

Ecological groups of birds of Zhytomyr region (Ukraine) in relation to thermal regime and their future prospects in the context of global climate change

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The potential impact of global climate change on the distribution of bird species can be predicted based on observed climate change and current knowledge of the factors affecting range boundaries. The concept of an ecological niche allows one to qualitatively and quantitatively characterise the impact of environmental factors on species. The study estimates the parameters of the thermal projection of the ecological niche of birds in Zhytomyr region, compares different approaches to modelling the response of species to the average annual temperature gradient, identifies ecological groups of birds based on their thermal gradient, and provides prospects for these ecological groups in the context of global climate change. The beta-function was found to reflect the reactions of different species within a single bell-shaped pattern across the entire gradient of the environmental factor. This makes it possible to estimate the optimal level for all bird species. Kurtosis can be used to distinguish between different response patterns within the beta model. Zero kurtosis indicates a symmetrical bell-shaped response. The relationship between the kurtosis of species response models and the optimum is complex. In general, species show negative kurtosis in the warm part of the range, indicating a sharp break in the species response curve in the warm part of the factor range. In the middle part of the factor range, the kurtosis value randomly fluctuates around zero, indicating a predominant tendency towards symmetrical response forms and the prevalence of the classical bell-shaped response model. The limits of variation of kurtosis are of great importance in the cold part of the range. The thermal projection of the ecological niche was used to divide bird species into ecological groups based on the position of the optimum zone and the width of the tolerance amplitude. It is shown that ecological groups differ in their prospects under global climate change. Stenotopic megatherms have the best prospects in the face of global climate change. The habitat conditions of all other bird species in the region will deteriorate over the next 70 years. The most threatening prospects should be expected for stenotopic microtherms. The stenotopic megatherms include 68 species, which is 25.9% of the total regional bird fauna. That is, global climate change poses a threat to 74.1% of the region's bird species. Stenotopic megatherms are typified by Anseriformes, Bucerotiformes, Gruiformes, and Pelecaniformes. It was predicted that *Ciconia ciconia* has the greatest prospects for expansion due to global climate change. The stenotopic microtherms are represented by 18 species, which is 6.9% of the regional avifauna. For these species, climatic conditions will significantly limit the number of favourable habitats. This ecological group is most strongly typified by Galliformes, Piciformes, and Strigiformes. Climate change will lead to a shift in the range of *Picus camus*, which will reduce the abundance of this species in the region.

Keywords: ecological niche factor analysis; Maxent; biogeographic predictors; prediction; climate warming.

Introduction

Climate is a significant determinant of the distribution of both species and land cover types (Thuiller et al., 2004; Barbet-Massin et al., 2012). Anthropogenic changes in atmospheric composition as a result of energy-related emissions are the key source of global climate transformation. The future scenarios that include a significant anthropogenic climate change also indicate a notable increase in global fossil fuel production, which is the primary source of carbon dioxide emissions. Urbanization and changes in land use also play an important role in generating climate change at the local and regional levels (Karl & Trenberth, 2003). The impact of climate on global biodiversity is typically assessed in terms of temperature, humidity and ecosystem productivity (Hawkins et al., 2003). The 20th century saw a moderate warming trend, as evidenced by geological events in the Earth's history. The mean surface temperature increased by approximately 0.5 °C over the course of the 20th century (Schneider & Root, 1996). Global surface temperatures have been observed to increase at a rate of approximately 0.2 °C per decade in recent years (Hansen et al., 2006). Global warming is associated with alterations in precipitation patterns and an increase in the frequency and intensity of extreme weather events. The global temperature increase is not uniform in space or time

(Hansen et al., 2006). The rate of increase in the daily minimum temperature is approximately twice that of the daily maximum temperature (Easterling et al., 2000). Although this moderate warming may pose risks to biota, the warming expected by 2100 AD will have far more negative consequences. The global average temperature is expected to rise by 1.1–5.4 °C (Arora et al., 2005). It is possible that different species may respond differently to global climate change as it progresses (Weiskopf et al., 2020). Climate change is becoming an increasingly significant factor influencing the distribution, abundance and life cycle of bird species, resulting in alterations to biodiversity and community composition. Variations in climate conditions are also affecting the productivity and adaptability of species (Muluneh, 2021). The spatial niches of numerous species are anticipated to undergo significant alterations in the future, with potential implications for the long-term survival of species and communities (Trautmann, 2018). There is already evidence that northern birds have shifted their breeding and non-breeding ranges to higher latitudes, and tropical birds to higher altitudes (La Sorte & Jetz, 2010). It is possible for species to develop new physiological tolerances in order to adapt to altered climatic conditions. Alternatively, they may move spatially in order to maintain existing physiological relationships with specific climatic conditions that define each species' climatic niche in the face of environmental change

(Skelly et al., 2007). The disruption of species interactions has been observed as a consequence of the differential responses of interacting species to warming. One of the most significant direct responses to changes in geographic climate complexes in space is the potential for species to adapt (Coelho et al., 2023). Ecological niches represent the long-term, stable factors that restrict the potential for species to spread. The adaptation of geographic niches is observed in climate change on geologic time scales due to the conservatism of niches (Martínez-Meyer et al., 2004). The responses of species to current climate change exhibit considerable variability, with a notable lag effect. The majority of bird species exhibit a strong correlation between their climatic niche and the geographic range they occupy. This correlation allows for the successful prediction of where and how to conserve species in the face of climate change (Tingley et al., 2009). The analysis of surface latitudinal and altitudinal temperature gradients is of particular importance in the context of geographic niche tracking, with a view to understanding past and present climate change (La Sorte et al., 2014). These gradients are natural ecological features that retain their location and general shape over ecological time scales. A climate thermostat mechanism has been identified in the geological record at a specific stage of the Earth's history, which is associated with the concentration of greenhouse gases. This mechanism is capable of mitigating tropical warming by redistributing heat to the poles in a greenhouse world. However, this mechanism ceased to function when greenhouse gas concentrations decreased, resulting in a transition from greenhouse to glacial conditions. The strongest latitudinal temperature gradients are observed outside the tropics, particularly in the Northern Hemisphere (Jonkers et al., 2023), where the largest land masses are located. It is possible that tropical biota may face a level of net biotic extinction that is unparalleled in higher latitudes. This is because climate change-induced range shifts can be offset by migration of species from lower latitudes (Colwell et al., 2008). The morphological and physiological traits of populations exhibit a correlation with latitudinal or altitudinal gradients (Jonas & Geber, 1999). Altitudinal temperature gradients are more intense and less variable than latitudinal gradients, although they are geographically more limited (De Frenne et al., 2013). It is evident that not all species are equally able to tolerate the latitudinal and altitudinal temperature gradients that are present in their respective geographic ranges. Furthermore, the distribution of these gradients within the ranges of species is not uniform. The absolute range of tolerance to high temperatures is the most reliable indicator of the latitudinal range and geographic location of a species (Calosi et al., 2010). It is predicted that latitudinal temperature gradients will decrease in the Northern Hemisphere as a consequence of the latitudinal asymmetry of the Earth's surface warming. The uneven distribution of warming will result in a decline in seasonal patterns and an acceleration of vegetation growth rates in high northern latitudes (Xu et al., 2013).

The life history, morphological and physiological traits of species populations exhibit variation at geographic scales (Zymaroeva et al., 2021). Geographical distance and differences in environmental conditions are significant factors in the divergence of species, emphasising the potential role of biotic and environmental parameters. The hypothesis of climate variability posits that the range of climatic fluctuations experienced by terrestrial animals increases with latitude. Consequently, it is proposed that individuals living in higher latitudes should exhibit greater plasticity than those living in lower latitudes (Naya et al., 2012). Climate change has been observed to cause shifts in the geographic ranges of birds. These shifts can be attributed to evolutionary adaptation, phenotypic adaptation, displacement, and extinction. The geographical response of species to environmental changes is complex in nature, a fortiori necessitating a detailed analysis of the ecological characteristics of individual species (Peterson et al., 2001). There is a substantial body of evidence indicating that the distribution of birds is influenced by climatic factors (Gaston, 2003). A study of North American passerine and non-passerine bird species has revealed that they have a northern range limit associated with a particular January isotherm. Different species are associated with different isotherms (Root, 1988). The northern limit of the range is influenced by physiological limitations, as well as the length of the day, which affects the period of time available for feeding and the availability of energy-rich food resources. High humidity can also affect the northern limits of the breeding range. The distribution of the grouse *Tetrao urogallus* in the UK may be

limited by high rainfall, which can lead to poor chick survival (Moss, 1986). There is evidence to suggest that the southern limit of the bird's range may be related to heat or water shortages (Li et al., 2021). For instance, the Eurasian magpie (*Pica pica*) in North America has a thermal limit of 40°C, whereas the related Yellow-billed magpie (*Pica nuttalli*) is more tolerant of heat. Consequently, the Eurasian magpie is confined to cooler areas, while the yellow-billed magpie can live in hotter areas (Hayworth & Weathers, 1984). A lack of drinking water can restrict the distribution of bird populations, as evidenced by the inability of most species to disperse into deserts (Morton et al., 1995). The creation of watering holes for cattle and sheep, as is the case in Australia, can result in the expansion of bird ranges due to the availability of water (Saunders & Curry, 1990). Furthermore, precipitation can indirectly affect birds through the availability of food sources, including insects, flowers and seeds (Scarpelli et al., 2023). The northern limit of the species' range is largely influenced by abiotic factors, such as low temperatures and high humidity (Bridle & Hoffmann, 2022). Consequently, the southern limit of the species' range may be influenced by climatic factors, such as heat or water shortages in regions where they are limiting factors, such as arid regions (Calosi et al., 2010). It can be posited that biotic factors such as interspecific competition, predation and parasitism may play a more pronounced role in wetter regions (Leach et al., 2016).

The potential effects of global climate change on the distribution of bird species can be predicted based on observed climate change and current knowledge of the factors affecting range boundaries (Sierra-Morales et al., 2021). It can be anticipated that the ranges of birds in temperate, boreal and arctic regions will expand in response to rising annual temperatures, particularly in areas where minimum temperatures are increasing and temperatures are rising most rapidly in high latitudes (Coristine & Kerr, 2015). The direction of climate change impacts will be opposite when approaching the equator. For example, a decrease in bird ranges in subtropical and tropical regions can be expected with rising temperatures and decreasing precipitation (Neate-Clegg et al., 2021). Indirect interactions between abiotic and biotic factors affect the quality of climate-influenced habitat change predictions (Zhukov et al., 2021). It is particularly challenging to anticipate changes in southern range boundaries when abiotic factors are not a limiting factor and when range boundaries are determined by a complex interaction of biotic factors or by certain vegetation types that may themselves be affected by climate change (Thomas & Lennon, 1999).

The impact of anthropogenic pressures on climate and land cover is resulting in significant alterations to ecosystems, with implications for the geographical distribution of species (Kunakh et al., 2022). This has created an urgent need to gain a deeper understanding of the spatial response of species to global change and to ensure the conservation of suitable habitats that support population resilience and conserve biodiversity (Zimaroeva et al., 2016). The accuracy of contemporary species distribution forecasting models is constrained by the disparate temporal and spatial resolutions of the datasets employed (Molozhon et al., 2023). The capacity of species to alter their geographic distributions is constrained by both macro-scale factors that delineate patterns across the range (Langraf et al., 2024), such as temperature and precipitation, and micro-scale factors that regulate the responses of individuals, such as biotic interactions and resource availability (Parmesan & Yohe, 2003). A wide range of factors can affect the response of species to changing climate regimes (Parmesan, 2006). It is possible that individuals do not have the flexibility to track relevant environmental cues in order to adjust the timing of life history events and adapt to new environmental circumstances (Simmonds et al., 2019). Although species may demonstrate flexibility in their responses to life-cycle events, they may lack the capacity to modulate their behaviour in response to environmental anomalies that affect the recovery of populations (Travis et al., 2013). To illustrate, the shifting of egg-laying dates to periods of earlier spring warming could have adverse effects on chick survival, particularly in the event that the probability of cold snaps is not associated with climate change-induced warming trends (Shiple et al., 2020). The potential for species to shift their spatial distribution in response to global change may vary considerably between species (Hallman & Robinson, 2020). The study of how specific areas of climate change affect species with disparate life cycle strategies, foraging guilds, or habitat affinities offers pro-

missing insights that can be extended to a broader range of unstudied species (Brawn et al., 2017). The prevailing approach to species distribution modelling can be divided into two main fields of study: species distribution models (SDMs), which incorporate both presence records and abiotic data, and ecological niche models (ENMs), which explicitly estimate the available habitat (Soberon & Peterson, 2005). These approaches are characterised by high spatial accuracy, yet they are not designed to identify the causal relationships between species and habitats (Merow et al., 2013). The models can be derived from different niche perspectives, which provide a unique framework for assessing the drivers of settlement within a species' range (Zymarioieva et al., 2019). A Grinnellian niche class reflects the abiotic drivers of site settlement, and SDM are mainly designed according to the Grinnellian niche concept (Saupe et al., 2012). It is often the case that broad-scale variables describing ecosystem features are the most relevant for predicting shift distributions over large spatial scales. In contrast, the Eltonian class of niches encompasses evaluations of biotic interactions and consumer-resource dynamics that can be quantified only at the local level (Soberon, 2007). Finally, Hutchinson's niche class is indicative of the functional role of a species, which is often evaluated based on functional traits and habitat requirements (Rosado et al., 2016), and also forecasts the possibility of colonisation of sites outside the study areas. The ability of a species to move beyond its current realised niche depends on the relative importance of abiotic factors, biotic interactions and dispersal probability at different spatial scales (Jankowski et al., 2013).

The aim of this study was to estimate the parameters of the thermal projection of the ecological niche of birds in Zhytomyr region, compare different approaches to modelling species response patterns in the mean annual temperature gradient, identify ecological groups of birds based on their thermal gradient, and establish the prospects of these ecological groups in the context of global climate change.

Materials and methods

The data on the species composition of the avifauna of Zhytomyr region were extracted from Avibase – World Bird Database (<https://avibase.bsc-eoc.org>). Records of bird species occurrences within Europe were obtained from the GBIF database (www.gbif.org) using the rgbif library. The following data sets were used as the predictors of bird ecological niche: climatic biogeographic variables, soil properties and indicators of landscape cover types. The nineteen bioclimatic variables were extracted from the WorldClim data and adapted to the geographical extent of the study area. The data was derived using the raster library. Forecast data on bioclimatic variables were obtained for the next 70 years based on the Coupled Model Intercomparison Project Phase 5 model (CMIP5) (Lynch et al., 2016). The information on the proportions of landscape cover types ("trees", "grassland", "shrubs", "cropland", "built", "bare", "snow", "water", "wetland", "moss") was obtained using the geodata library. The values were obtained from the ESA WorldCover dataset with a resolution of 0.3 seconds (<http://esa-worldcover.org>). Information on soil properties was obtained using the geodata library. The data were obtained from the SoilGRIDS database (Hengl et al., 2017). The ENFA procedure (Hirzel et al., 2002) was performed using the adehabitatHS library (Calenge, 2006). The results of the ENFA analysis were used to derive the marginalities of the ecological niche of 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). The assessment was made on the basis of both current predictors and projected climate variables.

The function β was employed to model the response function of species in a gradient of ecological regimes (Austin, 1976):

$$V = k \times (x - a)^\alpha \times (b - x)^\beta,$$

where V is the abundance of the species; k is a constant; a and b define the lower and upper limits of the species in the gradient of the variable x ; α and β are parameters of the distribution shape.

The location of the optimum and the asymmetry cannot be independently assessed in the case of beta functions, and the correlation between the response shape and the location of the optimum is an artefact of the response function. For this reason, the beta function cannot be used to estimate

the asymmetry of the species response (Oksanen, 1997), but it is this property that makes it possible to use the beta function to model different forms of species response when the actual form is unknown. In the range of values of a and b , the β -function can demonstrate a wide variety of possible distribution shapes: from a close approximation of the Gaussian distribution to an extremely asymmetric one. The shape parameters α and β determine three intuitive characteristics of the response function. The position of the maximum of the function, which can be interpreted as the optimum of the species in the environmental factor gradient, taking into account the endpoints a and b , can be determined as follows:

$$Opt = \frac{ab + \beta a}{\alpha + \beta}.$$

The optimum (maximum of the function) is in the middle of the range when $\alpha = \beta$. Asymmetry of the response, which is determined by the ratio of the parameters α and β . When $\alpha = \beta$, the response is symmetrical, and the asymmetry increases with the difference in the values of the parameters. The kurtosis (or flatness) of the response is described by the absolute values of the parameters α and β . The beta function parameters were estimated using the betafunctions library.

Results

Four types of response models were able to explain the response of bird species to mean annual air temperature (Fig. 1). The models II and III do not formally have a temperature value that can be clearly defined as the optimal level of the factor. For the model II, the threshold value of the factor under study is considered as optimal. The maximum limit of the factor under study will be considered optimal if the response is positive and the probability of occurrence increases with the average annual temperature. If the response is negative, then, on the contrary, the minimum boundary of the factor will be considered optimal. For model III, two values of the optimum are calculated. One value of the optimum is the same threshold value of the factor under study, and the other is the average of the factor values within the plateau with the highest probability of species occurrence. It should be noted that setting the boundary of such a plateau is a rather arbitrary procedure, although it is the same for all species whose response is described by Model III.

The species optimum for models IV and V is such that its value can be accurately estimated. The beta function makes it possible to display different species responses within a single bell-shaped pattern within the gradient of the environmental factor. This makes it possible to estimate the species optimum for all bird species. The different variants of the response shape within the beta model can be characterised by kurtosis. A kurtosis of zero corresponds to a symmetrical bell-shaped response pattern. As an example, we consider the case of the response model of *Phoenicurus ochruros* (S. G. Gmelin, 1774). A negative kurtosis indicates a shift of the response curve to the right. An example of such a response pattern is the case of *Falco naumanni* by J. G. Fleischer, 1818. In turn, a positive kurtosis indicates a shift in the response to the left, as observed in the case of *Nimicus phaeopus* (Linnaeus, 1758).

The kurtosis of beta model distributions differs between different types of HOF models ($R_{adj}^2 = 0.08$, $F = 6.5$, $P < 0.001$). The highest value of the beta-model kurtosis (0.46 ± 0.08) was found for the species whose response can also be described by the model II with a negative response of the species to an increase in the average annual air temperature (Planned comparison $F = 18.7$, $P < 0.001$). The kurtosis of the beta model for the positive responses of species to temperature increase according to this model is 0.02 ± 0.05 . The kurtosis did not differ from the kurtosis of species whose response can also be described by the VI model (Planned comparison $F = 0.07$, $P = 0.80$), but was smaller compared to all other models (Planned comparison $F = 18.6$, $P < 0.001$). The responses of the species described by the models II (positive response) and VI can also be described by a beta model with kurtosis that is not statistically different from zero (Planned comparison $F = 0.3$, $P = 0.58$). The asymmetric nature of the responses of the species described by model V also has high kurtosis estimates of the beta models (0.11 ± 0.04). The responses described by model III have a kurtosis of beta models equal to 0.04 ± 0.01 and statistically significantly different from zero (Planned comparison $F = 9.7$, $P < 0.001$) and from the V model (Planned comparison $F = 3.8$, $P = 0.05$).

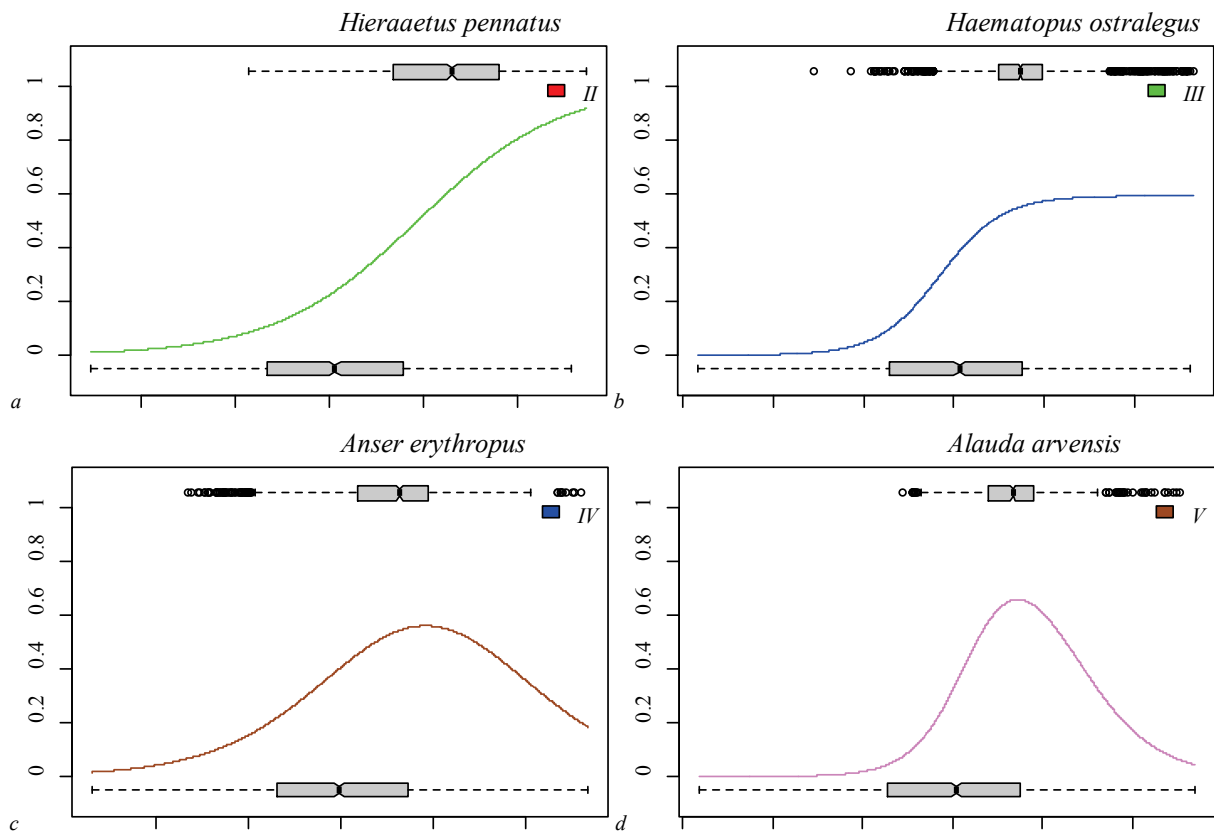


Fig. 1. The main patterns of species response in the mean annual temperature gradient: *a* is the model II, which indicates a monotonous response in the environmental factor gradient (it can be positive, which was established for 12 species, or negative, which was established for 2 species); *b* is the model III, which indicates the state of two plateaus with a transition between them (was established for 167 species); *c* is the model IV, which indicates a symmetrical bell-shaped response (was established for 53 species); *d* is the model V, which indicates an asymmetrical bell-shaped response (was established for 28 species)

The estimates of the optimum temperature ecological niches of birds obtained from the HOF model and the beta model are statistically significantly correlated (Fig. 2). The beta model provides more flexible estimates of optima for the model II, since the HOF approach for this species category provides marginal values of the environmental factor as a proxy for the ecological optimum. The estimates of the optimum for model III are systematically underestimated compared to models VI and V (the corresponding data cloud is shifted to the left along the abscissa axis).

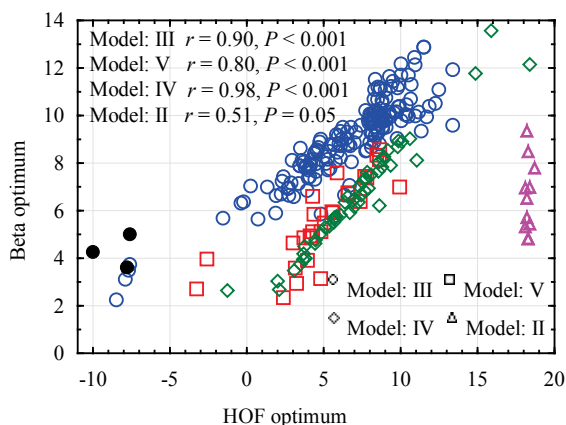


Fig. 2. The comparison of the estimates of the optimum temperature ecological niches of birds based on HOF models and beta models: the abscissa axis is the optimal values of the average annual temperature estimated from HOF models (°C); the ordinate axis is the optimal values of the average annual temperature estimated on the basis of the beta model (°C)

At the same time, the estimates in the warm part of the range for the model III correspond well to the beta model estimates, while in the cold

part of the range, the estimates of the optimum for the model III are more underestimated. On the contrary, models VI and V in the cold part of the range give estimates of the optimum close to those of the beta model, while in the warm part of the range the estimates are overestimated compared to the beta model.

The dependence of the kurtosis of species response models on the optimum is complicated (Fig. 3). The species typically exhibit a negative kurtosis in the warm part of the range, indicating a sharp break in the species response curve in the warm part of the factor range. The kurtosis randomly varies around zero in the middle part of the factor range, indicating a predominant tendency for symmetric response patterns and a preference for the classical bell-shaped response model. The kurtosis variation limits are very significant in the cold part of the range. There are species with significant positive kurtosis, indicating a sharp break in the response curve in the cold part of the factor range and a slow change in the response curve in the warm part of the gradient. Such species prefer colder habitats but are tolerant of warming. This group includes *Numenius phaeopus* (Linnaeus, 1758), *Calidris falcinellus* (Pontoppidan, 1763), and *Falco columbarius* Linnaeus, 1758. Of course, there are symmetric models and models with negative kurtosis, which indicates a sharp break in the model at higher temperatures. Obviously, these species are very sensitive to climate warming. The group of species most sensitive to warming includes *Tetrastes bonasia* (Linnaeus, 1758), *Lyrurus tetrix* (Linnaeus, 1758), *Glauclidium passerinum* (Linnaeus, 1758), and *Aegolius funereus* (Linnaeus, 1758).

The changes in the habitat preference index over the next 70 years due to global climate change depend on the ecological niche optimum and the kurtosis of the response curve (Fig. 4). The graph covers the entire space of combinations of optimum and kurtosis values of species response curves, although it should be noted that combinations of these parameters corresponding to real species occupy a more limited part of the graph in the diagonal area from the upper left to the lower right corner of the graph. Obviously, the bird fauna is the result of the selection of species that fit certain strategies. In fact, the fauna lacks species with the most dynamic

ecological niche, both in terms of increasing and decreasing habitat preference over time, corresponding to the upper right and lower left parts of the graph, which are currently empty. If the species' optimum is greater than 6 °C, then an increase in the kurtosis of the species' response curve is a factor that increases the prospects of improving the species' habitat conditions as a result of global climate change. If the species optimum is less than 6 °C, the relationship is reversed.

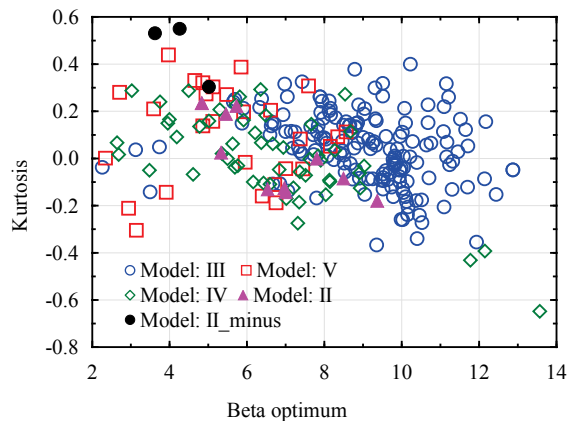
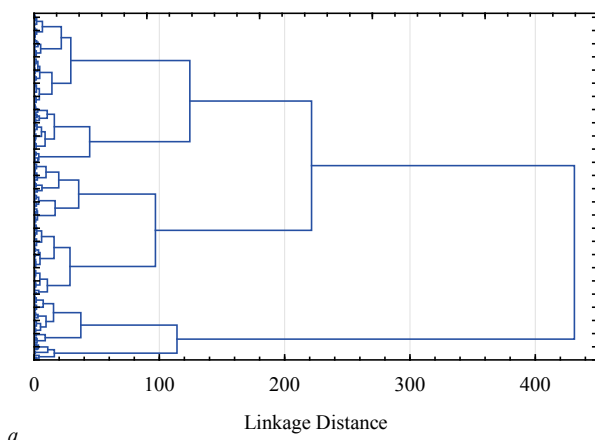
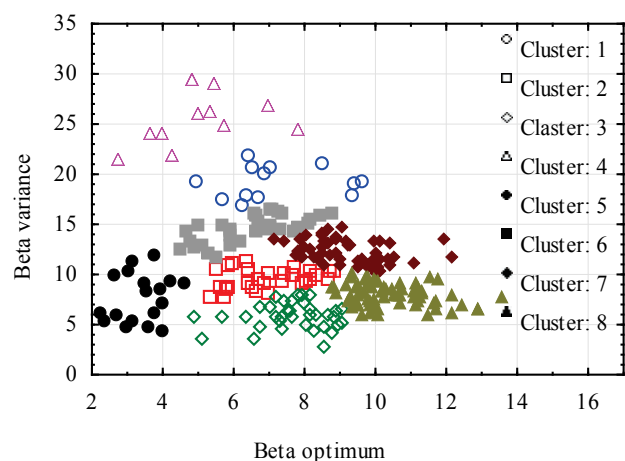


Fig. 3. Scatter plot of the estimates of the optimum (abscissa, °C) and kurtosis (ordinate) of the responses of bird species in the gradient of mean annual air temperature by the beta model: the best HOF models for the respective species are shown in colour

The cluster analysis of bird species based on estimates of their thermal optimum, tolerance and kurtosis of response to the mean annual air temperature gradient allowed us to identify eight relatively homogeneous clusters (Fig. 5). These clusters are well distinguished by the ecological properties of the bird species they contain ($F = 111.5$, $P < 0.001$). Therefore, the clusters can be interpreted as ecological groups. These ecological groups can be classified according to two features: ecological optimum and species tolerance in relation to the thermal factor. Microtherms (18 species, optimum 3.4 ± 0.7 °C), mesotherms (122 species, optimum 6.9 ± 1.4 °C) and megatherms (122 species, optimum 9.9 ± 1.2 °C) are distinguished in relation to the thermal regime (Table 1). According to the tolerance to the thermal factor, stenotopic species (122 species, temperature variation within the range 7.3 ± 1.7), hemistenotopic species (83 species, temperature variation within the range 11.3 ± 1.7), normotopic species (32 species, temperature variation within the range 14.6 ± 1.3), hemieurytopic species (13 species, temperature variation within the range of $19.2 \pm$



a



b

Fig. 5. Cluster analysis by Ward's method of bird species based on estimates of their thermal optimum, tolerance and kurtosis of response to the gradient of mean annual air temperature (a) and scatter plot of optimum and tolerance values (variance) depending on the bird species belonging to clusters (b): in Figure 6a, the abscissa indicates the distance between points according to the Euclidean metric, and the ordinate corresponds to bird species; in Figure 6b, the abscissa line indicates the optimum of the average annual air temperature (°C), and the ordinate line indicates the species' tolerance to the thermal factor, which is characterised by dispersion; the colour indicates the clusters

1.6) and eurytopic species (12 species, temperature variation within the range of 25.7 ± 2.7).

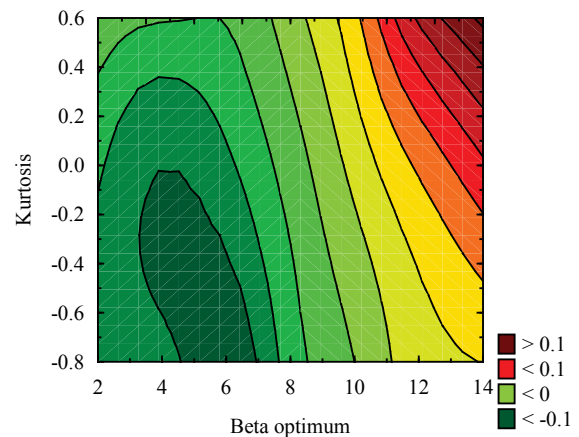


Fig. 4. The variation of the change in the habitat preference index of bird species in Zhytomyr region in the next 70 years induced by global climate change depending on the species' optimum in the gradient of mean annual air temperature (abscissa, °C) and the kurtosis of the species' response curve (spline approximation): the legend indicates the projected changes in the habitat preference index in the next 70 years due to global climate change compared to the current state

The ecological groups also differ in the kurtosis of the temperature gradient response distribution ($F = 5.5$, $P < 0.001$). Clusters 1 (hemieurytopic mesotherms), 7 (hemistenotopic megatherms) and 8 (stenotopic megatherms) have kurtosis that is not statistically significantly different from zero (Planned comparison $F = 0.2$, $P = 0.64$). Other ecological groups have a positive kurtosis (Planned comparison $F = 42.3$, $P < 0.001$). The highest kurtosis, which is statistically significantly different from all other ecological groups, was found for cluster 4 (eurytopic mesotherms) (Planned comparison $F = 12.2$, $P < 0.001$). The ecological groups differed in the level of predicted change in the bird habitat preference index in the next 70 years, taking into account global climate change ($F = 7.4$, $P < 0.001$, Fig. 6). Only birds belonging to cluster 8 (stenotopic megatherms) showed a tendency to increase in the habitat preference index (Planned comparison $F = 5.5$, $P = 0.02$). The representatives of all other clusters will see a decrease their habitat preference index in 70 years (Planned comparison $F = 60.0$, $P < 0.001$). The poorest prospects are for representatives of cluster 5 (stenotopic microtherms) (Planned comparison $F = 6.9$, $P = 0.009$).

Table 1
The ecological groups of birds in Zhytomyr region by their optimum, tolerance and symmetry of the response curve to the influence of average annual temperature

The width of the environmental amplitude	Characteristics	Ecological group in relation to the thermal regime		
		microtherm	mesotherm	megatherm
Stenotop	Number of species	18 (cluster 5)	36 (cluster 3)	68 (cluster 8)
	Optimum (mean±std. deviation, minimum-maximum)	3.4±0.7 (2.3–4.6)	7.7±1.0 (4.9–9)	10.4±1.1 (8.8–13.6)
	Tolerance (mean±std. deviation, minimum-maximum)	7.7±2.4 (4.4–11.9)	5.9±1.3 (2.8–8)	8.0±1.1 (5.9–10.2)
	Kurtosis (mean±std. deviation, minimum-maximum)	0.0±0.2 (–0.3–0.3)	0.0±0.2 (–0.3–0.4)	0.0±0.2 (–0.6–0.4)
Hemistenotop	Number of species	–	29 (cluster 2)	54 (cluster 7)
	Optimum	–	7.0±1.1 (5.4–8.8)	9.2±1.1 (7.1–12.2)
	Tolerance	–	9.6±1.0 (7.8–11.3)	12.2±1.2 (10.1–14.7)
	Kurtosis	–	0.1±0.1 (–0.2–0.4)	0.0±0.2 (–0.4–0.3)
Normotop	Number of species	–	32 (cluster 6)	–
	Optimum	–	6.5±1.2 (4.5–8.8)	–
	Tolerance	–	14.6±1.3 (11.7–16.5)	–
	Kurtosis	–	0.1±0.1 (–0.2–0.3)	–
Hemieurytop	Number of species	–	13 (cluster 1)	–
	Optimum	–	7.2±1.5 (4.9–9.6)	–
	Tolerance	–	19.2±1.6 (16.8–21.8)	–
	Kurtosis	–	0.0±0.2 (–0.4–0.3)	–
Eurytop	Number of species	–	12 (cluster 4)	–
	Optimum	–	5.0±1.4 (2.7–7.8)	–
	Tolerance	–	25.7±2.7 (21.5–29.5)	–
	Kurtosis	–	0.2±0.2 (–0.1–0.6)	–

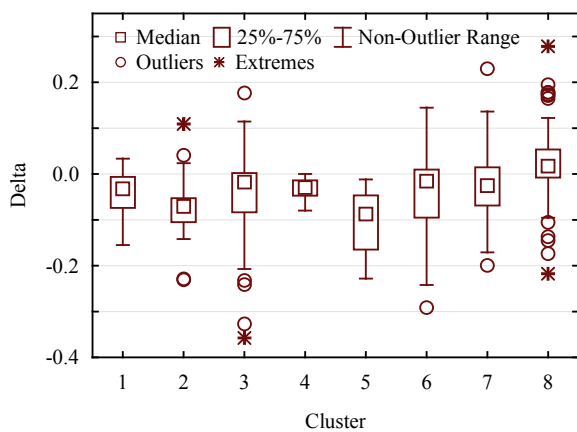


Fig. 6. Boxplot of variability of the predicted change in the bird habitat preference index depending on the ecological group (cluster): the abscissa axis is the ecological group (cluster), and the ordinate axis is the value of the predicted change in the bird habitat preference index over the next 70 years, taking into account global climate change

Discussion

Populations of species are responding to global climate change by shifting their geographical ranges to regions with suitable climatic conditions or by remaining in their current locations and adapting phenotypically or genetically. Birds are responding to recent climate change in a variety of ways, including shifting their geographic ranges to cooler climates. The ability of a species to change its geographic range depends on its ability to disperse, and on physiological and behavioural adaptations that are able to keep pace with the rate of climate change. The survival of species may depend not only on their ability to adapt to changing climates, but also on the extent to which the climate is stable (Loarie et al., 2009). Empirical evidence indicates that birds exhibit consistent behavioural responses to environmental gradients in the context of climate change. Climate change has resulted in alterations to migration strategies and the composition and structure of bird communities. Climatic gradients are of particular importance for populations of living organisms at large spatial and temporal scales. Temperature rise may lead to a shift in species ranges (Grimm et al., 2013; Krosby et al., 2015). There is a change in the geographical location of the climatic niche of the optimum blowing in the face of global warming. Thermophilisation of biological complexes is considered to be one of the main consequences of climate change. The species temperature index is designed to indicate the temperature niche of a species and can be calculated based on the temperature within the species' range (Kampichler et al., 2012; Roth et al., 2014).

The results demonstrate that the symmetrical bell-shaped model of species response to environmental factors is a visually informative model that indicates the qualitative features of species response to changes in environmental gradients. The most significant aspect of this fundamental model is that the response of a species to an environmental factor is conceptualised as exhibiting a nonlinear unimodal nature. Other response patterns may be considered as partial and derivative variants of the general bell-shaped model. The asymmetric nature of the response, while maintaining the bell-shaped nature of the response, can be seen as the influence of the scale of the factor on the response of the species. This is when the sensitivity of the species to changes in smaller and larger levels of the factor, measured in physical quantities, is different. This can be described as a situation of a certain mismatch between the "physical" and "biological" units of measurement of an environmental factor. Environmental factors are typically quantified in physical units, whereas the species in question perceives the factor in "biological" units. Furthermore, the approximation of the factor employed by the researcher as a convenient form for measurement with the help of instruments may not fully correspond to the nature of the impacts experienced by a particular species. For instance, the average annual temperature is a convenient climate marker. The observed changes in this marker over time are cited as evidence of global climate change. Nevertheless, the course of events in the avian life cycle throughout the year is contingent upon a complex interplay of temperature regimes. It can be observed that these regimes exhibit a correlation with the average annual temperature, although the extent of this correlation varies considerably both within and between species. Consequently, the average annual temperature serves as a convenient, albeit largely arbitrary, indicator of the species' ecological niche. One potential mechanism for the formation of an asymmetric response pattern is the contribution of different temperature regimes. Such a pattern may also be formed through the correlation of the temperature factor with other factors, such as precipitation. The impact of precipitation may be more or less sensitive at high or low temperatures, which will result in an asymmetric response to temperature. A bimodal response pattern is the consequence of interspecies interactions. Interspecific interactions are typically constrained to a limited spatial extent, rendering them inaccessible at the habitat level. This is why no patterns were observed that could be best described by HOF models VI and VII. The estimation of the occurrence or abundance along abiotic gradients is of significant importance for the prediction of future range shifts under the influence of global change, as it is directly related to the response of species and populations to the environment (MacPherson et al., 2021). The gradual alterations in temperature and precipitation patterns will be reflected in the responses of species, which will in turn result in changes in the probability of occurrence or abundance, as a consequence of changes in optimal environmental conditions (Meynard & Kaplan, 2012). The demographic information is also useful for more accurate predictions, as the theory of spatial ecology states that species respond to constant environmental

gradients by gradually changing in abundance as individuals sense changing conditions towards or away from an ecological optimum in space (Austin, 2007). Furthermore, the populations may exhibit thresholds of tolerance to abiotic factors or respond to biotic factors that alter the shape of their response, for example by creating asymmetric or skewed response functions (Oksanen & Minchin, 2002). The hypothesis of asymmetric limitation of abiotic stress predicts a more pronounced decline in the probability of species occurrence towards the more stressful end of the gradient (Dvorský et al., 2017). Other threshold-type effects can lead to asymmetric responses that are manifested in different species in communities (Janowski et al., 2013). Detection of reaction forms is of practical interest for understanding the impact of abiotic and biotic factors on the population. The selection of a species response model has a significant impact on the estimation of a species' ecological niche parameters. In theory, the species' optimum and tolerance are the most important parameters of the ecological niche, allowing for a meaningful assessment of the species' attitude to the impact of a particular environmental factor and, accordingly, the prediction of the species' state in the context of global climate change. The fundamental, unimodal, symmetric model enables the estimation of the species' optimum and tolerance. The asymmetric unimodal model also permits the estimation of the optimum, although the tolerance should be indicated by two numbers, rather than a single value, as is the case with the symmetric model. These two numbers define the limits of the tolerance zone for the species in question. With regard to other models on the HOF list, the estimation of optimum and tolerance is becoming less and less a defined procedure. It is important to note that real response patterns can be fitted by competing models, the accuracy of which may not be fundamentally different. Nevertheless, the estimation of the parameters of the optimum and tolerance of the species' ecological niche can diverge significantly, despite being derived from equivalent but distinct models.

A flexible alternative to modelling the response of species to environmental factors is the beta model. This approach permits the modelling of a diverse range of response patterns, encompassing symmetrical bimodal and monotonic types. All of these patterns are modelled using a single mathematical form, in which, in addition to the optimum and tolerance, another important parameter, kurtosis, can be estimated. The kurtosis indicates the varying sensitivity of a species to an environmental factor, contingent on its position relative to the optimum zone. The estimates of the parameters of the ecological niche of bird species obtained using alternative approaches demonstrate a high degree of correlation with each other. However, the beta model produces a smooth sequence of estimates, in contrast to the discrete sequences produced by estimates obtained using the HOF approach. The versatility of the mathematical form and the smoothness of the estimates allow us to select the beta model for modelling species responses to environmental factors and for comparing estimates with each other. In circumstances where the objective of the study is not to compare species responses, but to model them accurately, the HOF approach may be a more suitable strategy. Consequently, beta modelling represents the optimal methodology for estimating ecological niche parameters across a diverse range of species, given their disparate patterns of response to environmental factors. This approach is particularly suited to facilitating comparisons between species.

The parameters of an ecological niche determine the prospects for the status of bird species in the face of global climate change. Heat-loving bird species have better prospects for conservation in a warming climate. This is a somewhat trivial result. The original finding of the study is that the kurtosis of the species' response pattern to the temperature factor significantly affects the predicted change in the habitat preference index in the future. An increase in the kurtosis of thermophilic bird species has a positive impact on the prospects for survival under global climate change. In other words, in addition to being thermophilic, a species must also be tolerant of changes in temperature in the warm part of the gradient. Optimum, tolerance, and kurtosis allow us to distinguish ecological groups of birds in relation to the thermal regime. According to the position of the optimum, species can be divided into microthermals, mesothermals, and megathermals. Five categories have been identified based on the width of the ecological amplitude. Microtherms belong only to stenotopes, and megatherms to stenotopes and hemistenotopes. Mesotherms are represented by the greatest diversity of ecological groups in terms of the width of the

ecological amplitude in relation to the thermal factor. It should be noted that with an increase in the width of the ecological amplitude, the number of species in bird ecological groups decreases. Stenotopic megatherms have the best prospects under global climate change. Habitat conditions for all other bird species in the region will deteriorate over the next 70 years. The most threatening prospects should be expected for stenotopic microtherms.

The stenotopic megatherms include 68 species, which is 25.9% of the total regional bird fauna. That is, global climate change poses a threat to 74.1% of the regional bird species. Stenotopic megatherms are the most typical among Anseriformes: 14.7% of species of this ecological group belong to the order Anseriformes, while representatives of this order account for only 8.8% of the total bird fauna. Other predominantly stenotopic megatherms are representatives of the order Bucerotiformes (1.5% in the ecological group vs. 0.4% in the avifauna), Gruiformes (5.7% in the ecological group vs. 3.1% in the avifauna) and Pelecaniformes (4.9% in the ecological group vs. 2.8% in the avifauna). The only representative of Bucerotiformes in the regional fauna is *Upupa epops* Linnaeus, 1758. Climate warming is usually attributed to the increase in the number of this species observed in recent years in Europe (Kopij, 2016). Cool and rainy weather was found to have a negative effect on breeding rates and the availability of food. Rainfall had a negative effect on chick survival, while higher temperatures had a positive effect on chick survival (Arletaz et al., 2010). The greatest prospects for expansion due to global climate change are for *Ciconia ciconia* (Linnaeus, 1758). The evidence suggests that climate change has caused a gradual decline in the survival rates of Western European Storks. The decline in survival under global climate change is particularly noticeable for those storks nesting in Southern Europe (Martín et al., 2021). An increase in the average number of chicks was found in Central Europe as a result of an increase in average annual temperature. Higher temperatures and precipitation are favourable due to increased prey availability. A decrease in precipitation could lead to the loss of wetlands as suitable feeding grounds for this species (Gyalus et al., 2022). Researchers also point out the non-linear nature of this bird's response to climate change, which makes it difficult to make accurate predictions (Nevoux et al., 2008). The climate change will also be favourable for *Grus grus* (Linnaeus, 1758). This species is included in the Red Data Book of Ukraine. The population has increased in recent years, although hatching success has declined in recent years (Barwisch et al., 2022).

Stenotopic microtherms are represented by 18 species, which is 6.9% of the regional bird fauna. For these species, climatic conditions will significantly limit the number of favourable habitats. The largest proportion of species most vulnerable to global climate change is found in the orders Galliformes (16.7% in the ecological group vs. 2.3% in the bird fauna), Piciformes (11.1% in the ecological group vs. 3.8% in the bird fauna) and Strigiformes (22.2% in the ecological group vs. 4.2% in the bird fauna). Climate change will lead to a shift in the range of *Picus camus* J. F. Gmelin, 1788, which will result in a decrease in the number of this species in the region. This prediction is consistent with the recent population dynamics of this species. The trend of changes in the number of *P. camus* and *Poecile montanus* (Conrad von Baldenstein, 1827) is recognised as a moderate decrease (Gregory et al., 2007). *Aegolius funereus* (Linnaeus, 1758) is also at risk, with a decrease in population numbers also observed as a result of global climate change. The downward trend in chick production caused by starvation of offspring has led to a decline in the population of *A. funereus*. The main reason for the low level of population recovery is the loss and degradation of mature and old-growth forests due to clear-cutting, which leads to the loss of key habitats for the owls' primary (voles) and alternative (small birds) food, causing a shortage of food (Kouba et al., 2020). The abundance of *Eremophila alpestris* (Linnaeus, 1758) populations is also declining (Lehikoinen et al., 2014). The monitoring results also confirm the tendency of the *Acrocephalus dumetorum* Blyth, 1849 population decline due to global climate change (Lehikoinen & Virkkala, 2016). The Eastern European species *Phylloscopus trochiloides* (Sundevall, 1837) is expanding its range westwards in response to climate change and may soon be able to colonise new countries, including the UK (Leech & Crick, 2007). However, in Finland, this species and *Carpodacus erythrinus* (Pallas, 1770) show a declining trend in population density (Fraixendas et al., 2015). The group with a high risk of population decline includes

Tetrastes bonasia (Linnaeus, 1758), *Lyrurus tetrax* (Linnaeus, 1758), *Tetrao urogallus* (Linnaeus, 1758), *Strix uralensis* Pallas, 1771, *Strix nebulosa* Forster, 1772, *Picoides tridactylus* (Linnaeus, 1758), and *Glaucidium passerinum* (Linnaeus, 1758) that are listed in the Red Data Book of Ukraine. Thus, our projections are consistent with the observed trends in species abundance over the previous period of time since the beginning of noticeable and directed climate change.

Conclusion

Bird populations are shifting their geographical ranges to regions with more suitable climatic conditions in response to global climate change. Information about the properties of ecological niches is the basis for predicting changes in species ranges in response to global climate change in the future. The estimation of niche parameters depends on the model used to fit the observed data. HOF models are an effective tool for describing species-specific response patterns, but estimates of ecological niche parameters are only comparable within a single class of models, which significantly limits their ability to study multispecies species complexes. The beta model is a flexible and versatile tool that provides comparability for multispecies species complexes. Based on the parameters of the thermal projection of the ecological niche, bird species were divided into ecological groups based on the position of the optimum zone and the width of the tolerance amplitude. Ecological groups differ in their prospects in the context of global climate change. Improving trends can be predicted for stenotopic megatherms, while deteriorating trends will affect all other bird species, with the worst scenario expected for stenotopic microtherms.

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