

Annual course of temperature and precipitation as proximal predictors of birds' responses to climatic changes on the species and community level

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Abstract

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The study was conducted in the landscapes of south-eastern Ukraine during the nesting seasons 1988–2018. Within the landscape system associated with the Molochny Estuary, the ten most important ecosystem types were investigated, including the following: agricultural land, vegetated strips, meadows, islands and spits, reedbeds, urban areas, salt marshes, steppe, cliffs, artificial forests. Bird species responded to temperature and precipitation gradients. The patterns of responses were presented using Huisman, Olf and Fresco expanded by the Jansen-Oksanen hierarchical models. The nature of species response in the gradient of temperature or precipitation conditions depends on the type of particular ecosystem and is not uniform for all populations inhabiting the different landscape types. The bird communities were revealed to demonstrate an abrupt dynamic over time. The continuous changes in community structure initiated by the external environmental factors are combined with modifications of internal biotic interactions, which may lead to abrupt reorganization of the community.

Keywords

ecological niche, landscape diversity, ordination, temporal dynamic, trajectory analysis

Introduction

The climate affects a large number of major ecological mechanisms (WALTHER et al., 2009). Climate determines the structure of ecological systems at different hierarchical levels (MILLER, 2008). At the local level, a directed community turnover may be observed due to changes in the environment (DRESLEROVÁ, 2017; FAHRIG, 2003; LEE et al., 2019). The role of climate gradients becomes

crucial for communities on large spatial and temporal scales (METZ and TIELBÖRGER, 2016; MUCINA, 2019; PARMESAN, 2006). A disturbance of climatic regimes can lead to shifts in species ranges when temperatures rise (GRIMM et al., 2013; KROSBY et al., 2015). In the conditions of global warming, the geographical location of a species' climatic niche optimum changes, which affects the composition of communities in general (PAUTASSO, 2012; VELÁSQUEZ-TIBATÁ et al., 2013). Thermophilization

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of biological communities is considered as one of the main consequences of climate change (DE FRENNE et al., 2013; PARMESAN and YOHE, 2003). The influence of climate on bird community dynamics was estimated using the Community Temperature Index (CTI) (BOWLER and BÖHNING-GAESE, 2017; DEVICTOR et al., 2008). This index depends on the dominance of warm- and cold-dwelling species (DEVICTOR et al., 2012). The species temperature index (STI) is designed to identify the temperature niche of a species and can be calculated using temperature within the species' distribution range (KAMPICHLER et al., 2012; ROTH et al., 2014). CTI is derived from the abundance of species and their STIs and thus is a measure of the average temperature niche in a community (DEVICTOR et al., 2012; GODET et al., 2011).

The concept of an ecological niche allows us to give qualitative and quantitative characteristics of the influence of environmental factors on species (DEVICTOR et al., 2010; ZIMAROEVA et al., 2016). Application of Hutchinson's *n*-dimensional niche concept often focuses on the role of interspecific competition in the formation of species distribution models (PULLIAM, 2000). The habitat and climate components of the ecological niche are considered as independent dimensions of species response to global ecological trends (BARNAGAUD et al., 2012). The distribution of species and their changes are usually explained and predicted using large-scale climate variables, with the local habitat being considered as a secondary detailed filter with limited prognostic power (BLINKOVA and SHUPOVA, 2018; KORŇAN and ADAMÍK, 2014; OEDEKOVEN et al., 2017; PEARSON and DAWSON, 2003; TITEUX et al., 2017). Climate is the major driver of both species and land-cover distributions (BARBET-MASSIN et al., 2012; THULLER et al., 2004). Climate and habitats can simultaneously lead to shifts in species distribution (VELÁSQUEZ-TIBATÁ et al., 2013). The determinants of bird species distributions are hierarchically structured. A series of partial canonical ordinations were used to decompose species–environment relationships across hierarchical levels of organization to test different hypotheses about the importance of environmental control over community structure (CUSHMAN and MCGARIGAL, 2004). Climate variables are the determinants of the ecological niche on a large scale. Land cover becomes important at more granular spatial resolution (VIRKKALA, 2016). The integration of climate and land cover information can increase the predictive capabilities of biogeographic process models under conditions of global climate change (LUOTO et al., 2007). Climatic changes affect species range limits through processes that occur on a very local scale, including local adaptation, competitive exclusion, gradual dispersion and changes in biotic interactions (SEXTON et al., 2009). Species are often absent in a suitable habitat and are present in an unsuitable habitat as predicted by the theory of the ecological niche (PULLIAM, 2000). Implemented climate niches of species depend to varying degrees on ecological characteristics of their habitats, as the integration of climate variables and information on preferred habitats in species distribution models has

a controversial impact on their predictive efficiency (JETZ et al., 2007; LUOTO et al., 2007; THULLER et al., 2004).

The selection of appropriate environmental predictors of the niche is the key condition for the reliability of statistical models (AUSTIN and VAN NIEL, 2011). The proximal gradient is the causal variable determining the species response. The proximal variables determine the quality of the models as they are directly related to the regulation of physiological processes in individuals of the studied species (AUSTIN, 2002). Indirect gradients have no physiological effect on growth, development or competition (PIEDALLU et al., 2016). The variables that characterize indirect gradients are used in modeling species' responses to environmental factors and such variables are distal (AUSTIN, 1980). Models of species distribution will have only a local value either for prediction or for explanation when distal variables are used (BRADIE and LEUNG, 2017; GARDNER et al., 2019; MEROW et al., 2014). Direct gradients have a direct effect on species' physiology, while resource gradients create species' living conditions. Models based on proximal resource and direct gradients will be the most reliable and widely applicable (AUSTIN, 2002; ELITH et al., 2011). The species distribution models often use predictors that do not reflect the most important physiological features of species response to environmental factors. These are usually variables that reflect either seasonal or annual precipitation as simple surrogates of available plant moisture and neglect more direct measures such as soil water content. Predictors are usually results of seasonal or annual averaging and do not take into account the importance of climatic events during the critical period of a species' phenology (GARDNER et al., 2019).

Thus, global climate change affects the living conditions of individual species and their communities. These changes may affect the landscape diversity. In turn, the different types of ecosystems and climatic conditions determine a spatial distribution of species in space and time. The reliability of models based on climate predictors depends on the extent to which a relationship exists between a variable and biological features of a species. The models which use variables that reflect the causal relationships between environmental factors and species response are robust.

The objectives of the study were: 1) to evaluate the rate of temperature and precipitation increase during the first half of the year as proximal predictors of the ecological niche of birds; 2) to reveal the features of the response of bird populations to temperature and humidity gradients depending on ecosystem types; 3) to assess the influence of climatic changes on the temporal dynamics of bird communities.

Material and methods

Types of ecosystems investigated

The study was conducted in the landscapes of south-eastern Ukraine during the nesting seasons 1988–2018. Within the

landscape system associated with the Molochny Estuary, the ten most important ecosystem types were investigated, including the following: agricultural land, vegetated strips within or around fields, meadows, islands and spits, reedbeds, urban areas, salt marshes, steppe, cliffs, artificial forests. The Molochny Estuary is located within the north-western coast of the Sea of Azov (46°33'N, 35°24'E). The average depth of the estuary is 1.5–2.0 meters. The maximum length of the estuary is 36 km, the greatest width – 9 km in the southern part and the smallest – 4 km in the middle part of the water area. The total area of the estuary with the maximum water level is 21,945 thousand hectares. In the northern part, the Molochnaya River flows into the estuary, forming a delta with several branches. The southern part of the estuary is separated from the Sea of Azov by the whole body of the spit Peresyp, formed by sand and shell sediments (VOROVKA and DEMCHENKO, 2019). The Molochny Estuary is periodically connected to the Sea of Azov by an artificially created channel. Water salinity depends on season, precipitation and the degree of isolation of the estuary from the sea. In the years of strong desalination salinity decreased to 4–7 g l⁻¹, and in low water periods the salinity of the water of the Molochny Estuary sharply increases.

Field data collection

Bird surveys were conducted using the transect method (BIBBY et al., 2000; BLINKOVA et al., 2020; NOVIKOV, 1953). The width of the survey corridor with good visibility was 7–8 km, during rain – 2–4 km, in fog – up to 500 m (in the specified boundaries it was maximum for larger species, and minimal – for small birds and individuals which were in closed habitats with limited visibility). Point surveys were held during stops during the scanning of uniform open areas. In all cases, the territory was examined using 12-X binoculars and 60-X telescopes. Depending on the duration of the day and the quality of the light, the counts were carried out throughout the daylight hours from 7:00–7:30 to 15:30–16:00. The counts were recorded on special cards, applied to the scale of 1:200,000 maps, and then transferred to the geographic information database created in the software ArcMap 10.0.

Meteorological data

The information on the temperature and precipitation during 1988–2018 at the Henichesk weather station was obtained from the National Climatic Data Center (<https://www.ncdc.noaa.gov>) with the help of the *rnoaa* package (CHAMBERLAIN, 2020) for a language and environment R for statistical computing (R CORE TEAM, 2020).

Multivariate ordination techniques

The multivariate ordination techniques were applied to analyze the spatiotemporal variation in the bird species composition. Prior to analyses, species data were Hellinger-transformed (PIERRE LEGENDRE and GALLAGHER, 2001). We subjected the Hellinger-transformed abundance matrix

of species to constrained correspondence analysis (CCA) to extract the major patterns of variation (LEGENDRE and BIRKS, 2012; TER BRAAK and ŠMILAUER, 2015). The constrained ordination approaches allowed assessment of the effects of the temperature, precipitation and year as an explanatory variable on the bird community.

Statistical techniques

Huisman, Olf and Fresco hierarchical models (HOF) and Jansen-Oksanen models were used for explanation of the bird species response to the temperature or precipitation effects (HUISMAN et al., 1993; JANSEN and OKSANEN, 2013). Huisman, Olf and Fresco (HUISMAN et al., 1993) hierarchical models (HOF) along with a symmetric response also include a skewed response. Apart from the five HOF-models, two bimodal (skewed and symmetric) response shapes were included to cope with species that are restricted to gradient extremes due to competition (JANSEN and OKSANEN, 2013; MICHAELIS and DIEKMANN, 2017). The Huisman-Olf-Fresco models expanded by Jansen-Oksanen (HOFJO) are ranked according to the increasing complexity of biological information contained (HUISMAN et al., 1993; JANSEN and OKSANEN, 2013). Model I: no significant trend in space or time. Model II: an increasing or decreasing trend where the maximum is equal to the upper bound M. Model III: an increasing or decreasing trend where the maximum is below the upper bound M. Model IV: increase and decrease by the same rate – symmetrical response curve. Model V: increase and decrease by different rates – skewed response curve. Model VI: bimodal symmetric responses. Model VII: bimodal skewed responses. Huisman-Olf-Fresco models were fitted in the R statistical program (v. 3.3.1) (R DEVELOPMENTAL CORE TEAM, 2019) using the package “eHOF” (JANSEN, 2013). To improve modeling results even for small data sets, the stability of model choice was double-checked by bootstrapping (100 samplings, default package setting) to ensure model robustness. The Akaike information criterion corrected for small data sets (AICc) was used (BURNHAM and ANDERSON, 2002). In cases when the two procedures differed in their choice for the best model type, the bootstrapping model was preferred (MICHAELIS and DIEKMANN, 2017).

The dynamics of bird communities was assessed using the Community Trajectory Analysis (CTA) in the CCA-axis space. The calculations were performed using the package *vegclust* (DE CÁCERES et al., 2010, 2019). The types of trajectories of temporary changes in communities are given in accordance with an article by Matthews et al. (MATTHEWS et al., 2013). For the statistical analyses we used the appropriate procedures of Statistica (Version 5.5, StatSoft Inc., <http://www.statsoft.com>) or R (R CORE TEAM, 2020).

Results

The average daily temperatures during the first half of the year were found to be linearly dependent on the ordinal number of the day (Fig. 1A). The slope of the straight line

indicates the warming rate in a given year. This statistic was used to characterize the temperature regime of each of the years within the time range of the research. The warming rate and the average annual temperature were not statistically significantly correlated ($r = 0.10$, $p = 0.59$). The average annual temperature during the period of the investigations showed a tendency to increase, which was confirmed by a positive correlation with the ordinal value of the year ($r = 0.59$, $p < 0.001$) (Fig. 1). At the same time, the warming rate in the first half of the year was stationary during the period of studies (the correlation with the ordinal value of the year was $r = 0.29$, $p < 0.11$).

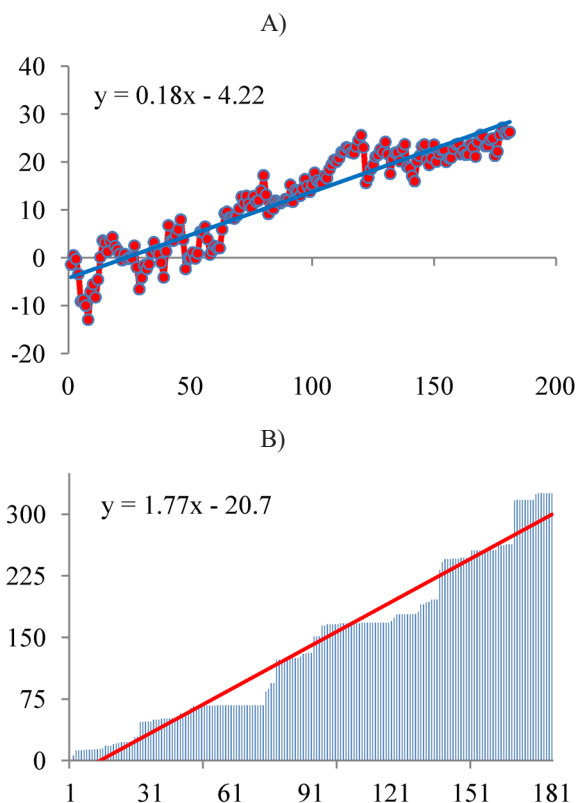


Fig. 1. Temporal dynamics of temperature course in the first half of 2005 (A) and cumulative precipitation (B). The abscissa axis is the order of days, starting from January 1; the ordinate axis is the temperature, °C (A); cumulative precipitation is the sum of precipitation with cumulative total for the previous days before this, mm (B).

The cumulative precipitation formed a trend, which can be described by a linear dependence (Fig. 1B). The slope of the straight line indicates the precipitation intensity in a given year and can also be used to characterize the precipitation regime. For the period of studies there was observed a trend of annual precipitation increase (correlation with the order of years was $r = 0.36$, $p = 0.04$) (Fig. 2). The annual precipitation and rate of precipitation in the first half of the year were strongly correlated ($r = 0.62$, $p < 0.001$). This explains the fact that the rate of precipitation in the first half of the year was also subject to an increasing trend over time ($r = 0.57$, $p < 0.001$) (Fig. 3).

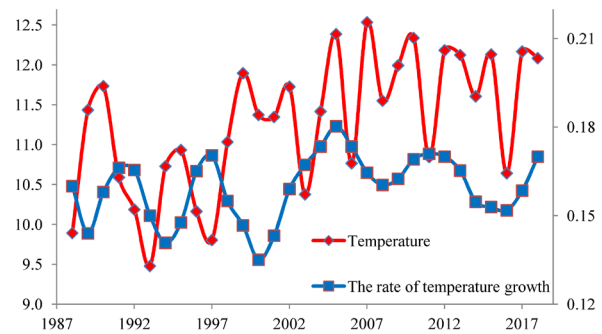


Fig. 2. Temporal dynamics of average annual temperature (red line) and temperature growth rate in the first half of the year (blue line). The abscissa axis is the order of years 1998, ..., 2018; the ordinate axis is the average annual temperature (on the left, °C); on the right is the average rate of temperature growth in the first half of the year (right, °C/day).

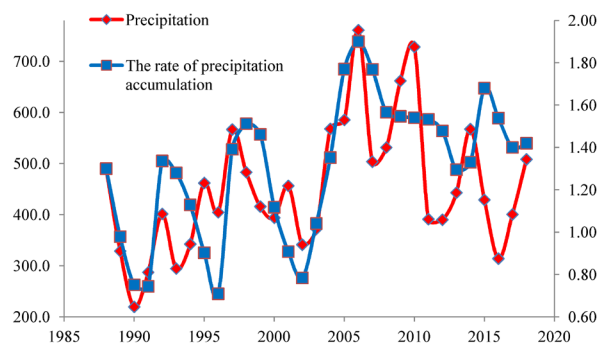


Fig. 3. Temporal dynamics of annual precipitation (red line) and precipitation accumulation rate in the first half of the year (blue line). The abscissa axis is the order of years 1998, ..., 2018; the ordinate axis is the annual precipitation (on the left, mm); on the right is the average rate of precipitation accumulation in the first half of the year (right, mm/day).

Bird species responded to temperature and precipitation gradients. The patterns of responses were presented using seven models (Fig. 4). Species that were found in more than one ecosystem type could show different patterns of response to similar environmental gradients (Table 1). It should be noted that in 38.24% of cases, the response of species to temperature was explained by the model I, which indicated the lack of a clear response to temperature variation (Fig. 5). In 34.5% of cases the response to precipitation gradient was also explained by the model I. The monotonic patterns of response (models II and III) were found to be suitable only in 11.8% of cases of response to temperature influence and in 20.6% of cases of response to precipitation gradient. The non-monotonic response patterns (unimodal – IV and V, as well as bimodal – VI and VII) were most typical for explaining the response of bird species to environmental gradients. To explain the response to temperature gradient, the non-monotonic models were the most preferable in 50.0% of cases, and to model the response to precipitation gradient were the most preferable in 44.9% of cases.

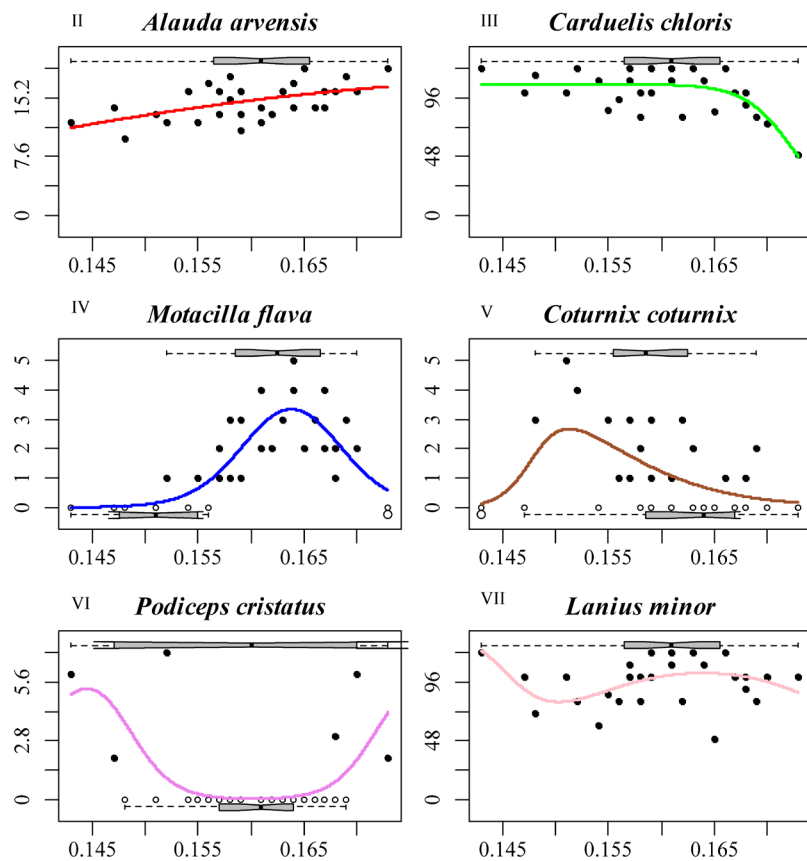


Fig. 4. HOFJO-models of species response to environment gradient. X-axis is the temperature growth rate in the first half of the year; Y-axis – the number of individuals. HOFJO-models: II – an increasing or decreasing trend where the maximum is equal to the upper bound; III – an increasing or decreasing trend where the maximum is below the upper; IV – increase and decrease by the same rate – symmetrical response curve; V – increase and decrease by different rates – skewed response curve; VI – bimodal symmetric responses; VII – bimodal skewed responses.

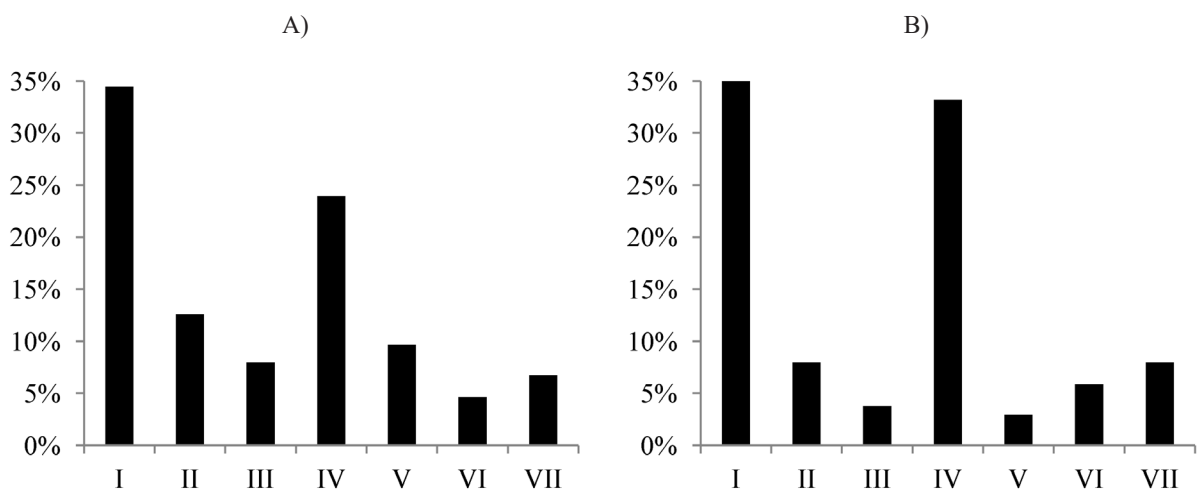


Fig. 5. The optimal models distribution of species response to the environment gradients. A – the temperature growth rate in the first half of the year; B – the precipitation accumulation rate in the first half of the year. X-axis – HOF and two additional models of the species responses to the soil moisture gradient, Y-axis – the % of the total number of species for which a model is the best according to AICc. HOFJO-models: I – no significant trend in space or time; II – an increasing or decreasing trend where the maximum is equal to the upper bound; III – an increasing or decreasing trend where the maximum is below the upper; IV – increase and decrease by the same rate – symmetrical response curve; V – increase and decrease by different rates – skewed response curve; VI – bimodal symmetric responses; VII – bimodal skewed responses.

Table 1. HOFJO-models of bird species response to temperature growth rate in the first half of the year and precipitation accumulation rate in the first half of the year

Species	Temperature growth rate in the first half of the year										Precipitation accumulation rate in the first half of the year									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
<i>Accipiter gentilis</i>	-	-	II	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Acrocephalus agricola</i>	-	-	-	-	III	-	VI	-	-	-	-	-	-	-	VII	-	VII	-	-	-
<i>Acrocephalus arundinaceus</i>	-	-	-	-	II	-	V	-	-	-	-	-	-	-	IV	-	IV	-	-	-
<i>Acrocephalus scirpaceus</i>	-	-	-	-	-	-	V	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Alauda arvensis</i>	II	-	-	-	-	-	-	I	V	I	I	I	-	-	-	-	-	I	IV	I
<i>Alcedo atthis</i>	-	-	-	-	II	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-
<i>Anas clypeata</i>	-	-	-	-	-	-	V	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Anas platyrhynchos</i>	-	V	-	-	-	-	V	-	-	-	-	IV	-	-	IV	-	IV	-	-	-
<i>Anas querquedula</i>	-	-	-	-	I	-	II	-	-	-	-	-	-	-	I	-	VII	-	-	-
<i>Anas strepera</i>	-	I	-	-	-	-	II	-	-	-	-	II	-	-	IV	-	IV	-	-	-
<i>Anser anser</i>	-	-	-	-	I	-	III	-	-	-	-	-	-	-	I	-	VI	-	-	-
<i>Anthus campestris</i>	I	-	-	-	IV	-	-	-	-	I	I	-	-	-	IV	-	-	-	-	I
<i>Anthus trivialis</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Ardea cinerea</i>	-	-	-	-	II	-	III	-	-	-	-	-	-	-	I	-	IV	-	-	-
<i>Ardea purpurea</i>	-	-	-	-	-	-	III	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Asio flammeus</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Asio otus</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Athene noctua</i>	-	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-
<i>Aythya ferina</i>	-	-	-	-	-	-	II	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Aythya nyroca</i>	-	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-
<i>Botaurus stellaris</i>	-	-	-	-	-	-	V	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Bucephala clangula</i>	-	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-
<i>Burhinus oedicephalus</i>	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-	-	-
<i>Buteo buteo</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Buteo rufinus</i>	-	IV	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-
<i>Calandrella rufescens</i>	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-	I

Table 1. Continued

Species	Temperature growth rate in the first half of the year										Precipitation accumulation rate in the first half of the year									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
<i>Caprimulgus europaeus</i>	-	I	VI	-	-	-	-	-	-	-	-	I	VI	-	-	-	-	-	-	-
<i>Carduelis cannabina</i>	-	I	II	-	-	-	-	-	-	-	-	I	IV	-	-	-	-	-	-	-
<i>Carduelis carduelis</i>	-	IV	III	-	-	-	-	I	-	-	-	II	III	-	-	-	-	I	-	-
<i>Carduelis chloris</i>	-	III	III	-	-	-	-	-	-	-	-	VII	III	-	-	-	-	-	-	-
<i>Casmerodius albus</i>	-	-	-	-	IV	-	V	I	-	-	-	-	-	-	IV	-	VII	I	-	-
<i>Charadrius alexandrinus</i>	-	-	-	-	II	-	-	-	II	-	-	-	-	-	IV	-	-	-	IV	-
<i>Charadrius dubius</i>	-	-	-	-	IV	-	-	-	III	I	-	-	-	-	IV	-	-	-	I	I
<i>Circus aeruginosus</i>	-	-	-	-	-	-	II	-	-	-	-	-	-	-	-	-	I	-	-	-
<i>Coccothraustes coccothraustes</i>	-	II	II	-	-	-	-	-	-	-	-	IV	IV	-	-	-	-	-	-	-
<i>Columba palumbus</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Coracias garrulus</i>	-	-	-	VI	-	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-
<i>Corvus corax</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Corvus cornix</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Corvus frugilegus</i>	-	V	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-
<i>Corvus monedula</i>	II	III	-	-	-	-	-	-	-	-	-	I	II	-	-	-	-	-	-	-
<i>Coturnix coturnix</i>	V	I	-	-	-	-	-	-	-	-	-	II	I	-	-	-	-	-	-	-
<i>Cuculus canorus</i>	-	V	-	-	IV	-	V	-	-	-	-	II	II	-	IV	-	VI	-	-	-
<i>Cygnus olor</i>	-	-	-	-	-	-	II	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Dendrocopos major</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Dendrocopos minor</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Dendrocopos syriacus</i>	-	I	I	-	-	-	-	V	-	-	-	I	I	-	-	-	-	VI	-	-
<i>Egretta garzetta</i>	-	V	-	-	-	-	IV	-	-	-	-	IV	-	-	-	-	IV	-	-	-
<i>Emberiza citrinella</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Emberiza hortulana</i>	-	I	-	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-	-	-
<i>Emberiza schoeniclus</i>	-	-	-	-	II	-	II	-	-	-	-	-	-	-	IV	-	V	-	-	-
<i>Erethacus rubecula</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Falco columbarius</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Falco subbuteo</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-

Table 1. Continued

Species	Temperature growth rate in the first half of the year										Precipitation accumulation rate in the first half of the year									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
<i>Falco tinnunculus</i>	-	II	I	I	-	-	-	-	-	-	-	IV	I	IV	-	-	-	-	-	-
<i>Falco vespertinus</i>	-	IV	I	-	-	-	-	-	-	-	-	II	I	-	-	-	-	-	-	-
<i>Ficedula albicollis</i>	-	-	I	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-	-	-
<i>Fringilla coelebs</i>	-	VI	VI	-	-	-	-	-	-	-	-	IV	IV	-	-	-	-	-	-	-
<i>Fulica atra</i>	-	-	-	-	VII	-	V	-	-	-	-	-	-	-	IV	-	IV	-	-	-
<i>Galerida cristata</i>	-	-	-	-	-	-	-	V	-	-	-	-	-	-	-	-	-	IV	-	-
<i>Gallinula chloropus</i>	-	-	-	-	IV	-	V	-	-	-	-	-	-	-	IV	-	VII	-	-	-
<i>Garrulus glandarius</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Glareola pratensis</i>	-	-	-	-	IV	-	-	IV	-	-	-	-	-	-	IV	-	-	-	VII	-
<i>Haematopus ostralegus</i>	-	-	-	-	V	-	-	-	V	-	-	-	-	-	III	-	-	-	III	-
<i>Himantopus himantopus</i>	-	-	-	-	V	-	-	-	V	-	-	-	-	-	VII	-	-	-	IV	-
<i>Hippoboscus icterina</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Hirundo rustica</i>	-	-	-	IV	-	-	-	V	-	-	-	-	-	IV	-	-	-	II	-	-
<i>Ixobrychus minutus</i>	-	-	-	-	II	-	IV	-	-	-	-	-	-	-	I	-	IV	-	-	-
<i>Jynx torquilla</i>	-	I	I	-	-	-	-	-	-	-	-	II	I	-	-	-	-	-	-	-
<i>Lanius collurio</i>	-	I	VI	-	-	-	-	-	-	-	-	VI	I	-	-	-	-	-	-	-
<i>Lanius minor</i>	-	VII	IV	-	-	-	-	-	-	-	-	VI	I	-	-	-	-	-	-	-
<i>Larus cachinnans</i>	-	-	-	-	VII	-	-	-	-	-	-	-	-	-	VII	-	-	-	-	-
<i>Larus genei</i>	-	-	-	-	VII	-	-	-	-	-	-	-	-	-	III	-	-	-	-	-
<i>Larus melanocephalus</i>	-	-	-	-	IV	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-
<i>Locustella tuscinioides</i>	-	-	-	-	II	-	IV	-	-	-	-	-	-	-	IV	-	VII	-	-	-
<i>Lullula arborea</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Luscinia luscinia</i>	-	-	IV	-	-	-	-	-	-	-	-	-	VII	-	-	-	-	-	-	-
<i>Luscinia svecica</i>	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Melanocorypha calandria</i>	II	-	-	-	-	-	-	-	I	-	-	I	-	-	-	-	-	-	I	-
<i>Merops apiaster</i>	-	-	-	IV	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-	-
<i>Miliaria calandria</i>	III	VII	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-	-
<i>Motacilla alba</i>	-	-	III	IV	-	-	-	IV	-	-	-	-	I	IV	-	-	-	VII	-	-

Table 1. Continued

Species	Temperature growth rate in the first half of the year										Precipitation accumulation rate in the first half of the year									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
<i>Motacilla citreola</i>	-	-	-	-	-	V	-	-	-	-	-	-	-	-	-	III	-	-	-	-
<i>Motacilla feldlegg</i>	-	-	-	-	-	IV	-	-	IV	-	-	-	-	-	-	I	-	-	II	-
<i>Motacilla flava</i>	IV	-	-	-	-	II	-	-	IV	-	-	-	-	-	-	IV	-	-	IV	-
<i>Muscicapa striata</i>	-	IV	IV	-	-	-	-	-	-	-	-	VI	-	-	-	-	-	-	-	-
<i>Netta rufina</i>	-	-	-	-	-	-	VI	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Oenanthe isabellina</i>	IV	-	-	-	-	-	-	-	-	II	II	-	-	-	-	-	-	-	-	III
<i>Oenanthe oenanthe</i>	I	-	-	-	-	-	-	IV	-	-	I	-	-	-	-	-	-	VI	-	-
<i>Oriolus oriolus</i>	-	I	IV	-	-	-	-	-	-	-	-	I	V	-	-	-	-	-	-	-
<i>Otus scops</i>	-	IV	IV	-	-	-	-	-	-	-	-	IV	I	-	-	-	-	-	-	-
<i>Panurus biarmicus</i>	-	-	-	-	VII	-	IV	-	-	-	-	-	-	-	IV	-	V	-	-	-
<i>Parus caeruleus</i>	-	VI	I	-	-	-	-	-	-	-	-	II	I	-	-	-	-	-	-	-
<i>Parus major</i>	-	I	I	-	-	-	-	-	-	-	-	I	V	-	-	-	-	-	-	-
<i>Passer domesticus</i>	-	-	I	-	-	-	-	I	-	-	-	-	I	-	-	-	-	I	-	-
<i>Passer montanus</i>	-	VII	I	II	-	-	-	-	-	-	-	II	I	VI	-	-	-	-	-	-
<i>Perdix perdix</i>	-	I	I	-	I	-	-	-	-	-	-	I	I	-	IV	-	-	-	-	-
<i>Phalacrocorax carbo</i>	-	-	-	-	IV	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-
<i>Phasianus colchicus</i>	-	I	III	-	-	-	IV	-	-	-	-	I	VI	-	-	-	IV	-	-	-
<i>Phoenicurus phoenicurus</i>	-	III	III	-	-	-	-	-	-	-	-	II	VII	-	-	-	-	-	-	-
<i>Phylloscopus collybita</i>	-	-	I	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Phylloscopus trochilus</i>	-	I	I	-	-	-	-	-	-	-	-	I	I	-	-	-	-	-	-	-
<i>Pica pica</i>	-	VII	IV	-	II	-	IV	-	-	-	-	VII	I	-	I	-	VI	-	-	-
<i>Plegadis falcinellus</i>	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Podiceps cristatus</i>	-	-	-	-	VI	-	VII	-	-	-	-	-	-	-	V	-	IV	-	-	-
<i>Podiceps grisegena</i>	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-	-	VII	-	-	-
<i>Porzana parva</i>	-	-	-	-	-	-	III	-	-	-	-	-	-	-	-	-	V	-	-	-
<i>Porzana porzana</i>	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-	-	I	-	-	-
<i>Rallus aquaticus</i>	-	-	-	-	I	-	IV	-	-	-	-	-	-	-	IV	-	IV	-	-	-
<i>Recurvirostra avosetta</i>	-	-	-	-	VII	-	I	-	IV	-	-	-	-	-	IV	-	I	-	IV	-

Table 1. Continued

Species	Temperature growth rate in the first half of the year										Precipitation accumulation rate in the first half of the year									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
<i>Remiz pendulinus</i>	-	I	-	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-	-	-
<i>Riparia riparia</i>	-	-	-	IV	II	-	-	-	-	-	-	-	VII	III	-	-	-	-	-	-
<i>Saxicola torquatus</i>	-	-	-	-	-	I	-	-	-	-	-	-	-	-	I	-	-	-	-	-
<i>Sterna albifrons</i>	-	-	-	-	IV	-	-	VI	-	-	-	-	-	IV	-	-	-	IV	-	-
<i>Sterna hirundo</i>	-	-	-	-	IV	-	III	-	VII	-	-	-	-	VII	-	III	-	-	V	-
<i>Sterna nilotica</i>	-	-	-	-	I	-	-	-	-	-	-	-	-	IV	-	-	-	-	-	-
<i>Sterna sandvicensis</i>	-	-	-	-	IV	-	-	-	-	-	-	-	-	VII	-	-	-	-	-	-
<i>Streptopelia decaocto</i>	-	VII	I	-	-	-	-	III	-	-	-	IV	IV	-	-	-	IV	-	-	-
<i>Streptopelia turtur</i>	-	I	I	-	-	-	-	-	-	-	-	I	VII	-	-	-	-	-	-	-
<i>Sturnus vulgaris</i>	-	IV	IV	IV	-	-	-	III	-	-	-	IV	IV	-	-	-	IV	-	-	-
<i>Sylvia atricapilla</i>	-	-	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Sylvia borin</i>	-	-	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Sylvia communis</i>	-	VII	I	-	-	-	-	-	-	-	-	II	I	-	-	-	-	-	-	-
<i>Sylvia nisoria</i>	-	I	I	-	-	-	-	-	-	-	-	II	I	-	-	-	-	-	-	-
<i>Tachybaptus ruficollis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	IV	-	-	-
<i>Tadorna ferruginea</i>	-	-	-	-	-	-	II	-	-	-	-	-	-	-	-	-	I	-	-	-
<i>Tadorna tadorna</i>	-	-	-	IV	IV	-	IV	-	-	-	-	-	-	IV	IV	-	IV	-	-	-
<i>Tringa totanus</i>	-	-	-	-	VII	-	-	-	II	-	-	-	-	II	-	-	-	-	-	VI
<i>Turdus merula</i>	-	I	IV	-	-	-	-	-	-	-	-	I	IV	-	-	-	-	-	-	-
<i>Turdus philomelos</i>	-	-	IV	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-	-	-
<i>Upupa epops</i>	-	-	I	VI	II	-	-	I	-	-	-	-	I	VI	I	-	-	I	-	-
<i>Vanellus vanellus</i>	-	-	-	-	IV	-	IV	-	IV	-	-	-	-	VI	-	IV	-	IV	-	-

I – Agricultural lands; 2 – Vegetated strips; 3 – Artificial forests; 4 – Cliffs; 5 – Islands and spits; 6 – Meadows; 7 – Reed beds; 8 – Rural territories; 9 – Salt marshes; 10 – Steepe.

The rates of temperature and precipitation increase in the first half of the year and the year as predictors were able to explain 5–51% variation of bird communities over time depending on the type of biotope (Table 2). These predictors were most important to explain the variation in bird community structure from Vegetated strips and Meadows. The bird communities from Cliffs and Islands and spits were the least sensitive to these predictors. Axis 1, extracted as a result of the CCA procedure, tended to reflect the time trend of community variability, which was closely related to the increase in temperature and precipitation. Axis 2 was not associated with a linear time trend in half of the cases. For bird assemblages from Islands and spits, axis 2 indicated a variation in response to rainfall. For Steppe communities, this axis indicated the

community's response to the temperature factor. For other communities, axis 2 indicated different combinations of temperature, precipitation and time effects on the variation of bird communities.

The trajectories of bird assemblages in the space of axes 1 and 2, which were extracted as a result of CCA procedure, indicated the presence of two or more quasicyclic states of the communities, the transition between which was almost saltatory (Fig. 6). The exception was the Steppe community, which exhibited a chaotic dynamic. The length of the trajectory was the longest for bird communities from Steppe and Meadows (Table 3). Obviously, the trajectory length indicated the degree of the community transformation over time. Bird communities from Salt marshes, Meadows, and Urban areas had the lowest mean

Table 2. Results of RDA ordination for bird communities from different biotopes with rates of temperature increase and precipitation in the first half of the year and year as predictors (only statistically significant correlation coefficients are shown)

Biotope	CCA1			CCA2			R^2_{adj}
	Temp	Prec	Year	Temp	Prec	Year	
Agricultural lands	0.47	0.67	0.98	-0.88	-	0.19	0.16
Vegetated strips	0.65	0.53	0.91	-0.76	-	0.40	0.47
Artificial forests	-0.44	-0.94	-0.81	0.20	0.31	-0.59	0.12
Cliffs	-	0.46	0.95	0.98	0.23	0.29	0.10
Islands and spits	-	0.51	0.99	-	0.81	-	0.20
Meadows	0.36	0.62	0.99	-0.71	-0.63	-	0.51
Reed beds	0.37	0.43	0.99	-0.36	0.70	-	0.10
Rural territories	-	0.46	0.99	-0.81	-0.73	-	0.36
Salt marshes	-	0.39	0.97	-0.62	-0.88	-0.23	0.29
Steepe	0.26	0.99	0.53	-0.96	-	-	0.05

Table 3. Trajectory lengths, angles, overall directionality of temporal change in communities

Biotope	Jump time	Lengths	Angles* (Mean \pm st. deviation)	Rho**	Directionality***
Agricultural lands	1993, 2003	29.54	94.79 \pm 0.93	0.65	0.43
Vegetated strips	2011	36.41	69.64 \pm 1.06	0.57	0.40
Artificial forests	2005	32.95	82.57 \pm 1.01	0.60	0.39
Cliffs	2015	46.49	93.66 \pm 1.03	0.59	0.40
Islands and spits	2010	33.74	79.53 \pm 0.94	0.64	0.39
Meadows	1998	56.49	107.93 \pm 1.28	0.44	0.33
Reed beds	2009	45.70	99.25 \pm 1.00	0.60	0.40
Rural territories	2012	39.31	95.41 \pm 1.14	0.52	0.41
Salt marshes	2006	37.59	95.77 \pm 1.19	0.49	0.42
Steepe	-	118.03	117.66 \pm 1.18	0.50	0.27

* – angles between consecutive segments in degrees; zero values point to segments that are along a straight line, and values equal to 180 degrees correspond to segments that are in opposite directions; ** – rho: mean resultant length of circular statistics which takes values between 0 and 1, and used to assess the degree of homogeneity of angle values and it will take a value of 1 if all angles are the same; *** – the measure of a overall directionality of a community trajectory and vary from 0 to 1 (the value 1 corresponds to the situation when all segments are located along a straight line).

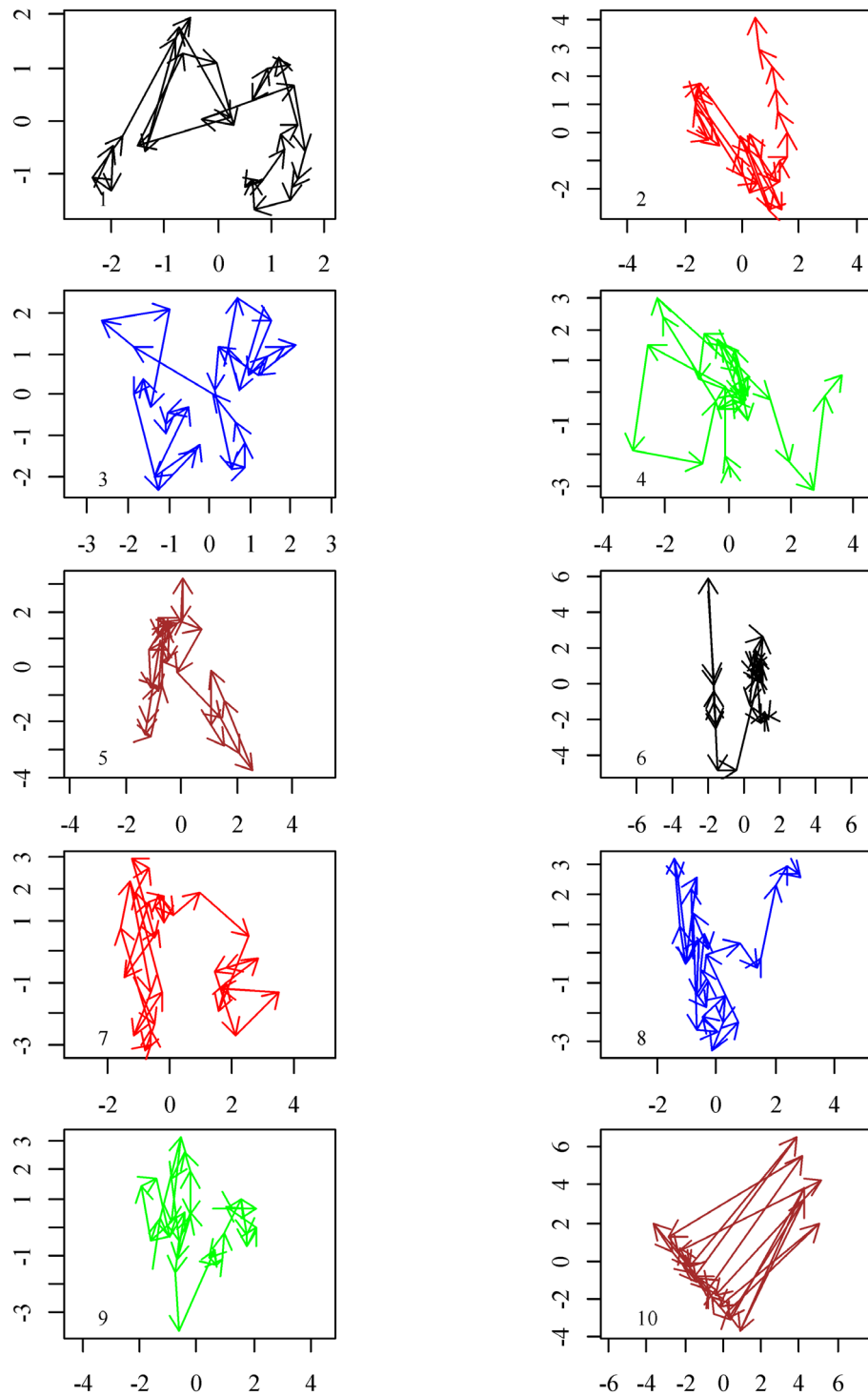


Fig. 6. Time trajectories of bird communities in the CCA axis space. The abscissa axis is CCA 1, the ordinate axis is CCA 2, and segments are transitions of the community state in successive years: 1988–1989, 1989–1990, ..., 2017–2018. The arrows show the directions of transitions. 1 – Agricultural lands, 2 – Vegetated strips within or around fields, 3 – Cliffs, 4 – Islands and Spits, 5 – Meadows; 6 – Reedbeds, 7 – Urban territories, 8 – Salt marshes, 9 – Steppe, 10 – Artificial forests.

resultant length of the circular statistics (ρ). Thus, for the specified habitats the degree of homogeneity of angle values was the lowest, which indicated greater chaotic dynamics. In turn, the highest degree of homogeneity of angle values was found for bird communities from the Steppe, Islands and spits, Agricultural lands.

Discussion

Global climate change affects the regimes of the most important meteorological variables, such as temperature and precipitation (KONAPALA et al., 2020). The temperature regimes influence various aspects of bird

biology (MAYFIELD et al., 2012; REIF et al., 2010; WATTS et al., 2018). The synchronization of the phenological stages of development of food objects with the breeding dynamics of birds is an important requirement for successful reproduction of birds (HALUPKA and HALUPKA, 2017; PAKHOMOV et al., 2019; PERRINS, 2008). The beginning of the breeding time of birds and the time of peak appearance of the food objects progressed due to the warming of the climate and was well explained by spring temperatures (VATKA et al., 2011). The spring phenological events show an earlier trend in the response to increasing spring temperatures (CARROLL et al., 2009). The role of precipitation is also important as a factor regulating the rhythm of the vegetation cover and the phenology of possible food objects for birds of plant origin (ZHOU and JIA, 2016). The state of plants also affects the animals on which the birds in turn feed (MÄNTYLÄ et al., 2011; ZHANG et al., 2018).

The landscape system considered covers a range of biotopes from steppe to aquatic ecosystems, for which the role of precipitation is crucial. There is a lack of water in the steppe communities, so the role of this environmental factor is extremely important. In wetland ecosystems, the precipitation regime determines the ratio of land or water surface in the respective areas, which affects the extent of island spaces. The island character of many locations is very important as a factor in protecting birds from predators (CLODE and MACDONALD, 2002; CÔTÉ and SUTHERLAND, 1997; SMITH et al., 2010). The precipitation also affects the level of salinity of soil and water bodies, which also significantly affects the structure of the vegetation cover and trophic objects of birds (SHRIVASTAVA and KUMAR, 2015).

However, the evaluation of the role of temperature and precipitation in the ecosystem dynamics suggests that these phenomena should be represented as the quantitative variables that can be used to model their role in a description of the state of bird populations and communities. The complexity of the problem is that the phenology is significantly different for different bird species. The most sensitive stages of life cycle for different bird species occur in different periods of the year. Therefore, the general variables such as the average annual temperature or the amount of precipitation for a year or other artificially specified period have a distant relation to the dynamics of the bird life cycle. In ecology, agriculture, forestry and hydrology the effective sum of temperatures is widely used, which is the sum of positive differences between the average diurnal temperature and a commonly-used threshold of temperature 5 °C (HEIKINHEIMO and LAPPALAINEN, 1997; THUM et al., 2009).

Under conditions of the linear temperature growth over time, which is observed in the first half of the year within the studied territory, the sum of effective temperatures will be proportional to the temperature increase rate. To study the coordinated changes in populations of different species in response to changes in the climatic conditions, the rate of temperature change eliminates the need to explicitly determine the sum of effective temperatures for the different species, which is practically very difficult to perform. In

addition, the rate of temperature increase is actually an invariant value for the thermal regime of a given year. It should be noted that the rate of temperature increase during the first half of the year does not demonstrate a stable growth trend throughout the whole period of research in contrast to the average annual temperature. The trend of average temperature increase can be explained by a global warming. The obtained results indicate that within the studied area the warming is shifted mostly to the second half of the year, when the main events related to the breeding of birds have already been completed. This result largely explains the observation that climatic changes are less important than landscape features of an area in terms of the variation of bird community structure (BONTHOUX et al., 2013; CRICK, 2004; TRAUTMANN, 2018; TRIVIÑO et al., 2011).

The quantification of precipitation dynamics is also a challenging task. The precipitation in the steppe zone should be also noted to be extremely irregular (KUNAH et al., 2019; MARCUZZI, 1979). The soil water balance depends on the daily precipitation and the actual evapotranspiration (TEIXEIRA and PEREIRA, 1992). Therefore, the cumulative sum of precipitation can be considered as a fairly good approximation that characterizes the water balance. The cumulative precipitation indicator gives a smoothed representation of the moisture dynamics (BONDAREV et al., 2019; BONDAREV and ZHUKOV, 2017). This indicator also reflects the presence of phenomena of moisture accumulation in the soil and water bodies, which provides a basis for the summation of the precipitation over a period.

The results obtained indicate that the birds did not show a significant pattern of response to the changes in temperature and precipitation in at least one third of the cases. According to 'Shelford's law of tolerance', all populations staying in the optimal condition do not demonstrate an unambiguous response to the ecological factors (SHELFORD, 1931). In contrast, switching the ecological factor from the pessimum to the optimum is commonly accompanied by the sensitive reaction of populations (ALASMARY et al., 2020; KUNAH et al., 2018). It is possible to assume that the species which are in an optimum zone do not appear insensitive to the variability of environmental factors. Thus, the observed climate changes for a considerable proportion of bird species do not exceed the limits of the optimum. Nevertheless, for 2/3 of the bird species, changes in the climatic conditions which are reflected in the variability of temperature and precipitation, affect their abundance. It is important to note that the nature of species response in the gradient of temperature or precipitation conditions depends on the type of particular ecosystem and is not uniform for all populations inhabiting the different landscape conditions. The results obtained are in accordance with the assumption that the responses to climatic warming are population, species and habitat specific (VATKA et al., 2011). The bimodal response types are associated with the role of biotic interactions such as the interspecific competition (AUSTIN, 1976; BATEMAN et al., 2012; JANSEN and OKSANEN, 2013). The bimodality is also the basis for the significant community rearrangements, which manifest

themselves as the discontinuous transitions of trajectories. Abrupt dynamics over time were observed for the bird communities of most of the ecosystem types studied. No drastic changes in the climatic conditions during the study period were detected. Therefore, we can conclude that the continuous changes in a community's structure initiated by the external environmental factors combined with changes in the internal biotic interactions, which is exactly what can lead to a drastic reorganization of the community. The climate changes have different effects on the distribution of resources in the various areas, creating a mismatch in resource use and availability between species (PIMM, 2009). This mismatch will eventually lead to cascading effects and asynchrony between reactions of different trophic groups, increasing negative and positive cumulative impacts of climate change on ecological communities (BELLARD et al., 2012; BROWN et al., 1997; MARTIN and MARON, 2012; MURPHY et al., 2020).

The variables considered, which describe temperature and precipitation conditions, can also explain the dynamics of bird communities. For community ordination, Redundancy Analysis or Correspondence Analysis may be considered as alternatives (VAN DEN WOLLENBERG, 1977). In comparison with other ordination techniques, these approaches have a constrained version (O'CONNOR, 1988; OKSANEN, 2012). The choice between these two techniques depends on the preferred type of species response to the effects of environmental gradients (TER BRAAK and PRENTICE, 1988). In case of monotonic responses, Redundancy Analysis has an advantage, while in case of bell-shaped responses, Correspondence Analysis has an advantage. The response of bird species to temperature and precipitation gradients most often has a symmetrical or asymmetrical bell-shaped type of response. It should be noted that the bimodal response type can be considered as a result of the strong competitive relationships of species in the optimum zone. Thus, Constrained (or Canonical) Correspondence Analysis (CCA) proved to be the most appropriate procedure for the ordination of bird communities.

For all communities, there was a trend of directed changes that is marked by a time variable. The increases in temperature and precipitation are associated with this trend. However, the correlation of these factors is specific to the different types of ecosystems. It should be noted that the importance of temperature may be lower than the role of precipitation or neutral trends for some ecosystems. Also, the community may not show a stable response to temperature changes. For example, no significant role of temperature was found for the bird communities of islands and spits. With global warming, the role of change in the rhythm of precipitation in the steppe zone is more important than temperature dynamics. These conclusions are in line with findings that the arid steppes with low vegetation productivity can respond strongly to the changing precipitation patterns, especially when warming occurs, highlighting the positive effects of increased precipitation on warming (XU et al., 2016). Obviously, the specificity of the impact of precipitation on vegetation cover and living birds has a clearly defined landscape context. The degree

of sensitivity to precipitation may vary significantly in different types of ecosystems. In addition, the mechanism of such influence will be different. In steppe ecosystems, the additional amount of water may stimulate plant growth and expand the trophic base for birds. In wetland ecosystems, the precipitation has a significant impact on the water levels in water bodies, which determines the areas suitable for nesting and the degree of protection of sites from the predators. In brackish estuaries, the precipitation affects the degree of salinity in water bodies and their level of food resources, which also determines the trophic base of the shorebird species.

Conclusion

The regime of temperature and precipitation has a significant impact on the temporal dynamics of both the studied bird populations and their communities. The warming and precipitation rates in the first half of the year may be considered as the proximal predictors both on species and community level. The type of response of bird populations to temperature or precipitation gradients varies depending on the ecosystem type. In the context of global warming, the role of changes in precipitation patterns is more important than changes in the temperature in transforming bird communities. The dynamics of bird communities under the influence of climatic factors are undergoing abrupt transitions, which are most likely due to the restructuring of biotic interactions within the communities.

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