



Climatic niche comparison between closely related trans-Palearctic species of the genus *Orthocephalus* (Insecta: Heteroptera: Miridae: Orthotylineae)

Anna A. Namyatova

Laboratory of Phytosanitary Diagnostics and Forecasts, All-Russian Institute of Plant Protection, St Petersburg, Russia

Laboratory of Insect Taxonomy, Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia

ABSTRACT

Previously climatic niche modelling had been studied for only a few trans-Palearctic species. It is unclear whether and to what extent those niches are different, and which climatic variables influence such a wide distribution. Here, environmental niche modelling is performed based on the Worldclim variables using Maxent for eight species of the genus *Orthocephalus* (Insecta: Heteroptera: Miridae: Orthotylineae). This group belongs to one of the largest insect families and it is distributed across Palearctic. *Orthocephalus bivittatus*, *O. brevis*, *O. saltator* and *O. vittipennis* are distributed across Europe and Asia; *O. coriaceus*, *O. fulvipes*, *O. funestus*, *O. proserpinae* have more limited distribution. Niche comparison using ENMTools was also undertaken to compare the niches of these species, and to test whether the niches of closely related species with trans-Palearctic distributions are more similar to each other, than to other congeners. It has been found that climatic niche models of all trans-Palearctic species under study are similar but are not identical to each other. This has been supported by niche geographic projections, climatic variables contributing to the models and variable ranges. Climatic niche models of all the trans-Palearctic *Orthocephalus* species are also very similar to two species having more restricted distribution (*O. coriaceus*, *O. funestus*). Results of this study suggest that trans-Palearctic distributions can have different geographic ranges and be shaped by different climatic factors.

Submitted 29 April 2020

Accepted 17 November 2020

Published 15 December 2020

Corresponding author

Anna A. Namyatova,
anna.namyatova@zin.ru

Academic editor

Jason Bond

Additional Information and
Declarations can be found on
page 26

DOI 10.7717/peerj.10517

© Copyright
2020 Namyatova

Distributed under
Creative Commons CC-BY 4.0

Subjects Biogeography, Ecology, Entomology, Zoology

Keywords Ecological niche modelling, Climate, Distribution, Palearctic, Miridae, Niche overlap, Insects

INTRODUCTION

Environmental niches are important characteristics of species. Studying them can help to identify the environmental factors responsible for maximizing the species' fitness, and lead to a better understanding of how environment is connected to speciation and how closely related species are different in their ecological preferences. Studying climatic niches of widespread species also can help to reveal the climatic variables, connected with the species ability to adapt to different conditions.

OPEN ACCESS

The Palearctic spans thousands of kilometers across different biomes and climatic zones. Species occupying large areas of Europe and Asia in this zoogeographic region are called “trans-Palearctic” and are often treated as having the same type of distribution (e.g., [Abe, Melika & Stone, 2007](#); [Hubenov, 2008](#); [Potikha, 2015](#)). However, the diversity of such distributions and corresponding climatic niches has never been quantitatively studied.

Most investigations of environmental niche differences treated allopatric vertebrate species (e.g., [Losos et al., 2003](#); [Graham et al., 2004](#); [Kozak & Wiens, 2006](#); [Kozak & Wiens, 2010](#); [McCormack, Zellmer & Knowles, 2010](#); [Blair et al., 2013](#)). There are only a few studies of ecological niche similarities of sympatric species (e.g., [Knouft et al., 2006](#); [Wellenreuther, Larson & Svensson, 2012](#); [Lisón & Calvo, 2013](#); [Mumladze, 2014](#); [López-Alvarez et al., 2015](#); [Dellicour et al., 2017](#)), and even fewer on insects ([Wellenreuther, Larson & Svensson, 2012](#); [Dellicour et al., 2017](#)). Many studies show that closely related sympatric species are different in their ecological niches ([Wellenreuther, Larson & Svensson, 2012](#); [Mumladze, 2014](#); [Aguirre-Gutiérrez et al., 2015](#); [López-Alvarez et al., 2015](#); [Dellicour et al., 2017](#)). However, only a few such works treat Palearctic insects (e.g., [Wellenreuther, Larson & Svensson, 2012](#); [Dellicour et al., 2017](#); [Avtaeva et al., 2019](#)), and such works on the trans-Palearctic insects are very rare (e.g., [Avtaeva et al., 2019](#)). Knowledge on climatic niches is also a prerequisite for studying the influence of climate on speciation, i.e., testing niche conservatism vs niche diversification hypotheses (e.g., [Losos et al., 2003](#); [Kozak & Wiens, 2006](#)). Therefore, it is essential to study climatic niches of the species widespread in Palearctic to understand the factors connected with such a wide distribution and how those factors relate to the phylogenetic history.

This current project describes the climatic niches and reveals their differences for closely related species of the Palearctic genus *Orthocephalus* Fieber, 1858 (Insecta: Heteroptera: Miridae: Orthotylinae). These species inhabit meadows and dry open areas, utilizing numerous species of Asteraceae, where at least the widely distributed taxa are likely to be polyphagous. *Orthocephalus* has been revised ([Namyatova & Konstantinov, 2009](#)), and a morphology-based phylogeny supporting its monophyly has been provided. Currently *Orthocephalus* includes 23 species, with *O. bivittatus* Fieber, 1864, *O. brevis* (Panzer, 1798), *O. saltator* (Hahn, 1835), and *O. vittipennis* (Herrich-Schaeffer, 1835) widely distributed in Europe and Asia ([Namyatova & Konstantinov, 2009](#)). This allows us to test whether the closely related species with wide distribution in the Palearctic occupy the same climatic niche, or whether their niches are significantly different.

Most of the *Orthocephalus* species have a low number (<15) of records, except for *O. coriaceus* (Fabricius, 1777), *O. fulvipes* Reuter, 1904, *O. funestus* Jakovlev, 1881, and *O. proserpinae* (Mulsant & Rey, 1852). The records of these species have also been used to build the climatic niches to find the factors influencing their distribution and compare them to those of the widely distributed species. Those niches will also allow testing whether the climatic niches of the species with trans-Palearctic distribution are more similar with each other than with those of the species having limited distribution. Comparisons of climatic niches of the *Orthocephalus* species will be the first step in answering the question, whether the niche conservatism or niche divergence or both can relate to speciation in this genus.

The aims of the current work are to: (1) compare the niches of widely distributed species with each other and with those of species with limited distribution to determine the main climatic variables responsible for the trans-Palearctic distribution and limited distribution; (2) to test whether the trans-Palearctic species are significantly similar and whether they are more similar to each other or to the species with a limited distribution; and (3) to draw conclusions on the presence of the niche conservatism or niche divergence processes in speciation within *Orthocephalus*, based on the phylogeny provided in [Namyatova & Konstantinov \(2009\)](#).

MATERIALS & METHODS

Specimens and localities sources

Eight species (and number of unique records) have been analyzed in this work *Orthocephalus bivittatus* (171), *O. brevis* (146), *O. coriaceus* (39), *O. fulvipes* (18), *O. funestus* (90), *O. proserpinae* (19), *O. saltator* (237), and *O. vittipennis* (208). *Orthocephalus vittipennis* is recorded from Western Europe to eastern Yakutia, including numerous records from Central Asia. The distributions of *O. saltator* and *O. brevis* are similar to that of *O. vittipennis*, but among Central Asian countries, they are known only from Kazakhstan. *Orthocephalus bivittatus* is not recorded from the northern Europe and eastern Siberia, however, is common in Central Asia ([Kerzhner & Josifov, 1999](#); [Namyatova & Konstantinov, 2009](#)). *Orthocephalus coriaceus* is mostly known from the middle and northern Europe with few specimens recorded from Kyrgyzstan. *Orthocephalus funestus* is known only from Northeast Asia. *Orthocephalus proserpinae* and *O. fulvipes* inhabit the Mediterranean region, *O. fulvipes* is additionally known from Arabian Peninsula and Iran ([Kerzhner & Josifov, 1999](#); [Namyatova & Konstantinov, 2009](#)). Numerous collecting expeditions have been taken in Central Asia, Mongolia, Siberia, Russian Far East, European part of Russia by the Russian and Soviet entomologists, and their collections are mainly preserved at the Zoological Institute of the Russian Academy of Sciences ([Konstantinov & Namyatova, 2019](#)). Although many records from European countries were excluded (see below), this region is still well represented in the current analysis. Therefore, it is likely, that the known distribution for *Orthocephalus* species probably reflects the real distribution.

Specimens used for this study are mostly preserved at the Zoological Institution of the Russian Academy of Sciences, St Petersburg, Russia. This collection holds one of the largest Palearctic collections of Heteroptera. The most label data for the *Orthocephalus* specimens are recorded in the Arthropod Easy Capture database (<https://research.amnh.org/pbi/locality/>). Some specimens are preserved at the Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Canada (CNC), Linnavuori Collection (LCRT), Matocq collection (MATOCQ), Bavarian State Museum in Zoology, Munich, Germany (ZSM), National Museum of Natural History, Paris, France (NMNH), Ribes Collection (JR), American Museum of Natural History, New York, USA (AMNH), Natural History Museum, Geneva, Switzerland (MHNG), Zoological Museum Amsterdam, Netherlands (ZMAN), Carapezza collection (AC), Finnish Museum of Natural History, Helsinki, Finland (MZH), Institute for Biological

Problems of Cryolithozone, Yakutsk, Russia (YIB). The specimens have been identified based on the revision of the genus *Orthocephalus* (Namyatova & Konstantinov, 2009). This revision corrected species identification errors of previous keys (e.g., Kerzhner & Jachewski, 1964; Wagner & Weber, 1965; Wagner, 1974) which were based on variable coloration and not male genitalia structure which proved crucial for accurate determination of the species. To decrease number of erroneous records, in most cases the localities from other papers have been added only if they cited the above-mentioned revision (Kment & Baňar, 2012; Matocq, Pluot-Sigwalt & Özgen, 2014; Heckmann, Strauss & Rietschel, 2015; Sofronova, 2017; Vinokurov, Golub & Zinovjeva, 2017) or provided the detailed illustrations of genitalia structures (Tamanini, 1981). All records from the literature have been added for *O. brevis* and *O. funestus* (Ribes, 1989; Melber, Günther & Rieger, 1991; Dioli, 1993; Gorczyca & Chłond, 2005; Arnold, 2008; Lim et al., 2011; Lim et al., 2012; Lim, Park & Lee, 2013a; Lim et al., 2013b; Nikolaeva, 2011; Frieß, 2006; Frieß, 2014; Roháčová, 2007; Cho et al., 2008; Cho et al., 2011; Kondorosy, 2011; Park et al., 2013; Halimi & Papparisto, 2014; Halimi, Papparisto & Topi, 2014; Shi, Li & Bao, 2016; Vinokurov, Kanyukova & Ostapenko, 2016; Gierlański, 2017; Jung, Kim & Duwal, 2017; Kozminykh & Naumkin, 2017; Taszakowski & Pasińska, 2017), as *O. brevis* can be easily separated from congeners by its widened antennal segment II and *O. funestus* inhabits Northeast Asia, and this is the only *Orthocephalus* species known from Northeast Asia (Namyatova & Konstantinov, 2009). The maps with all records used in this study are provided on Figs. 1 and 2 and the list of those records for all species and specimen information are provided in the Data S1.

Maps

Layers in 5-arc minute (~10 km) resolution representing different bioclimatic variables have been downloaded from Worldclim, Version 1.4 (<https://www.worldclim.org/version1>). In general, the finer resolution leads to more accurate predictions, as the data are averaged within the grid cell. For this study coarser resolution was chosen for two reasons. First, it is a trade-off between the high resolution data across large geographic space and computational efficiency, as there is only a little difference between the models built using different scales especially in broadly distributed species (e.g., Araújo et al., 2005; Seo et al., 2009). Seo et al. (2009) also has shown that with a spatial grid size below 16 × 16 km, there is a good agreement among model area estimated for species of all range sizes. Second, the coordinates for many localities are approximate, and high resolution might also lead to the erroneous interpretations (Graham et al. 2005; Hanberry, 2013). Layers have been trimmed for Palearctic (20°N–90°N, –30°W–180°E) and converted to ASCII format in DIVA-GIS (<https://www.diva-gis.org/>). Those layers have been uploaded to QGIS 3.10 and converted to vector and used to create “samples with data” files (swd files).

Environmental niche modelling

Maxent software (version 3.4.1) (https://biodiversityinformatics.amnh.org/open_source/maxent/) (Phillips, Anderson & Schapire, 2006) was chosen because it performs well in comparisons with other programs especially for rare species. It works with presence-only

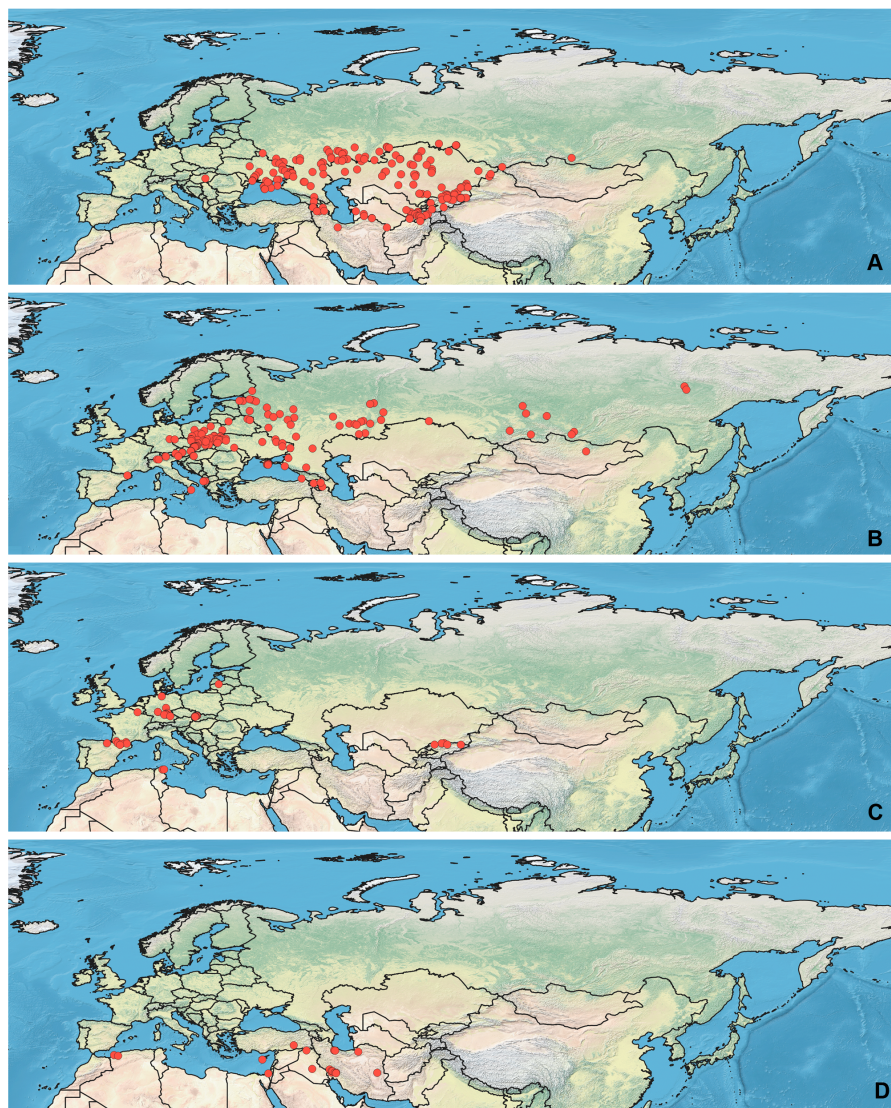



Figure 1 Maps of records used in the analysis. (A) *O. bivittatus*, (B) *O. brevis*, (C) *O. coriaceus*, (D) *O. fulvipes*. The background maps is taken from https://github.com/nvkelso/natural-earth-quick-start/tree/master/50m_raster/NE1_50M_SR_W. The layer with the country borders is taken from https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3. Full-size  DOI: 10.7717/peerj.10517/fig-1

data and is considered to produce robust results with sparse, irregularly sampled data and minor location errors, which is applicable to museum data (Elith *et al.*, 2006; Elith *et al.*, 2011; Pearson *et al.*, 2007; Kramer-Schadt *et al.*, 2013). The models have been built using swd files and bioclim layers in ASCII format. For the datasets with >50 localities, bootstrap replicated run type with 25% of localities assigned for the random test percentage were applied. Overall, ten replicates were conducted. For the datasets with <50 localities (*O. coriaceus*, *O. fulvipes* and *O. proserpinae*), crossvalidation with the replicate number

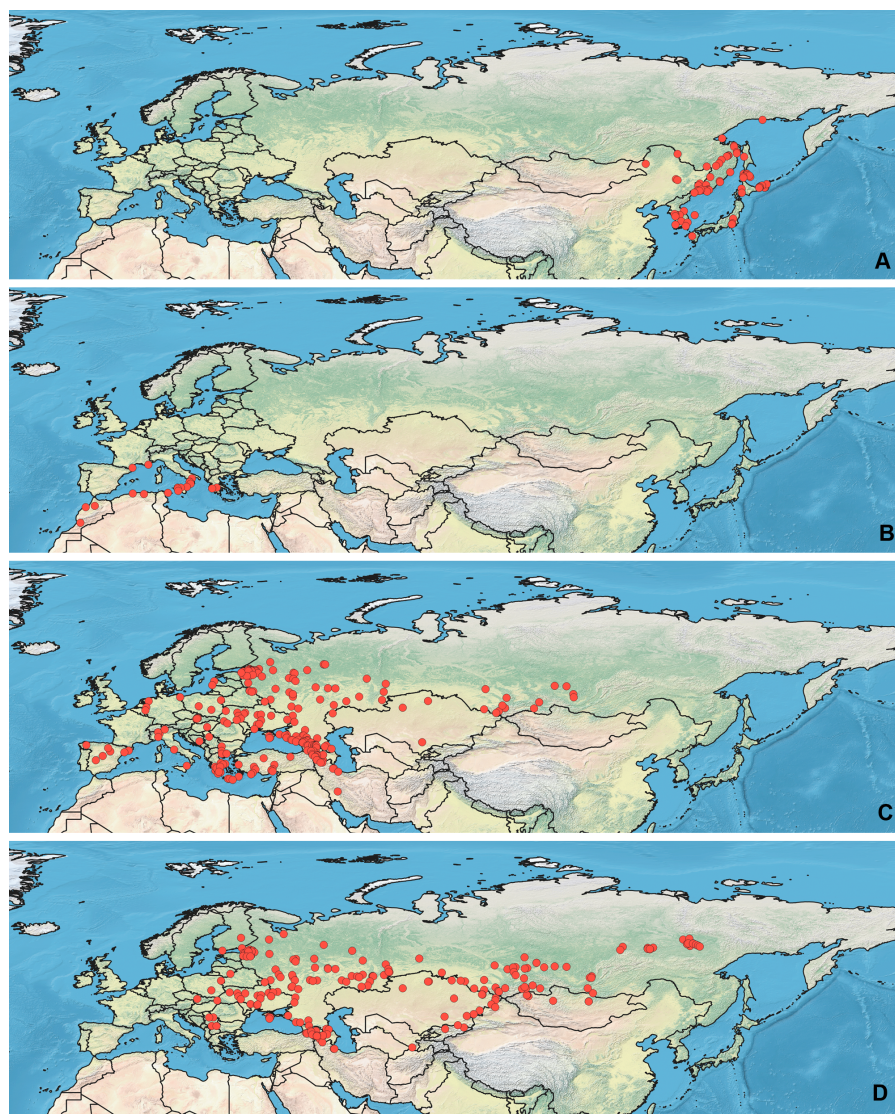


Figure 2 Maps of records used in the analysis. (A) *O. funestus*, (B) *O. proserpinae*, (C) *O. saltator*, (D) *O. vittipennis*. The background maps is taken from https://github.com/nvkelso/natural-earth-quick-start/tree/master/50m_raster/NE1_50M_SR_W. The layer with the country borders is taken from https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3.

Full-size  DOI: 10.7717/peerj.10517/fig-2

corresponding to the locality number was used (Pearson *et al.*, 2007; Shcheglovitova & Anderson, 2013).

The data used in this study are biased towards the easily accessed area, as most of the specimens were collected along major roads and railroads in the area currently corresponding to Russia, as well as Caucasus and Central Asia countries. This can exacerbate over-representation of some regions, which can lead to an inaccurate model. Sampling bias can be addressed by reducing the number of occurrence records in oversampled regions using spatial filtering (Kramer-Schadt *et al.*, 2013); however, it can lead to a situation where

the number of occurrences is too few to create a reliable model. Additionally, Maxent automatically discards the redundant records, appearing in the single grid cell (*Fourcade et al. 2014; Chiarenza et al., 2019*), which is ~ 10 km in this study. This is a quite large area, which might accommodate different climate regimes. Assigning the larger grid cell was needed for the filtering, and leading to further loss of information on species climatic preferences. Alternatively, it is possible to manipulate the background data by choosing background data with the same bias as occurrences (*Phillips et al., 2009; Elith et al., 2011; Kramer-Schadt et al., 2013*). As soon as there are < 20 occurrences for two of the analyzed species, the bias file approach was chosen. A previous study showed that using biased background data have increased the performance of the model and should be applicable for cases with small numbers of occurrence points (*Kramer-Schadt et al., 2013*). A bias file was created as a two-dimensional kernel density estimate, based on the coordinates of the occurrence points, using the `kde2d` function from the *MASS* package (*Ripley et al., 2020*) in R. This approach was applied in previous works (e.g., *Filazzola, Sotomayor & Lortie, 2018; Mudereri et al., 2020*). Bias files were converted to the raster ASCII format and have been implemented into the `biasfile` option in Maxent. Ten thousand background points, which is the default Maxent setting, was randomly selected from the area denoted in the bias file. The “cloglog” output was chosen for the visualization and further analysis.

Variable selection

Climatic niche modelling with two sets of variables was conducted. To avoid the model overfitting, it is possible to exclude the highly correlated variables and/or tune the model parameters (*Merow, Smith & Silander Jr, 2013*). It has been shown that Maxent can perform well with the correlating variables with tuned parameters (*Merow, Smith & Silander Jr, 2013; Morales, Fernández & Baca-González, 2017; De Marco Junior & Nobrega, 2018*); therefore, the first model type includes all bioclimatic variables (CF model). However, to test whether the model with all variables can be overfitted the highly correlated variables for each species were excluded (CR model) (see below for the details).

Parameter adjustment

There are two modifiable parameters in Maxent, which are feature classes and regularization multiplier. They should be adjusted for each particular case to avoid overfitting and/or over-complexity (*Morales, Fernández & Baca-González, 2017*). Feature classes correspond to the mathematical transformation of the variables and regularization multiplier (beta multiplier) limits the complexity of the model and generates a less localized prediction; i.e., smooths the model (*Phillips & Dudík, 2008; Elith et al., 2011; Merow, Smith & Silander Jr, 2013*). Best features and regularization multiplier set for the CF models has been selected using *ENMeval* package in R (*Muscarella et al., 2014a; Muscarella, Kass & Galante, 2014b*), using Maxent. The models have been tested against the regularization multipliers ranged from 0.5 to 6 and the 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” was chosen, because it accounts for spatial autocorrelation (*Muscarella et al., 2014a*). This analysis can result in different parameter sets in different runs, so the

analysis was done five times for each species. In case if the analyses resulted in different parameter sets, all of them were kept to run the environmental niche modelling in Maxent. All the parameter sets used for the modelling are provided in the [Table S1](#).

For the CR model, the *MaxentVariableSelection* package in R ([Jueterbock et al., 2016](#); [Jueterbock, 2018](#)) was used. It chooses the best set of variables, which has the lowest AICc value, based on the regularization multiplier and features. Comparisons were performed for the same parameters, as in the case of the *ENMeval*. A separate run was conducted to test the regularization multipliers for each feature class or combinations of classes. For the background data ten thousand background points were extracted from the bias file raster using R. For each feature (or combination of the features), its best regularization multiplier and variable set was kept for further analysis in Maxent, and they are provided in the [Table S1](#).

Maxent provides the list of the percent contribution (PC) and permutation importance (PI) for each variable in the model. The variables with PC and/or PI values higher than 10% are provided in [Table 1](#) for CF and CR models for each species.

Model evaluation

For model evaluation, training and test AUC values are provided, which is valid for model comparison over the same study area ([Bohl, Kass & Anderson, 2019](#)) (see [Table S1](#)). The differences between training and test AUC values and omission error rates have been also compared. It has been shown that the model with high differences between AUC values and omission error rate > 0.1 is likely to be overfitted ([Bohl, Kass & Anderson, 2019](#)). In the case of each model type (CF and CR), the model with the relatively high AUC values, low differences between training and test AUC and low omission error rates was chosen for the visualization and niche comparisons.

Environmental niche projection area and climatic variable ranges

The obtained environmental niche models were thresholded using the “Maximum training sensitivity plus specificity Cloglog threshold”, as the thresholds maximizing sensitivity and specificity perform well on presence only datasets ([Liu, Newell & White, 2016](#)). The total area of the thresholded niche projection was obtained using QGIS 3.10. The thresholded maps were used as masks to trim the bioclim layers to obtain the climatic variables ranges for each model. These areas and variable ranges were used to compare the models. The correlation of climatic variables was estimated for each species separately using Pearson’s correlations (PCor), as it is suitable for continuous variables. In this work PCor ≥ 0.9 is considered strong, as it is usually used to discriminate strongly correlated variables (e.g., [Jezkova, Olah-Hemmings & Riddle, 2011](#); [Dellicour et al., 2017](#)). I also considered $0.7 \leq \text{PCor} < 0.9$ as significant. Tables with Pearson’s correlations for the each species are provided in the [Data S2](#).

Niche overlap

Testing for niche overlap was performed in ENMTools ([Warren, Glor & Turelli, 2010](#)). First, the niche overlap was conducted to get the Schoener’s D (D) and Hellinger distance I (I) metrics, these measure similarities between species habitat suitability models. The

Table 1 Variables, contributing to the models CF (first column for each species) and CR 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 row.

	<i>bivittatus</i>		<i>brevis</i>		<i>coriaceus</i>		<i>fulvipes</i>		<i>funestus</i>		<i>proserpinae</i>		<i>saltator</i>		<i>vittipennis</i>	
	CF	CR	CF	CR	CF	CR	CF	CR	CF	CR	CF	CR	CF	CR	CF	CR
Bio1 Annual Mean Temp	PC PI	PC PI	PC PI	PC PI	X		X		PI		X		PI		PC PI	X
Bio2 Mean Diurnal Range	PI		X		X	X	X		X	X	X		X	X	X	PC
Bio3 Isothermality	PI	X	X		PC PI	PC PI	X		PC PI	PC PI	X		X	X	X	X
Bio4 Temp Seasonality	PI	X	X		X		X		X		PI	PC PI	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	X	PC PI	X		PI	PC PI	X	
Bio7 Temp Annual Range	PI		X		X		X		X		PC PI	X	PI		X	PC PI
Bio8 Mean Temp of Wettest Quarter	X	X	X		X		X		X		X		X	X	X	X
Bio9 Mean Temp of Driest Quarter	X	PC	X	X	X		PC PI		X		PC PI		X	X	PC	PI
Bio10 Mean Temp of Warmest Quarter	X	PC	X		X		X		X	PC	X		X		X	X
Bio11 Mean Temp of Coldest Quarter	PC		X		PI		X		X		X		PC		PI	
Bio12 Annual Precipitation	X		X	X	X		X		X		X		X	X	X	X
Bio13 Precipitation of Wettest Month	X	X	X	X	X		X		X		X		X	X	X	X
Bio14 Precipitation of Driest Month	X	X	PC PI	PC PI	PC	PC	X		X		PC	PC	X	X	X	X
Bio15 Precipitation Seasonality	PC	PC	X	PI	PI		X		X	PC PI	X	X	X	X	X	X
Bio16 Precipitation of Wettest Quarter	X		X		X	PI	X	PC PI	PI		X		X		X	PC
Bio17 Precipitation of Driest Quarter	X		X		X		X		X	PC PI	X		X		X	
Bio18 Precipitation of Warmest Quarter	X	PC PI	X	X	X	X	PC PI	PC PI	PC		X		X	X	X	PC PI
Bio19 Precipitation of Coldest Quarter	X	X	X		PC	PC	PC PI		X		PC	PC PI	X	PC	X	X
Area (x10 ⁶ km ²)	9.65	8.05	8.78	8.62	8.19	5.08	8.11	5.76	5.41	3.56	1.83	1.73	10.06	10.10	13.67	12.97

values of both metrics ranged from 0 (the niches do not overlap) to 1 (the niches are identical). Comparisons were run between all species within each model type, CF and CR, separately. Second, the “Identity test” for each pair of species was conducted. This test randomizes the occurrences for two species, creating the pseudopopulations, and compares the environmental niches for those datasets, creating permuted D and I values. If the D and I values for the actual data are significantly lower than those of the randomized (permuted) data the niches are interpreted to be different (Warren, Glor & Turelli, 2010). The identity test can be performed only for the same set of environmental layers for both compared species; therefore, the identity test was used for the models with all environmental variables. Third, the background test was also performed. It measures the difference between the similarity of two species on one side and the similarity between species and background of another species on the other side. The test should be undertaken for two sides, as it can yield different results for the reversed comparison. If the D and I metrics for actual niche overlap and obtained with background test are similar, this means that the similarity of niches between two species is the same as expected from random data. If the D and I metrics of actual datasets are higher or lower than those from background test, this means that the niches are more similar or more different than expected from random data respectively (Warren, Glor & Turelli, 2010). The background for each species equals to its bias file.

Maps visualization

All maps have been prepared in QGIS 10. The background for the Figs. 1–2 is the layer freely accessible at https://github.com/nvkelso/natural-earth-quick-start/tree/master/50m_raster/NE1_50M_SR_W, and it is not copyrighted. The maps for Figs. 3–6 have been created by the uploading the averaged maps resulted from the Maxent analysis to QGIS 10. The country borders layer is freely accessible at https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3, and it is not copyrighted.

RESULTS

Model evaluation

All the Maxent models have high discriminative power for the training datasets with high AUC. It is higher than 0.9 in all cases except for *O. vittipennis*, where AUC ranges vary from 0.87 to 0.89. The models are also able to predict the testing points with very similar AUC values, as in training datasets. The training AUC is higher than the test AUC, and the differences between the models chosen for the comparison vary from 0.002 (CF model for *O. bivittatus*) to 0.027 (CR model for *O. vittipennis*). Omission rates for the models chosen for the comparisons vary from 0.0789 (CR model for *O. funestus*) to 0.1620 (CF model for *O. vittipennis*). The AUC values and omission rates for all models are provided in the Table S1. The Maxent output files for each model chosen for the visualization and niche comparison are provided in the Data S3. The detailed descriptions of the climatic niches for each species are provided in the Data S4.

The model with all variables is supposed to be overfitted because of the correlated variables. Therefore, this model is expected to predict smaller areas of suitable conditions

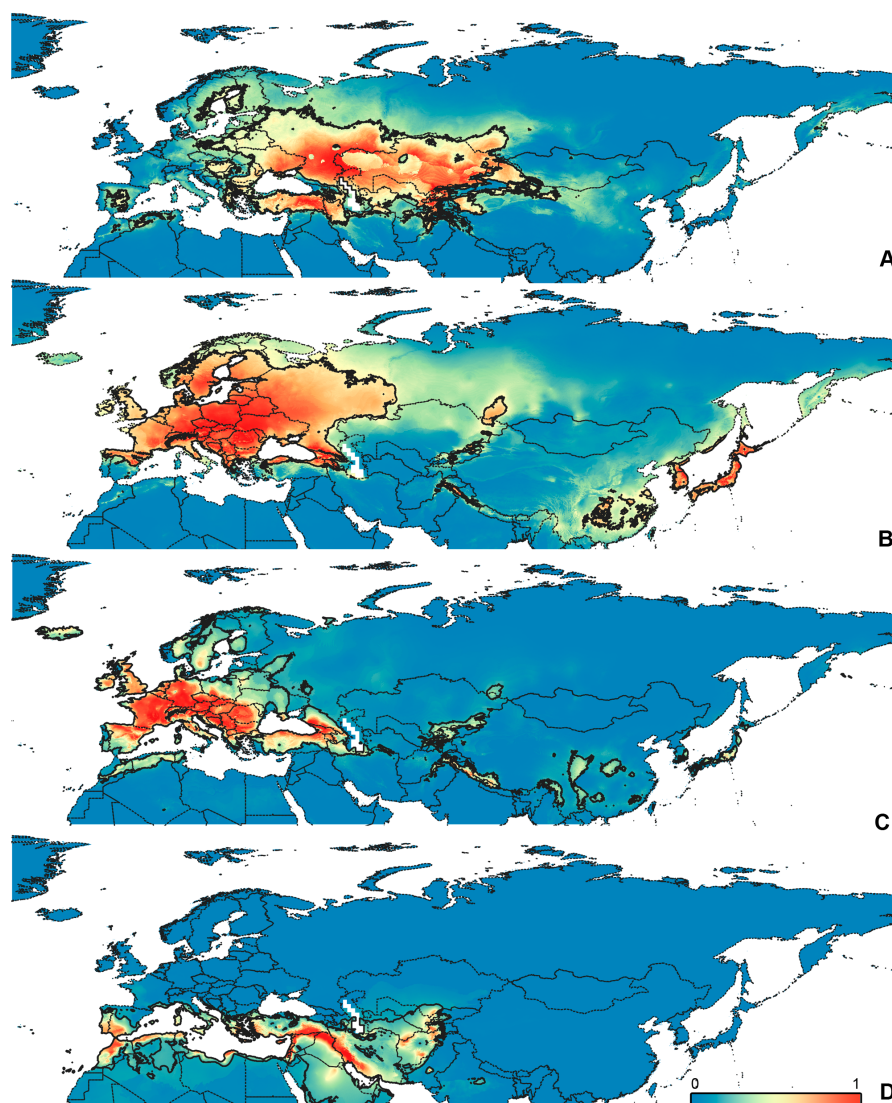


Figure 3 Geographical projections of the CF models. (A) *O. bivittatus*, (B) *O. brevis*, (C) *O. coriaceus*, (D) *O. fulvipes*. Threshold is indicated with the black line. Colors correspond to the suitability score at the bottom of the figure, with 0 corresponding to the most unsuitable places and 1 corresponding to the most suitable places. The layer with the country borders is taken from https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3.

Full-size DOI: 10.7717/peerj.10517/fig-3

and/or narrower ranges of the climatic variables, than the model with reduced set of variables (see Methods). However, the current results do not support this idea. The thresholded maps of the modelled areas with suitable conditions are provided in Figs. 3–6. Those areas of CF models are larger than or subequal to CR for all the species. In the case of variables ranges no model type is noticeably more restrictive than the other (Figs. 7–11). In rare cases, the CF models show significantly more restricted ranges, rather than CR models (e.g., bio12, bio13 for *O. bivittatus* and *O. proserpinae*, bio18 for *O. proserpinae*). The variables ranges for each model are shown on the Figs. 7–11.

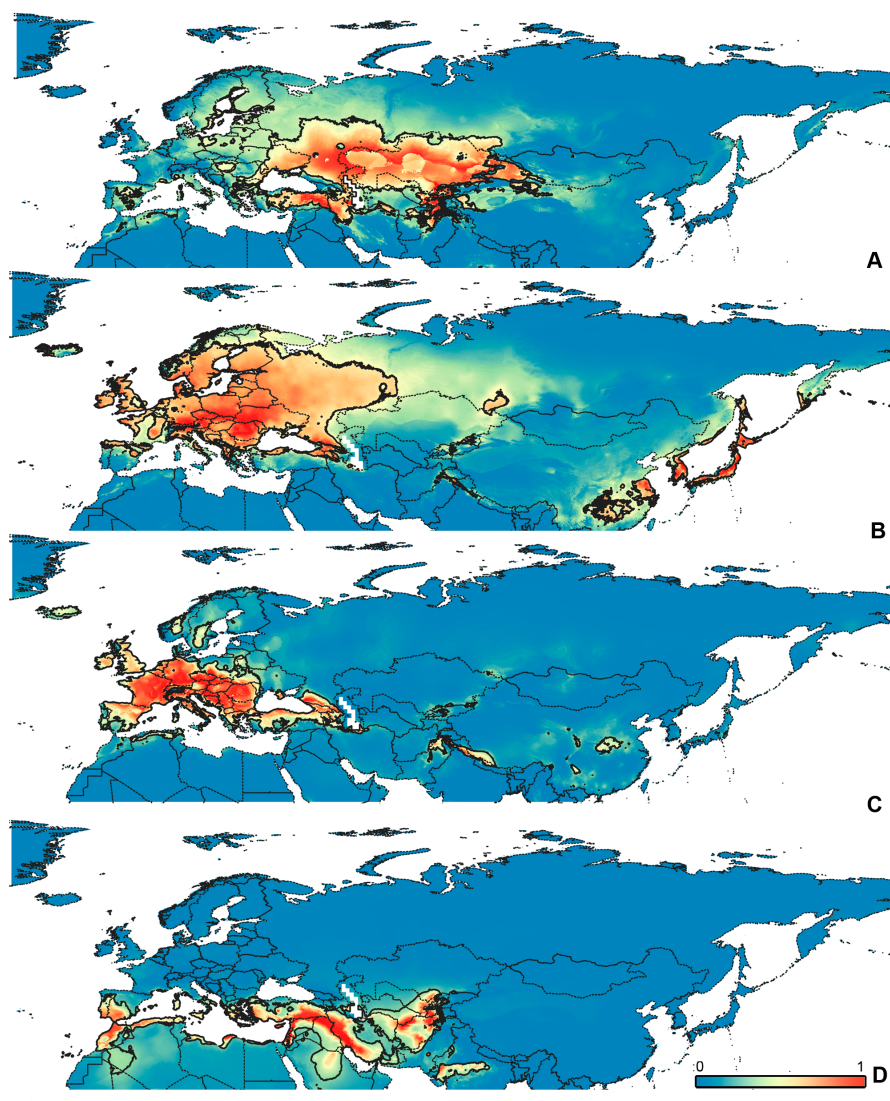


Figure 4 Geographical projections of the CR models. (A) *O. bivittatus*, (B) *O. brevis*, (C) *O. coriaceus*, (D) *O. fulvipes*. Threshold is indicated with the black line. Colors correspond to the suitability score at the bottom of the figure, with 0 corresponding to the most unsuitable places and 1 corresponding to the most suitable places. The layer with the country borders is taken from https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3.

Full-size  DOI: 10.7717/peerj.10517/fig-4

The climatic variables with high PC and PI for each model type and for each species are provided in the Table 1. Both models for the same species have different sets of climatic variables explaining their distribution, and each type of model (CF or CR) has different sets of climatic variables explaining the distribution in comparison between the species.

In most of the models both temperature related and precipitation related variables, are important for the species distribution, except for the CF models for *O. saltator* and *O. vittipennis*, having only temperature related variables significantly contributing. Most of the variables appear as important for at least one model, except for bio5 (max temperature of

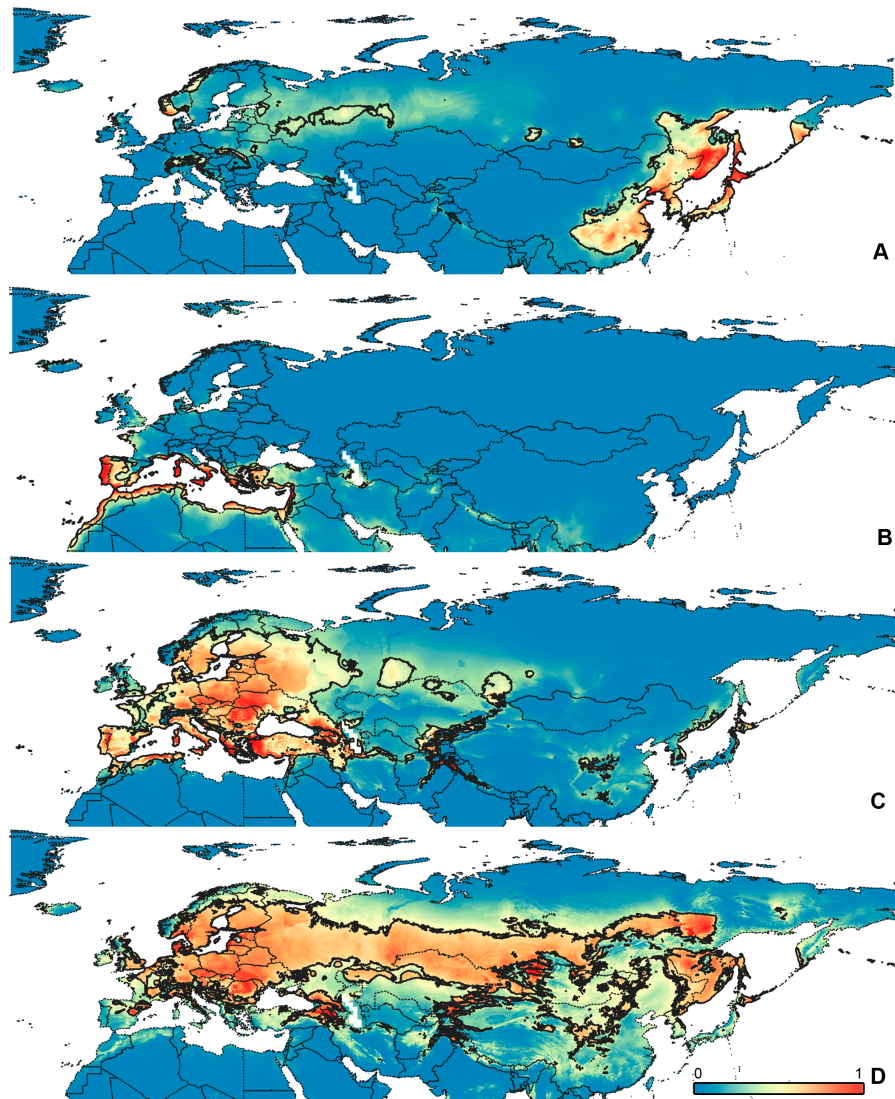


Figure 5 Geographical projections of the CF models. (A) *O. funestus*, (B) *O. proserpinae*, (C) *O. saltator*, (D) *O. vittipennis*. Threshold is indicated with the black line. Colors correspond to the suitability score at the bottom of the figure, with 0 corresponding to the most unsuitable places and 1 corresponding to the most suitable places. The layer with the country borders is taken from https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3.

Full-size  DOI: 10.7717/peerj.10517/fig-5

warmest month), bio8 (mean temperature of wettest quarter), bio12 (annual precipitation) and bio13 (precipitation of wettest month). In some cases, the same variable significantly contributes to the both type of models within the same species, i.e., bio1 (annual mean temperature for *O. bivittatus* and *O. brevis*), bio3 (isothermality) for *O. coriaceus* and *O. funestus*, bio4 (temperature seasonality) for *O. proserpinae*, bio14 (precipitation of driest month) for *O. brevis*, bio18 (precipitation of warmest quarter) for *O. fulvipes*, bio19 (precipitation of coldest quarter) for *O. coriaceus* and *O. proserpinae*.

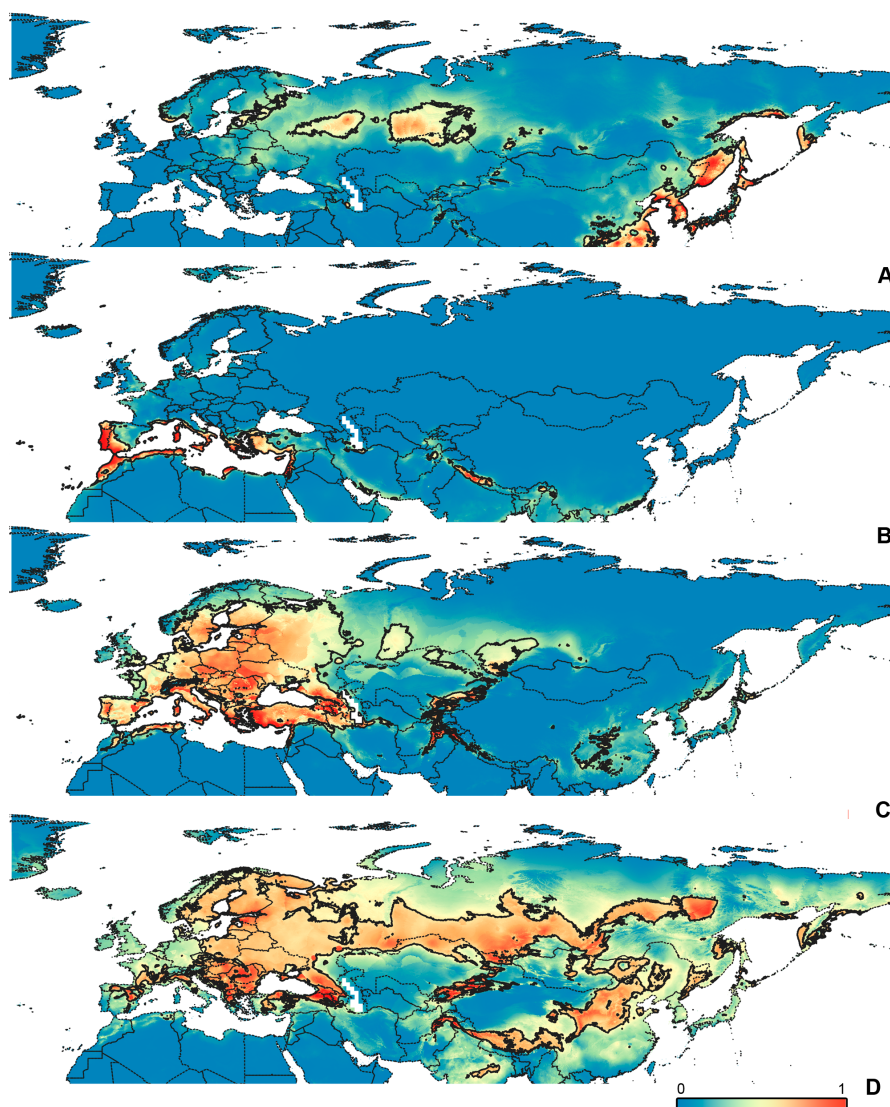


Figure 6 Geographical projections of the CR models. (A) *O. funestus*, (B) *O. proserpinae*, (C) *O. saltator*, (D) *O. vittipennis*. Threshold is indicated with the black line. Colors correspond to the suitability score at the bottom of the figure, with 0 corresponding to the most unsuitable places and 1 corresponding to the most suitable places. The layer with the country borders is taken from https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD_BORDERS-0.3.

Full-size DOI: 10.7717/peerj.10517/fig-6

Comparison of the variables for the species with similar environmental niches

Annual mean temperature (bio1) is important for all widely distributed species. In the case of the CR models for *O. saltator* and *O. vittipennis* this variable does not explain the distribution much. However, min temperature of coldest month (bio6) is important for this type of model in *O. saltator*, and mean temperature of driest quarter (bio9) is important for the CR model in *O. vittipennis*, and bio6 and bio9 significantly correlate with each other and bio1 (PCor > 0.87) in those two species (Table 1). Temperature

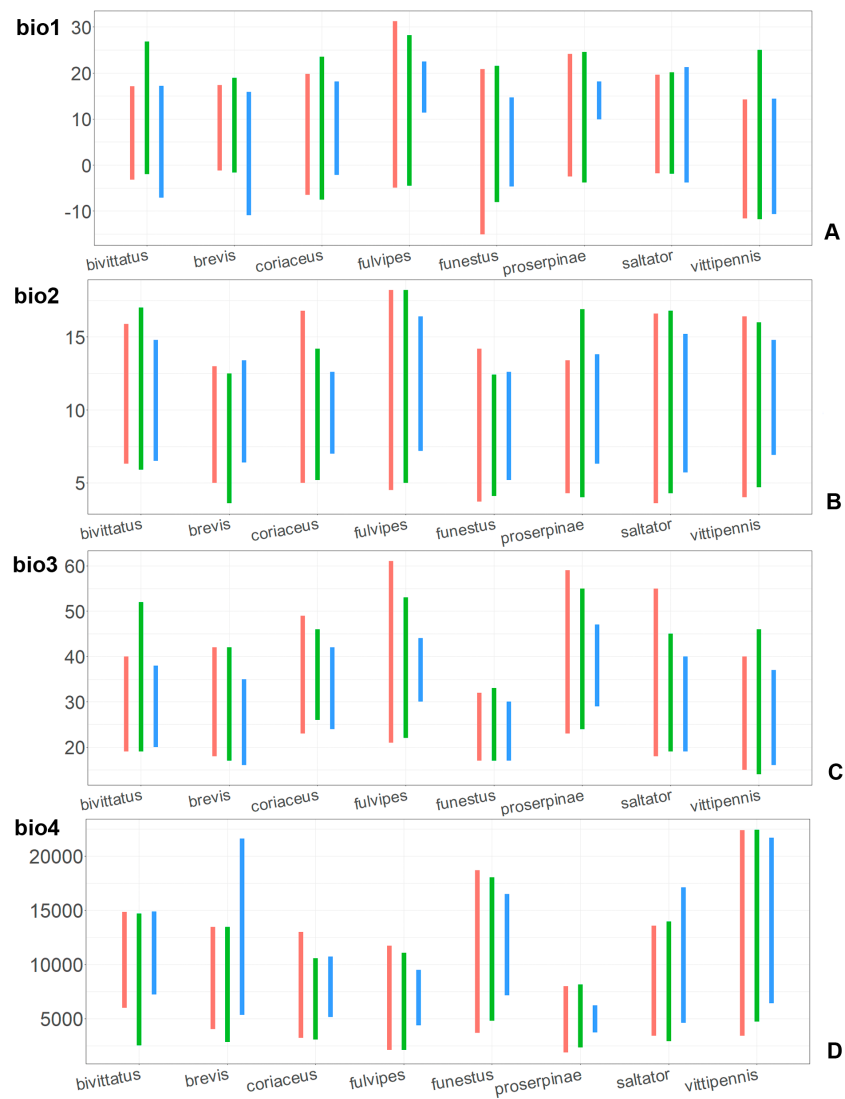


Figure 7 The ranges of (A) bio1, (B) bio2, (C) bio3, and (D) bio4. For each species, the first (red) line corresponds to the CF model, the second (green) line corresponds to the CR model, and the third (blue) line corresponds to the actual records.

Full-size  DOI: 10.7717/peerj.10517/fig-7

annual range (bio7) and mean temperature of coldest quarter (bio11) highly contribute to at least one of the models in *O. bivittatus*, *O. saltator* and *O. vittipennis*, and they also significantly correlate with each other in all those species, as well as with bio1, bio6 and bio9 for most of the species. In the models of two species, widely occurring in Central Asia (*O. bivittatus* and *O. vittipennis*), mean diurnal range (bio2), bio9, mean temperature of coldest quarter (bio11) and precipitation of warmest quarter (bio18) significantly contribute to at least one of the models. In *O. bivittatus* and *O. brevis* precipitation seasonality (bio15) is important for at least one of the models. In *O. brevis* precipitation of driest month (bio14) significantly contributes to both models. Max temperature of warmest month (bio5), mean temperature of wettest quarter (bio8), annual precipitation (bio12), precipitation of

wettest month (bio13), precipitation of driest quarter (bio17) only slightly contribute or do not contribute to the climatic models of the trans-Palearctic species.

Suitable conditions for *O. bivittatus* are shifted to drier places than in other species, whereas suitable conditions for *O. brevis* are predicted for the places with higher precipitation than in other species. In contrast to other species, suitable conditions for *O. vittipennis* are predicted in areas with very low temperatures over the winter and very strong seasonality. The models for *O. saltator* are similar to *O. brevis* in precipitation levels and temperature changes around the year; however, suitable conditions of the former are also predicted for the areas with warmer temperatures over the summer, than in *O. brevis*.

The models of *O. coriaceus* are more similar than random with all the models of widespread species (Table 2). It is different from all of them in the lower margins for isothermality (bio3) limited with higher values (Fig. 7), and suitable conditions are predicted for the places with low temperatures over summer (bio5, bio10) (Figs. 8 and 9). The models for *O. bivittatus* and *O. vittipennis* are additionally different from those of *O. coriaceus* in variables described in the model descriptions for those species (see Data S4). The models of *O. coriaceus* are most similar to those of *O. brevis* and *O. saltator*, which also occupy almost all Europe. Precipitation of driest month (bio14) significantly contributes to both models for *O. brevis* and *O. coriaceus* (Table 1). However, in contrast to *O. brevis*, suitable conditions for *O. coriaceus* are modelled for the places with very low values for this variable, as well as for precipitation of the driest quarter (bio17) (Figs. 10 and 11). The models of *O. coriaceus* differ from *O. saltator* in the upper margin of the precipitation of the driest month and quarter (bio14, bio17) range limited with higher values (Figs. 10 and 11), and the upper margin of seasonality (bio4) limited with lower values (Fig. 7).

The models for the northeastern *O. funestus* are more similar than random with *O. brevis*, *O. saltator* and *O. vittipennis*, and they are most similar to *O. brevis* and *O. vittipennis*. The models of *O. funestus* are different from those of abovementioned three widespread species in isothermality (bio3) range very narrow and shifted towards lower values (Fig. 7). In contrast to all other species, suitable conditions for *O. funestus* and *O. vittipennis* are modelled for the places with very low temperatures of coldest month, coldest and driest quarters (bio6, bio9, bio11) and strong seasonality (bio4) (Figs. 7–9). The upper margins of the diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4), temperature annual range (bio7) are limited with the lower values (Figs. 7–8), and the upper margins are limited with higher values for many precipitation variables (bio12–14, 16, 17–19) in *O. funestus* in comparison with *O. vittipennis* (Figs. 9–11).

Both, *O. funestus* and *O. brevis* have suitable conditions in places with high precipitation over the different seasons (bio12, bio14, bio17) (Figs. 9–11), but ranges of many temperature related variables (bio1, bio5, bio6, bio9, bio11) and seasonality (bio4) are limited with the lower margins in *O. funestus* than in *O. brevis* (Figs. 7–9). *Orthocephalus funestus* differs from *O. saltator* in the variable ranges modelled for the places with stronger annual temperature changes (bio4, bio7), lower temperatures over the different seasons (bio5, bio6, bio9, bio11) and higher precipitation (bio12–14, 16–19) (Figs. 7–11).

Both *O. fulvipes* and *O. proserpinae* inhabit southern areas of European Palearctic (Figs. 1D, 2B), but the variables contributing to their models are different (Table 1). For both

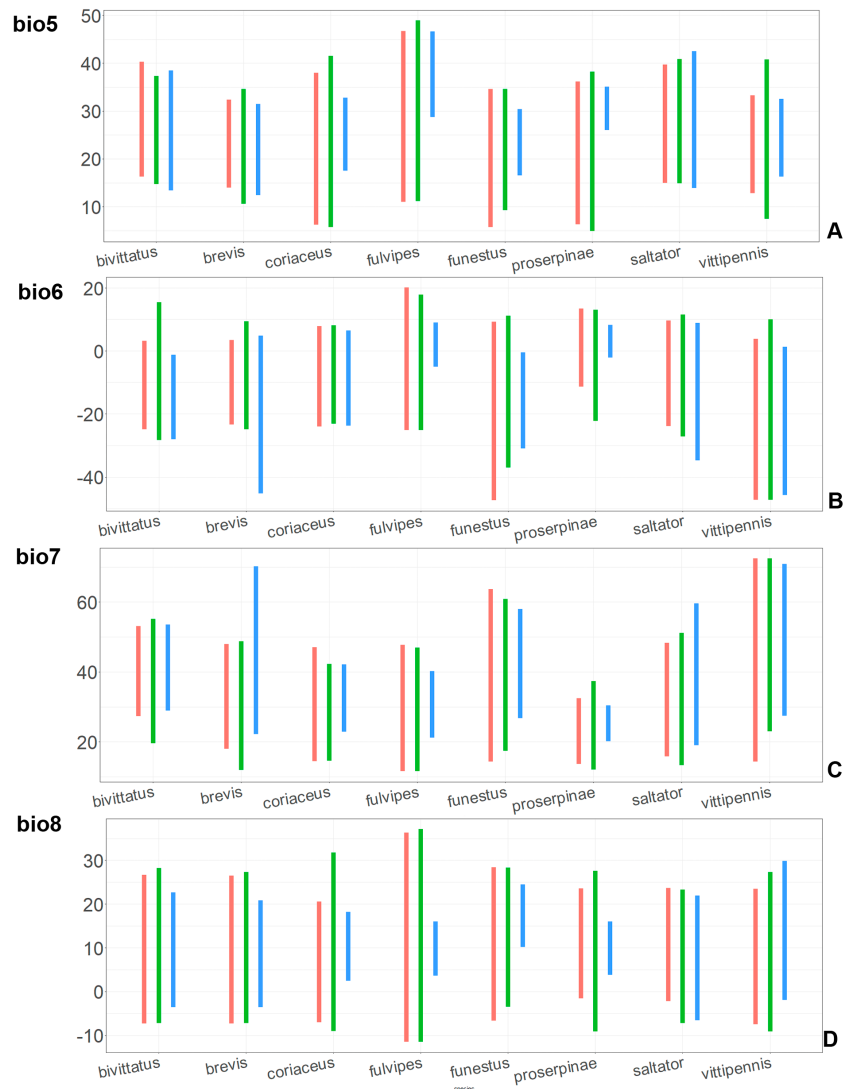


Figure 8 The ranges of (A) bio5, (B) bio6, (C) bio7, and (D) bio8. For each species, the first (red) line corresponds to the CF model, the second (green) line corresponds to the CR model, and the third (blue) line corresponds to the actual records.

Full-size  DOI: 10.7717/peerj.10517/fig-8

species in the CF model the mean temperature of driest quarter (bio9) is important. Precipitation over wettest or coldest quarters (bio16 and bio19) significantly contribute to the models of both species. They also have either precipitation of driest month (bio14) or precipitation of warmest quarter (bio18) with high PC. They have similar ranges for isothermality (bio3) and temperature seasonality (bio4), as well as higher temperatures of driest and coldest periods (bio6, bio9, bio11), and lower precipitations over the driest and warmest periods (bio14, bio17, bio18) (Figs. 7–11). The models of *O. fulvipes* differ from those of *O. proserpinae* in many temperature variables limited with higher values (bio5, bio6-bio11) (Figs. 8–9), as well as mean diurnal range and temperature seasonality and precipitation of driest month (bio2, bio4, bio14) (Figs. 7 and 10) .

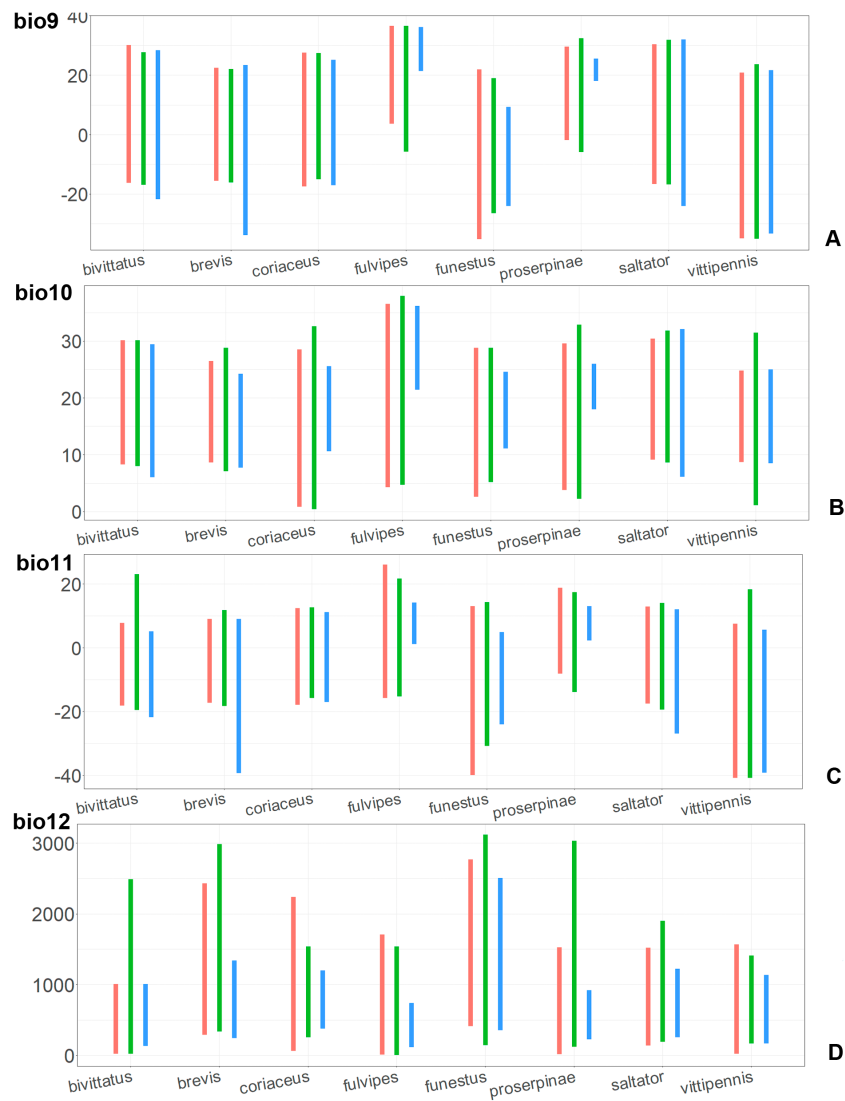


Figure 9 The ranges of (A) bio9, (B) bio10, (C) bio11, and (D) bio12. For each species, the first (red) line corresponds to the CF model, the second (green) line corresponds to the CR model, and the third (blue) line corresponds to the actual records.

Full-size DOI: 10.7717/peerj.10517/fig-9

Niche overlap, identity test and background test

The results for the niche overlap, identity test and background test are shown in the Table 2. The I and D metrics show that the niche overlap between all widely distributed species is relatively high in comparison to cases when widely distributed species is compared with locally distributed species, or locally distributed species are compared with each other ($I > 0.8$, $D > 0.5$). Similar values are for the overlap between the following pairs: *O. brevis* and *O. coriaceus*, *O. saltator* and *O. coriaceus*, *O. funestus* and *O. vittipennis*. The largest niche overlap is between *O. brevis* and *O. saltator* ($I > 0.9$, $D > 0.6$), as well as between *O. brevis* and *O. vittipennis* ($I > 0.8$, $D > 0.6$). However, identity test shows that those values do not

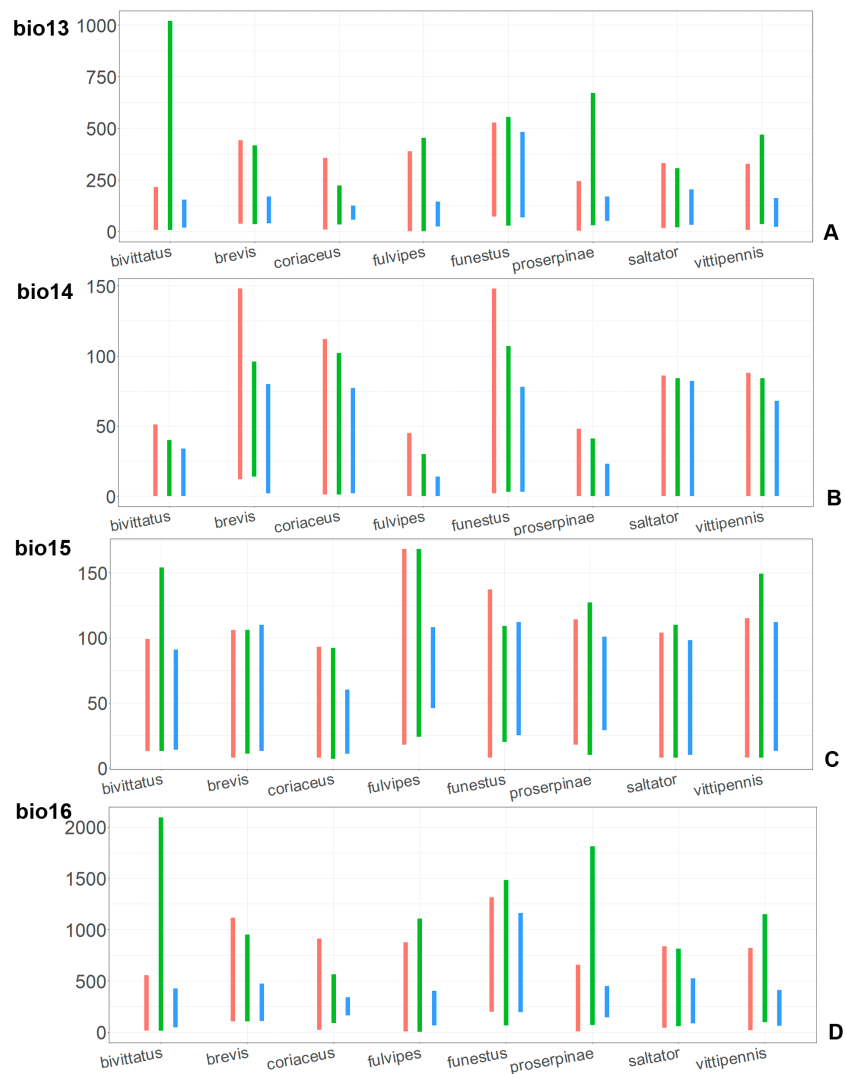


Figure 10 The ranges of (A) bio13, (B) bio14, (C) bio15, and (D) bio16. For each species, the first (red) line corresponds to the CF model, the second (green) line corresponds to the CR model, and the third (blue) line corresponds to the actual records.

Full-size  DOI: [10.7717/peerj.10517/fig-10](https://doi.org/10.7717/peerj.10517/fig-10)

reach 5% threshold for permuted I and D values, which means that we cannot conclude that the niches are identical.

The background test shows that all pairs of the widespread species are more similar to each other than expected for both CF and CR models and for comparisons in both sides, based on I and D metrics. The same result is shown for the comparisons of *O. coriaceus* with all widespread species, as well as for the following pairs: *O. funestus* and *O. brevis*, *O. saltator* and *O. vittipennis*, *O. funestus* and *O. saltator*, *O. funestus* and *O. vittipennis*, *O. coriaceus* and *O. proserpinae*, *O. fulvipes* with *O. proserpinae*. Background test undoubtedly shows that the niches are more different from each other only for *O. funestus* vs *O. proserpinae* comparison. In all other cases the results are dubious and differ depending on the type of

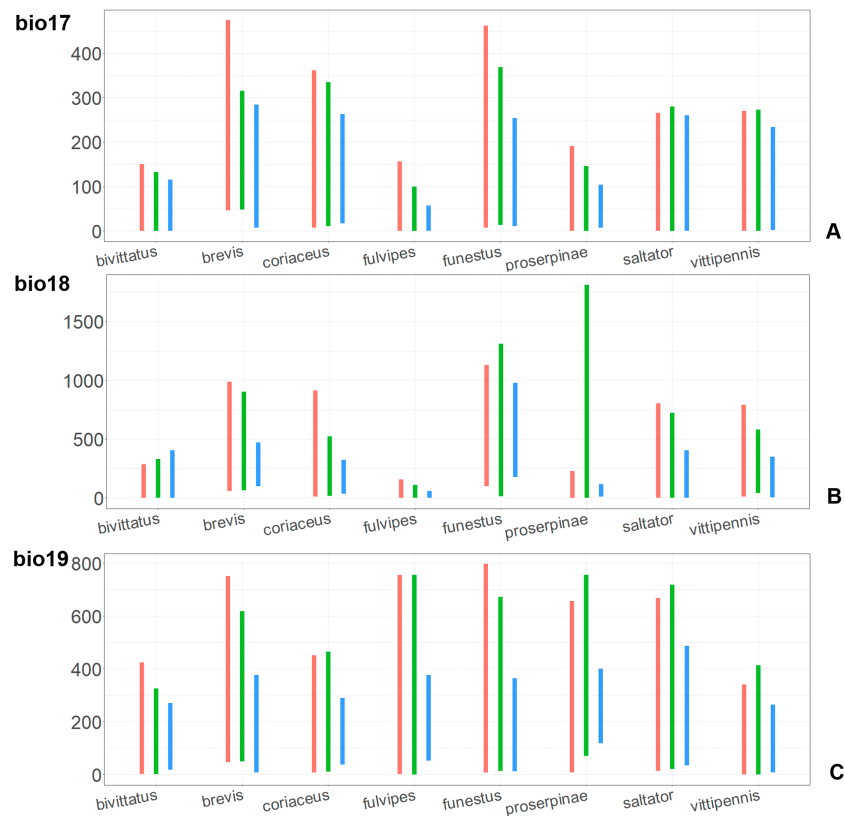


Figure 11 The ranges of (A) bio17, (B) bio18, (C) bio19. For each species, the first (red) line corresponds to the CF model, the second (green) line corresponds to the CR model, and the third (blue) line corresponds to the actual records.

Full-size DOI: 10.7717/peerj.10517/fig-11

model and statistical metric. The results also can differ for the pair of species, depending which species is used for the background. Generally, the CR models show more overlap with each other than the CF models, and background test is more often shows that the species are more similar to each other for the CR models. If two widespread species are compared, the background test results in very similar metrics values for both directions. If two species with very different areas of suitable conditions sizes are compared, the results depend on which of them is used for the background. In case when the species with larger distribution area is used as a background, the resulted metrics are lower, and therefore, the analysis shows that two species are more similar to each other than expected more often, rather than in the reversed comparison.

DISCUSSION

Climatic niches of *Orthocephalus* species comparison

The modelled environmental niches for the widespread species cover noticeably different areas. Areas in which conditions are suitable for *O. bivittatus* correspond with the other species the least. They are mostly projected on Central Asia and south of European part of Russia. (Figs. 3A, 4A). *Orthocephalus brevis* and *O. saltator* are more similar, having

Table 2 Niche overlap (in bold), identity test and background test results. If the niche overlap values are significantly lower than 5% threshold for permuted values, this means that the models are different. If the niche overlap values are higher or lower than those from background test, this means that the niches are more similar or more different than expected from random data respectively.

	Niche overlap I (CF models)	Niche overlap I (CR models)	Identity test 5% threshold for permuted I values	Background test I values, forward comparison	Background test I values, reverse comparison	Niche overlap D (CF models)	Niche overlap D (CR models)	Identity test 5% threshold for permuted D values	Background test D values, forward comparison	Background test D values, reverse comparison
bivittatus vs brevis	0.802	0.815	0.96	0.623	0.615	0.549	0.555	0.824	0.330	0.336
bivittatus vs coriaceus	0.7	0.628	0.928	0.626	0.536	0.39	0.326	0.735	0.334	0.257
bivittatus vs fulvipes	0.42	0.614	0.9	0.626	0.397	0.19	0.318	0.66	0.333	0.168
bivittatus vs funestus	0.504	0.649	0.95	0.634	0.433	0.28	0.373	0.78	0.34	0.204
bivittatus vs proserpinae	0.324	0.375	0.953	0.619	0.285	0.141	0.174	0.776	0.327	0.106
bivittatus vs saltator	0.854	0.83	0.968	0.622	0.613	0.593	0.575	0.838	0.329	0.337
bivittatus vs vittipennis	0.812	0.748	0.97	0.619	0.694	0.56	0.479	0.835	0.327	0.404
brevis vs coriaceus	0.836	0.798	0.902	0.608	0.540	0.522	0.485	0.69	0.332	0.259
brevis vs fulvipes	0.271	0.651	0.847	0.597	0.398	0.08	0.366	0.623	0.323	0.168
brevis vs funestus	0.79	0.814	0.94	0.614	0.439	0.505	0.539	0.78	0.335	0.208
brevis vs proserpinae	0.376	0.416	0.862	0.603	0.293	0.158	0.186	0.636	0.328	0.11
brevis vs saltator	0.905	0.929	0.961	0.615	0.618	0.724	0.758	0.818	0.335	0.342
brevis vs vittipennis	0.912	0.867	0.96	0.612	0.694	0.677	0.618	0.823	0.332	0.404
coriaceus vs fulvipes	0.397	0.697	0.87	0.522	0.382	0.169	0.378	0.633	0.248	0.161
coriaceus vs funestus	0.493	0.473	0.906	0.538	0.436	0.236	0.21	0.689	0.258	0.208
coriaceus vs proserpinae	0.533	0.579	0.863	0.526	0.287	0.276	0.292	0.625	0.251	0.108
coriaceus vs saltator	0.854	0.833	0.915	0.538	0.621	0.57	0.538	0.723	0.257	0.347
coriaceus vs vittipennis	0.723	0.723	0.930	0.531	0.699	0.41	0.389	0.748	0.253	0.411
fulvipes vs funestus	0.105	0.532	0.846	0.394	0.418	0.223	0.267	0.602	0.167	0.195
fulvipes vs proserpinae	0.76	0.711	0.841	0.397	0.282	0.484	0.267	0.593	0.168	0.104
fulvipes vs saltator	0.444	0.679	0.875	0.394	0.596	0.22	0.4	0.664	0.167	0.326
fulvipes vs vittipennis	0.274	0.651	0.882	0.386	0.687	0.09	0.337	0.662	0.161	0.4
funestus vs proserpinae	0.181	0.231	0.824	0.417	0.292	0.062	0.076	0.564	0.195	0.109
funestus vs saltator	0.646	0.713	0.951	0.435	0.618	0.366	0.431	0.791	0.206	0.343
funestus vs vittipennis	0.749	0.828	0.952	0.435	0.692	0.467	0.552	0.793	0.206	0.402
proserpinae vs saltator	0.493	0.533	0.867	0.296	0.604	0.253	0.261	0.627	0.11	0.331
proserpinae vs vittipennis	0.320	0.397	0.877	0.296	0.685	0.129	0.173	0.662	0.111	0.397
saltator vs vittipennis	0.846	0.819	0.97	0.613	0.693	0.599	0.573	0.84	0.338	0.403

the largest area of suitable conditions in Western Palearctic, however, the geographic projections of their environmental niches do not cover the Mediterranean region for *O. brevis*, whereas those areas are suitable for *O. saltator* (Figs. 3B, 4C, 5B, 6C). Suitable conditions for *O. vittipennis* extend through entire Eurasia, from Europe to Northeast Asia, including Central Asia, (Figs. 5D, 6D), whereas the Mediterranean area is not suitable for this species. Those differences in the areas of suitable conditions are also supported by the differences in the variables with highest contribution to the climatic models (Table 1) and comparisons of climatic variable ranges (see ‘Results’ for the details). Overall, all analyzed *Orthocephalus* species have different set of variables, most important for their climatic models and none of the pairs have identical climatic niches, which suggests that the climatic niche is species specific even for the closely related taxa. Finally, the differences in the environmental niches are also supported by the identity and background tests. Although in all widespread species niche overlap is high ($I > 0.8$, $D > 0.6$) and background test shows that the similarity between them is higher than that of random data, the identity test does not support the hypothesis that they are identical (Table 2). This supports the previous research, showing that the environmental niches in closely related species might be similar, but not identical (e.g., [Wellenreuther, Larson & Svensson, 2012](#); [López-Alvarez et al., 2015](#); [Dellicour et al., 2017](#)).

The climatic niche models of trans-Palearctic species are all more similar to each other than expected. The niches of *O. coriaceus* and *O. funestus*, distributed in Europe and Northeast Asia respectively, also highly overlap with some trans-Palearctic species. The climatic niche models of *O. fulvipes* and *O. proserpinae*, are not very similar with those of trans-Palearctic species.

[Schmitt \(2007\)](#) made an overview of the European types of distribution, and delimited three main types. Species with the center of dispersal in Mediterranean regions are “Mediterranean”, species having extra-Mediterranean center of dispersal belong to “Continental” type, and species with recent alpine or arctic distribution patterns are called “Alpine” or “Arctic”. Testing the center of the distribution for the *Orthocephalus* species is beyond the scope of the current paper: a phylogeography analysis combined with modelling of distribution during the glacial period is necessary for such a study. However, it is very likely that the trans-Palearctic *Orthocephalus* species belong at least to two Schmitt’s groupings (2007). Among the analyzed widespread species, suitable conditions in the Mediterranean region are generally not predicted for *O. bivittatus*, *O. brevis* and *O. vittipennis* and they probably belong to the “Continental” group. However, *O. saltator* has highly suitable climatic conditions in the Mediterranean region and might have its center of dispersal there (Figs. 5C, 6C).

Maps with the records and the areas of suitable conditions suggests that “trans-Palearctic” distribution is a term of convenience and might include many types of distributions connected with the different climatic conditions. Study of more species from different taxonomic groups, including closely related and unrelated species, are necessary to make conclusions on which types of environmental niches are suitable for the trans-Palearctic species and which climatic conditions are connected with such distributions.

Climatic variables important for the *Orthocephalus* distribution

Annual mean temperature (bio1), temperature annual range (bio7) and mean temperature of coldest quarter (bio11) are important for the models of at least three widely distributed *Orthocephalus* species. The results also correspond with the results of environment niche modelling of the trans-Palearctic beetle species *Pterostichus oblongopunctatus* (Fabricius, 1787), which showed that bio1 and bio11 had high contribution to the model of this species (Avtaeva et al. 2019). Modelling of the trans-Palearctic tick *Ixodes ricinus* (Linnaeus, 1758) showed that min temperature of coldest month (bio6) is among the variables with the highest PC in the climatic model of this species (Porretta et al., 2013). In all trans-Palearctic species bio6 and bio11 highly correlate with bio1 (PCor > 0.9), and this might mean that the distribution of the trans-Palearctic arthropods is limited at least partly by the winter temperatures. Overall, the set of the variables having high contribution to the climate models is unique for each *Orthocephalus* species, and analysis of more trans-Palearctic species is needed to make conclusions on how type of distribution correlates with the climatic variables.

Orthocephalus brevis, *O. coriaceus*, *P. oblongopunctatus* and *I. ricinus* are mostly distributed in the Western Palearctic, and their climatic models have precipitation of driest month (bio14) or precipitation of driest quarter (bio17) with high PC. This reflects the fact that the most suitable conditions for all those species cover middle and northern Europe, but not Mediterranean zones, and therefore prefer the places with relatively high precipitation around the year. This is also supported by the variable ranges of bio14 and bio17 variables for *O. brevis* and *O. coriaceus*, which show that these species inhabit places with high precipitation values over the driest period. Similarly to four mentioned species, *Orthocephalus saltator* is mostly distributed in Western Palearctic, but the areas with the most suitable conditions cover Mediterranean zones. In case of this species, bio14 and bio17 do not contribute much to the climatic model (<10% of PC and PI).

Although *O. coriaceus* and *O. funestus* have very different distribution, isothermality (bio3) has high PC and PI for both models in both species. However, according to the temperature ranges the former tends to inhabit places with high isothermality, whereas the latter prefers the areas with low values of this variable. The study with more European and East Asian species and species from Northeast Asia is needed to confirm that isothermality is connected with such distributions.

The precipitation related variables over the different seasons (bio14, bio15, bio18, bio19) are important for models for two species mostly distributed in the Mediterranean regions, and mean temperature of driest quarter (bio9) has high PC and PI in the CF model. This is similar to the Mediterranean species *Tomicus destruens* (Wollaston, 1865) (Sánchez-García, Galián & Gallego, 2015). It was shown that the variables bio19 and bio9 are also important for the climatic models of different clades and haplotypes of this species. Study of climatic preferences of more insect species from the Mediterranean region is needed to draw conclusions on how the climate is connected with the species distribution in this region.

Comparison of environmental niches between closely related *Orthocephalus* species in the phylogenetic context

Although, a morphology-based phylogeny for *Orthocephalus* has been published ([Namyatova & Konstantinov, 2009](#)), there are many unresolved clades, and, therefore, cannot be used to adequately analyze potential phylogenetic signal in climatic related tolerances and environmental niches. However, a few conclusions still can be reached. According to this phylogeny, *O. bivittatus*, *O. coriaceus*, *O. fulvipes*, *O. funestus*, *O. saltator* and *O. vittipennis* have very similar vestiture, color and genitalia, and in some cases the species can be identified only from the males. Those species form a clade, which also includes some other species. *Orthocephalus brevis* and *O. proserpinae* are very different morphologically, and are not closely related to other species.

Based on these relationships, it can be hypothesized that there are at least three processes in this genus related to climatic niches which might be at play. First, there might be phylogenetic conservatism, at least for some climatic variables. For example, *O. funestus* and *O. vittipennis* are very similar morphologically. They mostly differ only in hemelytron coloration in males. According to the current analysis, their niches are also more similar to each other than to random data, and both those species can tolerate strong seasonality and very low winter temperatures. Another example is *O. fulvipes*, inhabiting southwestern Palearctic, which morphologically is very similar to *O. saltator*, and the latter is the only widespread species in which the Mediterranean region is suitable.

Second, climatic niche convergence is also observed. This study found that climatic niches are very similar in *O. brevis* and *O. saltator*, as well as *O. brevis* and *O. vittipennis*, and those pairs are not closely related.

Third, the analysis shows the possibility of the distinct niche divergence in the distantly related taxa. According to the background test, the niches are undoubtedly more different from each other than from random data only for the *O. funestus* and *O. proserpinae* pair. According to [Namyatova & Konstantinov \(2009\)](#), those two species are not closely related. Those significant niche differences might be explained by differences in habitats, occupied by those two species. *Orthocephalus funestus* inhabits places in Northeast Asia with wide ranges of temperatures and high precipitation, whereas *O. proserpinae* lives in the Mediterranean region with narrow temperature ranges and low precipitation ([Figs. 5B, 5D, 6B, 6D](#)). However, *O. fulvipes*, which is more closely related to *O. funestus*, also prefers dry conditions including Mediterranean and desert climates ([Figs. 3D, 4D](#)). The background test for this species pair provides inconsistent results, suggesting that the niches between *O. funestus* and *O. fulvipes* are more similar with each other, than those of *O. funestus* and *O. proserpinae*. This leads to the hypothesis that the closely related species in *Orthocephalus* cannot diverge very quickly.

However, the robust molecular-based phylogeny and niche models for other *Orthocephalus* species are needed to test all those hypotheses on the niche evolution in this genus.

Based on this phylogeny, it is unclear whether the ability for the wide distribution has phylogenetic signal. On one hand, it is very likely that two closely related species can similarly adapt to the climatic conditions (e.g., [Losos, 2008](#); [Wiens et al., 2010](#)). On the

other hand, even though both sister species can potentially tolerate wide range of climatic conditions, one species might have significantly limited realized niche and distribution because of the strong competition with its sister species.

CONCLUSIONS

The study on the climatic niche modelling for eight insect species with trans-Palearctic distribution from the genus *Orthocephalus* has been performed. The niches of widely distributed trans-Palearctic species (*O. bivittatus*, *O. brevis*, *O. saltator*, *O. vittipennis*) are very similar to each other, but not identical. The differences are confirmed by the “Identity test” and “Background test” in ENMTools, as well as the comparison of the climatic variables contributing to the modes and variable ranges for the areas, covered by preferable conditions of different species. The niches of the trans-Palearctic species are also similar to two species having more limited distribution (*O. coriaceus*, *O. funestus*). Overall, the similarity of the niches of widely distributed species is higher than in cases when the niches of widely distributed and locally distributed species or only locally distributed species are compared. The annual mean temperature significantly contributes (bio1) to the climatic models of all trans-Palearctic species. Other temperature related variables, i.e., min temperature of coldest month (bio6), temperature annual range (bio7), mean temperature of driest quarter (bio9), mean temperature of coldest quarter (bio11) are likely to be important for the climatic niches of the trans-Palearctic species. For the trans-Palearctic species, widely distributed in Central Asia, mean diurnal range (bio2), min temperature of coldest quarter (bio11) and precipitation of warmest quarter (bio18) are also important for at least one of the models. For the Western Palearctic species with the most suitable conditions corresponding to the areas outside the Mediterranean regions (*O. brevis* and *O. coriaceus*), precipitation of driest month (bio14) is important. Isothermality (bio3) has high PC and PI for European *O. coriaceus* and East Asian *O. funestus*. For the species, distributed in the Mediterranean region (*O. fulvipes* and *O. proserpinae*), precipitation related variables over different seasons (bio14, bio16, bio18, bio19), significantly contribute to at least one of the model each. The discussion of the results based on the phylogeny suggests that within *Orthocephalus* there might be different processes connected to the climate niche differentiation, such as niche conservatism, niche convergence and niche divergence. More studies of climatic niches of the species distributed in the Palearctic are needed to better understand the types of possible climatic niches of widespread species, the main climatic variables shaping the distribution of the Palearctic taxa and how the climatic niches are related to phylogenetic history.

ACKNOWLEDGEMENTS

I am grateful to the curator of the Heteroptera collection (Zoological Institution of the Russian Academy of Science), Fedor Konstantinov and the Head of the Laboratory of Insect Taxonomy (Zoological Institution of the Russian Academy of Science), Sergey Sinev, for the access to the collection. I thank Liudmila Osipova (International Council of Clean Transportation, Berlin, Germany) for the assistance with the niche modelling

methodology and Elena Pazhenkova (St Petersburg State University, St Petersburg, Russia) for consultations on graphs visualizations with R. I'm grateful to Michael Schwartz (Agriculture & Agri-Food Canada, Canadian National Collection of Insects, Ottawa, Canada), Michael Elias (New South Wales Department of Primary Industries Biosecurity collections, Orange, Australia) and Igor Danilov (Zoological Institution of the Russian Academy of Science) for helping to revise the manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This work was supported by the Russian Science Foundation grant (no 19-74-00077). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the author:
Russian Science Foundation grant: 19-74-00077.

Competing Interests

The author declares there are no competing interests.

Author Contributions

- Anna A. Namyatova conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The records used in the analysis, as well as accession numbers and specimen information, including hosting collections, are available in the [Supplemental Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.10517#supplemental-information>.

REFERENCES

- Abe Y, Melika G, Stone GN. 2007.** The diversity and phylogeography of cynipid gallwasps (Hymenoptera: Cynipidae) of the oriental and eastern Palearctic regions, and their associated communities. *Oriental Insects* **41**(1):169–212
[DOI 10.1080/00305316.2007.10417504](https://doi.org/10.1080/00305316.2007.10417504).
- Aguierre-Gutiérrez J, Serna-Chavez HM, Villalobos-Arambula AR, Perezdela Rosa JA, Raes N. 2015.** Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines. *Diversity and Distributions* **21**(3):245–257
[DOI 10.1111/ddi.12268](https://doi.org/10.1111/ddi.12268).

- Araújo MB, Thuiller W, Williams PH, Reginster I. 2005.** Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography* **14**(1):17–30 DOI [10.1111/j.1466-822X.2004.00128.x](https://doi.org/10.1111/j.1466-822X.2004.00128.x).
- Arnold K. 2008.** Aktuelle Heteropteren-Funde nach 1980 aus dem Freistaat Sachsen (Insecta: Hemiptera)–2. Beitrag. *Faunistische Abhandlungen (Dresden)* **25**:79–89.
- Avtaeva TA, Sukhodolskaya RA, Skripchinsky AV, Brygadyrenko VV. 2019.** Range of *Pterostichus oblongopunctatus* (Coleoptera, Carabidae) in conditions of global climate change. *Biosystems Diversity* **27**(1):76–84 DOI [10.15421/011912](https://doi.org/10.15421/011912).
- Blair ME, Sterling EJ, Dusch M, Raxworthy CJ, Pearson RG. 2013.** Ecological divergence and speciation between lemur (Eulemur) sister species in Madagascar. *Journal of Evolutionary Biology* **26**(8):1790–1801 DOI [10.1111/jeb.12179](https://doi.org/10.1111/jeb.12179).
- Bohl CL, Kass JM, Anderson RP. 2019.** A new null model approach to quantify performance and significance for ecological niche models of species distributions. *Journal of Biogeography* **46**(6):1101–1111 DOI [10.1111/jbi.13573](https://doi.org/10.1111/jbi.13573).
- Chiarenza AA, Mannion PD, Lunt DJ, Farnsworth A, Jones LA, Kelland SJ, Allison PA. 2019.** Ecological niche modelling does not support climatically-driven dinosaur diversity decline before the Cretaceous/Paleogene mass extinction. *Nature Communications* **10**(1):1–14 DOI [10.1038/s41467-018-07882-8](https://doi.org/10.1038/s41467-018-07882-8).
- Cho YJ, Lee YH, Oh JB, Suh SJ, Choi DS. 2011.** Some notes on the insect fauna of Gadeok-do Island. *Journal of Korean Nature* **4**(4):319–324 DOI [10.7229/jkn.2011.4.4.319](https://doi.org/10.7229/jkn.2011.4.4.319).
- Cho YB, Yoon SJ, Yoon SM, Ryu JW, Min HK, Oh KS. 2008.** Insect Fauna of Gyeongju National Park, Korea. *Journal of Korean Nature* **1**(1):11–20 DOI [10.1016/S1976-8648\(14\)60122-5](https://doi.org/10.1016/S1976-8648(14)60122-5).
- De Marco Junior P, Nobrega CC. 2018.** Evaluating collinearity effects on species distribution models: an approach based on virtual species simulation. *PLOS ONE* **13**(9):e0202403 DOI [10.1371/journal.pone.0202403](https://doi.org/10.1371/journal.pone.0202403).
- Dellicour S, Kastally C, Varela S, Michez D, Rasmont P, Mardulyn P, Lecocq T. 2017.** Ecological niche modelling and coalescent simulations to explore the recent geographical range history of five widespread bumblebee species in Europe. *Journal of Biogeography* **44**(1):39–50 DOI [10.1111/jbi.12748](https://doi.org/10.1111/jbi.12748).
- Dioli P. 1993.** Eterotteri insubrici ed eterotteri xerothermici nei territori perilacustri della Lombardia e del Ticino. *Ecologia dell'Insubria e del Ticino: atti dell'XI convegno nazionale* **11**:81–86.
- Elith JH, Graham CP, Anderson R, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huetmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE. 2006.** Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**(2):129–151 DOI [10.1111/j.2006.0906-7590.04596.x](https://doi.org/10.1111/j.2006.0906-7590.04596.x).

- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011.** A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**(1):43–57 DOI [10.1111/j.1472-4642.2010.00725.x](https://doi.org/10.1111/j.1472-4642.2010.00725.x).
- Filazzola A, Sotomayor DA, Lortie CJ. 2018.** Modelling the niche space of desert annuals needs to include positive interactions. *Oikos* **127**(2):264–273 DOI [10.1111/oik.04688](https://doi.org/10.1111/oik.04688).
- Fourcade Y, Engler JO, Rödder D, Secondi J. 2014.** Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLOS ONE* **9**(5):e97122 DOI [10.1371/journal.pone.0097122](https://doi.org/10.1371/journal.pone.0097122).
- Frieß T. 2006.** Naturschutzfachliche Analyse der Wanzenfauna (Insecta, Heteroptera) unterschiedlicher Almflächen im Nationalpark Gesäuse (Österreich, Steiermark). *Denisia* **19**:857–873.
- Frieß T. 2014.** Die Wanzenfauna (Insecta: Heteroptera) des Nationalparks Gesäuse (Österreich, Steiermark). *Beiträge zur Entomofaunistik* **15**:21–59.
- Gierlański G. 2017.** Nowe dane o występowaniu pluskwiaków różnoskrzydłych (Hemiptera: Heteroptera) na użytkach zielonych w Masywie Śnieżnika (Sudety Wschodnie). *Heteroptera Poloniae –Acta Faunistica* **11**:7–13.
- Gorczyca J, Chłond D. 2005.** Orthotylinae of Poland—faunistic review (Hemiptera, Heteroptera, Miridae). *Annals of the Upper Silesian Museum (Entomology)* **13**:87–134.
- Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C. 2004.** Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* **58**(8):1781–1793 DOI [10.1111/j.0014-3820.2004.tb00461.x](https://doi.org/10.1111/j.0014-3820.2004.tb00461.x).
- Halimi E, Paparisto A. 2014.** Analysis of environmental factors in some ecosystems by studying the distribution of species: plant bugs (Miridae). In: *Proceeding of the 2nd international conference on research and education—challenges toward the future (ICRAE2014), 30–31 May 2014*. Shkodra, Albania: University of Shkodra Luigj Gurakuqi.
- Halimi E, Paparisto A, Topi D. 2014.** Systematic and ecological analysis on plant bugs (Miridae, Hemiptera) in the habitats of Lushnja region. *Albanian Journal of Agricultural Science 2014 Special Issue*:295–298.
- Hanberry BB. 2013.** Finer grain size increases effects of error and changes influence of environmental predictors on species distribution models. *Ecological Informatics* **15**:8–13 DOI [10.1016/j.ecoinf.2013.02.003](https://doi.org/10.1016/j.ecoinf.2013.02.003).
- Heckmann R, Strauss G, Rietschel S. 2015.** Die Heteropterenfauna Kretas. *Carolinea* **73**:83–130.
- Hubenov Z. 2008.** Composition and zoogeographical characteristics of the family Tachinidae (Diptera: Insecta) in Serbia and Bulgaria. *Advances in Arachnology and Developmental Biology* **12**:375–394.
- Jezkova T, Olah-Hemmings V, Riddle BR. 2011.** Niche shifting in response to warming climate after the last glacial maximum: inference from genetic data and niche assessments in the chisel-toothed kangaroo rat (*Dipodomys microps*). *Global Change Biology* **17**(11):3486–3502 DOI [10.1111/j.1365-2486.2011.02508.x](https://doi.org/10.1111/j.1365-2486.2011.02508.x).

- Jueterbock A. 2018.** MaxentVariableSelection: selecting the best set of relevant environmental variables along with the optimal regularization multiplier for maxent niche modeling. Available at <https://cran.r-project.org/web/packages/MaxentVariableSelection/MaxentVariableSelection.pdf> (accessed on 15 April 2020).
- Jueterbock A, Smolina I, Coyer JA, Hoarau G. 2016.** The fate of the Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling approach. *Ecology and Evolution* **6(6)**:1712–1724 DOI [10.1002/ece3.2001](https://doi.org/10.1002/ece3.2001).
- Jung S, Kim J, Duwal RK. 2017.** An annotated catalogue of the subfamily Orthotylinae (Hemiptera: Heteroptera: Miridae) from the Korean Peninsula. *Journal of Asia-Pacific Biodiversity* **10(3)**:403–408 DOI [10.1016/j.japb.2017.05.006](https://doi.org/10.1016/j.japb.2017.05.006).
- Kerzhner IM, Jaczewski TL. 1964.** Order Hemiptera (Heteroptera). In: Bei-Bienko GYa, ed. *Keys to the insects of the European USSR 1*. Leningrad: Nauka, 655–845 (In Russian).
- Kerzhner IM, Josifov M. 1999.** Cimicomorpha II: Miridae. In: Aukema B, Rieger C, eds. *Catalogue of the heteroptera of the palaearctic region*. vol. 3. Amsterdam: Entomological Society, 1–577.
- Kment P, Baňář P. 2012.** True bugs (Hemiptera: Heteroptera) of the Bílé Karpaty Protected Landscape Area and Biosphere Reserve (Czech Republic). *Acta Musei Moraviae, Scientiae Biologicae* **96(2)**:323–628.
- Knouft JH, Losos JB, Glor RE, Kolbe JJ. 2006.** Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology* **87(7)**:S29–S38 DOI [10.1890/0012-9658\(2006\)87\[29:PAOTEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[29:PAOTEO]2.0.CO;2).
- Kondorosy E. 2011.** Keszthely és környéke poloskafaunájának alapvetése (Heteroptera). *Folia Musei Historico-Naturalis Bakonyiensis A Bakonyi Természettudományi Múzeum Közleményei* **28**:105–145.
- Konstantinov FV, Namyatova AA. 2019.** Taxonomic revisions and specimen databases in the internet age: dealing with a species rich insect taxon. *Entomological Review* **99(3)**:340–361 DOI [10.1134/S0013873819030072](https://doi.org/10.1134/S0013873819030072).
- Kozak KH, Wiens J. 2006.** Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* **60(12)**:2604–2621 DOI [10.1111/j.0014-3820.2006.tb01893.x](https://doi.org/10.1111/j.0014-3820.2006.tb01893.x).
- Kozak KH, Wiens JJ. 2010.** Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters* **13(11)**:1378–1389 DOI [10.1111/j.1461-0248.2010.01530.x](https://doi.org/10.1111/j.1461-0248.2010.01530.x).
- Kozminykh VO, Naumkin DV. 2017.** True heteropterans (Insecta: Heteroptera) of the Basegi reserve and notes on heteropteran fauna of the Northern Urals. *Fauna Urala and Sibiri* **1**:90–100 [In Russian].
- Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckman I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Heribert H, Wilting A. 2013.** The importance of correcting for sampling bias in

- MaxEnt species distribution models. *Diversity and Distributions* **19**(11):1366–1379
DOI [10.1111/ddi.12096](https://doi.org/10.1111/ddi.12096).
- Lim JS, Lee BW, Park SY, Jo DG. 2011.** Insect fauna of Maebongsan mountain, Hongcheon-gun, Gangwon-do. *Journal of Korean Nature* **4**(4):293–307
DOI [10.7229/jkn.2011.4.4.293](https://doi.org/10.7229/jkn.2011.4.4.293).
- Lim JS, Park SY, Lee BW. 2013a.** A Study on the Insect Fauna in and Around Goseong-gun, Gangwon-do, South Korea. *Journal of Asia-Pacific Biodiversity* **6**(2):221–237
DOI [10.7229/jkn.2013.6.2.221](https://doi.org/10.7229/jkn.2013.6.2.221).
- Lim JS, Park SY, Lee BW, Jo DG. 2012.** A faunistic study of insects from Daebudo and Youngheungdo Islands in Korea. *Journal of Korean Nature* **5**(4):311–325
DOI [10.7229/jkn.2012.5.4.000](https://doi.org/10.7229/jkn.2012.5.4.000).
- Lim JS, Park SY, Lim JO, Lee BW. 2013b.** A Faunistic Study of Insects from Is. Ulleungdo and Its Nearby Islands in South Korea. *Journal of Asia-Pacific Biodiversity* **6**(1):93–121 DOI [10.7229/jkn.2013.6.1.093](https://doi.org/10.7229/jkn.2013.6.1.093).
- Lisón F, Calvo JF. 2013.** Ecological niche modelling of three pipistrelle bat species in semiarid Mediterranean landscapes. *Acta Oecologica* **47**:68–73
DOI [10.1016/j.actao.2013.01.002](https://doi.org/10.1016/j.actao.2013.01.002).
- Liu C, Newell G, White M. 2016.** On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution* **6**(1):337–348
DOI [10.1002/ece3.1878](https://doi.org/10.1002/ece3.1878).
- López-Alvarez D, Manzaneda AJ, Rey PJ, Giraldo P, Benavente E, Allainguillaume J, Mur L, Caicedo AL, Hazen SP, Breiman A, Ezrati S, Catalán P. 2015.** Environmental niche variation and evolutionary diversification of the *Brachypodium distachyon* grass complex species in their native circum-Mediterranean range. *American Journal of Botany* **102**(7):1073–1088 DOI [10.3732/ajb.1500128](https://doi.org/10.3732/ajb.1500128).
- Losos JB. 2008.** Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11**(10):995–1003 DOI [10.1111/j.1461-0248.2008.01229.x](https://doi.org/10.1111/j.1461-0248.2008.01229.x).
- Losos JB, Leal M, Glor RE, De Queiroz K, Hertz PE, Schettino LR, Lara AC, Jackman TR, Larson A. 2003.** Niche lability in the evolution of a Caribbean lizard community. *Nature* **424**(6948):542–545 DOI [10.1038/nature01814](https://doi.org/10.1038/nature01814).
- Matocq A, Pluot-Sigwalt D, Özgen İ. 2014.** Terrestrial Hemiptera (Heteroptera) collected in South-Eastern Anatolia (Diyarbakir, Mardin and Elaziğ provinces) (Turkey): second list. *Munis Entomology & Zoology* **9**(2):21–29.
- McCormack JE, Zellmer AJ, Knowles LL. 2010.** Does niche divergence accompany allopatric divergence in Aphelocoma jays as predicted under ecological speciation?: insights from tests with niche models. *Evolution* **64**(5):1231–1244
DOI [10.1111/j.1558-5646.2009.00900.x](https://doi.org/10.1111/j.1558-5646.2009.00900.x).
- Melber A, Günther H, Rieger C. 1991.** Die Wanzenfauna des österreichischen Neusiedlerseegebietes (Insecta, Heteroptera). *Wissenschaftliche Arbeiten aus dem Burgenland* **89**:63–192.

- Merow C, Smith MJ, Silander Jr JA. 2013.** A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**(10):1058–1069 DOI [10.1111/j.1600-0587.2013.07872.x](https://doi.org/10.1111/j.1600-0587.2013.07872.x).
- Morales NS, Fernández IC, Baca-González V. 2017.** MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ* **5**:e3093 DOI [10.7717/peerj.3093](https://doi.org/10.7717/peerj.3093).
- Mudereri BT, Mukanga C, Mupfiga ET, Gwatirisa C, Kimathi E, Chitata T. 2020.** Analysis of potentially suitable habitat within migration connections of an intra-African migrant-the Blue Swallow (*Hirundo atrocaerulea*). *Ecological Informatics* **57**:Article 101082 DOI [10.1016/j.ecoinf.2020.101082](https://doi.org/10.1016/j.ecoinf.2020.101082).
- Mumladze L. 2014.** Sympatry without co-occurrence: exploring the pattern of distribution of two *Helix* species in Georgia using an ecological niche modelling approach. *Journal of Molluscan Studies* **80**(3):249–255 DOI [10.1093/mollus/eyu045](https://doi.org/10.1093/mollus/eyu045).
- Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP. 2014a.** ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution* **5**(11):1198–1205 DOI [10.1111/2041-210X.12261](https://doi.org/10.1111/2041-210X.12261).
- Muscarella R, Kass JM, Galante R. 2014b.** ENMeval Vignette. Available at <https://cran.r-project.org/web/packages/ENMeval/vignettes/ENMeval-vignette.html#block> (accessed on 15 April 2020).
- Namyatova AA, Konstantinov FV. 2009.** Revision of the genus *Orthocephalus* Fieber, 1858 (Hemiptera: Heteroptera: Miridae: Orthotylinae). *Zootaxa* **2316**(1):1–118 DOI [10.11646/zootaxa.2316.1.1](https://doi.org/10.11646/zootaxa.2316.1.1).
- Nikolaeva AM. 2011.** The preliminary list of the terrestrial heteropteran species (Insecta: Heteroptera) of the Mescchera National Park. *Trudy Mordovskogo gosudarstvennogo prirodnogo zapovednika imeni P.G. Smidovicha* **14**:316–322 [In Russian].
- Park SJ, Kwon H, Park SK, Park DS. 2013.** Comparative insect faunas between Gangh-wado and six others Islands of West Coastal in Incheon, Korea. *Journal of Asia-Pacific Biodiversity* **6**(2):197–219 DOI [10.7229/jkn.2013.6.2.197](https://doi.org/10.7229/jkn.2013.6.2.197).
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson TA. 2007.** Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34**(1):102–117 DOI [10.1111/j.1365-2699.2006.01594.x](https://doi.org/10.1111/j.1365-2699.2006.01594.x).
- Phillips SJ, Anderson RP, Schapire RE. 2006.** Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**(3–4):231–259 DOI [10.1016/j.ecolmodel.2005.03.026](https://doi.org/10.1016/j.ecolmodel.2005.03.026).
- Phillips SJ, Dudík M. 2008.** Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. *Ecography* **31**:161–175 DOI [10.1111/j.0906-7590.2008.5203.x](https://doi.org/10.1111/j.0906-7590.2008.5203.x).
- Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. 2009.** Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* **19**(1):181–197 DOI [10.1890/07-2153.1](https://doi.org/10.1890/07-2153.1).

- Porretta D, Mastrantonio V, Amendolia S, Gaiarsa S, Epis S, Genchi C, Bandi C, Otranto D, Urbanelli S. 2013.** Effects of global changes on the climatic niche of the tick *Ixodes ricinus* inferred by species distribution modelling. *Parasites & Vectors* 6(1):Article 271 DOI 10.1186/1756-3305-6-271.
- Potikha EV. 2015.** A taxonomic list of the mayflies, Stoneflies and Caddisflies (Insecta: Ephemeroptera, Plecoptera and Trichoptera) of the Sikhote-Alin Biosphere Reserve. *Achievements in the Life Sciences* 9(1):22–31 DOI 10.1016/j.als.2015.05.004.
- Ribes J. 1989.** Mescellinea Fauna Iberica, (Heteroptera). *Sessió Conjunta d'Entomologia* VI:19–35.
- Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D. 2020.** Package MASS. Available at <https://cran.r-project.org/web/packages/MASS/MASS.pdf> (accessed on 15 April 2020).
- Roháčová M. 2007.** Ploštice (Heteroptera) Přírodní památky Kamenná u Staříče po dvaceti letech True bugs (Heteroptera) of the Natural Monument Kamenná after twenty years. *Práce a Studie Musea Beskyd, Přírodní Vědy (Frýdek-Místek)* 15:043–058.
- Sánchez-García FJ, Galián J, Gallego D. 2015.** Distribution of *Tomicus destruens* (Coleoptera: Scolytinae) mitochondrial lineages: phylogeographic insights and niche modelling. *Organisms Diversity & Evolution* 15(1):101–113 DOI 10.1007/s13127-014-0186-2.
- Schmitt T. 2007.** Molecular biogeography of Europe: pleistocene cycles and postglacial trends. *Frontiers in Zoology* 4(1):Article 11 DOI 10.1186/1742-9994-4-11.
- Seo C, Thorne JH, Hannah L, Thuiller W. 2009.** Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters* 5(1):39–43 DOI 10.1098/rsbl.2008.0476.
- Shcheglovitova M, Anderson RP. 2013.** Estimating optimal complexity for ecological niche models: a jackknife approach for species with small sample sizes. *Ecological Modelling* 269:9–17 DOI 10.1016/j.ecolmodel.2013.08.011.
- Shi K, Li Y, Bao C. 2016.** Study on species diversity, zoogeographical distribution and ecological properties of the miridae (hemiptera) family in the Hulun Buir City, Inner Mongolia of China. *International Proceedings of Chemical, Biological and Environmental Engineering* 91:43–47.
- Sofronova EV. 2017.** The true bugs (Hemiptera, Heteroptera) of the Baykalo-Lenskiy Reserve with new records from Irkutskaya Oblast' in East Siberia, Russia. *Euroasian Entomological Journal* 16(3):207–212 [In Russian].
- Tamanini L. 1981.** Gli eterotteri della Basilicata e della Calabria (Italia meridionale) (Hemiptera, Heteroptera). *Memorie del Museo civico di storia naturale di Verona, ser. 2, A* 3:1–164.
- Taszakowski A, Pasińska A. 2017.** New data on the occurrence of terrestrial true bugs (Hemiptera: Heteroptera) in Pieniny Mountains. *Fragmenta Faunistica* 60(1):15–22.
- Vinokurov NN, Golub VB, Zinovjeva AN. 2017.** Plant bugs (Heteroptera, Miridae) of the South Urals State Nature Reserve. II. Orthotylinae, Phylinae. *Euroasian Entomological Journal* 16(3):247–252.

- Vinokurov NN, Kanyukova EV, Ostapenko KA. 2016.** Homoptera (Cicadina) and Heteroptera of the Sikhote-Alin State Nature Biosphere reserve. *Amurian Zoological Journal* **8(4)**:233–249 [In Russian].
- Wagner E. 1974.** Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makaronesischen Inseln (Hemiptera, Heteroptera). In: *Teil 2. Entomologische Abhandlungen*. Leipzig: Akademische Verlagsgesellschaft Geest & Portig.
- Wagner E, Weber HH. 1965.** Héteroptères Miridae. *Faune de France* **67**:1–592.
- Warren DL, Glor RE, Turelli M. 2010.** ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33(3)**:607–611
[DOI 10.1111/j.1600-0587.2009.06142.x](https://doi.org/10.1111/j.1600-0587.2009.06142.x).
- Wellenreuther M, Larson KW, Svensson EI. 2012.** Climatic niche divergence or conservatism? Environmental niches and range limits in ecologically similar damselflies. *Ecology* **93(6)**:1353–1366 [DOI 10.1890/11-1181.1](https://doi.org/10.1890/11-1181.1).
- Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davis TJ, Grytnes J, Harrison SP, Hawkins BA, Halt RD, McCain CM, Stephens PR. 2010.** Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13(10)**:1310–1324 [DOI 10.1111/j.1461-0248.2010.01515.x](https://doi.org/10.1111/j.1461-0248.2010.01515.x).