Climatic niche comparison between closely related trans-Palearctic species from the genus *Orthocephalus* (Insecta: Heteroptera: Miridae: Orthotylinae) (#48200)

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

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Climatic niche modelling had previously only been performed for a handful of Palearctic species on a scale that included the entire region. The climatic niches of the species having trans-Palearctic distribution are poorly studied, and it is unclear whether and to what extent those niches can be different and which climatic variables are connected with such a wide distribution. Here, I perform environmental niche modelling based on the Worldclim climatic variables using Maxent and niche comparison using ENMTools for four species of the genus *Orthocephalus* (Insecta: Heteroptera: Miridae) (*O. bivittatus*, *O. brevis*, *O. saltator*, *O. vittipennis*), distributed across Europe and Asia to test whether their climatic niches are identical. The same analysis is also performed for four species from the same genus with more limited distribution (*O. coriaceus*, *O. fulvipes*, *O. funesuts*, *O. proserpinae*) to test whether the niches of the closely related species with trans-Palearctic distribution are more similar to each other, than to other congenerics. It has been found, that the climatic niche models of all trans-Palearctic species are similar to each other, but are not identical. This is supported by the niches geographic projections, climatic variables, contributing to the models, and variables ranges. The climatic niche models of all trans-Palearctic species are also very similar to two species having more restricted distribution (*O. coriaceus*, *O. saltator*). Results of this study suggest that the trans-Palearctic distribution can have different geographic ranges and can be shaped by different climatic factors.

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Abstract

Climatic niche modelling had previously only been performed for a handful of Palearctic species on a scale that included the entire region. The climatic niches of the species having trans-Palearctic distribution are poorly studied, and it is unclear whether and to what extent those niches can be different and which climatic variables are connected with such a wide distribution. Here, I perform environmental niche modelling based on the Worldclim climatic variables using Maxent and niche comparison using ENMTools for four species of the genus *Orthocephalus* (Insecta: Heteroptera: Miridae) (*O. bivittatus*, *O. brevis*, *O. saltator*, *O. vittipennis*), distributed across Europe and Asia to test whether their climatic niches are identical. The same analysis is also performed for four species from the same genus with more limited distribution (*O. coriaceus*, *O. fulvipes*, *O. funesuts*, *O. proserpinae*) to test whether the niches of the closely related species with trans-Palearctic distribution are more similar to each other, than to other congenerics. It has been found, that the climatic niche models of all trans-Palearctic species are similar to each other, but are not identical. This is supported by the niches geographic projections, climatic variables, contributing to the models, and variables ranges. The climatic niche models of all trans-Palearctic species are also very similar to two species having more restricted distribution (*O. coriaceus*, *O. saltator*). Results of this study suggest that the trans-Palearctic distribution can have different geographic ranges and can be shaped by different climatic factors.

Introduction

Environmental niches are important characteristics of species. Studying them can help to identify the environmental factors, responsible for maximizing the species’ fitness, and, therefore, lead to a better understanding of how environment is connected to speciation and how closely related species are different in their ecological preferences.

Most of the works on the environmental niche differences are made on the allopatric vertebrate species (e.g. Losos et al., 2003; Graham et al., 2004; Kozak & Weins, 2006, 2010; McCormack et al., 2010; Blair et al., 2013). There are only few works studying ecological niche similarities in species living in sympatry (e.g. Knouft et al., 2006; Wellenreuther et al., 2012; Lison & Calvo, 2013; Mumladze, 2014; López-Alvarez et al., 2015; Dellacour et al., 2016), and even fewer on insects (Wellenreuther et al., 2012; Dellacour et al., 2016). Many already published papers show that closely related species, occurring in sympatry, are different in their ecological niches (Wellenreuther et al., 2012; Mumladze, 2014; Aguirre-Gutierrez, 2015; López-Alvarez et al., 2015; Dellacour et al., 2017). However, only few such works have been performed for Palearctic insects (e.g. Wellenreuther et al. 2012; Dellacour et al., 2016), and no such work has been undertaken for the species with trans-Palearctic distribution, which spans thousands kilometres across different biomes and climatic zones. Studying climatic niches of widespread species can help to reveal the climatic variables, connected with the species ability to adapt to different conditions.

This work is concentrated on revealing the differences of the environmental niches between closely related species of the Palearctic genus *Orthocephalus* Fieber, 1858 (Insecta: Heteroptera: Miridae). It has been revised (Namyatova & Konstantinov, 2009), and a morphology-based phylogeny has been proposed for the group, which supported its monophyly. Currently *Orthocephalus* includes 23 species, and four of them are widely distributed in Europe and Asia, they are *Orthocephalus bivittatus* Fieber, 1864, *O. brevis* (Panzer, 1798), *O. saltator* (Hahn, 1835), and *O. vittipennis* (Herrich-Shaeffer, 1835) (Namyatova & Konstantinov, 2009). All of them are known from Western Europe to Siberia. *Orthocephalus vittipennis* is recorded from Western Europe to Eastern Siberia, 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* was not recoded from the northern Europe and Eastern Siberia, however, it is common in Central Asia (Kerzhner & Josifov, 1999; Namyatova & Konstantinov, 2009) This allows us to test, whether the closely related species with wide distribution in Palearctic occupy the same environmental niche, or whether they are significantly different.

Another four *Orthocephalus* species, *O. coriaceus* (Fabricius, 1777), *O. fulvipes* Reuter, 1904, *O. funestus* Jakovlev, 1881, and *O. proserpinae* (Mulsant & Rey, 1852), are also chosen to test whether the niches of the widespread species are more similar to each other, than with the species having more limited distribution. *Orthocephalus coriaceus* is mostly known from the middle and northern Europe with few specimens recorded from Kyrgyzstan. *O. funestus* is known only from Northeast Asia, *O. proserpinae* and *O. fulvipes* inhabit Mediterranean region, *O. fulvipes* is additionally known from Arabian Peninsula and Iran (Kerzhne & Josifov, 1999; Namyatova & Konstantinov, 2009).

The aims of the current work are as follows: (1) to build the climatic niche models and compare them between eight *Orthocephalus* species; (2) to test whether the trans-Palearctic species are significantly similar or even identical, and whether they are more similar to each other or to the species with a limited distribution; (3) to find the main climatic environmental factors, responsible for the niche differences.

Materials & Methods

Specimens and localities sources. The following species has been analyzed in this work *Orthocephalus bivittatus* (171 unique records), *O. brevis* (146 unique records), *O. coriaceus* (39 unique records), *O. fulvipes* (18 unique records), *O. funestus* (90 unique records), *O. proserpinae* (19), *O. saltator* (237 unique records), and *O. vittipennis* (208 unique records).

Data on the specimens, mostly preserved at the Zoological Institution, Russian Academy of Sciences, St Petersburg, Russia, have been used for this study. This collection holds one of the largest Palearctic collections of Heteroptera, and the data from the most specimen labels for *Orthocephalus*, preserved there, are plotted to the Arthropod Easy Capture database (https://research.amnh.org/pbi/locality/). The specimens have been identified based on the previously published revision (Namyatova & Konstantinov, 2009). To decrease number of erroneous records, in most cases the localities from other papers have been added only if they cited above-mentioned revision (Kment & Baňař, 2012; Matocq et al., 2014; Heckmann, 2015; Sofronova, 2017; Vinokurov et al., 2017). All records from the literature have been added for *O. brevis* and *O. funestus* (Ribes, 1989; Melber et al., 1991; Dioli, 1993; Gorczyca & Chłond, 2005; Arnold, 2008; Lim et al., 2011, 2012, 2013a, 2013b; Nikolaeva, 2011; Frieß, 2006, 2014; Roháčová, 2007; Cho et al. 2008, 2011; Kondorosy, 2011; Park et al., 2013; Halimi & Paparisto, 2014; Shi et al., 2016; Vinokurov, 2016; Gierlański, 2017; Jung et al., 2017; Kozminykh &

Naumkin, 2017), as *O. brevis* can be easily identified from congeners by its widened antennal segment II and *O. funestus* inhabits Northeast Asia, and this is the only *Orthocephalus* species, known from this area (Namyatova & Konstantinov, 2009). The maps with all records used in this study are provided on Figs 1 and 2 and the list of all the records for all species are provided in the Data S1.

Maps. Layers in 5-arc minute resolution representing different bioclimatic variables have been downloaded from Worldclim, Version 1.4 (https://www.worldclim.org/version1). 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, have been 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 et al., 2006) has been chosen, because it performs well in comparisons with other programmes especially for rare species. It works with the presence-only data and considered to produce robust results with sparse, irregularly sampled data and minor location errors, which is applicable to the museum data (Elith et al, 2006, 2011; Pearson et al, 2007; Kramer-Schadt et al., 2007). 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 and 10 replicates has been performed. For the datasets with <50 localities (*O. coriaceus*, *O. fulvipes* and O. *proserpinae*), crossvalidation with the replicates number corresponding to the localities number has been performed (Pearson at 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 vehicle 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 (Dormann et al., 2007; Kramer-Schadt et al., 2013), however, it can lead to the situation when the number of occurrences is too few to create the reliable model. 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 analysed species, the bias file approach has been chosen. The 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). Bias file has been 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 the previous works (e.g. Filazzola et al., 2018; Mudereri et al., 2020). Bias files have been 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, have been randomly selected from the area denoted in the bias file. The “cloglog” output was chosen for the visualisation and further analysis.

Variable selection. The climatic niche modelling with two sets of variables has been performed. To avoid the model overfitting, it is possible to exclude the highly correlated variables and/or tune the model parameters (Merrow et al., 2013). It was shown that Maxent can perform well with the correlating variables with tuned parameters (Merrow et al., 2013; Morales et al., 2017; De Marco Junior & Nobrega, 2019), therefore, the first model type includes all bioclimatic variables (CF model). However, to test whether the model with all variables can be overfitted, we excluded the highly correlated variables for each species (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 et al., 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, Merrow et al., 2013). Best features and regularization multiplier set for the CF models have been selected using *ENMeval* package in R (Muscarella et al., 2014a, 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” has been 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 performed five times for each species. In case if the analyses resulted in different parameter sets, all of them have been kept to run the environmental niche modelling in Maxent. All the parameter sets, used for the modelling, are provided in the Table S2.

In the case of the CR model, the *MaxentVariableSelection* package in R (Jueterbock et al., 2016; Jueterbock, 2018) has been used. It chooses the best set of variables, which has the lowest AICc value, based on the regularisation multiplier and features. The comparisons were performed for the same parameters, as in the case of the *ENMeval*. The separate run has been performed to test the regularization multipliers for the each feature class or combinations of the classes. For the background data ten thousands background points were extracted from the bias file raster using R. Each feature (or combination of the features), its best regularization multiplier and variable set was kept for the further analysis in Maxent, and they are provided in the Table S2.

Maxent provides the list of the percent contribution (PC) and permutation importance (PI) for the each variable in the model. We consider as important each variable, having PC and/or PI higher than 10%.

Model evaluation. For model evaluation, training and test AUC values are provided, which is valid for model comparison over the same study area (Bohl et al., 2019). The differences between training and test AUC values and omission error rates have been also compared, as well as, as the model with high differences between AUC values and omission error rate > 0.1 is likely to be overfitted (Bohl et al., 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 have been chosen for the visualization and niche comparisons.

Environmental niche projection area and climatic variable ranges. The obtained environmental niche models have been thresholded using the "Maximum training sensitivity plus specificity Cloglog threshold", as the thresholds, maximising the sensitivity and specificity perform well on the presence only datasets (Liu et al., 2016). The total area of the thresholded niche projection has been obtained. Second, the thresholded maps have been used as masks to trim the bioclim layers to obtain the climatic variables ranges for the each model. Those areas and variable ranges have been used to compare the models. The correlation of climatic variables has been estimated for each species separately using Pearson's correlations (PCor), as it is suitable for the continuous variables. Tables with Pearson's correlations for the each species are provided in the Data S3.

Niche overlap. Testing for niche overlap has been performed in *ENMTools* (Warren et al., 2010). First, the overlap niche was performed to get the Schoener's D (D) and Hellinger distance I (I) metrics, which measure the habitat suitability between two species. The values of both those metrics are ranging from 0 (the niches do not overlap) to 1 (the niches are identical). The comparisons were performed between all species within each model type, CF and CR, separately. Second, the "Identity test" for each pair of species performed, it 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 randomize data, it means that the niches are different (Warren et al., 2010). The identity test has been performed for the layers with all environmental variables. Third, the background test has been also performed. It measures the niche overlap with D and I metrics between the records of one species and random points taken from the background of another species. The test should be undertaken in 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 et al., 2010). The background for each species equals to its bias file.

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 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. Training AUC is higher than 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 0.162 (CF model for *O. vittipennis*). The AUC values and omission rates for all models are provided in the Table S2. The Maxent output files for the each model chosen for the visualization and niche comparison are provided in the Data S4.

The model with all variables is supposed to be overfitted because of the correlated variables, and, therefore, predict smaller areas of suitable conditions and/or narrow ranges of the climatic 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 the each model are shown on the Figs 7-11.

The climatic variables with high PC and PI for the each model type and for the 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 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, bio8, bio12 and bio13. In some cases, the same variable significantly contributes to the both type of models within the same species, i.e. bio1 for *O. bivittatus* and *O. brevis*, bio3 for *O. coriaceus* and *O. funestus*, bio4 for *O. proserpinae*, bio14 for *O. brevis*, bio18 for *O. fulvipes*, bio19 for *O. coriaceus* and *O. proserpinae*.

Descriptions of the climatic models and variables ranges for each species

Orthocephalus bivittatus

Geographic distribution Most specimens used in this analysis were collected in South Russia, Caucasus and Central Asian countries, the most western record is from Hungary, the most eastern is from Eastern Siberia near the lake Baikal, the most northern is from central European Russia (Bryansk Province), and the most southern is from the southern Turkmenistan near the boarders with Iran and Afghanistan (Fig. 1A).

In both models suitable conditions mainly extend from Eastern Europe (12-13°E) to Western China and Mongolia (95-96°E) in longitudinal direction, and from the middle of European Russia (30-31°N) to Iran and Afghanistan (58-59°N) in the latitudinal direction (Fig. 3A, 5A). Only very small patches of suitable conditions appear beyond those limits. However, the CF model predicts the large areas of suitable conditions in the eastern and northern Europe and central and northern European Russia up to northern Scandinavia and Karelia, whereas only small patches of suitable conditions are predicted there by the CR model. Both models do not predict Middle and Western Europe to be very suitable for *O. bivittatus*.

Climatic variables. Both models show that the annual average temperature (bio1) significantly contributes to the distribution, having both PC and PI high. In respect to other variables, the models are very different. the CF model bio11 is important too, and this model is also explained by the variables, connected with the annual, seasonal and diurnal temperature changes (bio2-4, bio7), as well as precipitation seasonality (bio15). In the CR model among the temperature variables, mean temperatures of driest quarter and month (bio9, bio10) are important, as well as precipitation seasonality (bio15) and precipitation of warmest quarter (bio18). Among all those variables, bio1 and bio11 (PCor = 0.93) and bio4 and bio7 (PCor=0.94) significantly correlate with each other.

The variable ranges show that precipitation in driest month, driest, warmest and coldest quarters (bio14, bio17-19) have relatively restricted ranges and shifted towards less precipitation in comparison to that of most other species (Figs10, 11). Suitable conditions for *O. bivitattus* are not modelled for the places with the low max temperature of warmest month (bio5) and annual temperature range (bio7), as the lowest values of these variables are higher than in other species (Fig. 8).

Orthocephalus brevis

Geographic distribution. Most records used in the current analysis are from Middle and Eastern Europe, western Russia, Caucasus and western Siberia (Fig 1B).

Both models predict a large area of suitable conditions in Western Palearctic from Portugal (8°W) to Ural Mountains (55-56°E) in longitudinal direction, and from north of Spain, Italy, Greece, Tukey and Iran (37-38°N) to northern Scandinavia (65-66°N) in the latitudinal direction. Additionally, Northeast Asia is predicted as suitable for *O. brevis*. There are also small patches of suitable conditions in Altai Mountains and Central Asia up to India (Figs 3B, 5B).

Climatic variables. Both the models show that the annual mean temperature (bio1) and precipitation of driest month (bio14) significantly contribute to the distribution with high PC and PI in both cases. In the CR model precipitation seasonality (bio15) has high PI. None of those variables significantly correlate with each other.

In comparison with other species, precipitations of driest month, driest and coldest quarters (bio14, bio17, bio19) in both models are high, and never reach 0 (Figs 10, 11). The lowest limit of annual precipitation (bio12) is also higher than in most of the other species (Fig. 9) and the upper limits of diurnal range (bio2) is low in comparison to most of the other species (Fig. 7). The precipitation ranges show that *O. brevis* generally prefers wetter places than other species.

Orthocephalus coriaceus

Geographic distribution. In this analysis the records from Central and Southern Europe, as well as from Kyrgyzstan and Tunisia, are used (Fig. 1C).

The overall size of areas with suitable conditions is distinctly smaller in the CR model than in the CF model, i.e. 8.19 x10^6 km^2 and 5.08 x10^6 km^2 respectively (Table 1). The models predict suitable conditions in most Europe and partly in Near East, up to Portugal in the west (8°W) up to Northern Iran in the east (54-55°E). However, the CR model mostly does not cover the areas in Belarus, Ukraine and western Russia, whereas in the CF model suitable conditions extend up to the middle parts of the European Russia. Both models estimate suitable conditions from northern Africa and northern Iran (34-36°N) up to Scandinavia in latitudinal direction. The CR model is more restrictive and estimates suitable conditions up to southern Scandinavia (61-62°N), whereas in the CF model they are extended more to the north (67°N). Both models predict suitable conditions in Iceland. Only small patches of suitable conditions are predicted beyond those areas.

Climatic variables. Both models show that isothermality, precipitation of driest month and coldest quarter (bio3, bio14, bio 19) significantly contribute to the distribution with high PC and PI. Among other variables, mean temperate of coldest quarter (bio11) and precipitation seasonality (bio15) are important for the CF model, and precipitation of wettest quarter (bio16) is important for the CR model. Among them bio19 significantly correlates with bio3 and bio14 (PCor = 0.71, 0.76 respectively), bio14 additionally correlates with bio15 and bio16 (PCor = -0.85, 0.79 respectively), and bio3 correlates with bio11 (PCor = 0.84).

Variable ranges for isothermality (bio3) have lowest limits with higher values than in other species and relatively small range in comparisons to most of other species (Fig. 7). The models predict the lowest margins of mean temperature of warmest quarter (bio10) to be lower than in many other species, and it is almost reaching 0 (Fig. 9), as the model predicts suitable conditions for *O. coriaceus* in the northern Scandindavia and Iceland.

Orthocephalus fulvipes

Geographic distribution. In this analysis only records from north Africa and Near East countries are used (Fig. 1D).

Both models are very similar and predict suitable conditions from Portugal and Morocco in the west (8-9°W) to Tadjikistan and Kyrgyzstan in the east (70-71°E), from the middle of Algeria and south of Arabian Peninsula (20-24°N) in the south to south Kazakhstan, north of Turkey as well as the Northern Mediterranean (39-42°N) in the north. Only small patches of suitable conditions are predicted beyond this area (Figs 3D, 5D).

Climatic variables. Precipitation of warmest quarter (bio18) is important for both models. In the CF model mean temperature of driest quarter (bio9) and precipitation of coldest quarter (bio19) are significantly important. In the CR model mean temperature of coldest month (bio6) and precipitation of warmest quarter (bio16) are additionally important. Among those variables only bio16 and bio19 strongly correlate with each other with PCor = 0.97.

The ranges of many temperature related variables are shifted towards higher values, which are annual mean temperature (bio1), isothermality (bio3), max temperature of warmest month (bio5), mean temperature of coldest month, driest, warmest and coldest quarters (bio6, bio9-bio11) (Figs 7-9). Precipitation variables values are often restricted by the relatively low values, e.g. annual precipitation (bio12), precipitation of direst month, driest and warmest quarters (bio14, bio17, bio18) (Figs 9-11). This suggests that that the suitable conditions cover many areas with relatively high temperatures all year and low precipitations at least over the warmest and driest periods.

Orthocephalus funestus

Geographic distribution. For the analysis the localities from Russian Far East, Japan, Korea, northeastern and northern China were used, and this area covers almost entire known distribution of *O. funestus*, except for Mongolia (Fig 2A).

Both models predict suitable conditions from southeastern China (23°N) in the south to the border between Khabarovsk Kray and Magadan Province, Russia (57-58°N) in the north. Both models cover Japan, Sakhalin Island and south of Kamchatka Peninsula. The CR model is more restricted in the east and suitable conditions extend up to 131-135°E in Russia (north of Khabarovsk Kray) and northern China (Heilongjiang Province) and up to 110°E in southeastern China (Hubei Province), whereas the CF model predicts suitable conditions up to 124°E in Russia (west of Amur Province) and 103°E in southeastern China (Sichuan Province). Both models predict large areas of suitable conditions in the European part of Russia and small patches in other Palearctic regions (Figs 4A, 6A).

Climatic variables. In both models isothermality (bio3) has both PC and PI high. Annual mean temperature (bio1) and precipitation of wettest and warmest quarters (bio16, bio18) also significantly contribute to the CF model. In the CR model mean temperature of coldest month and warmest quarter (bio6, bio10), precipitation seasonality (bio15) and precipitation of driest quarter (bio17) are important. All the temperature related variables correlate with each other with PCor > 0.7, except for bio6, which significantly correlates with bio1 only (PCor = 0.85). Bio1 and bio 3 correlate with bio16 and bio18 with PCor ~0.7-0.8. Bio15 and bio17 correlate with PCor =0.77, bio16 and bio18 strongly correlate with PCor = 0.99.

The annual mean temperature (bio1), min temperature of coldest month (bio6), mean temperature of driest and coldest quarters (bio9, bio11) have lower margin shifted towards lower values in comparison to other species (Figs 7-9). Isothermality (bio3) is limited with the lower values in comparison to other species, whereas temperature seasonality (bio4) and temperature annual range (bio7) are shifted towards higher values than in many other species (Figs 7, 8). Many ranges of precipitation related variables are shifted towards higher values or have upper margins limited with the higher values in comparison to many other species, i.e. annual precipitation (bio12), precipitations of wettest and driest months, wettest, driest and warmest quarters (bio13, 14, 16, 17, 18) (Figs 9-11). Those ranges suggest that *O. funestus* has suitable areas in places with strong seasonality, the temperature in coldest and driest periods lower than in other species, and relatively high precipitation in all periods.

Orthocephalus proserpinae

Geographic distribution. In this analysis the localities from south European countries and North Africa (Fig. 2B) are used. All models estimate suitable conditions around the

Mediterranean Sea from Morocco and Portugal (9-13°W) in the west to Syria and Jordan (36-37°W) in the east, from Morocco or Western Sahara (22-27°N) in the south to southern France, northern Italy, Greece and Turkey in the north (40-42°N) (Figs 4B, 6B).

Climatic variables. In the CF and CR models temperature seasonality (bio4), precipitation of driest month and coldest quarter (bio14, bio19) are also important. Temperature annual range (bio7) and mean temperature of driest quarter (bio9) significantly contribute to the CF model. None of those variables significantly correlate with each other.

Isothermality (bio3) range is shifted towards higher ranges, whereas temperature seasonality (bio4) and temperature annual range (bio7) are limited by the relatively low values (Figs 7, 8). The values of min temperature of coldest month (bio6), mean temperature of driest and coldest quarters (bio9, bio11) are confined by the relatively high values (Figs 8, 9), whereas precipitation of driest month and driest quarters (bio14, bio17) are confined to relatively low values (Figs 10, 11). Those ranges show that *O. proserpinae* prefers places with low temperature changes over the year, high temperatures of the coldest and driest periods, and low precipitation over the driest season.

Orthocephalus saltator

Geographic distribution. In this analysis numerous localities from around Europe, European and Asian Russia, Caucasus, Turkey, Iran, Kazakhstan are used (Fig. 2C). All models cover most of the Western Palearctic from Morocco and Spain (8-9°W) in the west to Volga River and northern Iran in the east (52-55°E), from northern Africa (30-31°N) in the south to northern Sweden and White Sea (64-65°N) in the north. Both models also predict large areas of suitable conditions in southern Urals and Altai Mountains. The small patches of suitable conditions also occur in Central Asia and Norheast Asia (Figs 4C, 6C).

Climatic variables. The models are mostly explained by the temperature related variables, min temperature of coldest month (bio6) is important for both models, and mean annual temperature (bio1) is important for the CF models, and those two variables strongly correlate with each other (PCor = 0.97). The CF model is also explained by the temperature annual range (bio7) and mean temperature of coldest quarter (bio11), which also strongly correlate with each other, as well as with bio1 and bio6 (PCor > 0.8 or PCor < -0.8). In the CF model precipitation of coldest quarter is important (bio19), which significantly correlates with bio6 and bio7 (PCor ~ 0.7-0.8).

Variable ranges for *O. saltator* do not show any noticeable peculiarities in comparison to most of the other species.

Orthocephalus vittipennis

Geographic distribution. In the current analysis the records from the Eastern and Middle Europe (Czech Republick, Poland) in the west to Yakutia in the east, from Finland and Karelia in the south to Balkans, Iran, Caucasus, and Turkmenistan in the south are used (Fig 2D).

The models predict suitable conditions from Spain to Japan. In the eastern Palearctic the models predict suitable conditions up to southern Europe, excluding most part of Mediterranean region, and northern Iran (38-39°N) in the south. In the north the models extend up to the northern Scandinavia and Kola Peninsula (65-69°N). In eastern Palearctic the models predict suitable conditions up to 62-64°N in the north, and up to Tajikistan and Kyrgyzstan (38-39°N) and south China (26-27°N) in the south.

Climatic variables. In both models mean temperature of driest quarter (bio9) significantly contributes. Annual temperature range (bio1) and mean temperature of coldest quarter (bio11) additionally significantly contribute to the CF model. Mean diurnal range (bio2), annual temperature range (bio7), precipitation of wettest and warmest quarters (bio16, bio18) are important for the CR model. All temperature related variables significantly or strongly correlate with each other (PCor = 0.7-1), except for bio2. Bio16 significantly correlates with bio18 (PCor = 0.76).

The variable ranges for mean annual temperature (bio1), mean temperature of coldest month (bio6), mean temperature of driest and coldest quarters (bio9, bio11) are limited by the values lower than in many other species (Figs 7, 8). Isothermality (bio3) reaches the lower values in comparison with many other species (Fig. 7), and temperature seasonality (bio4) and temperature annual range (bio7) reach the highest values among all species. The upper margin of the precipitation of coldest quarter (bio19) is limited by the relatively low values. Harsh conditions with extreme seasons and very low temperatures over winter can be suitable for *O. vittipennis*.

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 high ($I > 0.8$, $D > 0.5$). 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*, as well as between *O. brevis* and *O. vittipennis* (I > 0.9 , D > 0.6). However, identity test shows that those values do not 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. 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 model and statistic 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. 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 for the 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.

Comparison of the variables for the species with similar environmental niches

Widely distributed species. 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. All widespread species are different in other variables, explaining their distribution.

The ranges of the variable values show that both, temperature and precipitation might be important in characterizing the climatic niches for those 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 the warmer temperatures over the summer.

The models of *O. coriaceus* are more similar than random with all the models of widespread species. 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, 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. The models of *O. coriaceus* are most similar to those of *O. brevis* and *O. saltator*, which also occupy almost entire Europe. Precipitation of driest month (bio14) significantly contributes to both models for *O. brevis* and *O. coriaceus*. 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 driest quarter (bio17) (Fig. 10, 11). The models of *O. coriaceus* differ from *O. saltator* in the upper margin of the precipitation of driest month and quarter (bio14, bio17) range limited with higher values (Figs 10, 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 widepspread 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 of 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, but the variables contributing to their models are different. However, for both species in at least one model the summer temperature related variables (bio5, bio9) are important. Precipitation over wettest or coldest quarters (bio16 and bio19) significantly contribute to the models of both species. They have also similar ranges for isothermality (bio3) and temperature seasonality (bio4), as well as higher temperatures of driest and coldest periods (boi6, bio9, bio11), and lower precipitations over the driest and warmest periods (bio14, bio17, bio18). 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 (bio2, bio4) (Fig. 7) and precipitation of driest month (bio14) (Fig. 10).

Discussion

Trans-Palearctic distribution and environmental niches. The maps with records show that the distribution of *O. bivittatus* is mostly centered on Central Asia and south of European Russia. *Orthocephalus saltator* and *O. brevis* are more common in Western Palearctic, and *O. vittipennis* is more abundant in European Russia and Central Asia, spanning from Europe through Eastern Siberia and Central Asia to Western Siberia (Figs 1-2). Numerous expeditions have been performed to 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, Russian Academy of Sciences (Konstantinov & Namyatova, 2019). Although many records from European countries were excluded (see Methods), this region is still well represented in the current analysis. Therefore, it is likely, that the recorded distribution for *Orthocephalus* species somewhat reflects the real distribution.

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, 5A). *Orthocephalus brevis* and *O. saltator* are more similar, having largest area of suitable conditions in Western Palearctic, however, the geographic projections of their environmental niches does 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. The Mediterranean area is not suitable for this species either. Those differences in the areas of suitable conditions are also supported by the comparisons of climatic variable ranges (see Results section for the details). Finally, the differences in the environmental niches are also supported by the identity tests and comparisons of climatic variable ranges. 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.

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 of 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, and the phylogeohraphy 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. 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, ~~most~~ probably, belong to the “Continental” group. However, *O. saltator* has highly suitable climatic conditions in the Mediterranean region and might have center of dispersal there.

The 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 is 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.

Comparison of environmental niches between closely related Orthocephalus species. The results support the previous works, which showed that the environmental niches in closely related species might be similar, but not identical (e.g. Wellenreuther et al. 2012, López-Alvarez et al. 2015, Dellacour et al. 2016).

Although, a morphology-based phylogeny for *Orthocephalus* has been published (Namyatova & Konstantinov 2009), there are many unresolved clades, and, therefore, it cannot serve to analyze the phylogenetic signal of the climatic variables and environmental niches. However, a few conclusions still can be reached. According to this phylogeny, *Orthocephalus 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, we can hypothesize that there are at least two 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. 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. We found that climatic niches are very similar in *Orthocephalus brevis* and *O. saltator*, as well as *O. brevis* and *O. vittipennis*, and those pairs are not closely related. However, the robust molecular-based phylogeny is needed to test these hypotheses.

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 tough competition with its sister species.

Comparison of the Orthocephalus species environmental niches with those of other Palearctic species

The environmental niche modelling for Palearctic insect species is mostly regional (e.g. for Spain, Iran, Turkey), and only handful of papers exist with the modelling performed for the entire Europe and even less for the entire Palearctic (e.g. Sánchez-GarcÍa et al, 2013; Dellicour et al., 2014; Toth et al., 2013; Ataeva et al., 2019). No such work has been found covering entire Northeast Asia. The environmental niche, estimated for *O. brevis*, is similar to some of *Bombus* Latreille, 1802 (Dellicour et al., 2014) species and the beetle *Pterostichus oblongopunctatus* (Fabricius, 1787) (Ataeva et al. 2019). In the case of *P. oblongopunctatus*, annual mean temperature (bio1) and precipitation of driest month (bio14) are important for the distribution explanation, which contributes significantly to the model for *O. brevis* as well. The geographic projection of the environmental niche for *O. proserpinae*, covering only Mediterranean zones, is very similar to that of the beetle *Tomicus distruens* (Wollaston, 1865) (Sánchez-GarcÍa et al., 2013). However, I avoid reaching any conclusions on climatic niche comparisons of species from different insect groupings pending further research.

Conclusions

The study on the climatic niche modelling for four *Orthocephalus* species with trans-Palearctic distribution (*O. bivittatus*, *O. brevis*, *O. saltator*, *O. funestus*) has demonstrated that in all cases the niches are more similar to each other than what would be expected from a random dataset, but are not identical. Geographic projections of the models, climatic variables contributing to the models, and the modelled climatic variable ranges show that each of those species demonstrate a different climatic niche. The niches of the trans-paleartic species are also similar to two species having more limited distribution (*O. coriaceus*, *O. funestus*). More studies of species distributed in the Palearctic are needed to better understand the types of possible climatic niches of widespread species and the main climatic variables shaping the distribution of those taxa.

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Table 1(on next page)

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 raw.

Table 1:

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	bivittatus		*brevis*		*coriaceus*		*fulvipes*		*funestus*		*proserpinae*		*saltator*		*vittipennis*	
Bio1	PC PI	PC PI	PC PI	PC PI	X		X		PI		X		PI		PC PI	X
Bio2	PI		X		X	X	X		X	X	X		X	X	X	PC
Bio3	PI	X	X		PC PI	PC PI	X		PC PI	PC PI	X		X	X	X	X
Bio4	PI	X	X		X		X		X		PI	PC PI	X	X	X	
Bio5	X		X	X	X		X	X	X		X		X	X	X	
Bio6	X		X		X		X	PI	X	PC PI	X		PI	PC PI	X	
Bio7	PI		X		X		X		X		PC PI	X	PI		X	PC PI
Bio8	X	X	X		X		X		X		X		X	X	X	X
Bio9	X	PC	X	X	X		PC PI		X		PC PI		X	X	PC	PI
Bio10	X	PC	X		X		X		X	PC	X		X		X	X
Bio11	PC		X		PI		X		X		X		PC		PI	
Bio12	X		X	X	X		X		X		X		X	X	X	
Bio13	X	X	X	X	X		X		X		X		X	X	X	
Bio14	X	X	PC PI	PC PI	PC	PC	X		X		PC	PC	X	X	X	X
Bio15	PC	PC	X	PI	PI		X		X	PC PI	X	X	X	X	X	X
Bio16	X		X		X	PI	X	PC PI	PI		X		X		X	PC
Bio17	X		X		X		X		X	PC PI	X		X		X	
Bio18	X	PC PI	X	X	X	X	PC PI	PC PI	PC		X		X	X	X	PC PI
Bio19	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

Table 2(on next page)

Table 2.

Niche overlap, identity test and background test results. For the background test, the first value corresponds to the analysis with the records of the first species in the pair tested against the second species background, and the second value corresponds to the reverse analysis.

Table 2:

Niche overlap, identity test and background test results. For the background test, the first value corresponds to the analysis with the records of the first species in the pair tested against the second species background, and the second value corresponds to the reverse analysis.

	I (CF models)	I (CR models)	Background test I values	**5% threshold for permuted I values (climatic variables only)**	**5% threshold for permuted I values (climatic variables and biomes)**	D (CF models)	D (CR models)	Background test D values	**5% threshold for permuted D values (climatic variables only)**	**5% threshold for permuted D values (climatic variables and biomes)**
bivittatus vs brevis	0.802	0.815	0.623 0.615	0.96	0.953	0.549	0.555	0.330 0.336	0.824	0.801
bivittatus vs coriaceus	0.7	0.628	0.626 0.536	0.928	0.923	0.39	0.326	0.334 0.257	0.735	0.729
bivittatus vs fulvipes	0.42	0.614	0.626 0.397	0.9	0.886	0.19	0.318	0.333 0.168	0.66	0.651
bivittatus vs funestus	0.504	0.649	0.634 0.433	0.95	0.943	0.28	0.373	0.34 0.204	0.78	0.762
bivittatus vs proserpinae	0.324	0.375	0.619 0.285	0.953	0.886	0.141	0.174	0.327 0.106	0.776	0.654
bivittatus vs saltator	0.854	0.83	0.622 0.613	0.968	0.966	0.593	0.575	0.329 0.337	0.838	0.83
bivittatus vs vittipennis	0.812	0.748	0.619 0.694	0.97	0.965	0.56	0.479	0.327 0.404	0.835	0.82
brevis vs coriaceus	0.836	0.798	0.608 0.540	0.902	0.895	0.522	0.485	0.332 0.259	0.69	0.676
brevis vs fulvipes	0.271	0.651	0.597 0.398	0.847	0.855	0.08	0.366	0.323 0.168	0.623	0.633
brevis vs funestus	0.79	0.814	0.614 0.439	0.94	0.936	0.505	0.539	0.335 0.208	0.78	0.757
brevis vs proserpinae	0.376	0.416	0.603 0.293	0.862	0.876	0.158	0.186	0.328 0.11	0.636	0.649

brevis vs saltator	0.905	0.929	0.615 0.618	0.961	0.957	0.724	0.758	0.335 0.342	0.818	0.81
brevis vs vittipennis	0.912	0.867	0.612 0.694	0.96	0.96	0.677	0.618	0.332 0.404	0.823	0.813
coriaceus vs fulvipes	0.397	0.697	0.522 0.382	0.87	0.851	0.169	0.378	0.248 0.161	0.633	0.59
coriaceus vs funestus	0.493	0.473	0.538 0.436	0.906	0.89	0.236	0.21	0.258 0.208	0.689	0.676
coriaceus vs proserpinae	0.533	0.579	0.526 0.287	0.863	0.849	0.276	0.292	0.251 0.108	0.625	0.602
coriaceus vs saltator	0.854	0.833	0.538 0.621	0.915	0.914	0.57	0.538	0.257 0.347	0.723	0.714
coriaceus vs vittipennis	0.723	0.723	0.531 0.699	0.930	0.925	0.41	0.389	0.253 0.411	0.748	0.735
fulvipes vs funestus	0.105	0.532	0.394 0.418	0.846	0.74	0.223	0.267	0.167 0.195	0.602	0.469
fulvipes vs proserpinae	0.76	0.711	0.397 0.282	0.841	0.844	0.484	0.267	0.168 0.104	0.593	0.554
fulvipes vs saltator	0.444	0.679	0.394 0.596	0.875	0.865	0.22	0.4	0.167 0.326	0.664	0.634
fulvipes vs vittipennis	0.274	0.651	0.386 0.687	0.882	0.857	0.09	0.337	0.161 0.4	0.662	0.627
funestus vs proserpinae	0.181	0.231	0.417 0.292	0.824	0.776	0.062	0.076	0.195 0.109	0.564	0.487
funestus vs saltator	0.646	0.713	0.435 0.618	0.951	0.945	0.366	0.431	0.206 0.343	0.791	0.780
funestus vs vittipennis	0.749	0.828	0.435 0.692	0.952	0.951	0.467	0.552	0.206 0.402	0.793	0.788
proserpinae vs saltator	0.493	0.533	0.296 0.604	0.867	0.866	0.253	0.261	0.11 0.331	0.627	0.628
proserpinae vs vittipennis	0.320	0.397	0.296 0.685	0.877	0.861	0.129	0.173	0.111 0.397	0.662	0.649
Saltator vs vittipenis	0.846	0.819	0.613 0.693	0.97	0.967	0.599	0.573	0.338 0.403	0.84	0.833

Figure 1

Figure 1.

Maps of records used in the analysis. A. *O. bivittatus*, B. *O. brevis*, C. *O. coriaceus*, D. *O. fulvipes*.

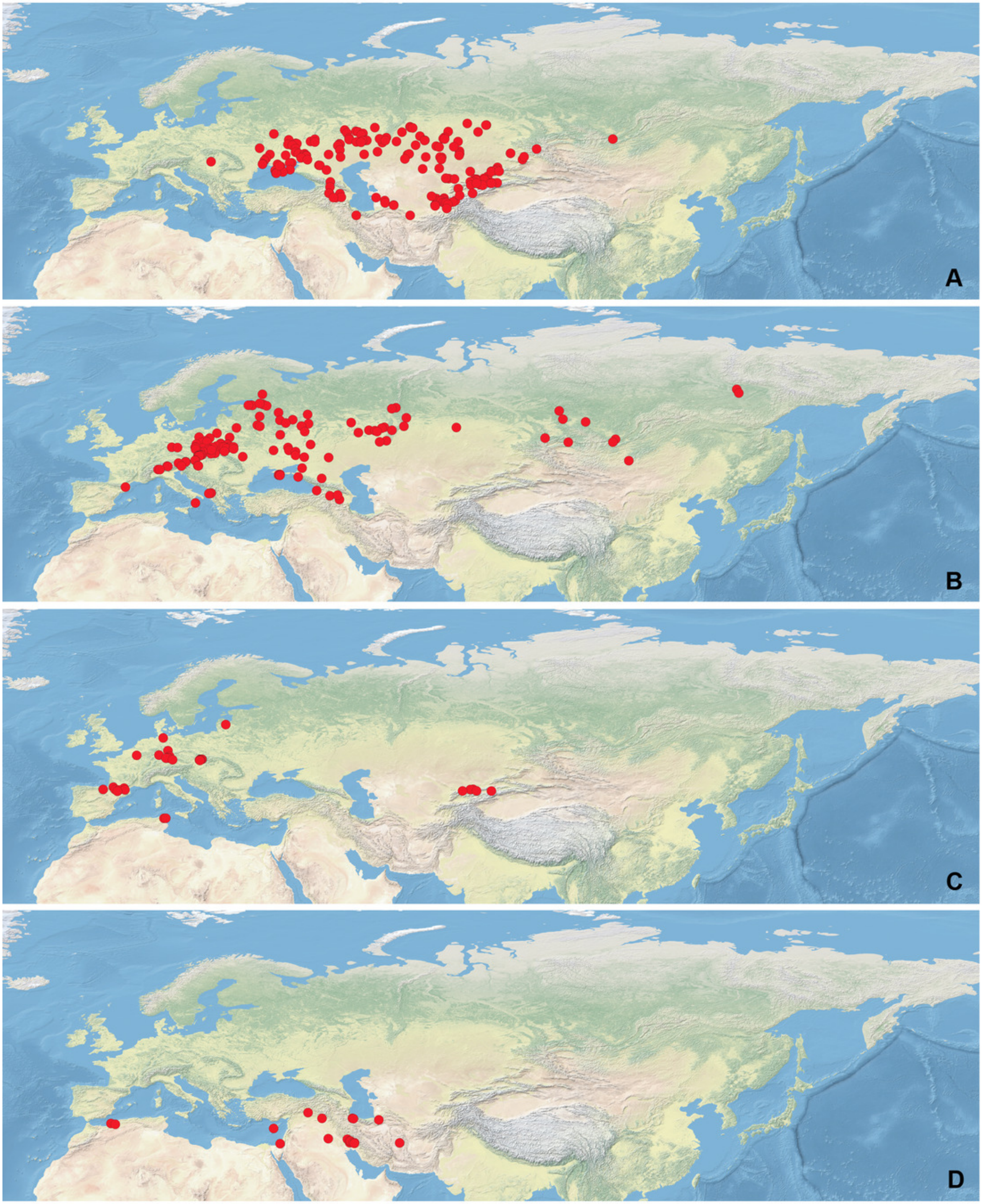

A
B
C
D

Figure 2

Figure 2.

Maps of records used in the analysis. A. *O. funestus*, B. *O. proserpinae*, C. *O. saltator,* D. *O. vittipennis*.

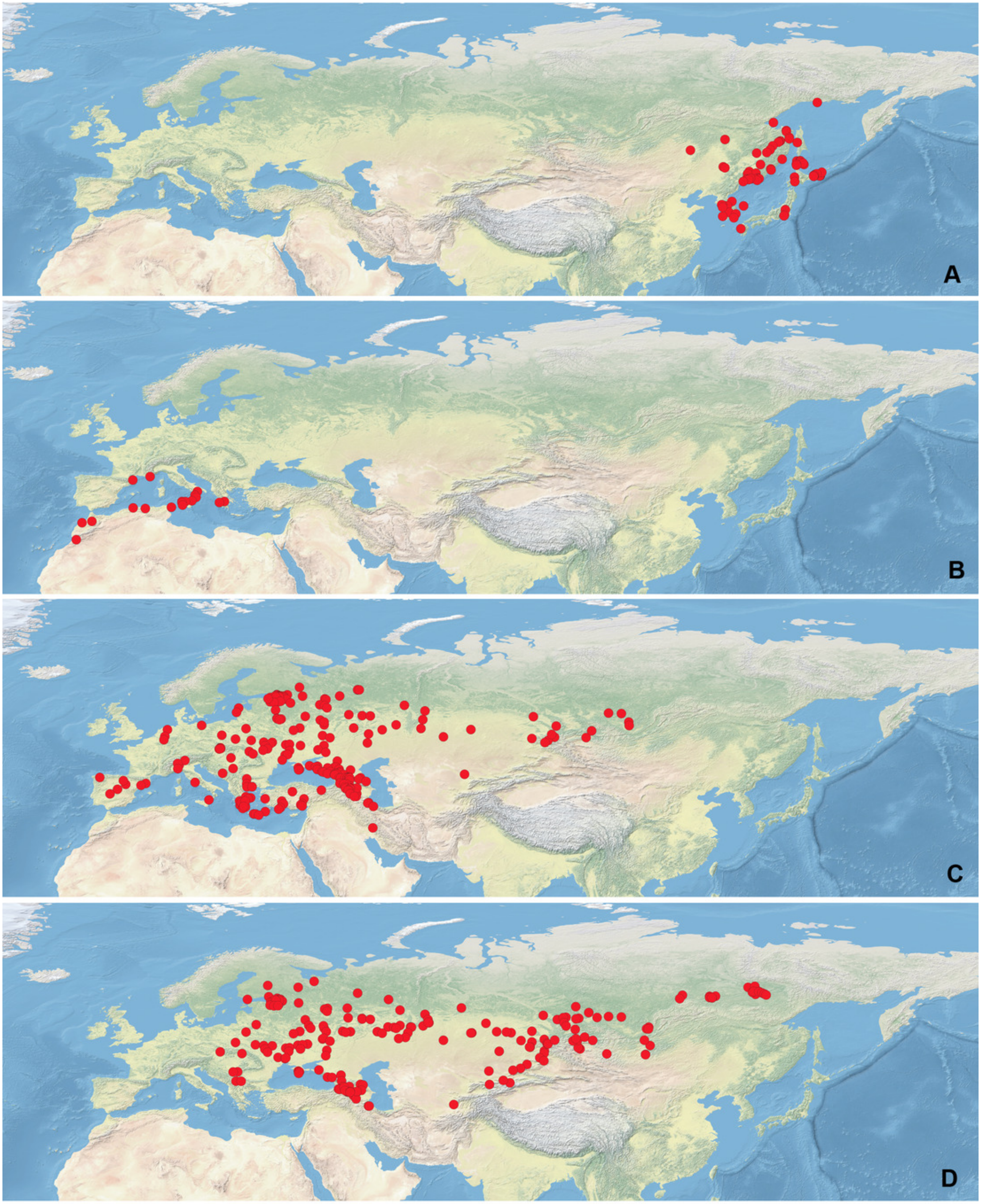

A
B
C
D

Figure 3

Figure 3.

Geographical projections of the CF model for A. *O. bivittatus*, B. *O. brevis*, C. *O. coriaceus*, D. *O. fulvipes*.

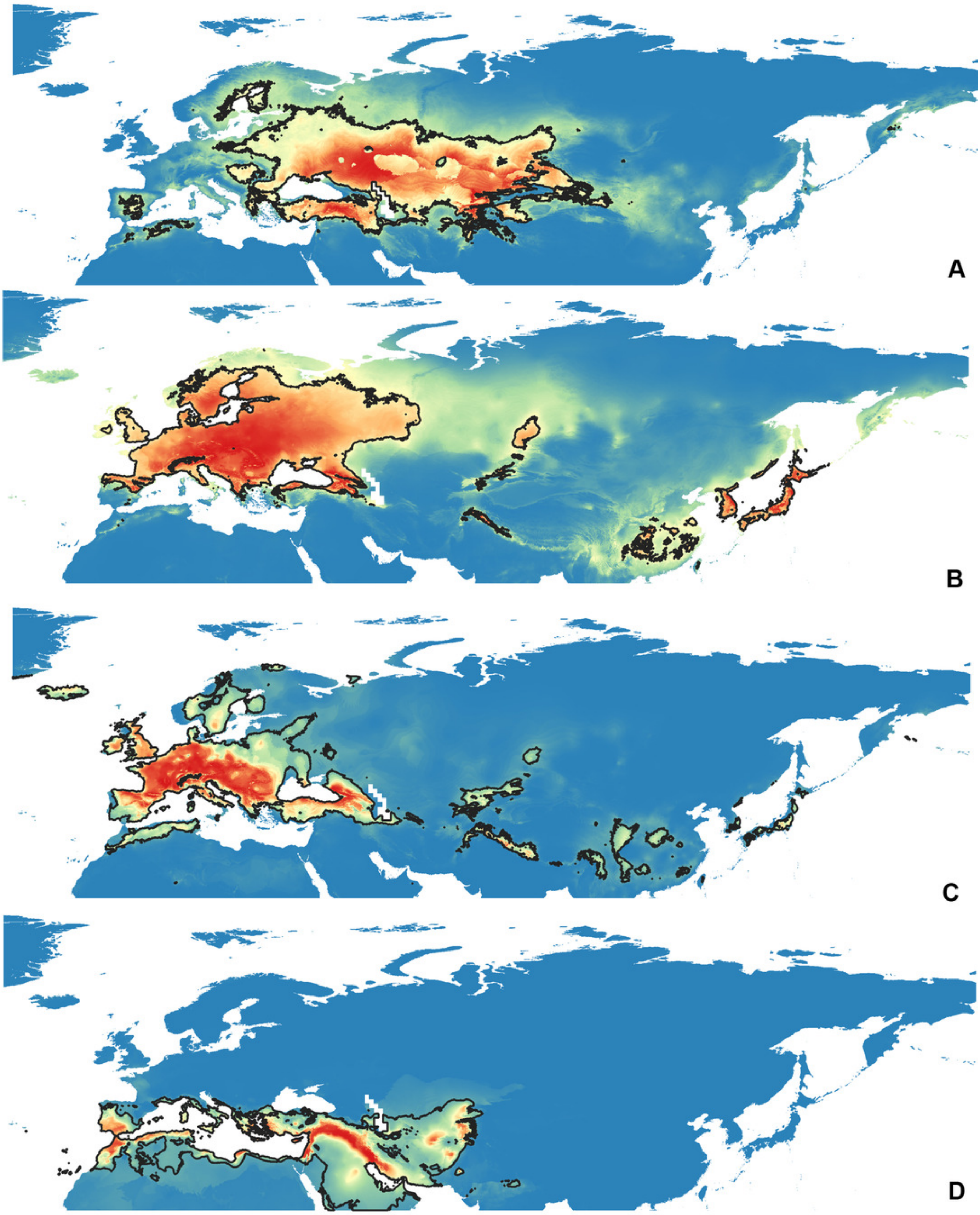

A
B
C
D

Figure 4

Figure 4.

Geographical projections of the CR model for A. *O. bivittatus*, B. *O. brevis*, C. *O. coriaceus*, D. *O. fulvipes*. Threshold is indicated with the black line.

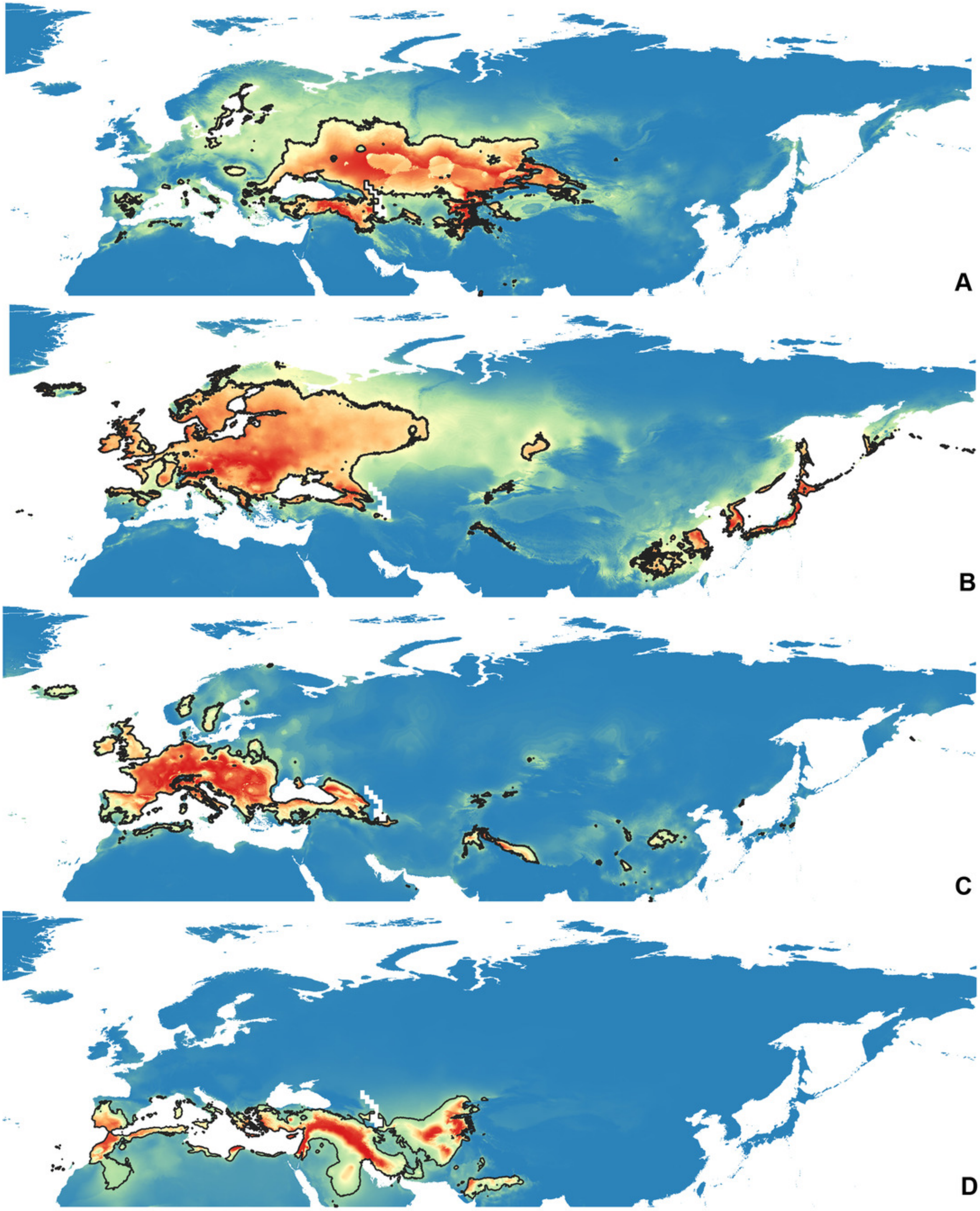

A
B
C
D

Figure 5

Figure 5.

Geographical projections of the CF models for A. *O. funestus*, B. *O. proserpinae*, C. *O. saltator,* D. *O. vittipennis*. Threshold is indicated with the black line.

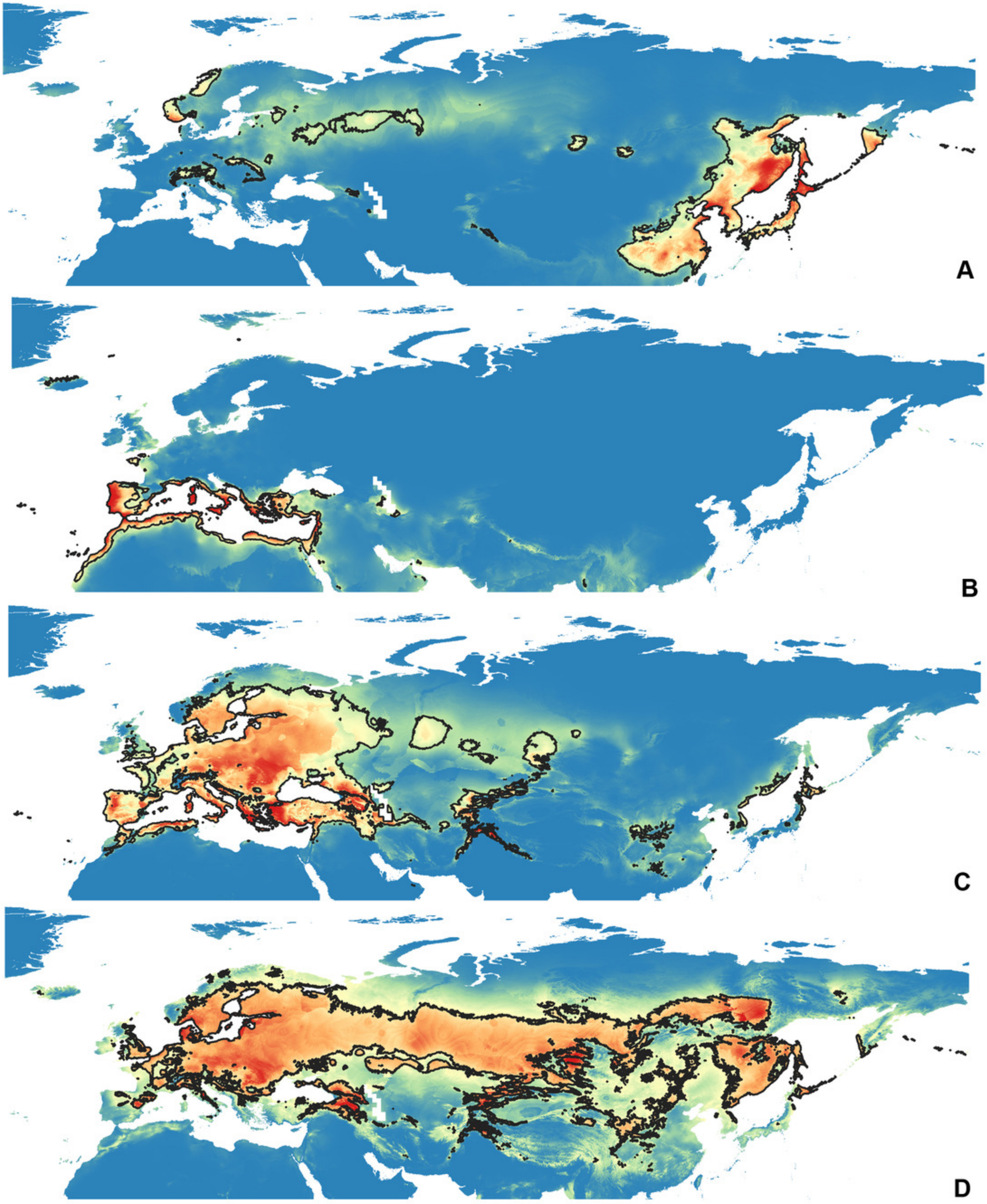

A
B
C
D

Figure 6

Figure 6.

Geographical projections of the CR models for O. A. *O. funestus*, B. *O. proserpinae*, C. *O. saltator,* D. *O. vittipennis*. Threshold is indicated with the black line.

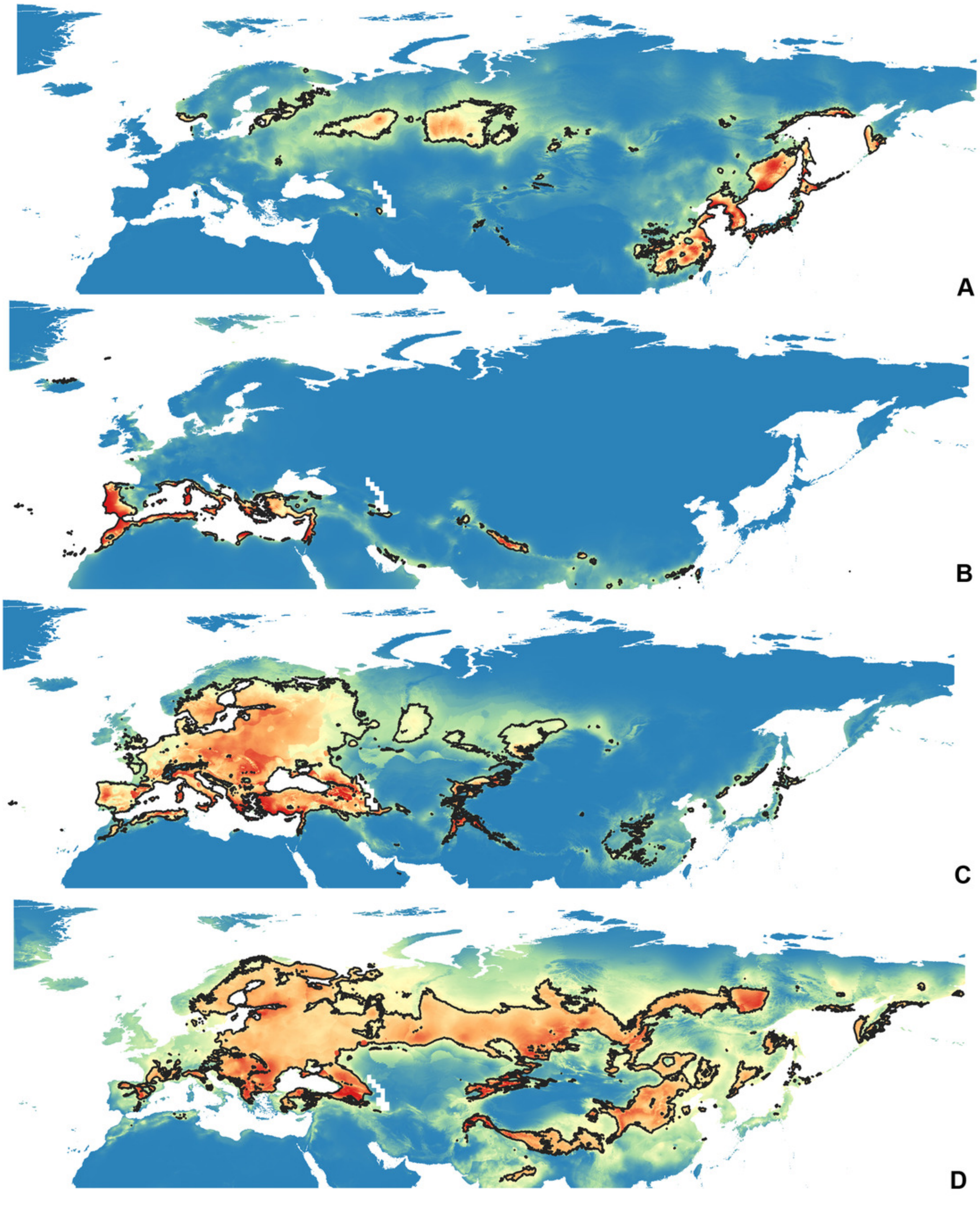

A
B
C
D

Figure 7

Figure 7.

The ranges of bio1, bio2, bio3, and 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.

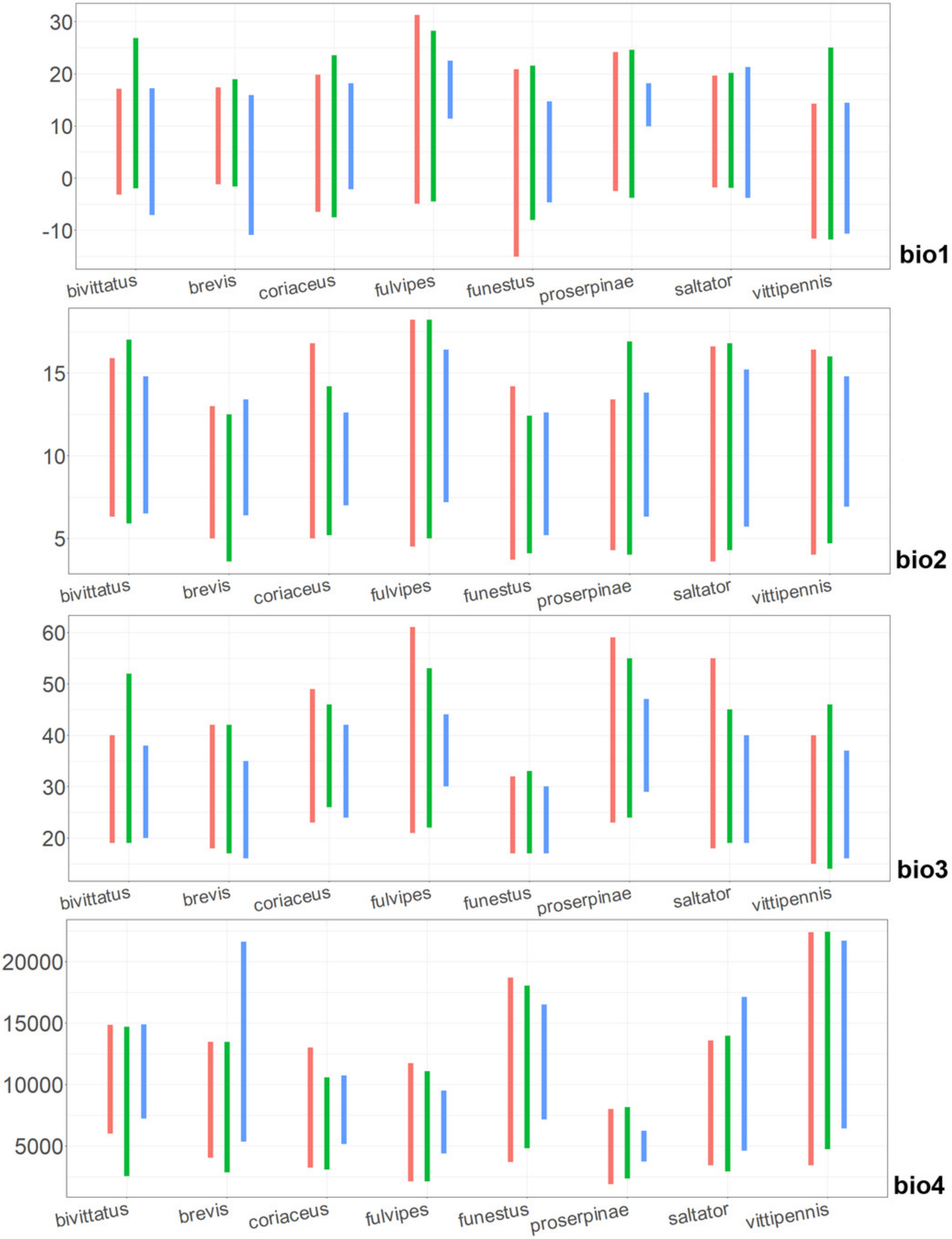

30
20
10
0
-10
bio1
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
15
10
5
bio2
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
60
50
40
30
20
bio3
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
20000
15000
10000
5000
bio4
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis

Figure 8

Figure 8.

The ranges of bio5, bio6, bio7, and 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.

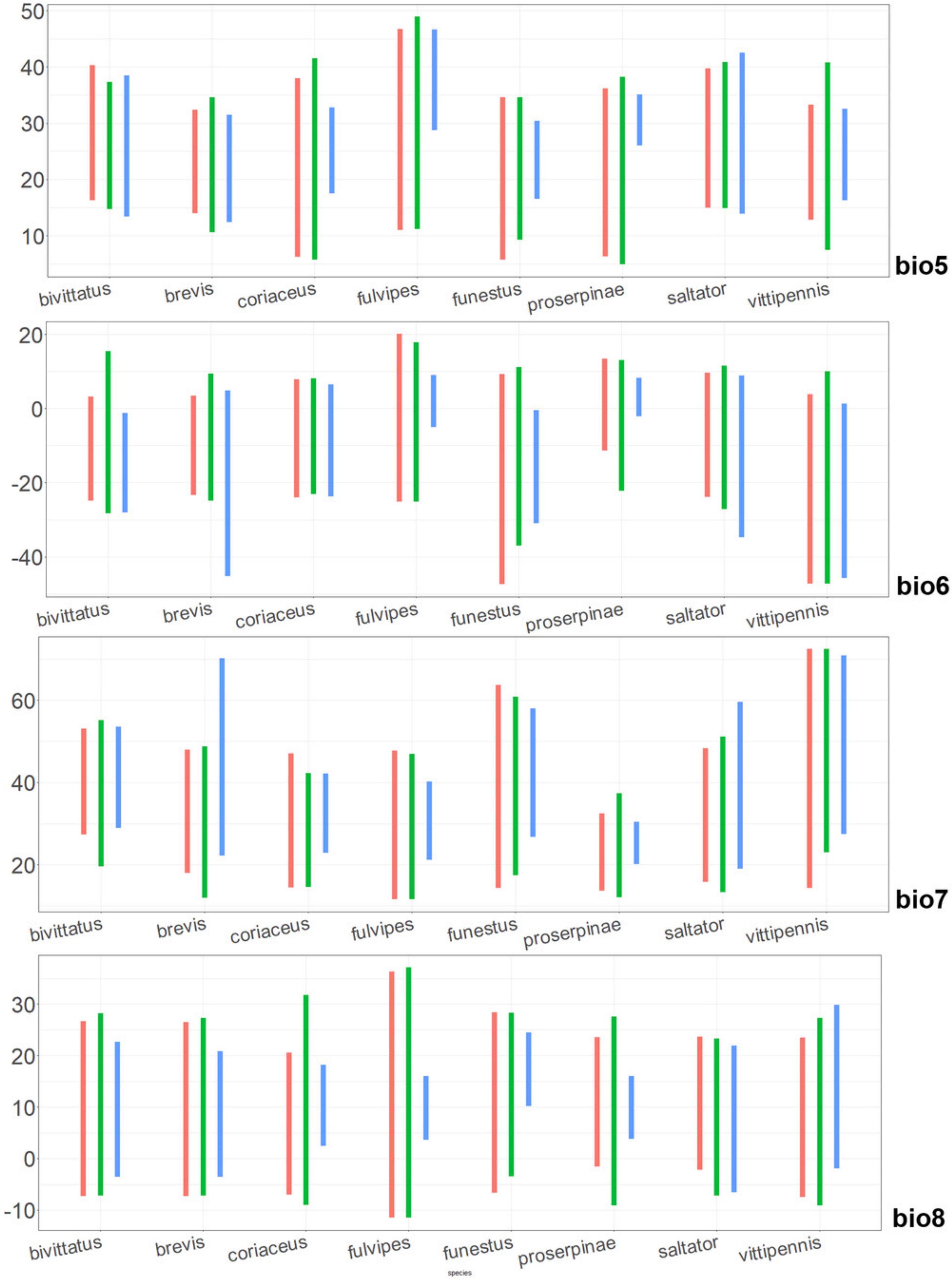

50
40
30
20
10
bio5
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
20
0
-20
-40
bio6
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
60
40
20
bio7
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
30
20
10
0
-10
bio8
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
species

Figure 9

Figure 9.

The ranges of bio9, bio10, bio11, and 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.

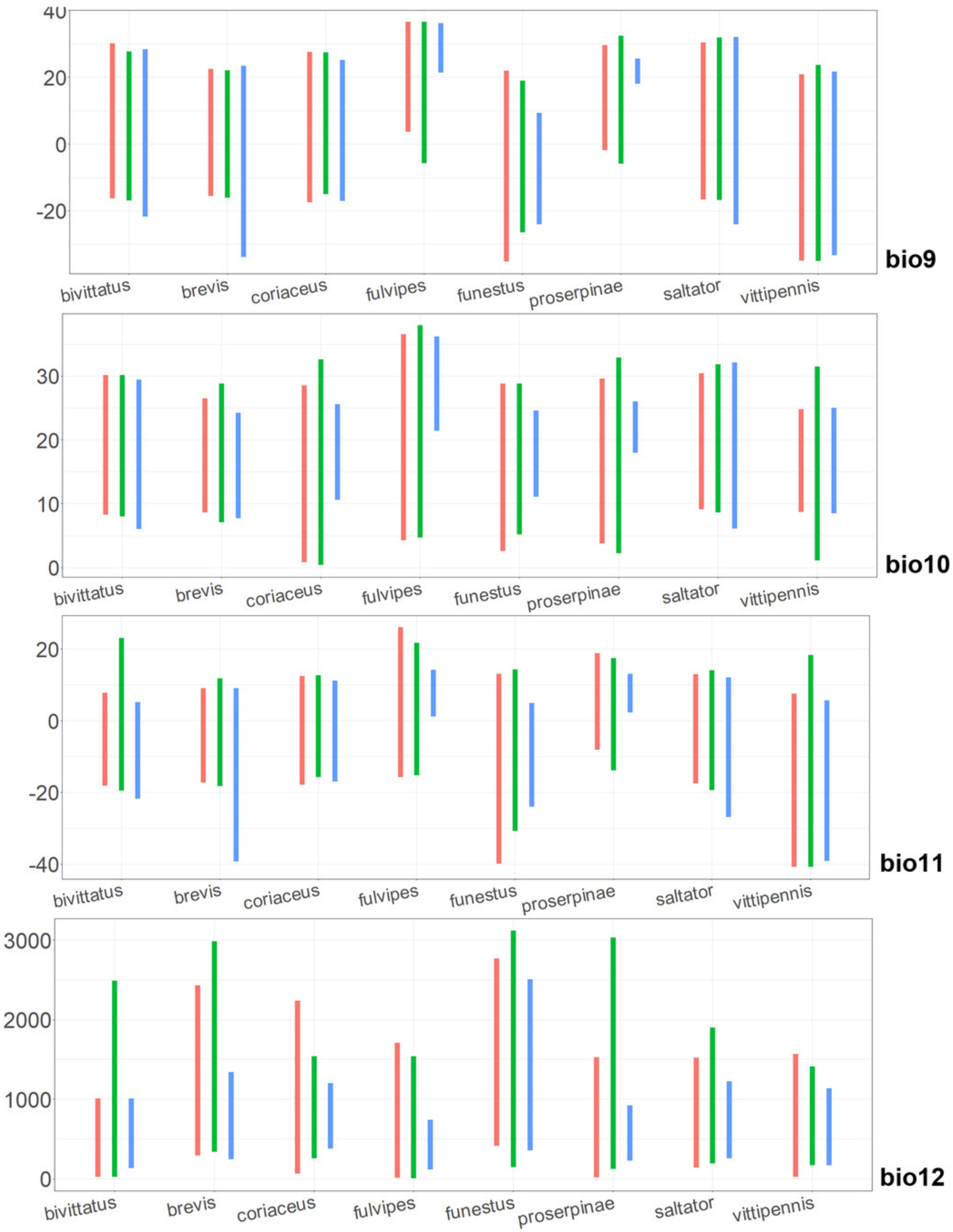

40
20
0
-20
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
bio9
30
20
10
0
bio10
20
0
-20
-40
bio11
3000
2000
1000
0
bio12

Figure 10

Figure 10.

The ranges of bio13, bio14, bio15, and 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.

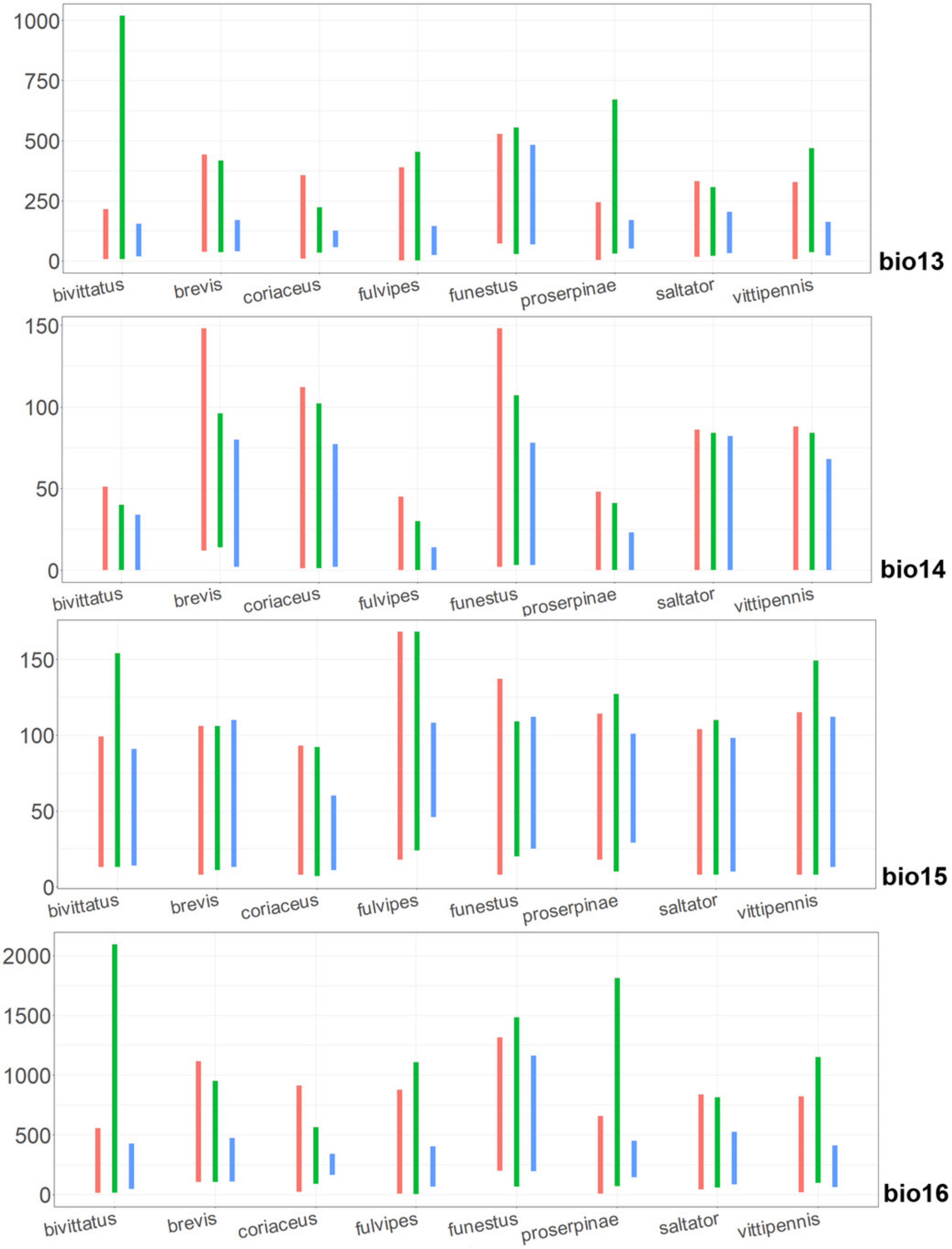
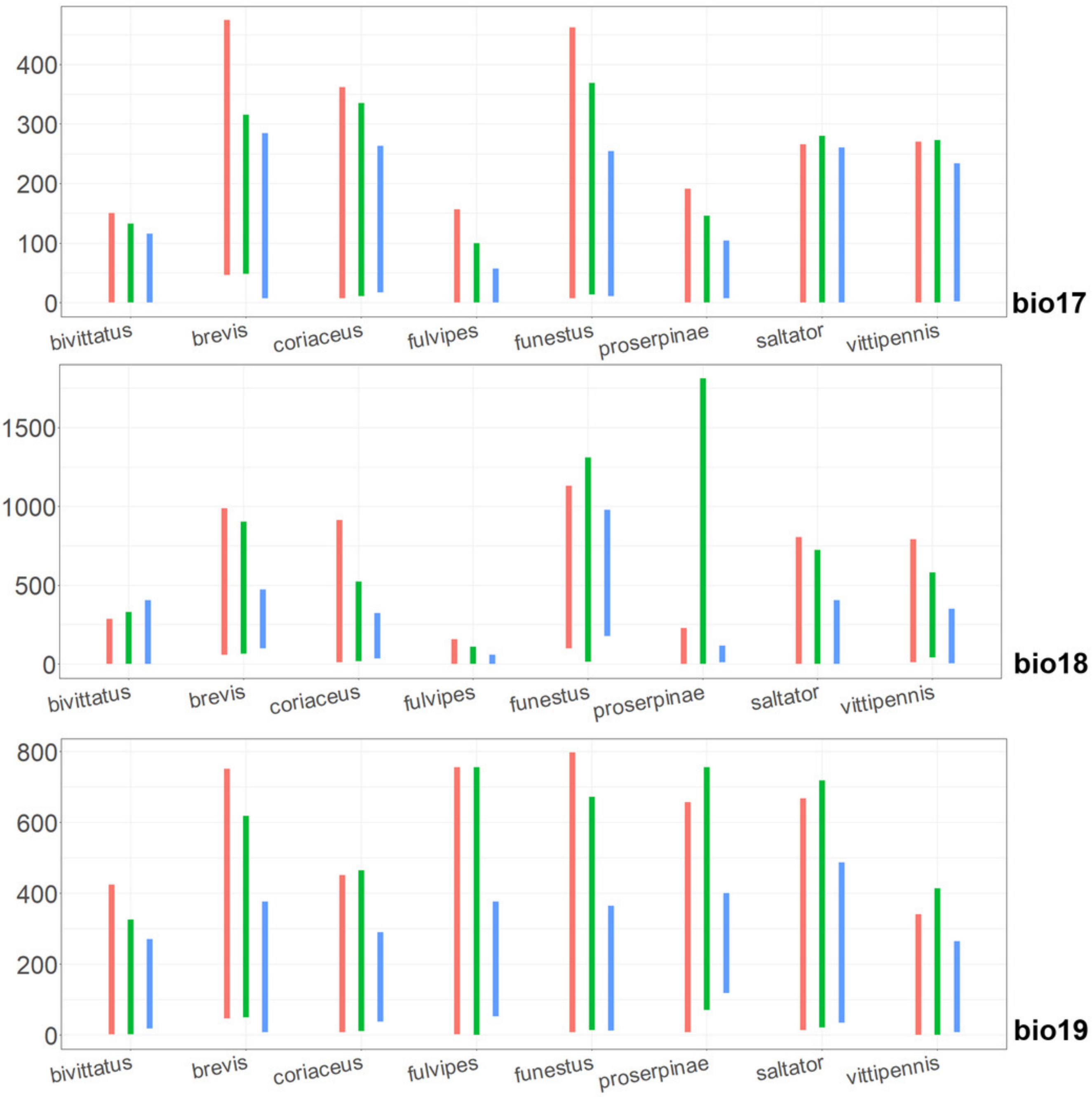

1000
750
500
250
0
bio13
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
150
100
50
0
bio14
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
150
100
50
0
bio15
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
2000
1500
1000
500
0
bio16
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis

Figure 11

Figure 11.

The ranges of bio17, bio18, 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.


400
300
200
100
0
bio17
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
1500
1000
500
0
bio18
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis
800
600
400
200
0
bio19
bivittatus
brevis
coriaceus
fulvipes
funestus
proserpinae
saltator
vittipennis