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

Anna A Namyatova [Corresp. 1, 2]

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

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

Corresponding Author: Anna A Namyatova
Email address: anna.namyatova@zin.ru

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: Orthotylinae). 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. funesuts*, *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.

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4 Anna A. Namyatova[1,2]

6 [1] Laboratory of Phytosanitary Diagnostics and Forecasts, All-Russian Institute of Plant
7 Protection, Pushkin-Saint Petersburg, Russia
8 [2] Laboratory of Insect Taxonomy, Zoological Institute, Russian Academy of Sciences, Saint
9 Petersburg, Russia

11 Corresponding Author:
12 Anna A. Namyatova
13 Universitetskaya emb. 1, Saint Petersburg, 199034, Russia
14 Email address: anna.namyatova@zin.ru

Abstract

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

Introduction

35 Environmental niches are important characteristics of species. Studying them can help to

36 identify the environmental factors responsible for maximizing the species' fitness, and lead

37 to a better understanding of how environment is connected to speciation and how closely

38 related species are different in their ecological preferences. Studying climatic niches of

39 widespread species also can help to reveal the climatic variables, connected with the species

40 ability to adapt to different conditions.

41   The Palearctic spans thousands of kilometers across different biomes and climatic

42 zones. Species occupying large areas of Europe and Asia in this zoogeographic region are

43 called "trans-Palearctic" and are often treated as having the same type of distribution (e.g.

44 Abe et al. 2007, Hubenov 2008, Potikha 2015). However, the diversity of such distributions

45 and corresponding climatic niches has never been quantitatively studied.

46   Most investigations of environmental niche differences treated allopatric vertebrate

47 species (e.g. Losos et al., 2003; Graham et al., 2004; Kozak & Weins, 2006, 2010;

48 McCormack et al., 2010; Blair et al., 2013). There are only a few studies of ecological niche

49 similarities of sympatric species (e.g. Knouft et al., 2006; Wellenreuther et al., 2012; Lison

50 & Calvo, 2013; Mumladze, 2014; López-Alvarez et al., 2015; Dellacour et al., 2016), and

51 even fewer on insects (Wellenreuther et al., 2012; Dellacour et al., 2016). Many studies show

52 that closely related sympatric species are different in their ecological niches (Wellenreuther

53 et al., 2012; Mumladze, 2014; Aguirre-Gutierrez, 2015; López-Alvarez et al., 2015;

54 Dellacour et al., 2017). However, only a few such works treat Palearctic insects (e.g.

55 Wellenreuther et al., 2012; Dellacour et al., 2016; Avtaeva et al., 2019), and such works on

56 the trans-Palearctic insects are very rare (e.g. Avataeva et al., 2019). Knowledge on climatic

57 niches is also a prerequisite for studying the influence of climate on speciation, i.e. testing

58 niche conservatism vs niche diversification hypotheses (e.g. Losos et al. 2003; Kozak &

59 Weins, 2006). Therefore, it is essential to study climatic niches of the species widespread in

60 Palearctic to understand the factors connected with such a wide distribution and how those

61 factors relate to the phylogenetic history.

62   This current project describes the climatic niches and reveals their differences for

63 closely related species of the Palearctic genus *Orthocephalus* Fieber, 1858 (Insecta:

64 Heteroptera: Miridae: Orthotylinae). These species inhabit meadows and dry open areas,

65 utilizing numerous species of Asteraceae, where at least the widely distributed taxa are likely

66 to be polyphagous. *Orthocephalus* has been revised (Namyatova & Konstantinov, 2009), and

67 a morphology-based phylogeny supported its monophyly. Currently *Orthocephalus* includes

68 23 species, with *O. bivittatus* Fieber, 1864, *O. brevis* (Panzer, 1798), *O. saltator* (Hahn,

69 1835), and *O. vittipennis* (Herrich-Shaeffer, 1835) widely distributed in Europe and Asia

70 (Namyatova & Konstantinov 2009). This allows us to test whether the closely related species

71 with wide distribution in the Palearctic occupy the same climatic niche, or whether their

72 niches are significantly different.

73 Most of the *Orthocephalus* species have a low number (<15) of records, except for

74 *O. coriaceus* (Fabricius, 1777), *O. fulvipes* Reuter, 1904, *O. funestus* Jakovlev, 1881, and *O.*

75 *proserpinae* (Mulsant & Rey, 1852). The records of these species have also been used to

76 build the climatic niches to find the factors influencing their distribution and compare them

77 to those of the widely distributed species. Those niches will also allow testing whether the

78 climatic niches of the species with trans-Palearctic distribution are more similar with each

79 other than with those of the species having limited distribution. Comparisons of climatic

80 niches of the *Orthocephalus* species will be the first step in answering the question, whether

81 the niche conservatism or niche divergence or both can relate to speciation in this genus.

82 The aims of the current work are to: (1) compare the niches of widely distributed

83 species with each other and with those of species with limited distribution to determine the

84 main climatic variables responsible for the trans-Palearctic distribution and limited

85 distribution; (2) to test whether the trans-Palearctic species are significantly similar and

86 whether they are more similar to each other or to the species with a limited distribution; and

87 (3) to draw conclusions on the presence of the niche conservatism or niche divergence

88 processes in speciation within *Orthocephalus*, based on the phylogeny, provided in

89 Namyatova and Konstantinov (2009).

90

91 **Materials & Methods**

92 ***Specimens and localities sources***. Eight species (and number of unique records) have been

93 analyzed in this work *Orthocephalus bivittatus* (171), *O. brevis* (146), *O. coriaceus* (39), *O.*

94 *fulvipes* (18), *O. funestus* (90), *O. proserpinae* (19), *O. saltator* (237), and *O. vittipennis* (208).

95 *Orthocephalus vittipennis* is recorded from Western Europe to eastern Yakutia, including

96 numerous records from Central Asia. The distributions of *O. saltator* and *O. brevis* are similar to

97 that of *O. vittipennis*, but among Central Asian countries, they are known only from Kazakhstan.

98 *Orthocephalus bivittatus* is not recoded from the northern Europe and eastern Siberia, however, is

99 common in Central Asia (Kerzhner & Josifov, 1999; Namyatova & Konstantinov, 2009).

100 *Orthocephalus coriaceus* is mostly known from the middle and northern Europe with few

101 specimens recorded from Kyrgyzstan. *Orthocephalus funestus* is known only from Northeast Asia.

102   *Orthocephalus proserpinae* and *O. fulvipes* inhabit the Mediterranean region, *O. fulvipes* is

103   additionally known from Arabian Peninsula and Iran (Kerzhner & Josifov, 1999; Namyatova &

104   Konstantinov, 2009). Numerous collecting expeditions have been taken in Central Asia, Mongolia,

105   Siberia, Russian Far East, European part of Russia by the Russian and Soviet entomologists, and

106   their collections are mainly preserved at the Zoological Institute of the Russian Academy of

107   Sciences (Konstantinov & Namyatova, 2019). Although many records from European countries

108   were excluded (see Methods), this region is still well represented in the current analysis. Therefore,

109   it is likely, that the known distribution for *Orthocephalus* species probably reflects the real

110   distribution.

111   Specimens used for this study are mostly preserved at the Zoological Institution of the

112   Russian Academy of Sciences, St Petersburg, Russia. This collection holds one of the largest

113   Palearctic collections of Heteroptera. The most label data for the *Orthocephalus* specimens are

114   recorded in the Arthropod Easy Capture database (https://research.amnh.org/pbi/locality/). Some

115   specimens are preserved at the Canadian National Collection of Insects, Agriculture and Agri-

116   Food Canada, Ottawa, Canada (CNC), Linnavuori Collection (LCRT), Matocq collection

117   (MATOCQ), Bavarian State Museum in Zoology, Munich, Germany (ZSM), National Museum of

118   Natural History, Paris, France (NMNH), Ribes Collection (JR), American Museum of Natural

119   History, New York, USA (AMNH), Natural History Museum, Geneva, Switzerland (MHNG),

120   Zoological Museum Amsterdam, Netherlands (ZMAN), Carapezza collection (AC), Finnish

121   Museum of Natural History, Helsinki, Finland (MZH), Institute for Biological Problems of

122   Cryolithozone, Yakutsk, Russia (YIB).The specimens have been identified based on the revision

123   of the genus *Orthocephalus* (Namyatova & Konstantinov, 2009). This revision corrected species

124   identification errors of previous keys (e.g. Kerzhner & Jachewski, 1964; Wagner & Weber, 1965;

125   Wagner, 1974) which were based on variable coloration and not male genitalia structure which

126   proved crucial for accurate determination of the species. To decrease number of erroneous records,

127   in most cases the localities from other papers have been added only if they cited the above-

128   mentioned revision (Kment & Baňař, 2012; Matocq et al., 2014; Heckmann, 2015; Sofronova,

129   2017; Vinokurov et al., 2017). All records from the literature have been added for *O. brevis* and

130   *O. funestus* (Ribes, 1989; Melber et al., 1991; Dioli, 1993; Gorczyca & Chłond, 2005; Arnold,

131   2008; Lim et al., 2011, 2012, 2013a, 2013b; Nikolaeva, 2011; Frieß, 2006, 2014; Roháčová, 2007;

132   Cho et al. 2008, 2011; Kondorosy, 2011; Park et al., 2013; Halimi & Paparisto, 2014; Shi et al.,

133   2016; Vinokurov, 2016; Gierlański, 2017; Jung et al., 2017; Kozminykh & Naumkin, 2017), as *O.*

134   *brevis* can be easily separated from congeners by its widened antennal segment II and *O. funestus*

135   inhabits Northeast Asia, and this is the only *Orthocephalus* species known from Northeast Asia

136   (Namyatova & Konstantinov, 2009). The maps with all records used in this study are provided on

137   Figs 1 and 2 and the list of those records for all species and specimen information are provided in

138   the Supplemental Data 1.

139   *Maps*. Layers in 5-arc minute (~10km) resolution representing different bioclimatic variables have

140   been downloaded from Worldclim, Version 1.4 (https://www.worldclim.org/version1). In general,

141   the finer resolution leads to more accurate predictions, as the data are averaged within the grid cell.

142   For this study coarser resolution was chosen for two reasons. First, it is a trade-off between the

143   high resolution data across large geographic space and computational efficiency, as there is only a

144   little difference between the models built using different scales especially in broadly distributed

145   species (e.g. Araújo et al., 2005; Seo et al., 2008). Seo et al. (2008) also has shown that with a

146   spatial grid size below 16×16km, there is a good agreement among model area estimated for

147   species of all range sizes. Second, the coordinates for many localities are approximate, and high

148   resolution might also lead to the erroneous interpretations (Graham et al. 2005; Hanberry et al.

149   2013). Layers have been trimmed for Palearctic (20°N - 90°N, -30°W - 180°E) and converted to

150   ASCII format in DIVA-GIS (https://www.diva-gis.org/). Those layers have been uploaded to

151   QGIS 3.10 and converted to vector and used to create "samples with data" files (swd files).

152   ***Environmental niche modelling***. Maxent software (version 3.4.1)

153   (https://biodiversityinformatics.amnh.org/open_source/maxent/) (Phillips et al., 2006) was chosen

154   because it performs well in comparisons with other programs especially for rare species. It works

155   with presence-only data and is considered to produce robust results with sparse, irregularly

156   sampled data and minor location errors, which is applicable to museum data (Elith et al, 2006,

157   2011; Pearson et al, 2007; Kramer-Schadt et al., 2007). The models have been built using swd files

158   and bioclim layers in ASCII format. For the datasets with >50 localities, bootstrap replicated run

159   type with 25% of localities assigned for the random test percentage were applied. Overall, ten

160   replicates were conducted. For the datasets with <50 localities (*O. coriaceus*, *O. fulvipes* and O.

161   *proserpinae*), crossvalidation with the replicate number corresponding to the locality number was

162   used (Pearson at al., 2007; Shcheglovitova & Anderson, 2013).

163   The data used in this study are biased towards the easily accessed area, as most of the

164   specimens were collected along major roads and railroads in the area currently corresponding to

165   Russia, as well as Caucasus and Central Asia countries. This can exacerbate over-representation

166   of some regions, which can lead to an inaccurate model. Sampling bias can be addressed by

167   reducing the number of occurrence records in oversampled regions using spatial filtering

168   (Dormann et al., 2007; Kramer-Schadt et al., 2013); however, it can lead to a situation where the

169   number of occurrences is too few to create a reliable model. Additionally, Maxent automatically

170   discards the redundant records, appearing in the single grid cell (Fourcade et al. 2014, Chiarenza

171   et al. 2019), which is ~10km in this study. This is a quite large area, which might accommodate

172   different climate regimes. Assigning the larger grid cell was needed for the filtering, and leading

173   to further loss of information on species climatic preferences. Alternatively, it is possible to

174   manipulate the background data by choosing background data with the same bias as occurrences

175   (Phillips et al., 2009; Elith et al., 2011; Kramer-Schadt et al., 2013). As soon as there are <20

176   occurrences for two of the analyzed species, the bias file approach was chosen. A previous study

177   showed that using biased background data have increased the performance of the model and should

178   be applicable for cases with small numbers of occurrence points (Kramer-Schadt et al., 2013). A

179   bias file was created as a two-dimensional kernel density estimate, based on the coordinates of the

180   occurrence points, using the kde2d function from the *MASS* package (Ripley et al., 2020) in R.

181   This approach was applied in previous works (e.g. Filazzola et al., 2018; Mudereri et al., 2020).

182   Bias files were converted to the raster ASCII format and have been implemented into the biasfile

183   option in Maxent. Ten thousand background points, which is the default Maxent setting, was

184   randomly selected from the area denoted in the bias file. The "cloglog" output was chosen for the

185   visualization and further analysis.

186   *Variable selection*. Climatic niche modelling with two sets of variables was conducted. To avoid

187   the model overfitting, it is possible to exclude the highly correlated variables and/or tune the model

188   parameters (Merrow et al., 2013). It has been shown that Maxent can perform well with the

189   correlating variables with tuned parameters (Merrow et al., 2013; Morales et al., 2017; De Marco

190   Junior & Nobrega, 2019); therefore, the first model type includes all bioclimatic variables (CF

191   model). However, to test whether the model with all variables can be overfitted the highly

192   correlated variables for each species were excluded (CR model) (see below for the details).

193 ***Parameter adjustment***. There are two modifiable parameters in Maxent, which are feature classes

194 and regularization multiplier. They should be adjusted for each particular case to avoid overfitting

195 and/or over-complexity (Morales et al., 2017). Feature classes correspond to the mathematical

196 transformation of the variables and regularization multiplier (beta multiplier) limits the complexity

197 of the model and generates a less localized prediction; i.e. smooths the model (Phillips & Dudík,

198 2008; Elith et al. 2011, Merrow et al., 2013). Best features and regularization multiplier set for the

199 CF models has been selected using *ENMeval* package in R (Muscarella et al., 2014a, 2014b), using

200 Maxent. The models have been tested against the regularization multipliers ranged from 0.5 to 6

201 and the default feature classes and their combinations, i.e. L, LQ, LQH, H, LQHP, LQHPT (L =

202 linear, Q = quadratic, H = hinge, P = parameter, T = threshold). The method "block" was chosen,

203 because it accounts for spatial autocorrelation (Muscarella et al., 2014a). This analysis can result

204 in different parameter sets in different runs, so the analysis was done five times for each species.

205 In case if the analyses resulted in different parameter sets, all of them were kept to run the

206 environmental niche modelling in Maxent. All the parameter sets used for the modelling are

207 provided in the Supplemental Table 1.

208 For the CR model, the *MaxentVariableSelection* package in R (Jueterbock et al., 2016;

209 Jueterbock, 2018) was used. It chooses the best set of variables, which has the lowest AICc value,

210 based on the regularization multiplier and features. Comparisons were performed for the same

211 parameters, as in the case of the *ENMeval*. A separate run was conducted to test the regularization

212 multipliers for each feature class or combinations of classes. For the background data ten thousand

213 background points were extracted from the bias file raster using R. For each feature (or

214 combination of the features), its best regularization multiplier and variable set was kept for further

215 analysis in Maxent, and they are provided in the Supplemental Table 1.

216 Maxent provides the list of the percent contribution (PC) and permutation importance (PI)

217 for each variable in the model. The variables with PC and/or PI values higher than 10%2 are

218 provided in Table 1 for CF and CR models for each species.

219

220 ***Model evaluation***. For model evaluation, training and test AUC values are provided, which is valid

221 for model comparison over the same study area (Bohl et al., 2019) (see Supplemental Table 1).

222 The differences between training and test AUC values and omission error rates have been also

223 compared. It has been shown that the model with high differences between AUC values and

224   omission error rate > 0.1 is likely to be overfitted (Bohl et al., 2019). In the case of each model

225   type (CF and CR), the model with the relatively high AUC values, low differences between

226   training and test AUC and low omission error rates was chosen for the visualization and niche

227   comparisons.

228   ***Environmental niche projection area and climatic variable ranges***. The obtained environmental

229   niche models were thresholded using the "Maximum training sensitivity plus specificity Cloglog

230   threshold", as the thresholds maximizing sensitivity and specificity perform well on presence only

231   datasets (Liu et al., 2016). The total area of the thresholded niche projection was obtained using

232   QGis 3.10. The thresholded maps were used as masks to trim the bioclim layers to obtain the

233   climatic variables ranges for each model. These areas and variable ranges were used to compare

234   the models. The correlation of climatic variables was estimated for each species separately using

235   Pearson's correlations (PCor), as it is suitable for continuous variables. In this work $PCor \geq 0.9$ is

236   considered strong, as it is usually used to discriminate strongly correlated variables (e.g. Jezkova

237   et al., 2011; Dellicour et al., 2014). I also considered $0.7 \leq PCor > 0.9$ as significant. Tables with

238   Pearson's correlations for the each species are provided in the Supplemental Data 2.

239   ***Niche overlap***. Testing for niche overlap was performed in ENMTools (Warren et al., 2010). First,

240   the niche overlap was conducted to get the Schoener's D (D) and Hellinger distance I (I) metrics,

241   these measure similarities between species habitat suitability models. The values of both metrics

242   ranged from 0 (the niches do not overlap) to 1 (the niches are identical). Comparisons were run

243   between all species within each model type, CF and CR, separately. Second, the "Identity test" for

244   each pair of species was conducted. This test randomizes the occurrences for two species, creating

245   the pseudopopulations, and compares the environmental niches for those datasets, creating

246   permuted D and I values. If the D and I values for the actual data are significantly lower than those

247   of the randomized (permuted) data the niches are interpreted to be different (Warren et al., 2010).

248   The identity test can be performed only for the same set of environmental layers for both compared

249   species; therefore, the identity test was used for the models with all environmental variables. Third,

250   the background test was also performed. It measures the difference between the similarity of two

251   species on one side and the similarity between species and background of another species on the

252   other side. The test should be undertaken for two sides, as it can yield different results for the

253   reversed comparison. If the D and I metrics for actual niche overlap and obtained with background

254   test are similar, this means that the similarity of niches between two species is the same as expected

255   from random data. If the D and I metrics of actual datasets are higher or lower than those from

256   background test, this means that the niches are more similar or more different than expected from

257   random data respectively (Warren et al., 2010). The background for each species equals to its bias

258   file.

259   ***Maps visualization***. All maps have been prepared in QGis 10. The background for the Figs 1-2 is

260   the layer freely accessible at https://github.com/nvkelso/natural-earth-quick-

261   start/tree/master/50m_raster/NE1_50M_SR_W, and it is not copyrighted. The maps for Figs 3-6

262   have been created by the uploading the averaged maps resulted from the Maxent analysis to QGis

263   10. The country borders layer is freely accessible at

264   https://github.com/petewarden/openheatmap/tree/master/mapfileprocess/test_data/TM_WORLD

265   _BORDERS-0.3, and it is not copyrighted.

266

Results

268   ***Model evaluation.*** All the Maxent models have high discriminative power for the training datasets

269   with high AUC. It is higher than 0.9 in all cases except for *O. vittipennis*, where AUC ranges from

270   0.87 to 0.89. The models are also able to predict the testing points with very similar AUC values,

271   as in training datasets. The training AUC is higher than the test AUC, and the differences between

272   the models chosen for the comparison vary from 0.002 (CF model for *O. bivittatus*) to 0.027 (CR

273   model for *O. vittipennis*). Omission rates for the models chosen for the comparisons vary from

274   0.0789 (CR model for *O. funestus*) to 0.1620 (CF model for *O. vittipennis*). The AUC values and

275   omission rates for all models are provided in the Supplemental Table 1. The Maxent output files

276   for each model chosen for the visualization and niche comparison are provided in the Supplemental

277   Data 3. The detailed descriptions of the climatic niches for each species are provided in the

278   Supplemental Data 4.

279   The model with all variables is supposed to be overfitted because of the correlated

280   variables. Therefore, this model is expected to predict smaller areas of suitable conditions and/or

281   narrow ranges of the climatic variables, than the model with reduced set of variables (see

282   Methods). However, the current results do not support this idea. The thresholded maps of the

283   modelled areas with suitable conditions are provided in Figs 3-6. Those areas of CF models are

284   larger than or subequal to CR for all the species. In the case of variables ranges no model type is

285   noticeably more restrictive than the other (Figs 7-11). In rare cases, the CF models show

286   significantly more restricted ranges, rather than CR models (e.g. bio12, bio13 for *O. bivittatus* and

287   *O. proserpinae*, bio18 for *O. proserpinae*). The variables ranges for each model are shown on the

288   Figs 7-11.

289   The climatic variables with high PC and PI for each model type and for each species are

290   provided in the Table 2. Both models for the same species have different sets of climatic variables

291   explaining their distribution, and each type of model (CF or CR) has different sets of climatic

292   variables explaining the distribution in comparison between the species.

293   In most of the models both temperature related and precipitation related variables, are

294   important for the species distribution, except for the CF models for *O. saltator* and *O. vittipennis*,

295   having only temperature related variables significantly contributing. Most of the variables appear

296   as important for at least one model, except for bio5 (max temperature of warmest month), bio8

297   (mean temperature of wettest quarter), bio12 (annual precipitation) and bio13 (precipitation of

298   wettest month). In some cases, the same variable significantly contributes to the both type of

299   models within the same species, i.e. bio1 (annual mean temperature for *O. bivittatus* and *O. brevis*,

300   bio3 (isothermality) for *O. coriaceus* and *O. funestus*, bio4 (temperature seasonality) for *O.*

301   *proserpinae*, bio14 (precipitation of driest month) for *O. brevis*, bio18 (precipitation of warmest

302   quarter) for *O. fulvipes*, bio19 (precipitation of coldest quarter) for *O. coriaceus* and *O.*

303   *proserpinae*.

304   ***Comparison of the variables for the species with similar environmental niches***

305   Annual mean temperature (bio1) is important for all widely distributed species. In the case of the

306   CR models for *O. saltator* and *O. vittipennis* this variable does not explain the distribution much.

307   However, min temperature of coldest month (bio6) is important for this type of model in *O.*

308   *saltator*, and mean temperature of driest quarter (bio9) is important for the CR model in *O.*

309   *vittipennis*, and bio6 and bio9 significantly correlate with each other and bio1 (PCor > 0.87) in

310   those two species (Table 2). Temperature annual range (bio7) and mean temperature of coldest

311   quarter (bio11) highly contribute to at least one of the models in *O. bivittatus*, *O. saltator* and *O.*

312   *vittipennis*, and they also significantly correlate with each other in all those species, as well as with

313   bio1, bio6 and bio9 for most of the species. In the models of two species, widely occurring in

314   Central Asia (*O. bivittatus* and *O. vittipennis*), mean diurnal range (bio2), bio9, precipitation of

315   driest quarter (bio11) and precipitation of warmest quarter (bio18) significantly contribute to at

316   least one of the models. In *O. bivittatus* and *O. brevis* precipitation seasonality (bio15) is important

317 for at least one of the models. In *O. brevis* precipitation of driest month (bio14) significantly

318 contributes to both models. Max temperature of warmest month (bio5), mean temperature of

319 wettest quarter (bio8), annual precipitation (bio12), precipitation of wettest month (bio13),

320 precipitation of driest quarter (bio17) only slightly contribute or do not contribute to the climatic

321 models of the trans-Palearctic species.

322  Suitable conditions for *O. bivittatus* are shifted to drier places than in other species,

323 whereas suitable conditions for *O. brevis* are predicted for the places with higher precipitation than

324 in other species. In contrast to other species, suitable conditions for *O. vittipennis* are predicted in

325 areas with very low temperatures over the winter and very strong seasonality. The models for *O.*

326 *saltator* are similar to *O. brevis* in precipitation levels and temperature changes around the year;

327 however, suitable conditions of the former are also predicted for the areas with warmer

328 temperatures over the summer, than in *O. brevis*.

329  The models of *O. coriaceus* are more similar than random with all the models of

330 widespread species (Table 1). It is different from all of them in the lower margins for isothermality

331 (bio3) limited with higher values (Fig. 7), and suitable conditions are predicted for the places with

332 low temperatures over summer (bio5, bio10) (Figs 8, 9). The models for *O. bivittatus* and *O.*

333 *vittipennis* are additionally different from those of *O. coriaceus* in variables described in the model

334 descriptions for those species (see Supplemental data 4). The models of *O. coriaceus* are most

335 similar to those of *O. brevis* and *O. saltator*, which also occupy almost all Europe. Precipitation

336 of driest month (bio14) significantly contributes to both models for *O. brevis* and *O. coriaceus*

337 (Table 2). However, in contrast to *O. brevis*, suitable conditions for *O. coriaceus* are modelled for

338 the places with very low values for this variable, as well as for precipitation of the driest quarter

339 (bio17) (Fig. 10, 11). The models of *O. coriaceus* differ from *O. saltator* in the upper margin of

340 the precipitation of the driest month and quarter (bio14, bio17) range limited with higher values

341 (Figs 10, 11), and the upper margin of seasonality (bio4) limited with lower values (Fig. 7).

342  The models for the northeastern *O. funestus* are more similar than random with *O. brevis*,

343 *O. saltator* and *O. vittipennis*, and they are most similar to *O. brevis* and *O. vittipennis*. The models

344 of *O. funestus* are different from those of abovementioned three widespread species in

345 isothermality (bio3) range very narrow and shifted towards lower values (Fig. 7). In contrast to all

346 other species, suitable conditions for *O. funestus* and *O. vittipennis* are modelled for the places

347 with very low temperatures of coldest month, coldest and driest quarters (bio6, bio9, bio11) and

348   strong seasonality (bio4) (Figs 7-9). The upper margins of the diurnal range (bio2), isothermality

349   (bio3), temperature seasonality (bio4), temperature annual range (bio7) are limited with the lower

350   values (Figs 7-8), and the upper margins are limited with higher values for many precipitation

351   variables (bio12-14, 16, 17-19) in *O. funestus* in comparison with *O. vittipennis* (Figs 9-11).

352   Both, *O. funestus* and *O. brevis* have suitable conditions in places with high precipitation

353   over the different seasons (bio12, bio14, bio17) (Figs 9-11), but ranges of many temperature

354   related variables (bio1, bio5, bio6, bio9, bio11) and seasonality (bio4) are limited with the lower

355   margins in *O. funestus* than in *O. brevis* (Figs 7-9). *Orthocephalus funestus* differs from *O. saltator*

356   in the variable ranges modelled for the places with stronger annual temperature changes (bio4,

357   bio7), lower temperatures over the different seasons (bio5, bio6, bio9, bio11) and higher

358   precipitation (bio12-14, 16-19) (Figs 7-11).

359   Both *O. fulvipes* and *O. proserpinae* inhabit southern areas of European Palearctic (Figs

360   1D, 2B), but the variables contributing to their models are different (Table 2). For both species in

361   the CF model the mean temperature of driest quarter (bio9) is important. Precipitation over wettest

362   or coldest quarters (bio16 and bio19) significantly contribute to the models of both species. They

363   also have either precipitation of driest month (bio14) or precipitation of warmest quarter (bio18)

364   high PC. They have also similar ranges for isothermality (bio3) and temperature seasonality (bio4),

365   as well as higher temperatures of driest and coldest periods (boi6, bio9, bio11), and lower

366   precipitations over the driest and warmest periods (bio14, bio17, bio18) (Figs 7-11). The models

367   of *O. fulvipes* differ from those of *O. proserpinae* in many temperature variables limited with

368   higher values (bio5, bio6-bio11) (Figs 8-9), as well as mean diurnal range and temperature

369   seasonality and precipitation of driest month (bio2, bio4, bio14) (Fig. 7, 10) .

370

371   **Niche overlap, identity test and background test**

372   The results for the niche overlap, identity test and background test are shown in the Table 1. The

373   I and D metrics show that the niche overlap between all widely distributed species is relatively

374   high in comparison to cases when widely distributed species is compared with locally distributed

375   species, or locally distributed species are compared with each other (I > 0.8, D > 0.5). Similar

376   values are for the overlap between the following pairs: *O. brevis* and *O. coriaceus*, *O. saltator* and

377   *O. coriaceus*, *O. funestus* and *O. vittipennis*. The largest niche overlap is between *O. brevis* and *O.*

378   *saltator* (I > 0.9 , D > 0.6), as well as between *O. brevis* and *O. vittipennis* (I > 0.8 , D > 0.6).

379 However, identity test shows that those values do not reach 5% threshold for permuted I and D
380 values, which means that we cannot conclude that the niches are identical.
381   The background test shows that all pairs of the widespread species are more similar to each
382 other than expected for both CF and CR models and for comparisons in both sides, based on I and
383 D metrics. The same result is shown for the comparisons of *O. coriaceus* with all widespread
384 species, as well as for the following pairs: *O. funestus* and *O. brevis*, *O. saltator* and *O. vittipennis*,
385 *O. funestus* and *O. saltator*, *O. funestus* and *O. vittipennis*, *O. coriaceus* and *O. proserpinae*, *O.*
386 *fulvipes* with *O. proserpinae*. Background test undoubtedly shows that the niches are more
387 different from each other only for *O. funestus* vs *O. proserpinae* comparison. In all other cases the
388 results are dubious and differ depending on the type of model and statistical metric. The results
389 also can differ for the pair of species, depending which species is used for the background.
390 Generally, the CR models show more overlap with each other than the CF models, and background
391 test is more often shows that the species are more similar to each other for the CR models. If two
392 widespread species are compared, the background test results in very similar metrics values for
393 both directions. If two species with very different areas of suitable conditions sizes are compared,
394 the results depend on which of them is used for the background. In case when the species with
395 larger distribution area is used as a background, the resulted metrics are lower, and therefore, the
396 analysis shows that two species are more similar to each other than expected more often, rather
397 than in the reversed comparison.

Discussion

399

400   ***Climatic niches of* Orthocephalus *species comparison*.** The modelled environmental
401 niches for the widespread species cover noticeably different areas. Areas in which conditions are
402 suitable for *O. bivittatus* correspond with the other species the least. They are mostly projected on
403 Central Asia and south of European part of Russia. (Figs 3A, 4A). *Orthocephalus brevis* and *O.*
404 *saltator* are more similar, having the largest area of suitable conditions in Western Palearctic,
405 however, the geographic projections of their environmental niches do not cover the Mediterranean
406 region for *O. brevis*, whereas those areas are suitable for *O. saltator* (Figs 3B, 4C, 5B, 6C). Suitable
407 conditions for *O. vittipennis* extend through entire Eurasia, from Europe to Northeast Asia,
408 including Central Asia, (Figs 5D, 6D), whereas the Mediterranean area is not suitable for this
409 species. Those differences in the areas of suitable conditions are also supported by the differences

410   in the variables with highest contribution to the climatic models (Table 1) and comparisons of

411   climatic variable ranges (see Results section for the details). Overall, all analyzed *Orthocephalus*

412   species have different set of variables, most important for their climatic models and none of the

413   pairs have identical climatic niches, which suggests that the climatic niche is species specific even

414   for the closely related taxa. Finally, the differences in the environmental niches are also supported

415   by the identity tests and comparisons of climatic variable ranges. Although in all widespread

416   species niche overlap is high (I>0.8, D>0.6) and background test shows that the similarity between

417   them is higher than that of random data, the identity test does not support the hypothesis that they

418   are identical (Table 1). This supports the previous research, showing that the environmental niches

419   in closely related species might be similar, but not identical (e.g. Wellenreuther et al. 2012, López-

420   Alvarez et al. 2015, Dellacour et al. 2016).

421   The climatic niche models of Trans-Palearctic species are all more similar to each other

422   than expected. The niches of *O. coriaceus* and *O. funestus*, distributed in Europe and northeast

423   Asia respectively, also highly overlap with some Trans-Palearctic species. The climatic niche

424   models of *O. fulvipes* and *O. proserpinae*, are not very similar with Trans-Palearctic species.

425   Schmitt (2007) made an overview of the European types of distribution, and delimited three

426   main types. Species with the center of dispersal in Mediterranean regions are "Mediterranean",

427   species having extra-Mediterranean center of dispersal belong to "Continental" type, and species

428   with recent alpine of arctic distribution patterns are called "Alpine" or "Arctic". Testing the center

429   of the distribution for the *Orthocephalus* species is beyond the scope of the current paper: a

430   phylogeography analysis combined with modelling of distribution during the glacial period is

431   necessary for such a study. However, it is very likely that the trans-Palearctic *Orthocephalus*

432   species belong at least to two Schmitt's groupings (2007). Among the analyzed widespread

433   species, suitable conditions in the Mediterranean region are generally not predicted for *O.*

434   *bivittatus*, *O. brevis* and *O. vittipennis* and they probably belong to the "Continental" group.

435   However, *O. saltator* has highly suitable climatic conditions in the Mediterranean region and might

436   have its center of dispersal there (Figs 5C, 6C).

437   Maps with the records and the areas of suitable conditions suggests that "trans-Palearctic"

438   distribution is a term of convenience and might include many types of distributions connected with

439   the different climatic conditions. Study of more species from different taxonomic groups,

440   including closely related and unrelated species, are necessary to make conclusions on which types

441   of environmental niches are suitable for the trans-Palearctic species and which climatic conditions

442   are connected with such distributions.

443   **Climatic variables important for the *Orthocephalus* distribution**

444   Annual mean temperature (bio1), temperature annual range (bio7) and mean temperature of coldest

445   quarter (bio11) are important for the models of at least three widely distributed *Orthocephalus*

446   species. The results also correspond with the results of environment niche modelling of the trans-

447   Palearctic beetle species *Pterostichus oblongopunctatus* (Fabricius, 1787), which showed that bio1

448   and bio11 had high contribution to the model of this species (Avtaeva et al. 2019). Modelling of

449   the trans-Palearctic tick *Ixodes ricinus* (Linnaeus, 1758) showed that min temperature of coldest

450   month (bio6) is among the variables with the highest PC in the climatic model of this species

451   (Porretta et al. 2013) In all trans-Palearctic species bio6 and bio11 highly correlate with bio1 (PCor

452   > 0.9), and this might mean that the distribution of the trans-Palearctic arthropods is limited at least

453   partly by the winter temperatures. Overall, the set of the variables having high contribution to the

454   climate models is unique for each *Orthocephalus* species, and analysis of more trans-Palearctic

455   species is needed to make conclusions hon ow type of distribution correlates with the climatic

456   variables.

457   *Orthocephalus brevis*, *O. coriaceus*, *P. obongopunctatus* and *I. ricinus* are mostly distributed in

458   the Western Palearctic, and their climatic models have precipitation of driest month (bio14) or

459   precipitation of driest quarter (bio17) with high PC. This reflects the fact that the most suitable

460   conditions for all those species cover middle and northern Europe, but not Mediterranean zones,

461   and therefore prefer the places with relatively high precipitation around the year. This is also

462   supported by the variable ranges of bio14 and bio17 variables for *O. brevis* and *O. coriaceus*,

463   which show that these species inhabit places with high precipitation values over the driest period.

464   Similarly to four mentioned species, *Orthocephalus saltator* is mostly distributed in Western

465   Palearctic, but the areas with the most suitable conditions cover Mediterranean zones. In case of

466   this species, bio14 and bio17 do not contribute much to the climatic model (<10% of PC and PI).

467   Although *O. coriaceus* and *O. funestus* have very different distribution, isothermality (bio3) has

468   high PC and PI for both models in both species. However, according to the temperature ranges the

469   former tends to inhabit places with high isothermality, whereas the latter prefers the areas with low

470   values of this variable. The study with more European and East Asian species is needed to confirm

471   that isothermality is connected with such distributions.

472   The precipitation related variables over the different seasons (bio14, bio15, bio18, bio19) are
473   important for models for two species mostly distributed in the Mediterranean regions, and mean
474   temperature of driest quarter (bio9) has high PC and PI in the CF model. This is similar to the
475   Mediterranean species of *Tomicus destruens* (Wollaston, 1865) (Sánchez-García et al., 2013). It
476   was shown that the variables bio19 and bio9 are also important for the climatic models of different
477   clades and haplotypes of this species. Study of climatic preferences of more insect species from
478   the Mediterranean region is needed to draw conclusions on how the climate is connected with the
479   species distribution in this region.
480
481   ***Comparison of environmental niches between closely related* Orthocephalus *species in the***
482   ***phylogenetic context***
483   Although, a morphology-based phylogeny for *Orthocephalus* has been published
484   (Namyatova & Konstantinov 2009), there are many unresolved clades, and, therefore, cannot be
485   used to adequately analyze potential phylogenetic signal in climatic related tolerances and
486   environmental niches. However, a few conclusions still can be reached. According to this
487   phylogeny, *O. bivittatus*, *O. coriaceus*, *O. fulvipes*, *O. funestus*, *O. saltator* and *O. vittipennis* have
488   very similar vestiture, color and genitalia, and in some cases the species can be identified only
489   from the males. Those species form a clade, which also includes some other species.
490   *Orthocephalus brevis* and *O. proserpinae* are very different morphologically, and are not closely
491   related to other species.
492   Based on these relationships, it can hypothesized that there are at least three processes in
493   this genus related to climatic niches which might be at play. First, there might be phylogenetic
494   conservatism, at least for some climatic variables. For example, *O. funestus* and *O. vittipennis* are
495   very similar morphologically. They mostly differ only in hemelytron coloration in males.
496   According to the current analysis, their niches are also more similar to each other than to random
497   data, and both those species can tolerate strong seasonality and very low winter temperatures.
498   Another example is *O. fulvipes*, inhabiting southwestern Palearctic, which morphologically is very
499   similar to *O. saltator*, and the latter is the only widespread species in which the Mediterranean
500   region is suitable.

501   Second, climatic niche convergence is also observed. This study found that climatic niches

502   are very similar in *O. brevis* and *O. saltator*, as well as *O. brevis* and *O. vittipennis*, and those pairs

503   are not closely related.

504   Third, the analysis shows the possibility of the distinct niche divergence in the distantly

505   related taxa. According to the background test, the niches are undoubtedly more different from

506   each other than from random data only for the *O. funestus* and *O. proserpinae* pair. According to

507   Namyatova and Konstantinov (2010), those two species are not closely related. Those significant

508   niche differences might be explained by differences in habitats, occupied by those two species.

509   *Orthocephalus funestus* inhabits places in northeast Asia with wide ranges of temperatures and

510   high precipitations, whereas *O. proserpinae* lives in the Mediterranean region with narrow

511   temperature ranges and low precipitation (Figs 5B, D, 6B, D). However, *O. fulvipes*, which is more

512   closely related to *O. funestus*, also prefers dry conditions including Mediterranean and desert

513   climates (Figs 3D, 4D). The background test for this species pair provides inconsistent results,

514   suggesting that the niches between *O. funestus* and *O. fulvipes* are more similar with each other,

515   than those of *O. funestus* and *O. prosepinae*. This leads to the hypothesis that the closely related

516   species in *Orthocephalus* cannot diverge very quickly.

517   However, the robust molecular-based phylogeny and niche models for other

518   *Orthocephalus* species are needed to test all those hypotheses on the niche evolution in this genus.

519   Based on this phylogeny, it is unclear whether the ability for the wide distribution has

520   phylogenetic signal. On one hand, it is very likely that two closely related species can similarly

521   adapt to the climatic conditions (e.g. Losos 2008, Wiens et al. 2010). On the other hand, even

522   though both sister species can potentially tolerate wide range of climatic conditions, one species

523   might have significantly limited realized niche and distribution because of the strong competition

524   with its sister species.

525

Conclusions

526

527   The study on the climatic niche modelling for eight insect species with trans-Palearctic distribution

528   from the genus *Orthocephalus* has been performed. The niches of widely distributed trans-

529   Palearctic species (*O. bivittatus*, *O. brevis*, *O. saltator*, *O. vittipennis*) are very similar to each

530   other, but not identical. The differences are confirmed by the "Identity test" and "Background test"

531   in ENMTools, as well as the comparison of the climatic variables contributing to the modes and

532   variable ranges for the areas, covered by preferable conditions of different species. The niches of
533   the trans-Palearctic species are also similar to two species having more limited distribution (*O.*
534   *coriaceus*, *O. funestus*). Overall, the similarity of the niches of widely distributed species is higher
535   than in cases when the niches of widely distributed and locally distributed species or only locally
536   distributed species are compared. The annual mean temperature significantly contributes (bio1) to
537   the climatic models of all trans-Palearctic species. Other temperature related variables, i.e. min
538   temperature of coldest month (bio6), temperature annual range (bio7), mean temperature of driest
539   quarter (bio9), mean temperature of coldest quarter (bio11) are likely to be important for the
540   climatic niches of the trans-Palearctic species. For the trans-Palearctic species, widely distributed
541   on Central Asia, mean diurnal range (bio2), min temperature of coldest quarter (bio11) and
542   precipitation of warmest quarter (bio18) are also important for at least one of the models. For the
543   Western Palearctic species with the most suitable conditions corresponding to the areas outside the
544   Mediterranean regions (*O. brevis* and *O. coriaceus*), precipitation of driest month (bio14) is
545   important. Isothermality (bio3) has high PC and PI for European *O. coriaceus* and East Asian *O.*
546   *funestus*. For the species, distributed in Mediterranean region (*O. fulvipes* and *O. proserpinae*),
547   precipitation related variables over different seasons (bio14, bio16, bio18, bio19), significantly
548   contribute to at least one of the model each. The discussion of the results based on the phylogeny
549   suggests that within *Orthocephalus* there might be different processes connected to the climate
550   niche differentiation, such as niche conservatism, niche convergence and niche divergence. More
551   studies of climatic niches of the species distributed in the Palearctic are needed to better understand
552   the types of possible climatic niches of widespread species, the main climatic variables shaping
553   the distribution of the Palearctic taxa and how the climatic niches are related to phylogenetic
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555

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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.

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

	bivittatus		*brevis*		*coriaceus*		*fulvipes*		*funestus*		*proserpinae*		*saltator*		*vittipennis*	
	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	
Bio13 Precipitation of Wettest Month	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 |

Niche overlap (in bold), identity test and background test results.

The results for the I and D metrics are separated with the bold line. 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.

1 Table 2:

2 Niche overlap (in bold), identity test and background test results. The results for the I and D metrics are separated with the bold line. If

3 the niche overlap values are significantly lower than 5% threshold for permuted values, this means that the models are different. If the

4 niche overlap values are higher or lower than those from background test, this means that the niches are more similar or more different

5 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

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 .
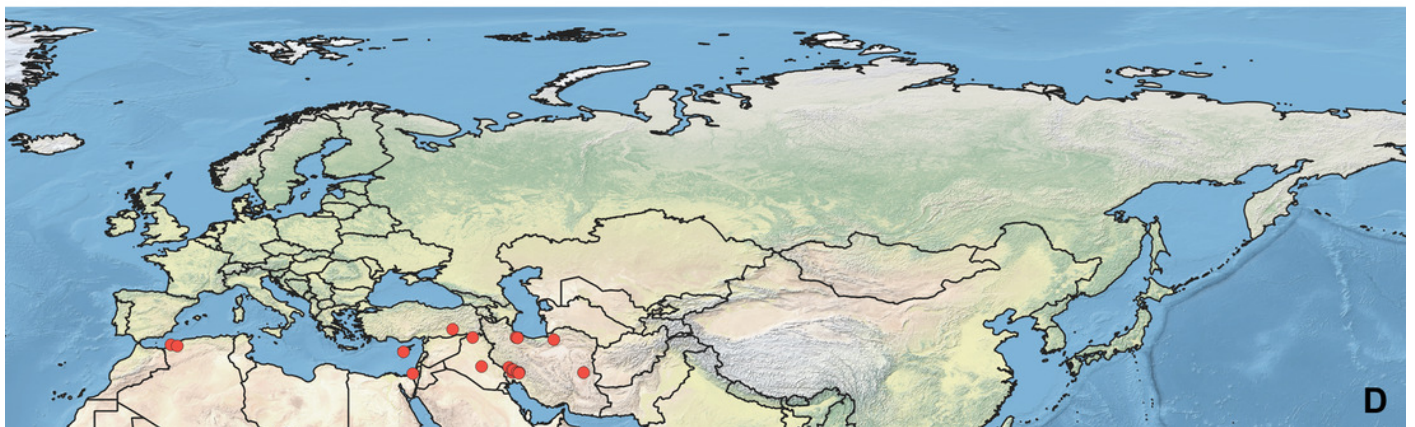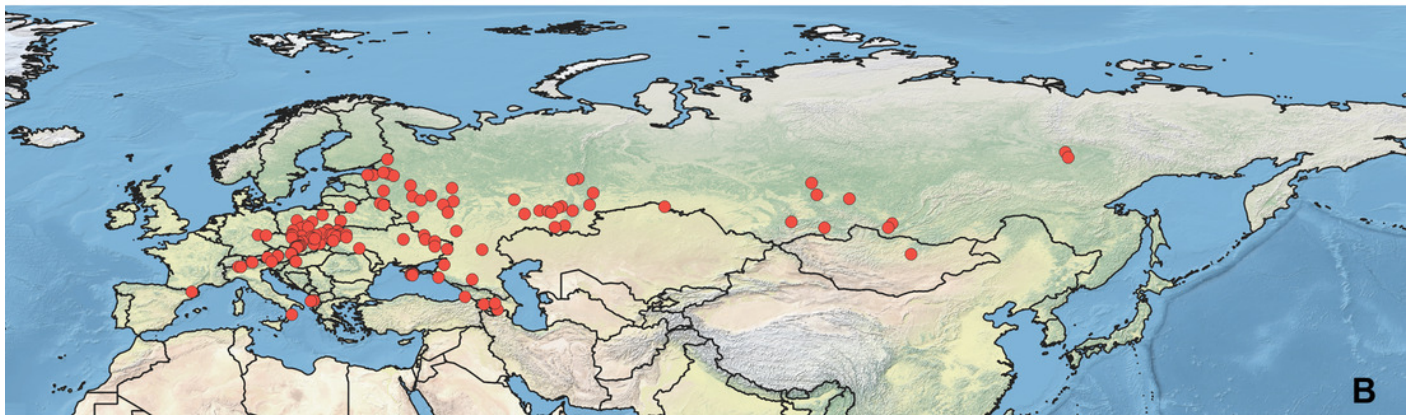
Figure 2

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_WOR
LD_BORDERS-0.3 .
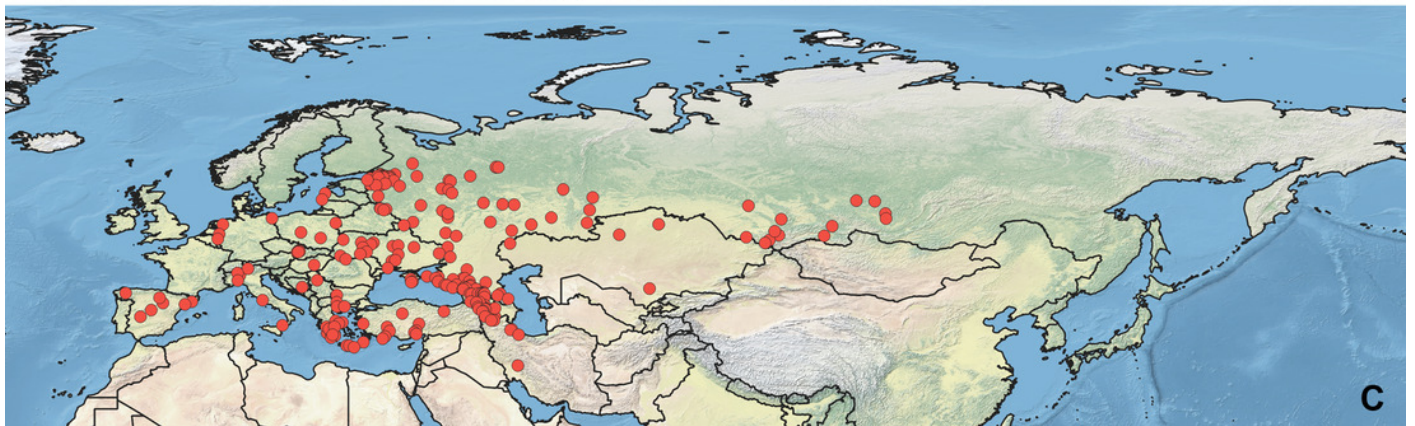
Figure 3

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 .

A

B

C

D
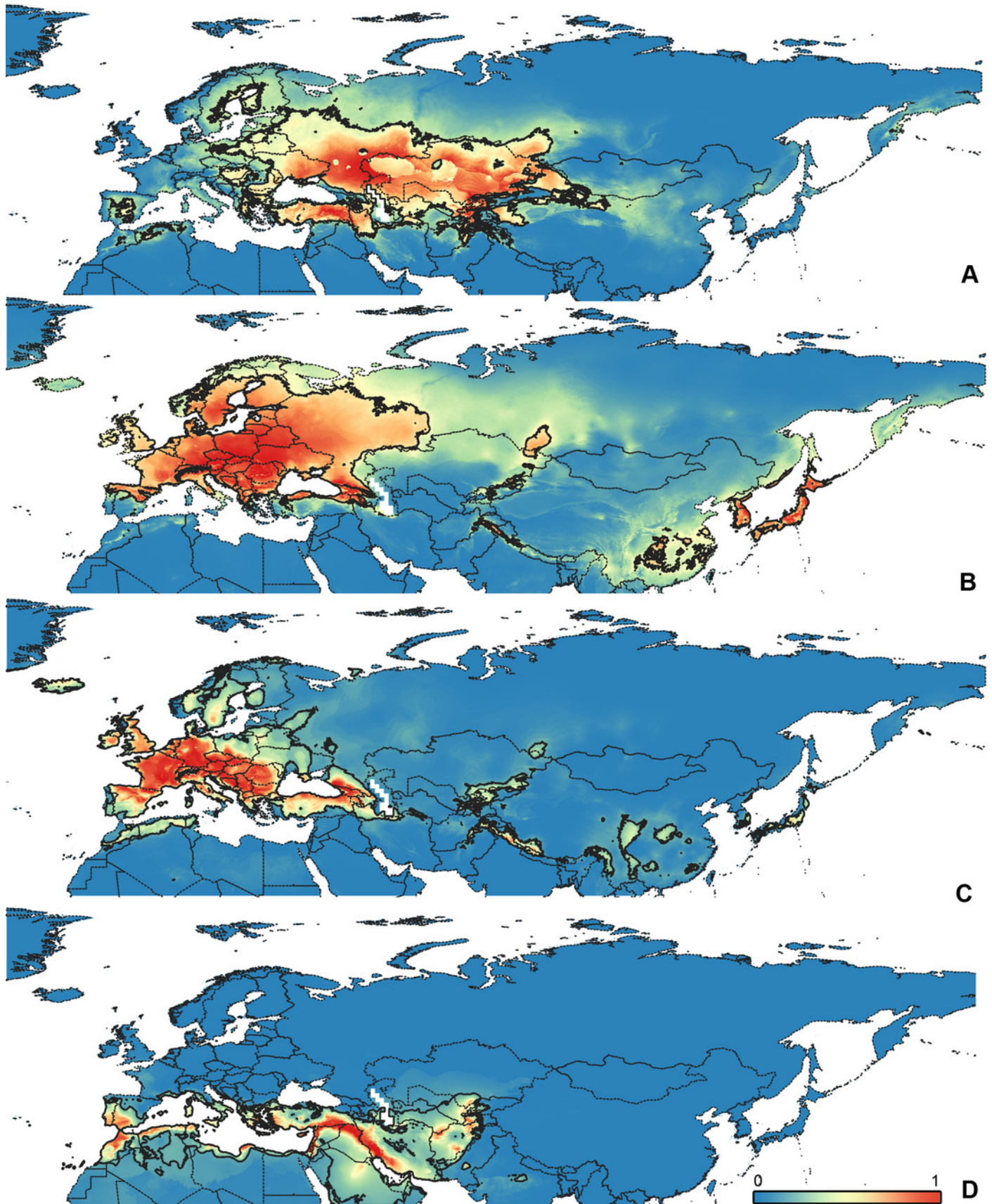
Figure 4

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 .
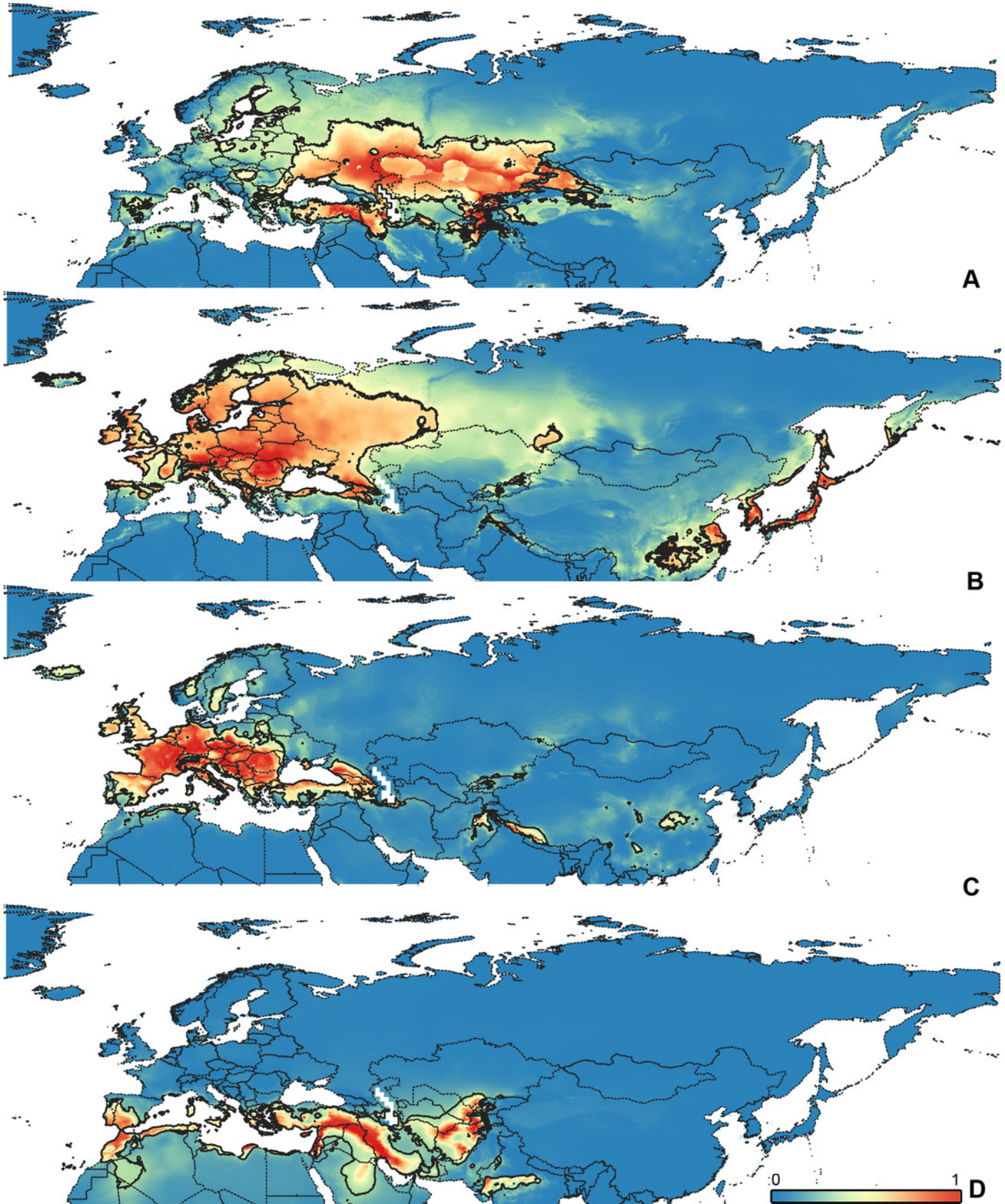
Figure 5

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 .
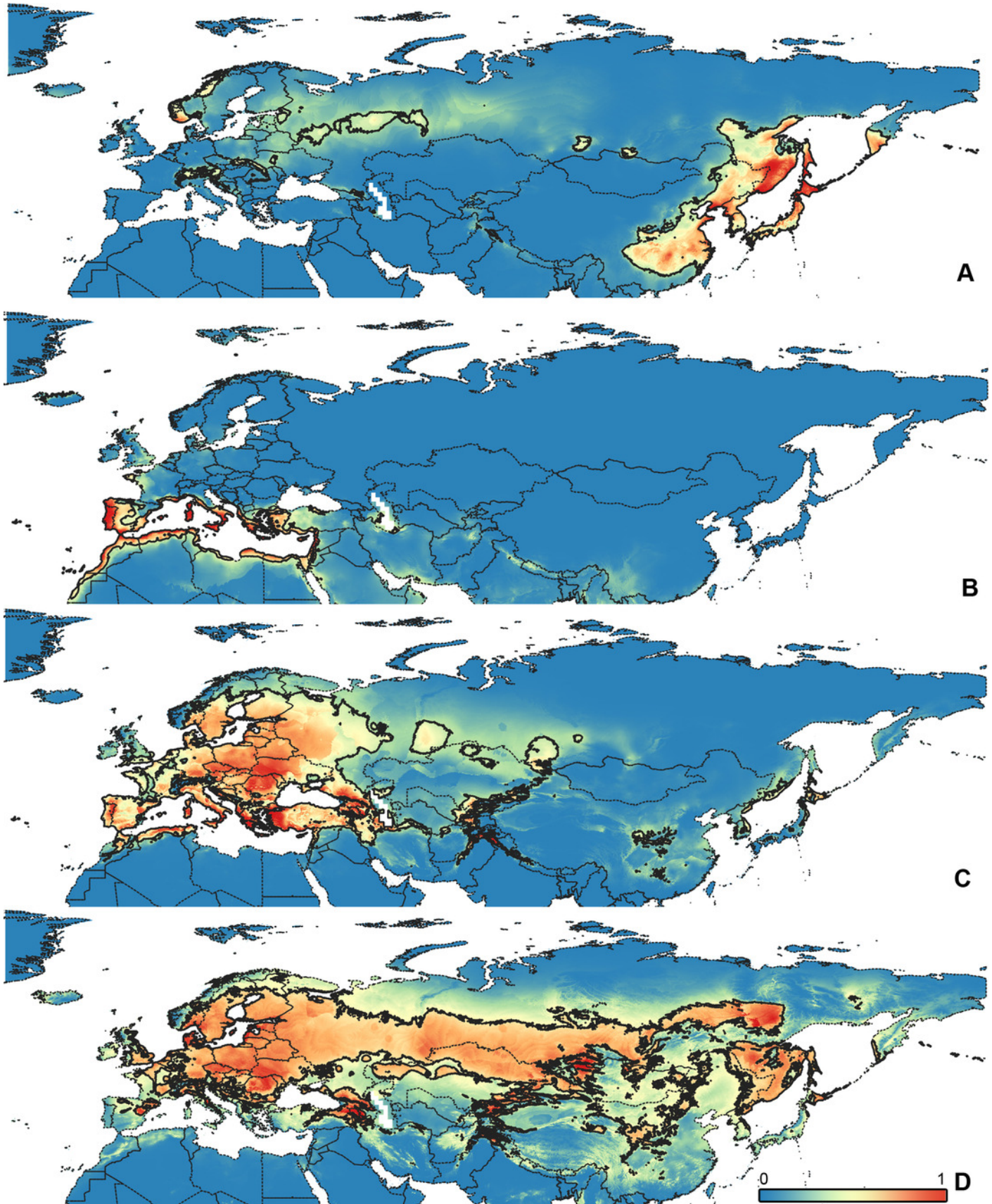
Figure 6

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 .

A

B

C

0   1   D
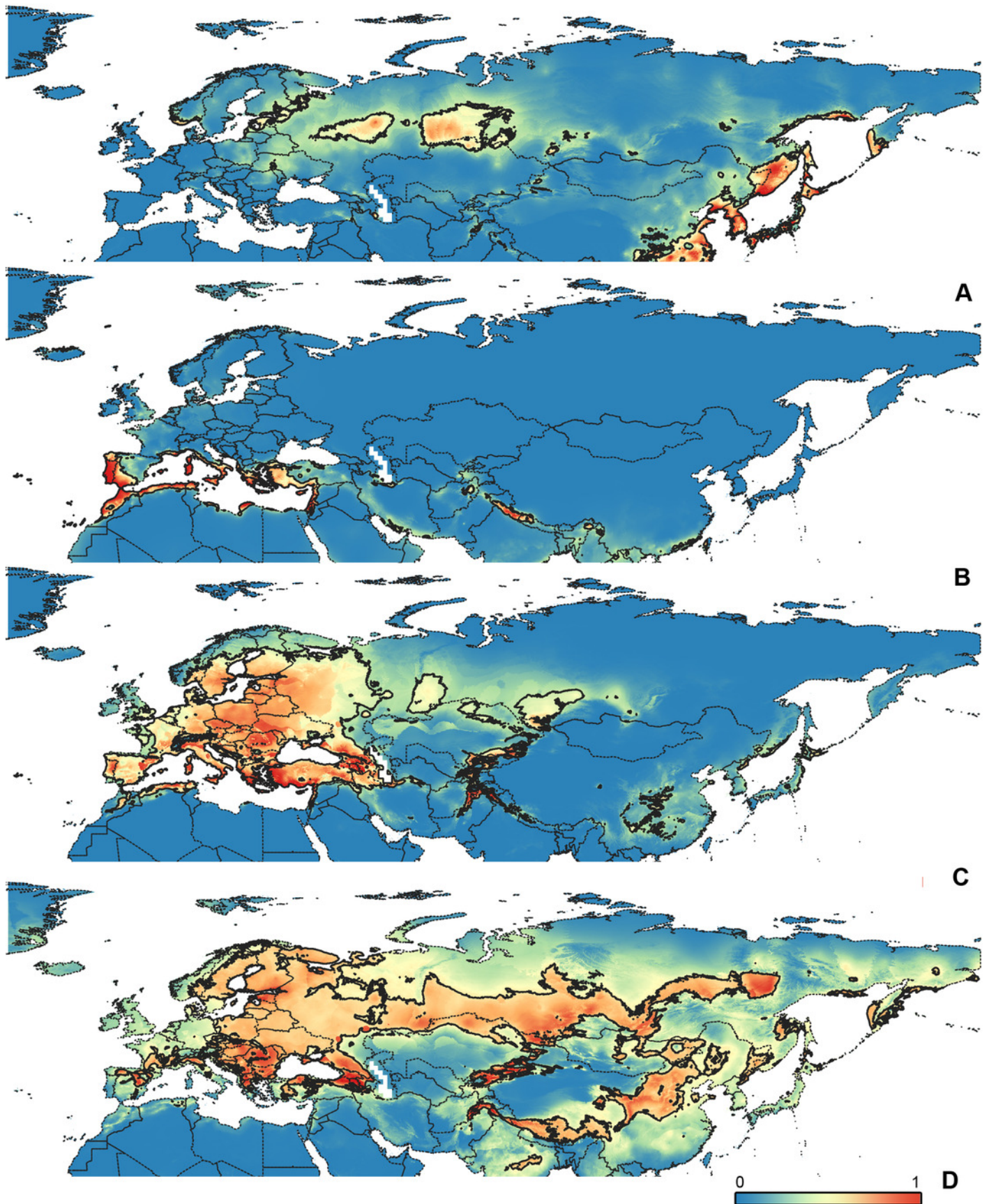
Figure 7

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.
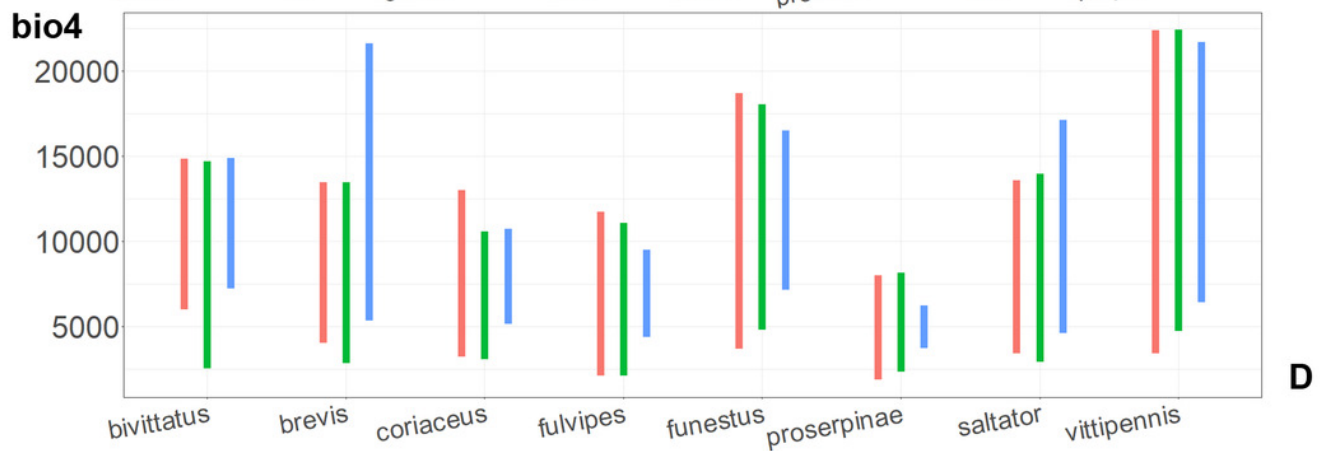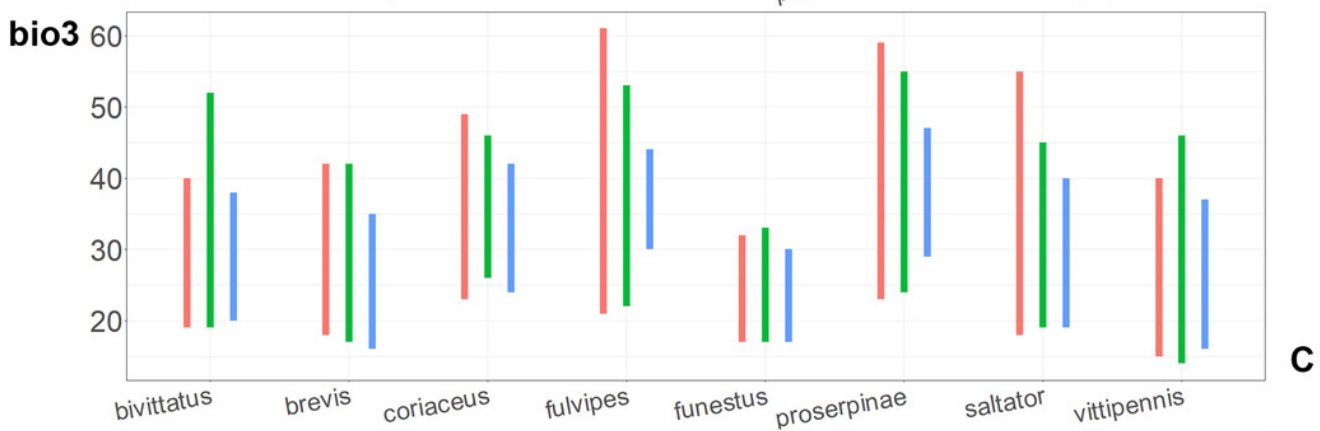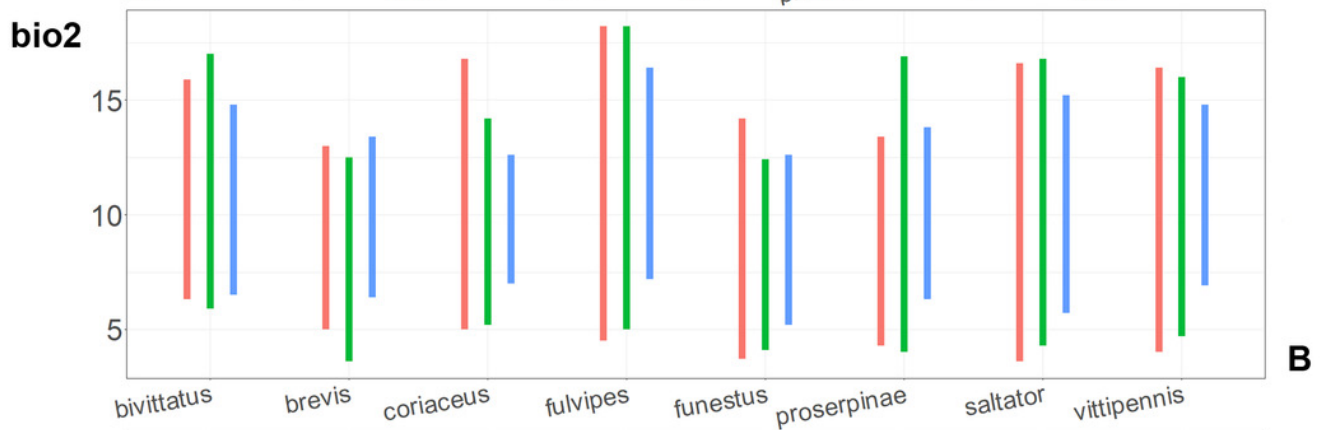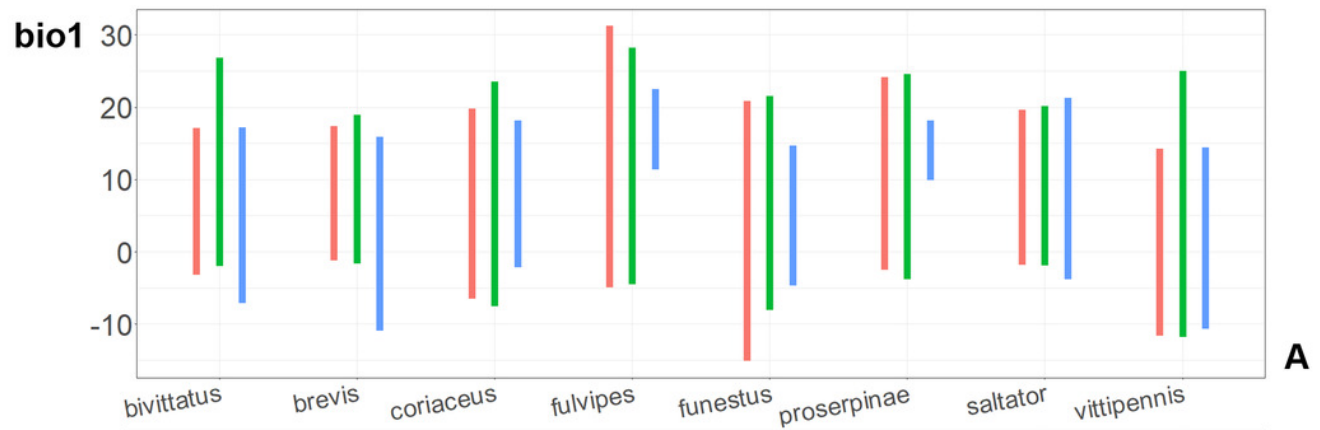
Figure 8

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.
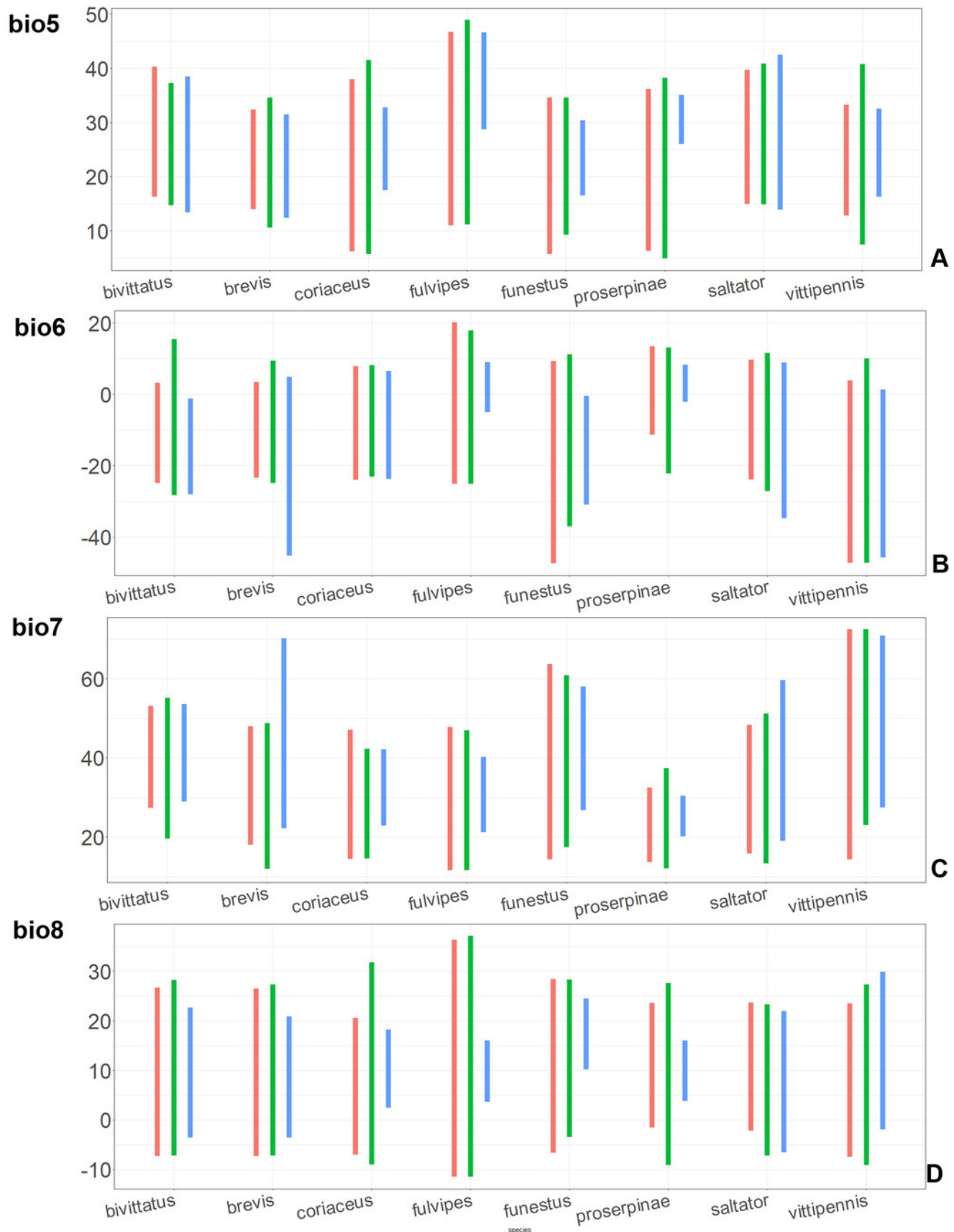
Figure 9

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.
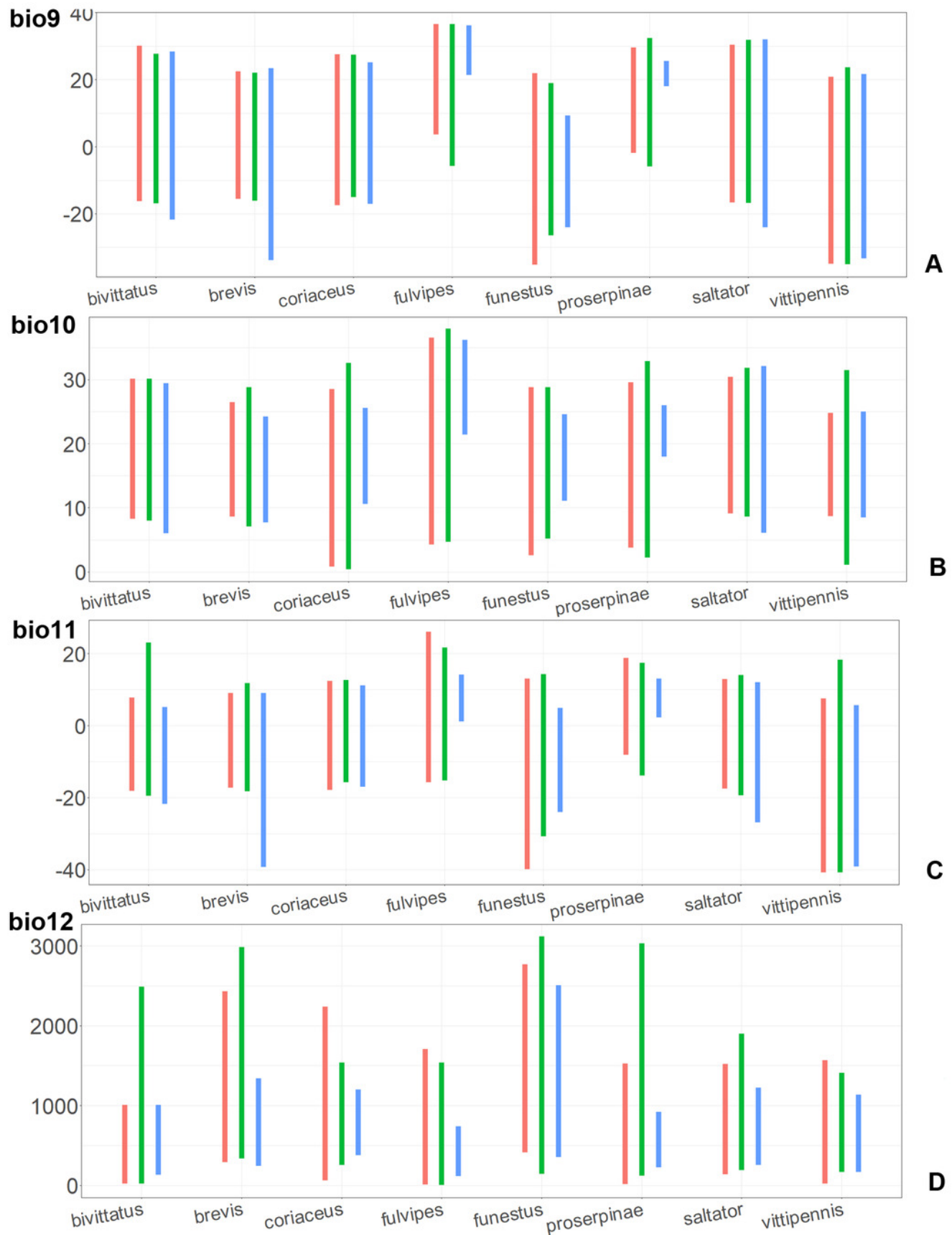
Figure 10

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.
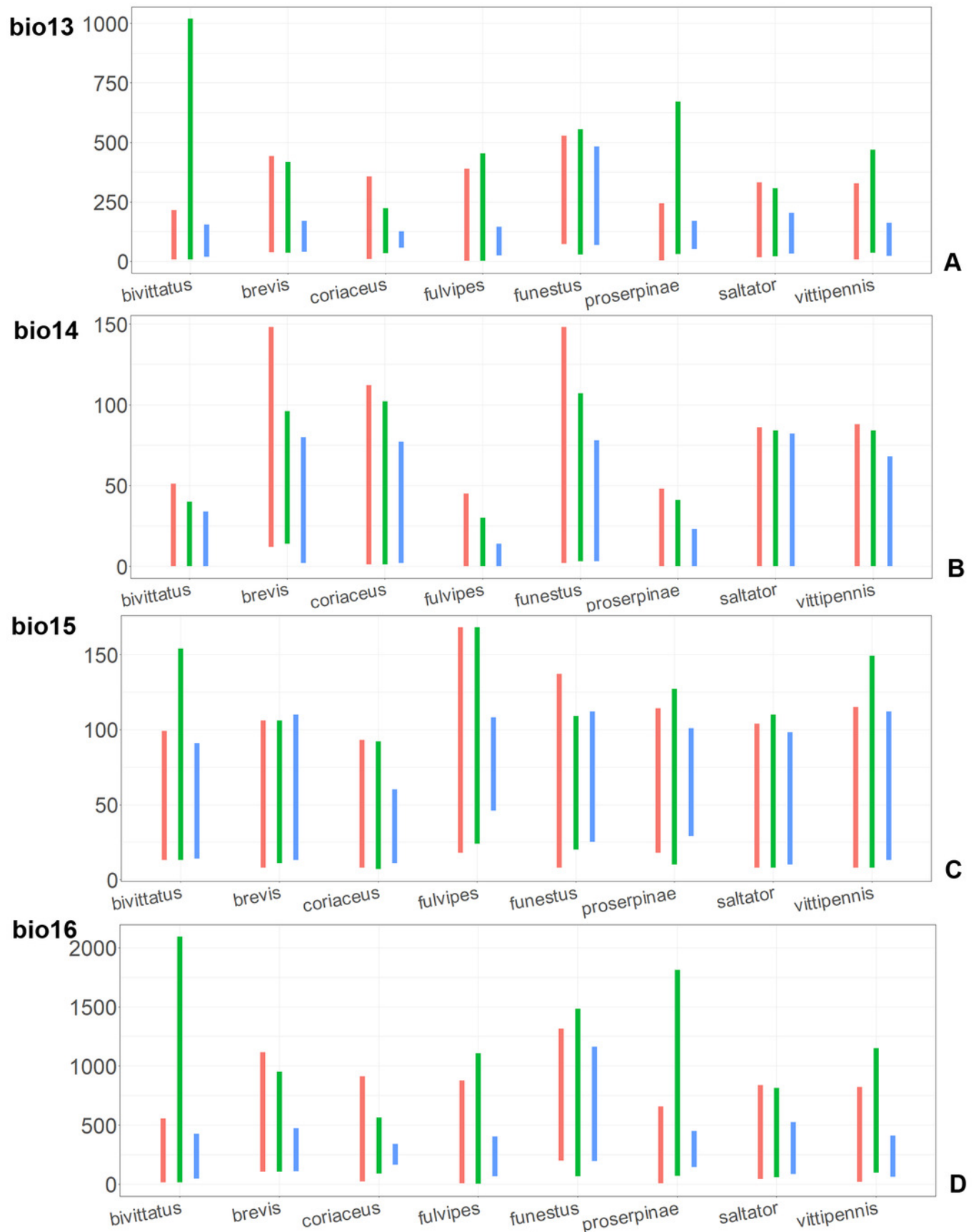
Figure 11

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.

bio17

bio18

bio19