Preferable and limiting conditions of trans-Palearctic *Orthocephalus* species (Heteroptera: Miridae)

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Abstract

The environmental conditions limiting the distribution of trans-Palearctic species from various groups remain poorly studied. This work addresses the topic from three perspectives: (1) analysis of climatic variables, biomes and climate zones corresponding to the actual records; (2) assessment of environmental niches and contribution of biomes to those niches; (3) comparison of the distributional limits of trans-Palearctic and more local species. The genus *Orthocephalus* (Insecta: Heteroptera: Miridae) is used as a model taxon. The results have demonstrated that all trans-Palearctic species of this genus are known from numerous biomes and climate zones, but each of them has unique preferences. Biomes significantly contribute to the environmental niches of some of those species. None of the trans-Palearctic species were recorded from the hot steppe and desert climate zones, which occupy large areas in the Palearctic, although certain rare and local species inhabit those regions. This means that the trans-Palearctic species cannot easily adapt to those conditions.

Keywords: distribution, climatic variables, climate zones, biomes, plant bugs, insects, environmental niche modelling

Introduction

In recent years, different aspects of widely distributed species from various groups have been studied, including the peculiarities of native and introduced species, population structure, and climatic condition preferences, as well as the differences in tolerance of heat and cold between widespread species and those with comparatively small ranges (Lohman, Peggie, Pierce and Meier, 2008; Pyron and Burbrink, 2009; Overgaard, Kristensen, Mitchell and Hoffmann, 2011; Stohlgren et al., 2011; McDowell, Benson and Byers, 2014; Beukema et al., 2018; Namyatova, 2020). Widely distributed species can successfully complete their life cycle in a wide range of environmental conditions. This raised the following interesting questions. What are the factors that limit the distribution of widespread species? Are there similar preferable and limiting conditions for various widespread species inhabiting the same continent?

The current study addresses these questions for a number of trans-Palearctic species, i. e., widely distributed in the Palearctic. These taxa represent an important component of the biodiversity of Europe and Asia. The relation between the distribution and the environmental preferences for trans-Palearctic species is likely to be of great importance for better understanding of the biogeographical patterns, species migrations, invasions and the effect of climate change on biodiversity in this zoogeographic realm. However, this topic has been poorly studied, while works published earlier mostly cover Western Palearctic and are very scarce for its Asian part (e. g., Estrada-Peña, Sánchez and Estrada-Sánchez, 2012; Estrada-Peña et al., 2013; Beukema et al., 2018; Namyatova, 2020).

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The model taxon for this work is the genus *Orthocephalus*, Fieber, 1858, from the family of plant bugs, or Miridae Hahn, 1831 (Insecta: Hemiptera: Heteroptera). Bugs from this genus are dark-colored, 3–7 mm long, feed on herbs and mostly live in meadows and steppe biotopes. The genus includes 23 species with different distributions. Four of them, namely *O. bivittatus* (Fieber, 1864), *O. brevis* (Panzer, 1798), *O. saltator* (Hahn, 1835) and *O. vittipennis* (Herrich-Schaeffer, 1835), are trans-Palearctic. *Orthocephalus coriaceus* (Fabricius, 1777) is widespread mostly in Europe and *O. funestus* (Jakovlev, 1881) inhabits large areas in Northeast Asia. *Orthocephalus fulvipes* (Reuter, 1904) and *O. proserpinae* (Mulsant and Rey, 1852) are known from different Mediterranean and arid areas in the southwest Palearctic. The 15 other species are either distributed very locally or known only from few localities (10 or less). *Orthocephalus* was revised morphologically and its distribution was carefully documented (see Namyatova and Konstantinov, 2009, and Namyatova, 2020, for further details on *Orthocephalus*).

The current work addresses the question on the preferable and limiting conditions for the trans-Palearctic species from three perspectives. First, it was hypothesized, that the ectotherm organisms occupying heterogeneous habitats develop physiological or behavioral capacities to optimize performance in variable thermal environments (e. g., Ghalambor et al., 2006; Overgaard, Kristensen, Mitchell and Hoffmann, 2011). This relates to trans-Palearctic species, the distribution of which spans across thousands of kilometers, covering different biomes and climate zones. These taxa must be able to adjust to different conditions, and they are very likely to be well-adapted to the most common conditions in the regions, which include the largest biomes and climate zones. In the previous paper, based on the climatic data only, it was shown that four closely related trans-Palearctic *Orthocephalus* species are differently adapted to the climatic conditions, and their ecological niches are not identical (Namyatova, 2020). However, the species' preferences for the particular biomes and climate zones were not studied. If some large biomes and climate zones are avoided by the trans-Palearctic species that means that there are conditions to which they cannot easily adapt.

Second, it is possible to test whether the biome variable contributes to the ecological niche models for the trans-Palearctic species, and therefore, influences their distribution. Previously biomes were used for environmental niche modelling for plants (e. g., Thuiller et al., 2005; Wan, Wang and Yu, 2017). Should the trans-Palearctic species be evenly distributed across different biomes, it is likely that they do not have a strong preference for particular biomes. However, a biome might be a restricting factor for the species with a more local distribution. Biomes are supposed to correlate with the climatic variables, as long as they represent the broad vegetation type, which is at least partly defined by the climate (Crisp et al., 2009). Therefore, adding biomes to the analysis might not improve the model performance or even make it overfitted. However, the differences between the models that are based on the climatic variables only and those which also include biome variable, have never been tested.

Third, it was shown that the ecological niches of the trans-Palearctic species are similar to each other and to those of widespread species, which are distributed mostly in Europe (*O. coriaceus*) and Northeast Asia (*O. funestus*) (Namyatova, 2020). At the same time, the niches of the trans-Palearctic species are less similar to those of more local species inhabiting the Mediterranean areas of the western Palearctic (*O. fulvipes* and *O. proserpinae*). However, the species known from <11 localities were not studied.

The current work is aimed to extend the previous research on *Orthocephalus* species and assess the actual distribution of the trans-Palearctic species in comparison with the more local ones. Therefore, the investigated question is: are there any conditions suitable for the rare and local species, but avoided by the trans-Palearctic species? If the answer is positive, this will mean that some conditions are suitable for certain representatives of this genus, but the trans-Palearctic species cannot develop adaptations to them quickly and those conditions can represent the limiting factors for the distribution of these taxa.

To sum up, this paper explores the preferable and limiting environmental conditions for the distribution of the trans-Palearctic species. Specifically, the objectives are as follows: (1) to test, based on the records and ecological niche models, whether there are biomes and climate zones preferable and avoided by the trans-Palearctic *Orthocephalus* species; (2) to test whether biomes contribute to the ecological niches of *Orthocephalus* species, and whether there is a difference between more local and widespread species; (3) to compare the climatic variables, biomes and climatic zones suitable for all species of the genus *Orthocephalus* and to find the possible limiting conditions for the widespread and more local species.

ANIMAL ECOLOGY

Material and methods

Specimens

All *Orthocephalus* species (numbers of unique records are provided in brackets) were analysed in this paper, they are *O. arnoldii* (10), *O. bivittatus* (171), *O. brevis* (146), *O. championi* Saunders, 1894 (3), *O. coriaceus* (39), *O. fulvipes* (18), *O. funestus* (90), *O. medvedevi* Kiritshenko, 1951 (4), *O. melas* Seindestucker, 1962 (2), *O. minimus* Drapolyuk and Kerzhner, 2000 (1), *O. modaressi* Linnavuori, 1997 (3), *O. proserpinae* (19), *O. putshkovi* Namyatova and Konstantinov, 2009 (2), *O. rhyparopus* Fieber, 1864 (1), *O. saltator* (237), *O. scorzonerae*

Drapolyuk and Kerzhner, 2000 (10), *O. sefrensis* Reuter, 1895 (2), *O. solidus* (Seidenstucker, 1971) (1), *O. styx* Reuter, 1908 (4), *O. tibialis* (Reuter, 1894) (2), *O. tristis* (Reuter, 1894) (1), *O. turkmenicus* Namyatova and Konstantinov, 2009 (6), *O. vittipennis* (208). The localities for *O. bivittatus*, *O. brevis*, *O. coriaceus*, *O. fulvipes*, *O. funestus*, *O. proserpinae*, *O. saltator* and *O. vittipennis* are listed in Data S1 in Namyatova (2020) and the maps with the localities of those species are provided in Figs 1, 2 in Namyatova (2020). The list of the localities for the rare and local species are listed in Data SI1.

Specimens used for this study are mostly preserved at the Zoological Institute of the Russian Academy of Sciences (ZISP), which possesses the largest collection of Palearctic Miridae. Some of the specimens used in this study are preserved in other institutions: Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Canada (CNC), Museum of Natural History, London, Great Britain (BMNH), National Museum of Wales, Cardiff, Great Britain (NMWC), Hungarian Natural History Museum, Budapest, Hungary (HNHM), Linnavuori Collection (LCRT), Matocq collection (MATOCQ), Bavarian State Museum in Zoology, Munich, Germany (ZSM), National Museum of Natural History, Paris, France (MNHN), Ribes Collection (JR), American Museum of Natural History, New York, USA (AMNH), Natural History Museum, Geneva, Switzerland (MHNG), Zoological Museum, Amsterdam, Netherlands (ZMAN), Zoological Museum, Moscow, Russia (ZMAM), Carapezza collection (AC), Finnish Museum of Natural History, Helsinki, Finland (MZH), Institute for Biological Problems of Cryolithozone, Yakutsk, Russia (YIB). Additional localities were taken from the following papers: Putshkov, 1961; Ribes, 1989; Melber, Günther and Rieger, 1991; Dioli, 1993; Gorczyca and Chłond, 2005; Arnold, 2008; Lim, Lee, Park and Jo, 2011; Lim, Park, Lee and Jo, 2012; Lim, Park and Lee, 2013a; Lim, Park, Lim and Lee, 2013b; Nikolaeva, 2011; Frieß, 2006, 2014; Roháčová, 2007; Cho et al., 2008, 2011; Kondorosy, 2011; Kment and Baňař, 2012; Park, Kwon, Park and Park, 2013; Halimi, Paparisto and Topi, 2014; Heckmann, 2015; Shi, Li and Bao, 2016; Vinokurov, Kanyukova and Ostapenko, 2016; Gierlański, 2017; Jung, Kim and Duwal, 2017; Kozminykh and Naumkin, 2017; Sofronova, 2017; Vinokurov, Golub and Zinovjeva, 2017.

In this paper, the following types of distribution are compared: (1) trans-Palearctic (*O. bivittatus*, *O. brevis*, *O. saltator*, *O. vittipennis*), (2) European (*O. coriaceus*), (3) Northeast Asian (*O. funestus*) (4) southwestern (*O. fulvipes*, *O. proserpinae*) (5) rare and local species, known from 10 or less localities, and these include the rest of the taxa. The species from the types 1–3 inhabit large regions of the Palearctic, and are common in at least some parts of it. The species from type 5 are mostly collected from the eastern and southern Europe, northern Africa, the Near East, and Central Asia, and some of them are known only from one to three locations, and apparently are very local. For example, *O. championi* is known only from Corsica (France), while a few specimens of *O. rhyparopus* have been collected in a single locality in the Volgograd Province (Russia) and have never been recollected. Representatives of some taxa from type 5 distribution have been collected in the localities separated by thousands of kilometers (*O. arnoldii*, *O. putshkovi*, *O. scorzonerae*, *O. turkmenicus*). However, few records and specimens are known of each, therefore, they are not abundant in their habitats and cannot easily spread and become common in new areas; in this paper they are treated as rare. Species from type 4 are known from 18 or 19 localities and small series, and there are very few records of them in the literature, therefore, they could be considered rare. However, these species inhabit large areas and have enough points to undertake ecological niche modelling and have been placed in a separate group for comparison purposes.

Maps and map visualization

The layers with 19 bioclimatic variables were downloaded from Worldclim Version 1.4 (https://www.worldclim.org/version1) in 5-arc minute (~10 km). Refer to O'Donnel and Ignizio (2012) for the detailed explanation of each variable. This resolution was chosen for higher computational efficiency. Additionally, many coordinates for the localities are approximate and higher resolution can lead to erroneous conclusions (e. g., Graham et al., 2005; Hanberry, 2013). The maps with biomes according to the TNC Terrestrial Ecoregions map as defined in Olson et al. (2011) and the maps with the Köppen — Geiger climate zones (Peel, Finlayson and McMahon, 2007; Rubel and Kottek, 2010) were downloaded from the following open resources: http://maps.tnc.org/gis_data.html and https://datacatalog.worldbank.org/dataset/world-maps-k%C3%B6ppen-geiger-climate-classification, respectively.

The maps with the bioclimatic variables and biomes were trimmed for Palearctic (20°N–90°N, –30°W–180°E) and converted to ASCII format using DIVA-GIS and QGIS.

All maps were prepared using QGIS 3.16. Fig. 1A is a colored representation of the biomes and Fig. 2A is a colored representation of the Köppen — Geiger climate zones. The maps for Figs 3, 4 and Figs SI1, SI2 were created by uploading the averaged maps generated from the Maxent analysis to QGis 3.16. The country borders layer is freely accessible at https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3, and is not copyrighted. The background for Fig. 6, D–G, is the layer freely accessible at https://github.com/nvkelso/natural-earth-quick-start/tree/master/50m_raster/NE1_50M_SR_W and is not copyrighted.

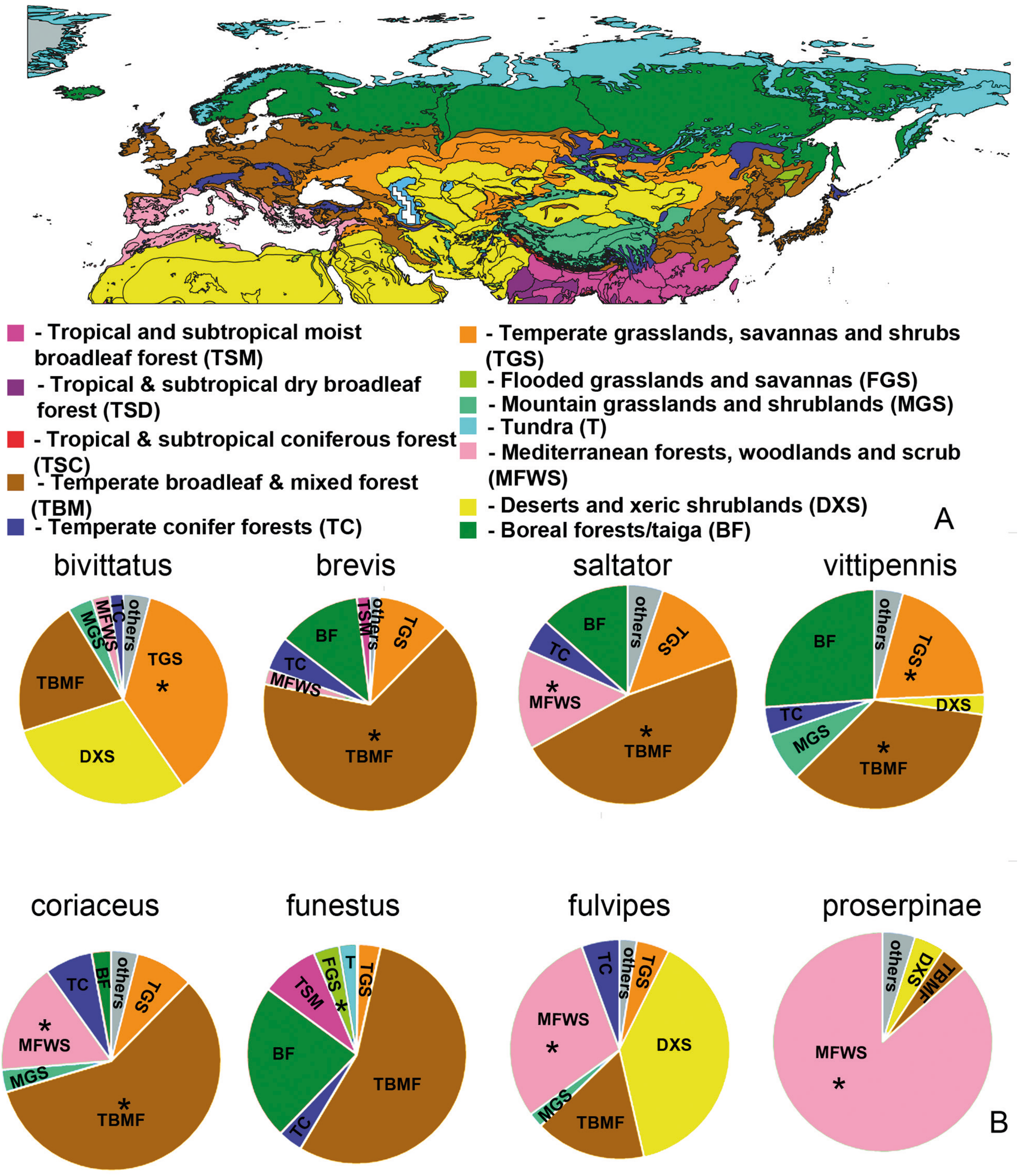

Fig. 1. A. Colored representation of the biomes from Olson et al. (2011). B. Diagrams showing the percentage of geographic projection of climatic niche occupied by biomes for species used for the niche modelling. The percentage of geographic projection for each biome is average calculated from four niches obtained in this work and Namyatova (2020). Biomes occupying less than 2 % of geographic projections in average are included in the "others" sector. The sector is marked with an asterisk if the area of the corresponding biome in at least one geographic projection of the models exceeds 50 % of total biome area in Palearctic.

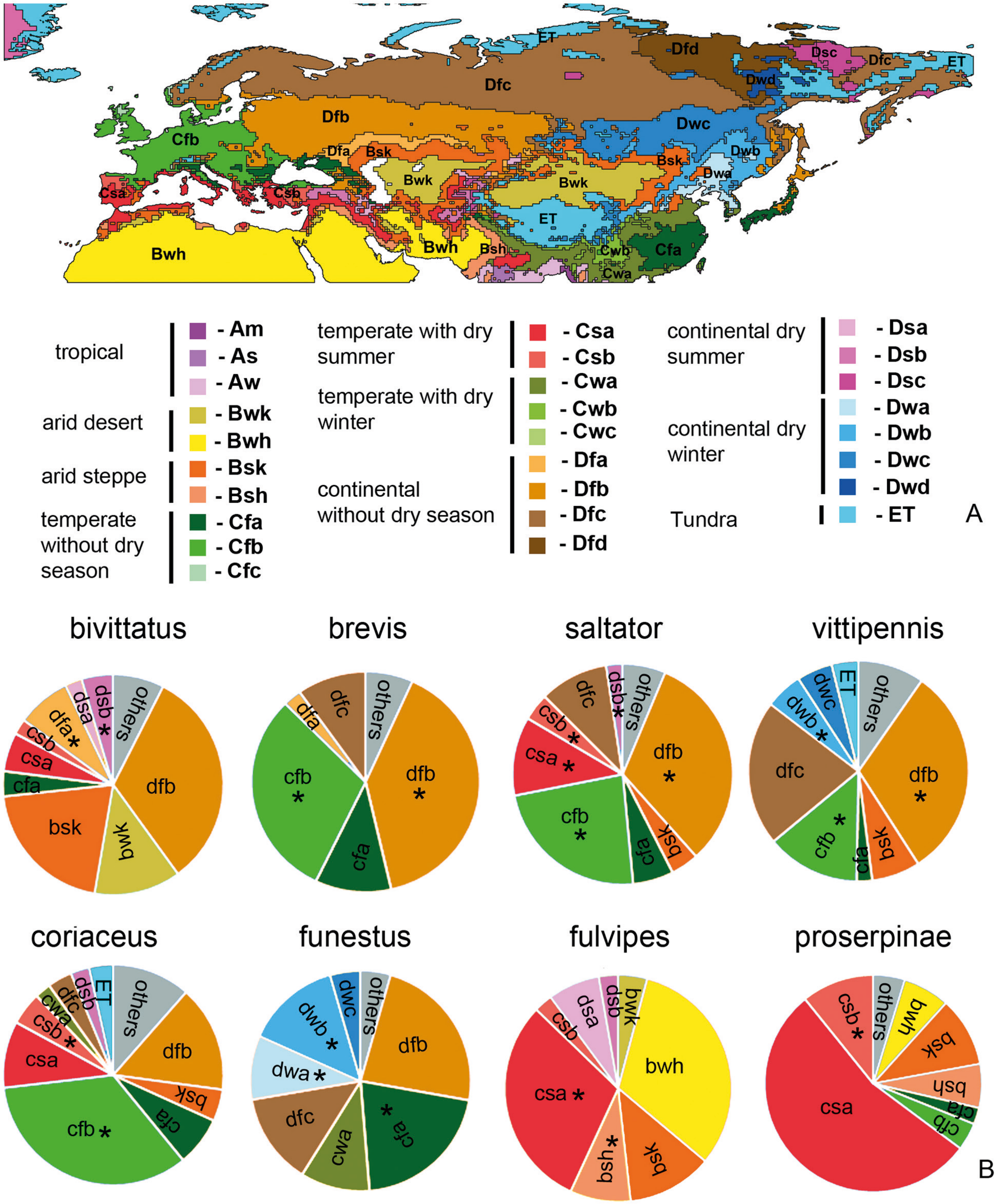

Fig. 2. A. Colored representation of the Koppen — Geiger climate zones from Rubel and Kottek (2010). B. Diagrams showing the percentage of geographic projections of climatic niche occupied by climatic zone for all species used for the niche modelling. The percentage of geographic projection for each climatic zone is average calculated from four niches obtained in this work and Namyatova (2020). Climate zones occupying less than 2 % of geographic projections in average are included in the "others" sector. A sector is marked with an asterisk if the area of the corresponding climatic zone in at least one geographic projection of the models exceeds 50 % of total climate zone area in Palearctic.

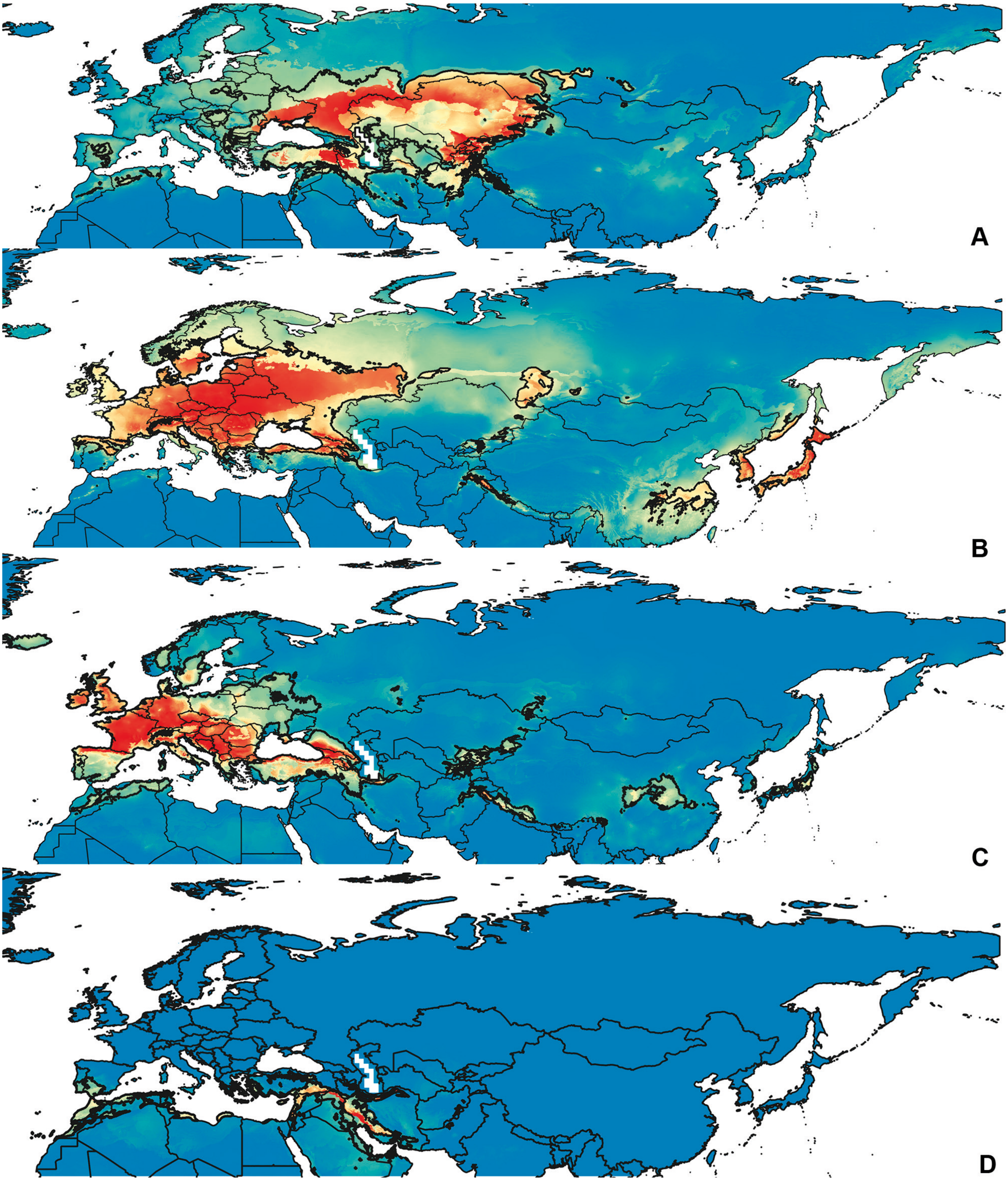

Fig. 3. Environmental niche models obtained with all climatic variables and biomes (CBF). A. *O. bivittatus*, B. *O. brevis*, C. *O. coriaceus*, D. O. *fulvipes*.

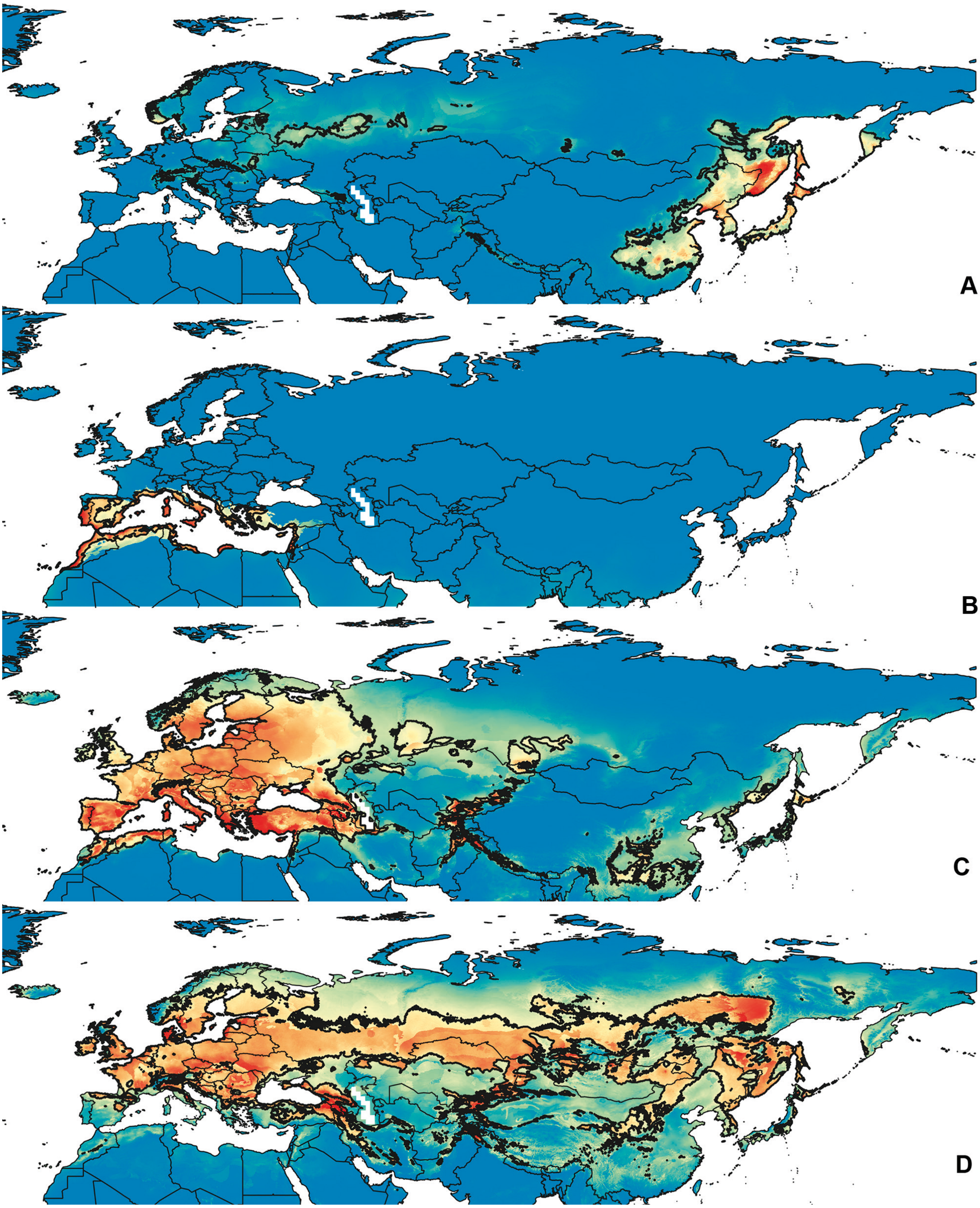

Fig. 4. Environmental niche models obtained with all climatic variables and biomes (CBF). A. *O. funestus*, B. *O. proserpinae*, C. *O. saltator*, D. *O. vittipennis*.

Environmental niche modelling

The procedures mostly follow Namyatova (2020), as it is important for the comparison of the results. The analysis has been performed in Maxent 3.4.1 with swd files and layers with climatic variables and biomes in ASCII format. For the datasets with >50 localities, the bootstrap replicated run type has been applied. In this case, 25 % of the localities were assigned for the random test percentage. Overall, ten replicates were conducted. For the datasets with <50 localities (*O. coriaceus*, *O. fulvipes* and *O. proserpinae*), the cross-validation run type was used. The replicate number corresponded to the locality number, which is advised for small datasets (Pearson, Raxworthy, Nakamura and Peterson, 2007; Shcheglovitova and Anderson, 2013). Sampling bias was addressed by choosing the background data with the same bias as localities (Phillips et al., 2009; Elith et al., 2011; Kramer-Schadt et al., 2013). Bias file was created using the kde2d function from the *MASS* package in R (Filazzola, Sotomayor and Lortie, 2018; Mudereri et al., 2020; Ripley et al., 2020). Bias file for each species in ASCII format has been implemented into the biasfile option in Maxent and used to randomly select ten thousand background points, which is the default Maxent setting. The "cloglog" output was used for the models of the geographic projection, visualization and further analysis.

Variable selection

Similar to the study based on the climatic variables only (Namyatova, 2020), in the current work, an analysis with two sets of variables has been performed. The first set included all climatic variables and biomes (climate and biome full dataset or CBF). Since using the highly correlated variables can lead to overfitting and narrowing the niche distribution (Beaumont, Hughes and Poulsen, 2005), reduced datasets (climate and biome reduced dataset or CBR), created for each species separately, have also been used to obtain the model. To create this set of variables, the highly correlated variables have been excluded. Biome variable has categorical data type and climatic variables have continuous data type. The data have been tested for normality using Shapiro — Wilk normality test in R, and it was found that most of them do not have normal distribution. The correlation of the climatic variables was tested using the Pearsons' correlation method, which is suitable for this type of data. The correlation >0.9 is considered as high. The correlation between biomes and climatic variables has been tested using Kruskal — Wallis test, which is suitable for calculating correlation between categorical and continuous variables, and it does not assume the normal variable distribution. For this test the correlation with p-value >0.05 has been considered as high for most of the cases. For *O. proserpinae* Kruskal — Wallis test p-values are >0.05 for all pairs; therefore, the correlation with p-value >0.5 has been considered as high for this species. For the CBR dataset for each species, only those climatic variables which do not have high correlation with biomes and other climate variables have been chosen. The tables with the Pearsons' correlations are provided in Data S2 in Namyatova (2020) and Kruskal — Wallis correlations are provided in Table SI1. The sets of variables chosen for the CBR model for each species is provided in Table 1.

To avoid overfitting and over-complexity, feature classes and regularization multiplier (beta-multiplier) have been adjusted with *ENMeval* package in R (Muscarella et al., 2014a; Muscarella, Kass and Galante, 2014b) using Maxent. The models have been tested for the regularization multipliers ranging from 0.5 to 8 and default feature classes and their combinations, i. e., L, LQ, LQH, H, LQHP, LQHPT (L = linear, Q = quadratic, H = hinge, P = parameter, T = threshold). The method "block" has been chosen because it accounts for spatial autocorrelation (Muscarella et al., 2014a). The analysis has been run five times for each species and for each dataset. All resulting parameter sets have been saved and used for environmental niche modelling with Maxent. *ENMeval* has not provided conclusive results for the CBR datasets for *O. fulvipes* and *O. prosepinae*, and for those species the same parameter sets as in the CBF dataset have been applied to the CBR dataset. The full list of the parameter sets used for the modelling are provided in Table SI2.

Model evaluations

Training and test area under ROC curve (AUC) values, provided by Maxent, are valid for comparing the models calculated for the same study area (Bohl, Kass and Anderson, 2019) (Table SI2). The models have also been evaluated based on the differences between training and test AUC and omission error rates, as models with high differences between AUC values and omission error rates >0.1 are likely to be overfitted (Bohl et al., 2019). Therefore, the models with relatively high AUC values, and low differences between training and test AUC and omission rates have been chosen for the model visualization and further analysis (Table SI2).

Environmental niche projection

The obtained environmental niche models have been thresholded using the "Maximum training sensitivity plus specificity Cloglog threshold", as maximizing sensitivity and specificity performs well on presence only datasets (Liu, Newell and White, 2016). The total area of the thresholded niche projection for the models CBF and CBR has been obtained using QGIS 3.10 and provided in Table 1.

Variable comparison between models

The thresholded maps have been used as masks to trim the layers with climatic variables, biomes and climate zones to obtain the climatic variable ranges, as well as

Table 1. Variables contributing to the models CBF (first column for each species) and CBR model (second column for each species). The variables used for modelling are marked with "X". PC and PI denote the variables having PC and PI higher than 10 %. Total area of the suitable conditions projected area for each model is provided in the last raw

	bivittatus		*brevis*		*coriaceus*		*fulvipes*		*funestus*		*proserpinae*		*saltator*		*vittipennis*	
	CBF	**CBR**	**CBF**	**CBR**	**CBF**	**CBR**	**CBF**	**CBR**	**CBF**	**CBR**	**CBF**	**CBR**	**CBF**	**CBR**	**CBF**	**CBR**
Bio1 Annual Mean Temp	PC PI	PC PI	PI	PI	X	X	X	PC	PI	PI	X	X	PC PI	PC PI	PC PI	PI
Bio2 Mean Diurnal Range	X	X	X	X	X	X	X	X	X	X	X	PI	X	X	X	X
Bio3 Isothermality	X	X	X	X	PC PI	PC PI	X		PC PI	PC PI	X	X	X	X	X	X
Bio4 Temp Seasonality	X		X	X	X	X	X	X	X		X		X		X	X
Bio5 Max Temp of Warmest Month	X	X	X	X	X		X		X		X		X	X	X	
Bio6 Min Temp of Coldest Month	X		X		X	X	PI	PI	X		X		PI		X	
Bio7 Temp Annual Range	X	X	X		X		X		X	X	PI		X	X	X	
Bio8 Mean Temp of Wettest Quarter	X	X	X	X	X		X		X	X	X	X	X	X	X	X
Bio9 Mean Temp of Driest Quarter	X	X	X	X	X	X	PC PI		X	PI	X	PI	X	X	X	PI
Bio10 Mean Temp of Warmest Quarter	X		X		X	X	X	X	X		X	X	X		X	PI
Bio11 Mean Temp of Coldest Quarter	PI		X	X	X		X		X		X		X		X	
Bio12 Annual Precipitation	X	X	X	X	X		X		X	X	X		PC	X	X	X
Bio13 Precipitation of Wettest Month	X		X		X		X		X		X		X		X	
Bio14 Precipitation of Driest Month	X	X	PC PI	PC PI	X	PC	X	PC PI	X	X	X		X	X	X	X
Bio15 Precipitation Seasonality	X	X	X	X	PI	PI	X		X	X	X		X	X	X	X
Bio16 Precipitation of Wettest Quarter	X	X	X	PI	X	X	X		PI		X	X	X	X	X	PC PI
Bio17 Precipitation of Driest Quarter	X		PI		X		X		X		X		X		X	
Bio18 Precipitation of Warmest Quarter	PI	PI	X	X	X	X	PI		PC	PC PI	X		X	X	X	
Bio19 Precipitation of Coldest Quarter	PC	PC PI	X	X	X	PC	X	PC	X		X	X	PC PI	PC	X	PC PI
Biomes	PC PI	PC PI	PC	PC	PC	PC	PC PI	PC PI	PC	PC	PC PI	PC PI	X	PC	PC	X
Area (x10^6 km^2)	8.05	7.36	7.80	7.36	7.59	8.32	1.80	3.81	4.51	4.97	1.22	2.11	11.53	9.80	13.83	17.20

biomes and climate zones, covered by the geographic projections of the models.

For the comparison of the climatic variables between the models, the graphs with the climatic variable ranges for each species have been created in R. The graphs on Figs 5, 6, A–C, show the averaged ranges for the chosen climatic variables for each species used for the niche modelling, Figs SI3–SI12 show the ranges of all variables for each model obtained in this work and Namyatova (2020).

To compare the biomes and climate zones suitable for the species, two ratios have been calculated for each taxon and for each model including CBF and CBR, as well as the models based on full climatic data (CF) and

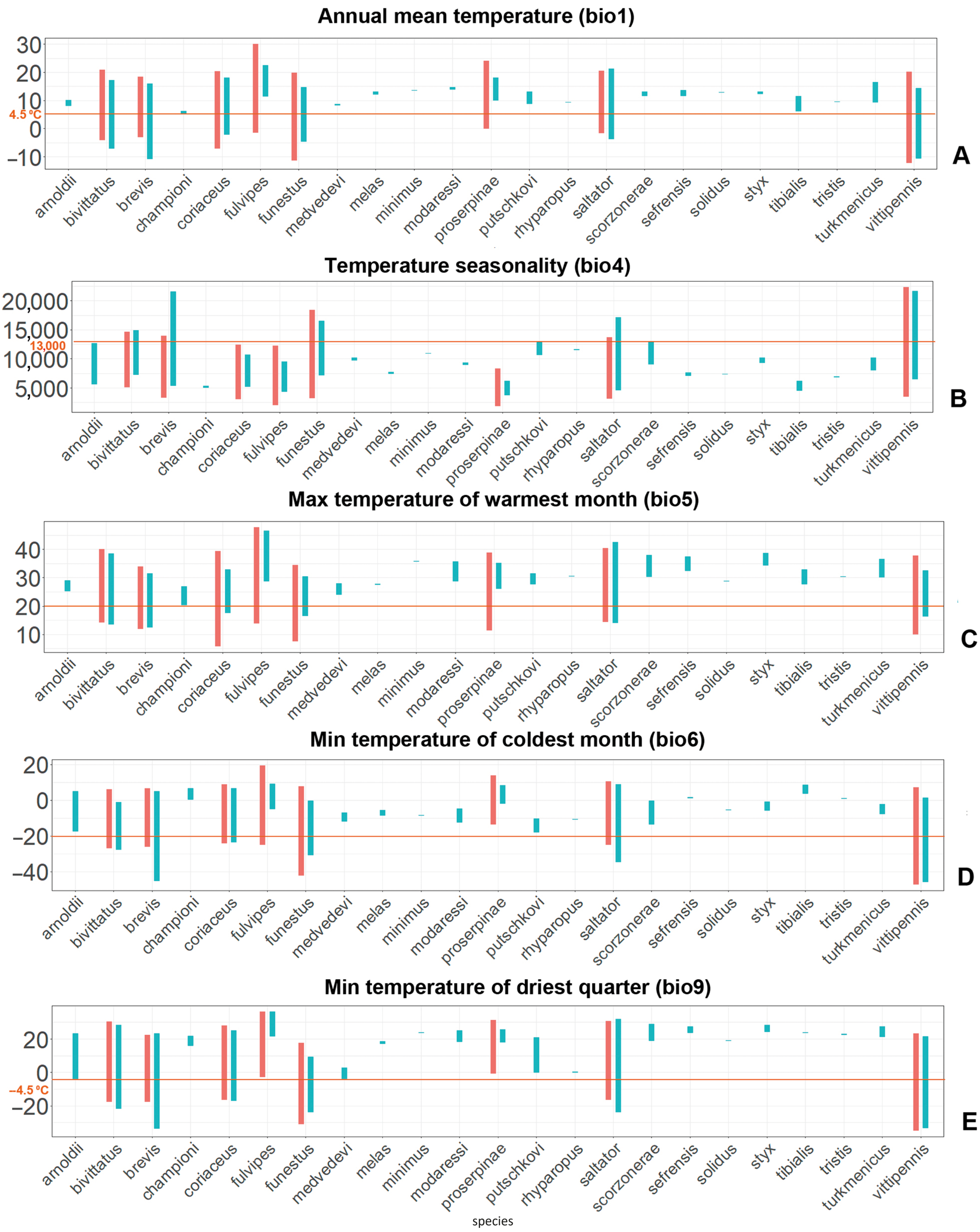

Fig. 5. Ranges for climatic variables important for explaining the *Orthocephalus* species' distribution. The ranges of actual records are shown in blue, the averaged ranges obtained from models are shown in rose. The possible limiting value for each variable is shown with the orange line. A. Annual mean temperature (bio1), B. Temperature seasonality (bio4), C. Max temperature of warmest month (bio5), D. Min temperature of coldest month (bio6), E. Min temperature of driest quarter (bio9).

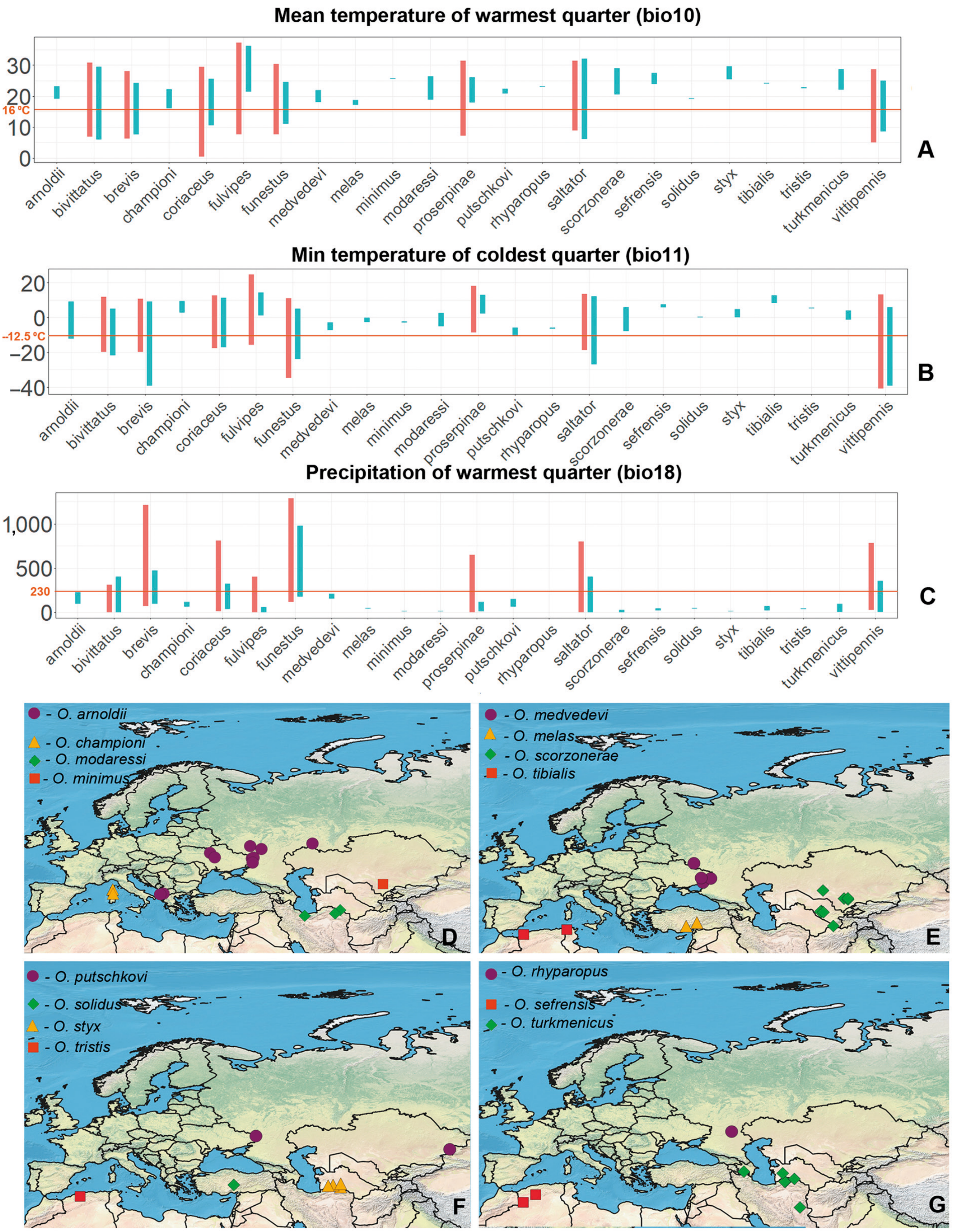

Fig. 6. Ranges for climatic variables important for explaining the *Orthocephalus* species' distribution. The ranges of actual records are shown in blue, the averaged ranges obtained from models are shown in rose. The possible limiting value for each variable is shown with the orange line. A. Mean temperature of warmest quarter (bio10), B. Min temperature of coldest quarter (bio11), C. Precipitation of warmest quarter (bio18). Distribution of rare and local *Orthocephalus* species. D. *O. arnoldii*, *O. championi*. *O. minimus*, *O. modaressi*. E. *O. medvedevi*, *O. melas, O. scorzonerae*, *O. tibialis*. F. *O. putschkovi*, *O. solidus*, *O. styx*, *O. tristis*. G. *O. rhyparopus*, *O. sefrensis*, *O. turkmenicus*.

reduced climatic data (CR). (1) The ratio between the area of a particular biome or climatic zone, occupied by the geographic projection of the model, and the total area of this geographic projection. If the ratio is 1 (or 100 %), this means that geographic projection covers a single biome or climate zone, meaning that those conditions are very suitable for species, and others are not (Figs 1, 2, Table SI6, Data SI2–SI3). The geographic projections of models of widely distributed species might occupy the entire small biome or climate zone, meaning that this area is suitable for the species. However, in this case the area of this biome or climate zone could be small in comparison with the entire geographic projection of the model, and the first ratio will also be small. Therefore, the second ratio has been calculated: (2) The ratio between the biome or climate zone area occupied by the geographic projection of the model and the entire area of the corresponding biome or climate zone in the Palearctic. If the second ratio is 1 (or 100 %), this means that the geographic projection covers the entire particular biome or climate zone in the Palearctic, and those conditions should be very suitable for the studied taxon (Figs 1, 2, Table SI6).

All areas have been calculated in QGis using the “Statistics by category” tool. The comparisons have been performed for CBF, CBR, as well as for CF and CR. All geographic projections were in WGS 84 coordinate system.

Niche overlap

The niche overlap has been completed in ENMTools (Warren, Glor and Turelli, 2010) in three stages. (1) Schoener’s D (D) and Hellinger distance I (I), measuring niche overlap with values ranging from 0 to 1, have been obtained. Comparisons have been run between all species within each model type, CBF and CBR, separately. (2) The identity test was performed to test whether the models of different species are identical. It can be performed only for the same set of variables for both species; therefore, only CBF models have been compared in this case. This test randomizes the occurrences for two species, compares the environmental niches for those datasets and creates permuted D and I values for them. The niches are considered as different, if the values obtained from actual data are significantly lower than those obtained from randomized data (Warren, Glor and Turelli, 2010). (3) The background test creates the niche based on random distribution with the chosen species background. It compares one species’ actual occurrences with the random background occurrences of the other species and calculates I and D values for the niche overlap. The test should be performed on both sides. If I and D values of actual records are higher or lower than those obtained from the background test, this means that the niches are more similar or more different than expected from random data, respectively (Warren, Glor and Turelli, 2010). For this study the background for each species corresponds to its bias file.

Results

Model evaluation results

In the most resulted Maxent models training and test AUC are higher than 0.9, except for *O. vittipennis*, where training AUC ranges from 0.79 to 0.88 and test AUC ranges from 0.74 to 0.86. In most cases training AUC is higher than test AUC, except for two models for *O. funestus*. The differences between test and training AUC in the models chosen for the further analysis range from 0.001 (*O. funestus*) to 0.03 (*O. vittipennis*). Omission rates for the chosen models vary from 0.0631 (*O. funestus*) to 0.1667 (*O. fulvipes* and *O. proserpinae*) (see Table SI2 for the list of all values for AUC and omission rates). This is very similar to the results obtained in the research based on climate data only (Namyatova, 2020). The differences between test and training AUC and omission rates can be higher or lower for the models with biomes in comparison with the models without biomes.

Comparison of the geographic projections of the models with and without biomes

The geographic projections of the niches with biomes are provided in Figs 3, 4 (CBF) and Figs SI1–SI2 (CBR). The areas of the geographic projections of the models are provided in Table 1, and for the models CBF and CBR they can be smaller or larger than the corresponding areas of CF and CR models (Table 1 in Namyatova (2020) with two corrections: the areas for the CR models of *O. bivittatus* and *O. funestus* equal 7.69 x10^6 km^2 and 3.85 x10^6 km^2, respectively). The geographic projections of the models with and without biomes are similar.

For some species, some geographic projections reflect the species distribution better than others. For example, CF model for *O. bivittatus* predicts extending favorable conditions to the north of Russia, however, this species has never been reported from there. In case of CR and CBR models of *O. vittipennis*, the favorable conditions extend to the almost entire northern Russia, but, again, it has never been collected there. Considering the large number of mirid samplings from those regions (Konstantinov and Namyatova, 2019), it is very unlikely that *O. bivittatus* and *O. vittipennis* live in the north of Russia.

The geographic projections of the CBF and CBR models for *O. fulvipes* are much more restricted in the Near East than those of the CF and CR models; however, those areas remain poorly studied and the actual distribution of this species is unknown.

Biome contribution to the models

According to the Kruskal — Wallis test, a biome correlates with climatic variables for *O. bivittatus* (bio6 and bio11), *O. coriaceus* (bio8), *O. fulvipes* (bio3, bio5, bio8, bio9, bio11, bio12, bio15), and *O. proserpinae* (all variables) (Table SI1). Biomes significantly contribute to the niche models of the southwestern species, i. e. PC > 30 % and PI > 20 % for *O. fulvipes*, PC > 90 % and PI > 40 % for *O. proserpinae*. This variable has high PC for the European *O. coriaceus* (>40 %) and Northeast Asian *O. funestus* (>14 %). As to the trans-Palearctic species, biomes significantly contribute to both models of *O. bivittatus* (PC > 50 %, and PI ~ 20 %) and *O. brevis* (PC > 25 %). Biomes do not contribute much to the models of *O. saltator*, it only has PC ~ 10 % for the CBR model. This variable has the highest PC (41.5 %) for the CBF model of *O. vittipennis*; however, it does not contribute much to the CBR model (Table 1). These results only partly support the hypothesis that biomes should contribute more to the models of local species rather than to more widespread species. Indeed, this variable has high PC and PI for more local species (*O. fulvipes* and *O. proserpinae*); however, it also significantly contributes to all models of trans-Palearctic *O. bivittatus*.

Comparisons of climatic variables contributing to the models with and without biomes

The climate variables highly (>10 %) contributing to the CBF and CBR models are summarized in Table 1, and those for CF and CR models are summarized in Table 1 in Namyatova (2020). The set of variables with significant contribution to the models is identical for the CBF and CF models of *O. funestus* only. Overall, the number of climatic variables significantly contributing to CBF and CBR models is equal to or less than those significantly contributing to CF and CR models. Temperature seasonality (bio4), Max temperature of the warmest month (bio5), Mean temperature of the wettest quarter (bio8) and Precipitation of the wettest month (bio13) only slightly contribute or do not contribute to the CBF and CBR models, which only partly fits the results for the CF and CR models. Similar to the CF and CR models, in the CBF and CBR models, Annual mean temperature (bio1) significantly contributes to at least one of the models of all trans-Palearctic species, and it is very likely to be an important variable for the trans-Palearctic *Orthocephalus* species' distribution. Precipitation of the driest month (bio14) seems to be very important for *O. brevis*, because it has high PC and PI for all the models. Precipitation of the warmest quarter (bio18), Min temperature of the coldest month (bio6) and Mean temperature of the driest quarter (bio9) might be important for *O. bivittatus*, *O. saltator* and *O. vittipennis*, respectively, because they significantly contribute to at least three models of the corresponding species.

This analysis confirms that Isothermality (bio3) is important for both *O. coriaceus* and *O. funestus*. Other variables highly contributing to at least three models of those species are bio14 and bio19 for *O. coriaceus* and bio18 for *O. funestus*.

For southwestern species, the variables noticeably differ in their importance for the model. However, bio6 and bio18 contribute to three models of *O. fulvipes*.

The climatic variable ranges of the models with biomes are in general similar to and not narrower than those without biomes (Figs SI3–SI12).

Niche overlap for ecological niches with and without biomes

The results of niche overlap for the models with biomes are similar to those without biomes (compare Table SI3 in the current paper and Table 2 in Namyatova, 2020). Trans-Palearctic species show high niche overlap, and the identity test shows that none of those niches are identical. *Orthocephalus coriaceus* models have high niche overlap with *O. brevis* and *O. saltator*. As in the previous work (Namyatova, 2020), the largest niche overlap (I>0.9 and D>0.7) is demonstrated for the pair *O. brevis* and *O. saltator*. However, there are also differences in the niche overlap results between the datasets with and without biomes. For example, the niche overlap based on D metrics for the CBF and CBR models of the pairs *O. bivittatus* and *O. brevis*, *O. funestus* and *O. vittipennis* show lower values in comparison to the results for the CF and CR models. Additionally, background tests for the CBF and CBR models do not show consistent results for those two pairs, whereas the background tests for those two pairs for CF and CR models consistently show that the niches of those pairs are more similar than expected from the random data. The situation is opposite for the pair *O. bivittatus* and *O. coriaceus*, their niches are more similar than expected from the random data when the models with biomes are compared, and the results have been inconsistent in the previous work.

In case of *O. fulvipes*, the background test for the CBF and CBR models shows that the niche of this species is more different than expected from random data from all other species, except for *O. coriaceus*, and those results are inconsistent for the same comparisons of the CF and CR models. Although in the previous work it has been shown that the niches of *O. proserpinae* and *O. funestus* are more different than expected from random data, the current study does not show consistent results for this pair.

Comparisons of the climate variable ranges of widespread and more local species and rare species

The ranges of the climatic variables for *Orthocephalus* species are summarized in Figs 5, 6, A–C, and Figs SI3–SI12. The results show that rare species are distributed

Table 2. Number of *Orthocephalus* species collected from all biomes. Biomes with no records are highlighted in grey. The percentage of the biome area relatively to the entire Palearctic area is provided in the second column. The biomes with the largest number of species are in bold

Biome	% of total Palearctic area	Total number of species	Number of trans-Palearctic species	*O. coriaceus* (widespread European species)	*O. funestus* (widespread northeastern species)	*O. fulvipes* and *O. proserpinae* (widespread southwestern species)	Number of rare species
Tropical and subtropical moist broadleaf forests	5 %	0	0	0	0	0	0
Tropical and subtropical dry broadleaf forests	1 %	0	0	0	0	0	0
Tropical and subtropical coniferous forests	<1 %	0	0	0	1	0	0
Temperate broadleaf and mixed forests	**16 %**	**12**	**4**	**1**	**1**	**1**	**5**
Temperate conifer forests	**3 %**	**9**	**4**	**1**	**1**	**2**	**2**
Boreal forests/taiga	18 %	5	4	0	1	0	0
Tropical and subtropical grasslands, savannas and shrublands	<1 %	0	0	0	0	0	0
Temperate grasslands, savannas and shrublands	**8 %**	**12**	**4**	**1**	**1**	**0**	**6**
Flooded grasslands and savannas	1 %	1	0	0	1	0	0
Montane grasslands and shrublands	6 %	6	3	0	0	0	3
Tundra	7 %	0	0	0	0	0	0
Mediterranean forests, woodlands and scrub	**4 %**	**10**	**2**	**1**	**0**	**2**	**5**
Deserts and xeric shrublands	**29 %**	**8**	**4**	**0**	**0**	**1**	**4**
Mangroves	<1 %	0	0	0	0	0	0

in warm areas and, in comparison to trans-Palearctic species, as well as *O. funestus* and *O. coriaceus*, they do not occur in cold climates. In particular, the annual mean temperature (bio1) for rare species does not surpass 4.5 °C, though it can be below 0 °C for the trans-Palearctic species, as well as in *O. coriaceus* and *O. funestus* (Fig. 5A). Max temperature of the warmest month (bio5) is relatively high in all rare and local species and it is always higher than 20 °C, whereas it can be less than 20 °C in all trans-Palearctic species, as well as in *O. coriaceus* and *O. funestus* (Fig. 5C). Min temperature of the coldest month (bio6) is above –20 °C for all rare and local species, whereas it can be well below –20 °C in trans-Palearctic species, *O. coriaceus* and *O. funestus* (Fig. 5D). Mean temperature of the driest quarter (bio9) is higher than –5 °C in the rare and local species, whereas in trans-Palearctic species, *O. funestus* and *O. coriaceus* it can reach –20 °C and below (Fig. 5E). Mean temperature of the warmest quarter (bio10) is above 16 °C in rare and local species, and it can be less than 10 °C in all trans-Palearctic species (Fig. 6A). Mean temperature of the coldest quarter (bio11) is higher than –12.5 °C in rare and local species and it can reach –13 °C and below in trans-Palearctic species, *O. coriaceus* and *O. funestus* (Fig. 6B). The rare and local species are also distributed in the zones with dry summer, i. e. Precipitation of the warmest quarter (bio18) for them does not reach above 230 mm, whereas in trans-Palearctic species, *O. funestus* and *O. coriaceus* it can be higher than 300 mm (Fig. 6C). Additionally, Temperature seasonality (bio4) does not surpass 13,000 in rare and local species, whereas all trans-Palearctic species and *O. funestus* are distributed in the places with higher values of the seasonal differences (Fig. 5B). The climatic variables corresponding to the records of *O. fulvipes* and *O. proserpinae* are very similar to those of the rare and local species, however, their models suggest adaptation for the broader variable ranges. *Orthocephalus fulvipes* can tolerate higher temperatures over the warmest and driest periods (bio5, bio9, bio10) than all other species (Figs 5, C, E, 6A).

Comparison of biomes of widespread species and of more local and rare species

None of the *Orthocephalus* species were collected in the tropical and subtropical biomes, as well as Tundra and Mangroves biomes. The greatest number of species (12 in each) were collected in the Temperate broadleaf and mixed forests and Temperate grasslands, savannas and shrublands biomes.

Each trans-Palearctic species was collected from 6 or 7 biomes and sets of biomes with records are identical only for *O. bivittatus* and *O. vittipennis* (Table SI4). All trans-Palearctic species were collected in Temperate broadleaf and mixed forests, Temperate grasslands, savannas and shrublands, Temperate conifer forests, Deserts and xeric shrublands and Boreal forests/taiga biomes. This list includes four largest biomes in the Palearctic (Table 2). Temperate broadleaf and mixed forests and Temperate grasslands, savannas and shrublands biomes, which are the third and the fourth largest Palearctic biomes respectively, occupy significant areas of the geographic projections of the trans-Palearctic species ecological niche models (Fig 1B, Table SI6, Data SI2).

Orthocephalus brevis, *O. saltator* and *O. vittipennis* are more similar to each other in that the largest area of the geographic projection of their models is occupied by the Temperate broadleaf and mixed forests biome, and Boreal forests/taiga biome is one of the most important biomes for them (Figs 1B, Table SI6, Data SI2). *Orthocephalus saltator* differs from all other species in the preferable conditions occupying more than 50 % of the Mediterranean forests, woodlands and scrubs biome, whereas this biome is not very important for other trans-Palearctic species. *Orthocephalus bivittatus* is different from other trans-Palearctic species in that the Temperate grasslands, savannas and shrublands biome occupies the largest area of the geographic projections of its models, and, unlike other trans-Palearctic species, the Deserts and xeric shrublands biome is also very important for this species in terms of preferable conditions.

Northeast Asian species *Orthocephalus funestus* and European *O. coriaceus* were recorded from six and five biomes respectively (Table SI4). Similar to the trans-Palearctic species, the Temperate broadleaf and mixed forests biome occupies the largest area of the geographic projection of the models of those species (Fig 1B, Table SI6, Data SI2). However, unlike the trans-Palearctic species, neither of the two species was found in the Deserts and xeric shrublands, which is the largest biome in Palearctic. Additionally, *O. funestus* has never been collected from the Temperate grasslands, savannas and shrublands biome and *O. coriaceus* has not been recorded in the Boreal forests/taiga biome.

Both southwestern species, *O. fulvipes* and *O. proserpinae*, were collected from the Temperate conifer forests and Mediterranean, forests, woodlands and scrubs biomes (Tables 2, SI4). These two biomes occupy a significant area of the geographic projection for the models of *O. proserpinae* (Fig 1, Table SI6, Data SI2). *Orthocephalus fulvipes* was also collected from Temperate broadleaf and mixed forests and Deserts and xeric shrubands biomes. All four biomes occupy a significant area of the geographic projections for the models of *O. fulvipes* (Table 2).

All rare and local species were collected from biomes inhabited by the trans-Palearctic species as well. However, no rare and local species were collected from the Boreal forest/taiga biome, where all trans-Palearctic species and *O. funestus* were found there (Tables 2, SI4). The greatest number of the rare and local species (6) were collected from the Temperate grasslands, savannas and shrublands biome. Five rare and local species were collected from the Mediterranean, forests, woodlands and scrubs and Temperate broadleaf and mixed forests biomes each.

Comparisons of climatic zones of widespread and more local species and rare species

None of the *Orthocephalus* species were collected from the following climate zones: all tropical climates (type A), Subtropical highland climate or temperate oceanic climate with dry winters (Cwb), Cold subtropical highland climate or subpolar oceanic climate with dry winters (Cwc), Mediterranean-influenced extremely cold subarctic climate (Dsd) and Ice cap climate (EF).

Each trans-Palearctic species was collected from 11–13 climate zones (Tables 3, SI5). All of them were collected in the Cold desert (Bsk), Humid subtropical (Cfa), Temperate oceanic (Cfb), Warm-summer humid continental (Dfb), Subarctic (Dfc) and Monsoon-influenced subarctic (Dwc) climates. This list includes the second and third largest climate zones in the Palearctic, but does not include the first, fourth and fifth largest climate zones (Table 2). Warm-summer humid continental climate (Dfb) occupies the largest area of the geographic projection of the models of all trans-Palearctic species in comparison with other climate zones (Fig 2, Table SI6, Data SI3). Temperate oceanic climate (Cfb) and Subarctic climate (Dfc) occupy a significant area of the geographic projection for the models of *O. brevis*, *O. saltator* and *O. vittipennis* (Table SI6, Data SI3). Among them, preferable conditions for only *O. saltator* correspond to large parts of the Mediterranean climates (Csa, Csb) (Fig 2B, Table SI6, Data SI3). Unlike all other species, the preferable conditions for

Table 3. Number of *Orthocephalus* species collected from all climate zones. Climate zones with no records are highlighted in grey. The percentage of the climate zone area relatively the entire Palearctic area is provided in the second column. The climate zones with the largest number of species are in bold

Climate zone	% of total Palearctic area	Total number of species	Number of trans-Palearctic species	*O. coriaceus* (widespread European species)	*O. funestus* (widespread northeastern species)	*O. fulvipes* and *O. proserpinae*	Number of rare species
Tropical climates (type A)	1 %	0	0	0	0	0	0
Cold desert, climate (Bsk)	**7 %**	**10**	**4**	**0**	**0**	**1**	**5**
Hot semi-arid (steppe) climate (Bsh)	2 %	2	0	0	0	1	1
Cold desert, climate (Bwk)	6 %	4	1	0	0	1	2
Hot desert climate (Bwh)	18 %	3	0	0	0	1	2
Humid subtropical climate (Cfa)	**4 %**	**8**	**4**	**1**	**1**	**0**	**2**
Temperate oceanic climate (Cfb)	5 %	5	4	1	0	0	0
Subpolar oceanic climate (Cfc)	<1 %	1	1	0	0	0	0
Hot-summer Mediterranean climate (Csa)	**4 %**	**12**	**3**	**1**	**0**	**2**	**6**
Warm-summer Mediterranean climate (Csb)	1 %	6	2	0	0	0	4
Monsoon-influenced humid subtropical climate (Cwa)	4 %	1	0	0	1	0	0
Subtropical highland climate or temperate oceanic climate with dry winters (Cwb)	1 %	0	0	0	0	0	0
Cold subtropical highland climate or subpolar oceanic climate with dry winters (Cwc)	<1 %	0	0	0	0	0	0
Hot-summer humid continental climate (Dfa)	1 %	6	4	0	0	0	2
Warm-summer humid continental climate (Dfb)	**9 %**	**9**	**4**	**1**	**1**	**0**	**3**
Subarctic climate (Dfc)	16 %	6	4	1	1	0	0
Extremely cold subarctic climate (Dfd)	2 %	2	2	0	0	0	0
Hot, dry-summer continental climate (Dsa)	**<1 %**	**7**	**3**	**1**	**0**	**0**	**3**
Warm, dry-summer continental climate (Dsb)	1 %	5	3	1	0	0	1
Dry-summer subarctic climate (Dsc)	1 %	1	1	0	0	0	0
Mediterranean-influenced extremely cold subarctic climate (Dsd)	<1 %	0	0	0	0	0	0
Monsoon-influenced hot-summer humid continental climate (Dwa)	1 %	1	0	0	1	0	0
Monsoon-influenced warm-summer humid continental climate (Dwb)	2 %	1	0	0	1	0	0
Monsoon-influenced subarctic climate (Dwc)	5 %	4	4	0	0	0	0
Monsoon-influenced extremely cold subarctic climate (Dwd)	<1 %	1	1	0	0	0	0
Ice cap climate (EF)	<1 %	0	0	0	0	0	0
Tundra (ET)	**7 %**	3	3	0	0	0	0

O. vittipennis correspond to a large part (42–72 %) of the Monsoon-influenced warm summer humid continental climate (Dwb) (Fig 2B, Table SI6, Data SI3). The preferable conditions for *O. bivittatus* largely correspond to the dry climates of type B (Bsk and Bwk), and they also occupy more than 50 % of the Hot-summer humid continental (Dfa) and Warm, dry-summer continental (Dsb) climates (Fig 2B, Table SI6, Data SI3).

Northeast Asian *Orthocephalus funestus* and European *O. coriaceus* were recorded from six and seven climate zones respectively, and none of them belong to the dry climates (type B) (Tables 3, SI5). Similarly to the trans-Palearctic species, Warm-summer humid continental climate (Dfb) occupies the largest area of the geographic projection of the models for *O. funestus*, and Subarctic climate (Dfc) is also important for this species. Preferable conditions for *O. funestus* also correspond to the Humid subtropical climate (Cfa) and monsoon climate zones (Dwb, Cwa, Cwb) (Table SI6, Data SI3). For *Orthocephalus coriaceus* Temperate oceanic climate (Cfb) occupies the largest area of the geographic projections of the models (Fig. 3, Table SI6, Data SI3). Warm-summer humid continental climate (Dfb) and Mediterranean climate types (Csa, Csb) are also important for the models of this species.

Southwestern species, *O. fulvipes* and *O. proserpinae*, are both found in Hot-summer Mediterranean climate (Csa) and in the dry climates of type B (Table 3, Table SI5). For both of them, Hot-summer Mediterranean climate (Csa) occupies the largest area of the geographic projections of the models (Fig 2B, Table SI6, Data SI3).

The rare and local species are known from ten climate zones. They are absent from the cold climate types, even though in some of them at least three trans-Palearctic species have been collected, e. g. Subarctic climate (Dfc), Tundra (ET) and Monsoon-influenced subarctic climate (Dwc). In addition, the rare and local species have never been collected from the Temperate oceanic climate (Cfb), though it is the largest climate zone in Europe and occupies a significant part of the geographic projections of the models of all trans-Palearctic species. Three rare and local species were collected from very dry and hot climates, Hot semi-arid (steppe) climate (Bsh) and Hot desert climate (Bwh), no trans-Palearctic species were collected from these areas (Tables 3, SI5).

Discussion

Biomes and climate zones suitable for trans-Palearctic species

Each of the trans-Palearctic species was collected from six or seven biomes and 11, 12, or 13 climate zones. *Orthocephalus funestus* was also collected from six biomes; however, its localities correspond to only six climate zones, and the rest of the species were collected from a smaller number of biomes and climate zones (Tables 2, 3, Data SI2–SI3). This supports the idea that trans-Palearctic species are adapted to a wider range of variable conditions better than less widespread species. The set of biomes is different for most pairs of the trans-Palearctic species (except for *O. bivittatus* and *O. vittipennis* pair), and the set of climate zones is different for all pairs of the trans-Palearctic species. The fact that four trans-Palearctic *Orthocephalus* species have different climate and biome preferences confirms the finding of the previous study that closely related trans-Palearctic species can differ among each other in adaptation to external conditions (Namyatova, 2020).

Temperate Broadleaf and mixed forest and Temperate grasslands, savannas and shrubs biomes occupy most parts of the geographic projections of the trans-Palearctic species (Figs 1, 2, Table SI6). These are the third and the fourth largest biomes in Palearctic, occupying 16 % and 8 % of the total Palearctic area respectively. The most parts of those two biomes correspond to the Warm-summer humid continental climate (Dfb), which is the third largest climate zone in the Palearctic, occupying the biggest part of the geographic projections of the models of all trans-Palearctic species (Fig. 2, Table SI6).

The area covered by the Boreal forest/taiga biome, the second largest biome in the Palearctic, mostly fits the area of the Subarctic climate (Dfc) (Figs 1, 2). This biome and climate zone are suitable for the trans-Palearctic *Orthocephalus* species, as all of them have been recorded there. All these species are also found in the Temperate conifer forest biome, which is relatively small, occupying only 3 % of the Palearctic's total area, and it corresponds to different climates. The other two climate zones, suitable for all trans-Palearctic species are Temperate oceanic climate in the west and Monsoon-influenced subarctic climate (Dwc) in the east (Figs 1B, 2B).

Although all trans-Palearctic species are adapted to a wide range of climatic conditions, not all biomes and climate zones are suitable for those species. The suggestion that the trans-Palearctic species are adapted to the most widespread conditions in the Palearctic has not been confirmed. They were not recorded in the Hot desert climate (Bwh), which is the largest Palearctic climate zone, occupying ~18 % of its total area, and from the hot steppe climate (Bsh). This also means that trans-Palearctic species cannot adapt quickly to some conditions.

Environmental conditions limiting widespread and more local *Orthocephalus* species distributions

The distribution of all trans-Palearctic *Orthocephalus* species in the south is limited by climates combining very hot and dry conditions, but is not limited by biome. Although all four species with trans-Palearctic distribution were collected from Deserts and xeric shrublands biome, they were collected mostly from the Cold semi-arid (steppe) climate (Bsk), and never from the Hot desert (Bwh) and Hot semi-arid (steppe) (Bwk) climates (Tables 2, 3, SI4, SI5).

In the north, the distribution of the trans-Palearctic species is more limited by biomes, rather than by climate. They are all known from the extremely cold climates, such as Extremely cold subarctic (Dfd) and Monsoon-influenced extremely cold subarctic (Dwd) climates, as well as climates with long periods of average temperatures below 0 °C for more than six months, i. e. Tundra (ET). However, they were not recorded from the Tundra biome, though the majority of this biome area is covered with Tundra climate. This might be an indicator that the type of vegetation or lack of a particular plant species influences the distribution of the trans-Palearctic *Orthocephalus* species (Tables 2, 3, SI4, SI5).

Adaptation to the colder climates can be more important for the trans-Palearctic species, rather than adaptation to the hot and dry climates (Bsh, Bwh), though hot and dry climates are suitable for other *Orthocephalus* species, i. e. *O. fulvipes*, *O. scorzonerae*, *O. tibialis* and *O. turkmenicus* (Fig. 2B, Tables 3, SI5). These four species are not very closely related (Namyatova and Konstantinov, 2009), and possibly have obtained the ability to survive the hot desert and steppe climates independently, which means that there are capacities to develop the adaptation to those climates in *Orthocephalus*. It was demonstrated before that there is a connection between tolerance to cold and desiccation, as they have many similar effects on cellular levels (e. g., Clark and Worland, 2008; Sinclair, Ferguson, Salehipour-Shirazi and McMillan, 2013; Terhzaz et al., 2015). Likewise, there is evidence of cross-tolerance for heat and cold in insects as well (e. g., Rinehart et al., 2007; Koštál and Tollarová-Borovanská, 2009; King and McRae, 2015). However, it was also shown for Australian *Drosophila* that widespread species demonstrated a significantly larger cold-hardening response than more locally distributed tropical species, and tropical species showed a slightly larger heat-hardening response (Overgaard, Kristensen, Mitchell and Hoffmann, 2011), meaning that the selection for adaptation to the colder environment did not automatically select for adaptation to heat. Therefore, the trans-Palearctic *Orthocephalus* species might still have limitations in their physiology to become adapted to both the extremely cold and very hot climates, and adaptation to extremely cold temperatures is more important for their wide distribution in the Palearctic.

Both widely distributed, but not trans-Palearctic species, *O. coriaceus* and *O. funestus*, are not found in the extremely cold climates (Dfd, Dwd) and Tundra (ET), as well as steppe and desert areas (Tables 2, 3, SI4, SI5). The lack of adaptation to those conditions can be an important factor preventing these two species from spreading to the center of the Eurasian continent. However, it seems that their distribution is limited by other conditions as well. *Orthocephalus funestus* is widely distributed in Northeast Asia, but it does not reach eastern Siberia. It has been found on the borders with the Monsoon-influenced subarctic climate (Dfc), but does not cross it, and apparently cannot inhabit areas with Dfc, Dwd and Dfd climates to spread west (Fig. 2A in Namyatova, 2020). However, *O. funestus* tolerates low temperatures, and it is recorded in places with low values of Min temperature of the coldest month (bio6) (up to ~–30 °C) and Mean temperature of the coldest quarter (bio11) (up to ~–25 °C), which are slightly higher than for *O. saltator* and *O. vittipennis* and even lower than for *O. bivittatus* (Figs 5D, 6B). Which climatic or other factor or combination of factors prevents *O. funestus* from inhabiting Dfc, Dwd and Dfd climate zones is unclear. The distribution of *Orthocephalus coriaceu*s in Europe is limited to biome, as in that area it is only known in the Temperate and broadleaf forest biome. In Kyrzgyzstan, this species is found in other biomes; however, there is a significant distribution disjunction between the European and Kyrgyzstan records, and they might represent two cryptic species (Fig. 1C in Namyatova, 2020).

Orthocephalus fulvipes and *O. proserpinae* share similar climatic variable ranges with rare and local species, and, therefore, all these taxa are discussed together (see Results). These two species together were collected in almost every biome, where trans-Palearctic species were also found, except for the Boreal/forest taiga biome (Table 2). Most likely, it is not the biome itself, but the cold Subarctic climate (Dfc), covering most of this biome, that limits the distribution of these species.

The rare and locally distributed species, as well as *O. fulvipes* and *O. proserpinae*, are found in the warm and hot climates, including dry and humid ones, which are steppe, deserts, Mediterranean and subtropical climates. However, some rare species also inhabit continental climates (Dfb, Dsa, Dsb), where the average temperature of the coldest month is below 0 °C. None of them was collected in the Temperate Oceanic climate (Cfb), where the average temperature of the coldest month is above 0 °C, and this climate type occurs in most parts of Europe (Fig. 6B, Tables 3, SI5; Figs 1D, 2B in Namyatova, 2020). This means that the occurrence of temperatures below 0 °C for a continuous period is not a limiting factor for the wider distribution across Europe or the Palearctic. The ability of rare and locally distributed *Orthocephalus* species to survive long periods of freezing temperatures is additionally supported by the values of Min temperature of the coldest month (bio6) and Mean temperature of the coldest quarter (bio11), which can be negative for many of those species (Figs 5D, 6B).

There are at least three possible ways how temperature can limit the distribution of the rare and local and southwestern *Orthocephalus* species. First, they or their host plants might need a longer period of high temperatures in the summer to complete a life cycle, since the Max temperature of the warmest month (bio5) for rare and more locally distributed species is always higher than 20 °C, whereas for the wider distributed species it can be as low as 11 °C (Fig. 5C). Second, it was shown that for some species of insects, long periods of the chill between 0 °C and 15 °C during cold and warm seasons can be fatal as well (Fields, 1992; Bale, 1996; Renault, Salin, Vannier and Vernon, 2002). The widely distributed species might develop an adaptation to survive and remain active over such temperatures (average between 0 °C and 15 °C) in the summer, common in northern and temperate regions of the Palearctic. There is an argument that insect species living in the milder climates have high risk to die in case of exposure to temperatures slightly above 0° (Overgaard and McMillan, 2016). This is also supported by the range of the Mean temperature of the warmest quarter (bio10), which can be below 12 °C for all trans-Palearctic species, as well as *O. funestus* and *O. coriaceus*, and it is always higher than 16 °C for other species (Fig. 6A). Finally, the rare and local species, as well as southwestern species, might not have adaptation to survive long periods of very cold temperatures (<–20 °C). Min temperature of the coldest month (bio6) for the rare and local species, as well as *O. proserpinae* and *O. fulvipes*, is higher than –19 °C, whereas this variable for the widely distributed species can be below –22 °C (Fig. 5D).

These three explanations do not exclude each other, and species might need to be adapted to both, the cooler summers and the extremely cold winters, to be able to become widespread.

Comparison of climatic niches built on different variable sets

The comparison of different environmental datasets' performance helps to obtain more accurate distribution and ecological niche models (e. g., Peterson and Nakazawa, 2008; Parolo, Rossi and Ferrarini, 2008; Williams et al., 2009). Altogether in Namyatova (2020) and this work, four different datasets have been used to obtain the environmental niche models for the same eight *Orthocephalus* species. They are as follows (1) a full dataset with 19 climatic variables and biomes (CBF); (2) reduced climatic variable sets and biomes (CBR); (3) 19 climatic variables and no biomes (CF); and (4) reduced climatic variables sets and no biomes (CR). The comparison of the AUC values, omission rate values, area size and variable ranges does not indicate that the models with the full set of variables are more overfitted than those with reduced variables sets (cf. Table SI2 this work and Table S1 in Namyatova, 2020), which has also been shown previously for European plant species (Parolo, Rossi and Ferrarini, 2008). Most likely, the correlation between variables is compensated with parameter adjustments for the Maxent modelling. Neither of the models performs significantly better if AUC and omission rate values are compared. Modelling produced similar areas with the most suitable conditions for each species in most cases. The size of the geographic projection areas significantly varies only for *O. fulvipes* and *O. vittipennis* (Table 1 in this work and Table 1 in Namyatova, 2020). The variable ranges are also similar when compared within the species, though the values of some variables are drastically higher for the CR model rather than for other models, i. e. bio12, bio13 and bio16 for *O. bivittatus* and *O. proserpinae* (Figs SI8–S10), bio15 for *O. bivittatus* (Fig. SI10), bio18 for *O. fulvipes* and *O. proserpinae* (Fig. SI11). All these variables are related to precipitation. Preferable conditions for *O. bivittatus*, *O. fulvipes* and *O. proserpinae* mostly correspond to the arid and sclerophyll areas with low precipitation levels. Therefore, their ecological niches should not show high values for those variables, which in most cases are higher than for other species when CR models are compared. This might mean that the variable ranges inferred from the reduced dataset without biomes (CR) are less reliable than those of other models. The set of variables for the CR models have been chosen using *MaxentVariableSelection* package for R (Jueterbock, Smolina, Coyer and Hoarau, 2016; Jueterbock, 2018), which chooses the best variable set using the Akaike information criterion (AIC) values as the model performance indicator (Namyatova, 2020). However, there is an argument that this criterion should not be used as a measure of the model performance (Velasco et al., 2019).

The climatic variable contribution to the model is different depending on the dataset, although, some of the variables show consistent results for all the models (e. g., bio1 for all trans-Palearctic species, bio3 for *O. coriaceus* and *O. funestus*, bio14 for *O. brevis*). The biomes have very high contribution to the models of *O. proserpinae* (PC > 90 %); therefore, climatic variables cannot show high contribution to the models. However, in this case, all climatic variables highly correlate with the biomes (Table SI1) and their contribution should be assessed using the dataset without biomes.

Although biomes highly contribute to the models of many analyzed *Orthocephalus* species, they do not influence the geographic projection and climatic variable ranges of the models much. This might be because biomes correlate with the climate, and the absence of biomes in the dataset is compensated by climatic variables. However, the variable dataset might influence the test for niche overlap using the background test. For some cases, the results of this test for the models based on different variable sets are inconsistent, the niches of two species can be more different than random data if we use one dataset, and the comparison can produce an opposite result if we use another dataset. This is true if we compare models built on the datasets with and without biomes, and the models built on the datasets with reduced and full sets of variables. The differences between the niche overlap results based on the models with different variable datasets demonstrate that the results of the background test can depend on the presence of a single variable and should be interpreted with caution.

Perspectives

The current research is the first to study the distribution limits and preferable conditions of the species using the comparison of the environmental preferences of closely related trans-Palearctic species with each other, as well as the comparison of the preferences of widely distributed species with more locally distributed species. In Namyatova (2020) and this paper it has been found that the niches of the trans-Palearctic species are divergent in all cases. It can be explained by the fact that all those species occupy similar biotopes and feed on similar plants; therefore, they may adjust to different conditions to decrease competition pressure. Studies of the environmental preferences of more species distributed across the Palearctic are needed to find whether it is also true for other closely related trans-Palearctic species or sister species that might share the same ecological niche. Additionally, the future work on the distribution and ecological niche modelling of the species widely distributed in this region will demonstrate whether the preferences and limitations of other trans-Palearctic and rare species are similar to those of *Orthocephalus*. Faunistic works show that other trans-Palearctic plant bugs can differ in preferences and distribution limits. For example, there are records of some of those species from the treeless areas of Chukotka (Tundra biome) (Vinokurov and Khruleva, 2021), avoided by the *Orthocephalus* species (see above).

It was also found that in some cases the models do not reflect the real distribution (e. g., *O. bivittatus* and *O. vittpennis*) and show suitable conditions for the areas where those species do not live. In those works, only temperature- and precipitation-related climatic variables have been used, as well as biomes. It is likely that some other factors, e. g. humidity, wind characteristics, solar radiation level, number of sunny days, snow depth, presence of permafrost, etc., might also limit the distribution of some trans-Palearctic species. Therefore, including other abiotic factors can improve the ecological niche models for those species.

Another step in understanding the trans-Palearctic distribution and adaptation for a wide range of conditions is to study them in the phylogenetic context. Such studies will reveal the evolution of the ability to inhabit large areas, as well as morphological, behavioral and ecological features linked to distribution.

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