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The distribution patterns of the two-coloured bush-cricket *Bicolorana bicolor* (Philippi, 1830) (Orthoptera: Tettigoniidae) across the Asian part of its range

Закономерности распространения двуцветного скачка *Bicolorana bicolor* (Philippi, 1830) (Orthoptera: Tettigoniidae) в азиатской части его ареала

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КЛЮЧЕВЫЕ СЛОВА: травянистые ландшафты, лесостепь, степь, луг, моделирование, прогноз.

ABSTRACT. The spatial distribution of the two-coloured bush-cricket *Bicolorana bicolor* over the Asian part of its range is characterized by the set of known localities for the first time. Abundance levels and general ecological preferences of the species are described. The first Maxent models of the *B. bicolor* distribution were generated for 3 periods (current, 2021–2040, 2041–2060) and 3 Shared Socioeconomic Pathways. The species is widely distributed in temperate Asia and its populations occur in many applicable habitats (especially in plain and mountain meadows and meadow steppes). In several areas of Kazakh Uplands and the Altai Mts., the species populations may be very abundant. The predicted changes in the *B. bicolor* distribution are significant and relatively unidirectional. The optimal areas may shift northward and northeastward.

РЕЗЮМЕ. Впервые по совокупности известных местонахождений охарактеризовано распространение двуцветного скачка *Bicolorana bicolor* в азиатской части его ареала. Описаны уровни численности и общие экологические предпочтения вида. Впервые сгенерированы модели распределения *B. bicolor* методом максимальной энтропии для трёх периодов (современность, 2021–2040, 2041–2060 гг.) и для трёх сценариев социально-экономического развития. Показано, что вид широко распространён в умеренных районах Азии, а его популяции встречаются

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в различных пригодных местообитаниях (особенно на равнинных и горных лугах и в луговых степях). В некоторых районах Казахского мелкосопочника и Горного Алтая популяции вида могут быть многочисленными. Прогнозируемые изменения в распространении *B. bicolor* значительны и сравнительно однонаправлены. Оптимальные для вида районы обитания могут сместиться на север и северо-восток.

Introduction

The two-coloured (or bicolor meadow) bush-cricket *Bicolorana bicolor* (Philippi, 1830) is widely distributed species across the southern parts of the temperate forest areas, the forest-steppes and the steppes of Eurasia. A. Liana [1987] published the map of the species range, but some data concerning the species distribution in the Asian part of its range were missed (cf. Storozhenko [2004]). However, this part of the species range is very important, because its local populations are numerous and often abundant. The goals of this paper are, first, to characterize the general distribution of *Bicolorana bicolor* in the Asian part of its range, second, to produce the species distribution models based on several sets of bioclimatic variables for different periods (contemporary and future) and, third, to compare these models and to discuss some possible shifts in the species distribution.

Materials and Methods

We collected data on the species distribution from 1976 until 2023 in the Asian parts of its range: from the Ural Mts. on the west and Pacific Ocean on the east and mainly between the southern border of the taiga life zone (about 56°N), and the southern border of the temperate deserts (about 40°N) including the Tien (Tian) Shan and Tarbagatai Mts. The native vegetation of these areas was quite diverse and included different forests, forest-steppes, steppes, semi-deserts, and northern deserts. However, many local ecosystems were transformed and are used as agricultural fields and rangelands [Isachenko, 1985]. There were and are different meadows, especially along local river valleys and in mountains. Across the local plains, average temperatures are relatively moderate (mean temperatures of the warmest month are between 16 to 32°C, the same for the coldest month may be from –4 to –37 °C), and average annual precipitation amounts vary between 125 to 860 mm [Isachenko, 1985].

We described the species distribution on the basis of quantitative and qualitative samples from natural, semi-natural and transformed ecosystems, usually in July and August. Two main quantitative methods were used: (1) sampling during a fixed period of time in each habitat studied [Gause, 1930; Sergeev, 1986, 1997]: insects were collected with a standard net (commonly 40 cm diameter) over a period of 10–30 minutes and results have been recomputed to an hour; (2) the standard sweep nettings were done (from 50 to 200 sweep numbers) and results have been recalculated to 100 sweeps.

We estimated geographic coordinates by the Glonass/GPS handheld devices during our field studies after 1998 and also used Google Earth Pro (©Google 2022) to determine them for localities investigated before 2000. Besides our own data, we used some old data too, especially collected during the field trips of Novosibirsk State University (1960–1986) and the Institute of Systematics and Ecology of Animals (the former Biological Institute, Novosibirsk, Russia). We also used the data from different publications [Zubowsky, 1900; Adelung, 1906; Pylnov, 1911; Bey-Bienko, 1925, 1927, 1930, 1949; Tarbinskij, 1925; Wnukowskij, 1926; Miram, 1928; Nefedov, Miram, 1939; Popov, 1965; Čejchan, 1968; Mistshenko, 1968; Bazyluk, 1970, 1972; Chogsomzhav, 1972, 1974; Akulova, 2008; Ermakova, 2014] and data from the collections of Novosibirsk State University, Gorno-Altaisk State University, and the Institute of Systematics and Ecology of Animals. The studied specimens are chiefly in the collections of Novosibirsk State University, the Institute of Systematics and Ecology of Animals (Novosibirsk), and the Federal Scientific Center of the East Asia Terrestrial Biodiversity (Vladivostok). Our set of data includes the geographic coordinates of 216 localities.

To generate the species distribution models over the Asian parts of *B. bicolor* range we used the machine learning, maximum entropy modelling, namely Maxent 3.4.4 [Phillips *et al*., 2006, 2017; Elith *et al*., 2011]. This approach is based only on presence data. To generate the Maxent models we used the full sets of the applicable bioclimatic variables at the 30 arcsecond spatial resolution [Fick, Hijmans, 2017; WorldClim, 2022] to compare results for the same territory, but for different periods. We rated accuracy of these models by using the AUC (the area under the receiver operating characteristic curve) values for sets of 25 replicates with cross-validation. Significance of climatic variables was determined on the basis of their predictive contributions and Jackknife tests. To forecast some possible shifts in the species distribution the "Future climate data" (19 standard averaged bioclimatic variables) for 2021–2040 and 2041–2060 downscaled from the global climate model CNRM-ESM2-1 (Centre National de Recherches Météorologiques and Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique, France) [Séférian, 2018] at the 30 arcsecond spatial resolution and for the three Shared Socioeconomic Pathways (1-2.6, 2-4.5, 3-7.0) [Meinshausen *et al*., 2020] were used. A Lambert conformal conic projection was chosen as the basic map. Maps of species distribution were generated on the basis of geographic coordinates with QGIS 3.18.3.

Results

GENERAL DISTRIBUTION. *Bicolorana bicolor* occurs mainly across the southern parts of the forest life-zone, the forest-steppes and the steppes. In Europe, its range occupies territories mainly between North and Baltic Seas on the north and the northern boundary of Mediterranean Europe on the south. However, the local populations of the species occur in the southernmost parts of Sweden [Kindwall, 1995], in the Pskov Region (Russia) [Ozerski, 2019] and in the south taiga of the Komi Republic (Russia) [Kulakova, Tatarinov, 2020]. It is known from the steppes of East European Plain [Medvedev, 1928]. *B. bicolor* is also distributed across the mountains of Mediterranean Europe [Puissant, Voisin, 1999; Fontana et al., 2004; Agabiti, Fontana, 2005; Bramanti, 2017; Mulder, 2023], the Crimean (Yayla) Mts. [Likhovid, 1997], and the Caucasus [Mulder, Mulder, 2020]. However, all specimens from the Caucasus should be checked, because they may belong to *Bicolorana burri* (Uvarov) [Tarbinsky, 1940].

Bicolorana bicolor is more or less common in the central parts of Europe and is associated with meadows and

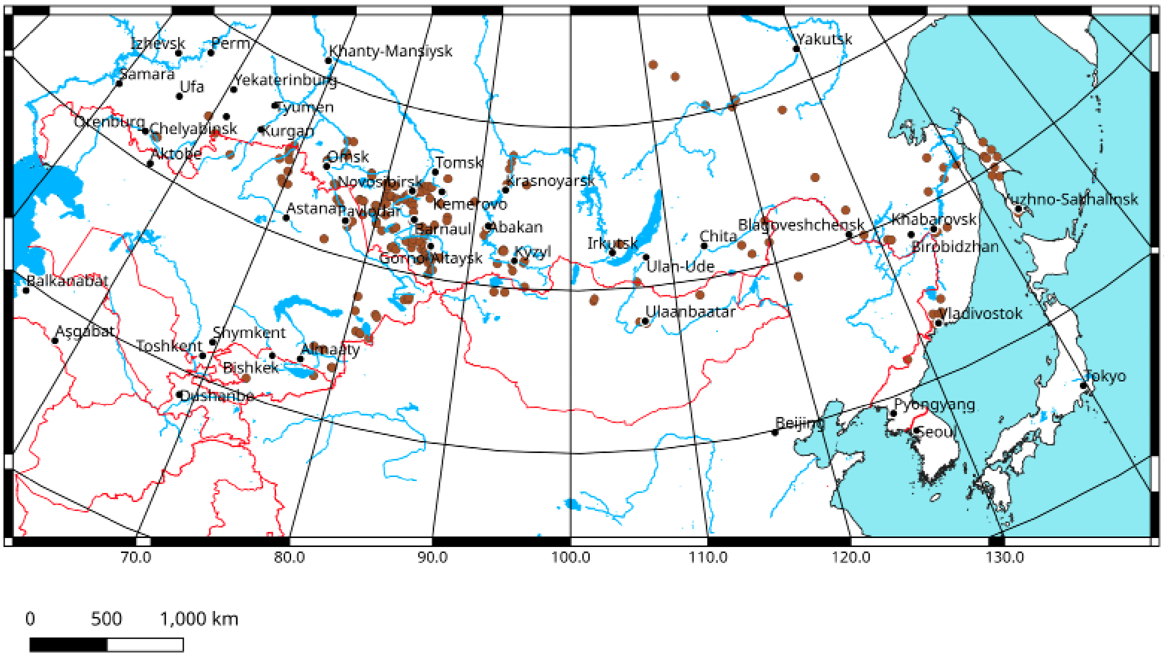


Fig. 1. General distribution of *Bicolorana bicolor* across the Asian part of the species range.
Рис. 1. Распространение *Bicolorana bicolor* в азиатской части ареала вида.

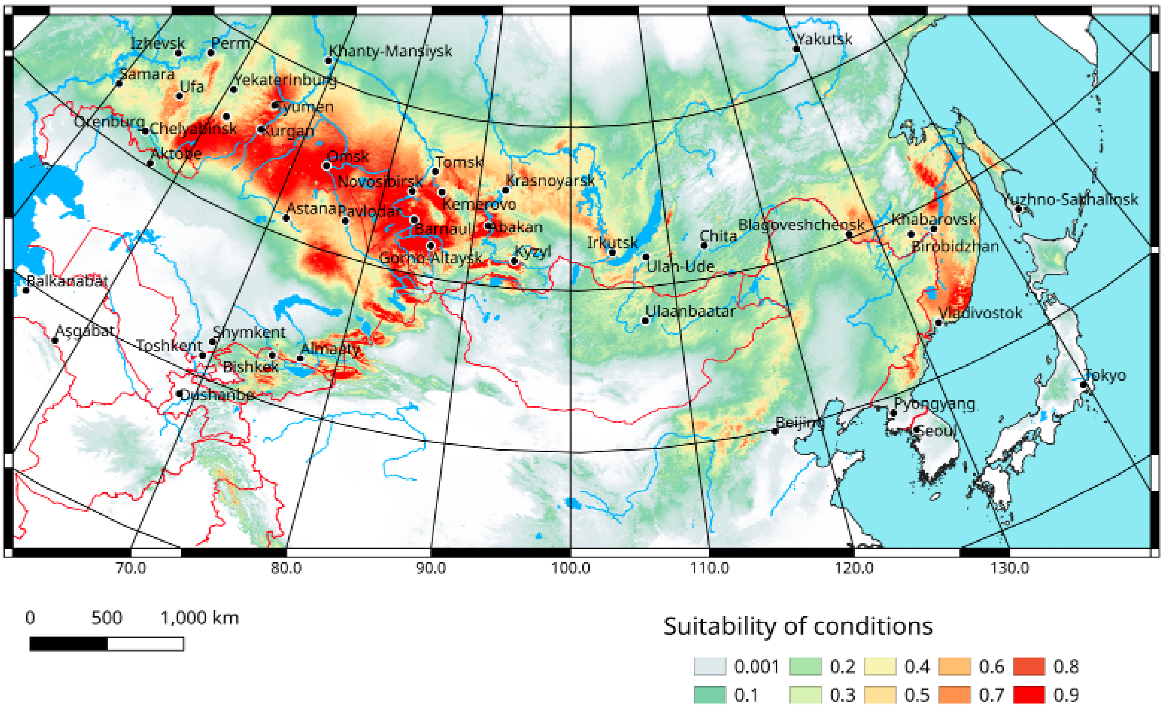


Fig. 2. Predicted probabilities of suitable conditions for *Bicolorana bicolor* (all bioclimatic variables for 1970–2000; point-wise means for 25 replicates with cross-validation).
Рис. 2. Оценка пригодности местообитаний *Bicolorana bicolor* (все биоклиматические переменные для периода 1970–2000 гг.; средние по пикселям по 25 повторностям с кроссвалидацией).

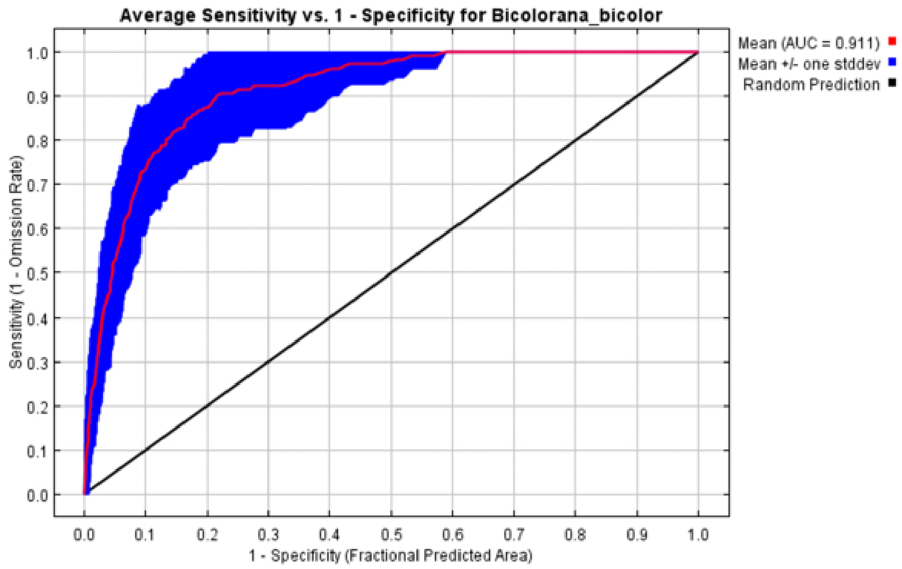


Fig. 3. Reliability test for the *Bicolorana bicolor* distribution model (all bioclimatic variables for 1970–2000; 25 replicates with cross-validation).
Рис. 3. Тест на надежность модели распространения *Bicolorana bicolor* по площади под кривой (AUC) (все биоклиматические переменные для периода 1970–2000 гг.; 25 повторностей с кроссвалидацией).

Table 1. Predictive contributions for all data.
Таблица 1. Предсказательный вклад биоклиматических переменных.

Bioclimatic variables	Percent contribution	Permutation importance
1 — Annual mean temperature	**27.7**	26.1
2 — Mean diurnal range	7.4	3.6
3 — Isothermality	6.9	5.9
4 — Temperature seasonality	1.6	14.3
5 — Max temperature of warmest month	0.9	6.1
6 — Min temperature of coldest month	6.5	0.9
7 — Temperature annual range	**11**	2.8
8 — Mean temperature of wettest quarter	0.9	0.1
9 — Mean temperature of driest quarter	0.5	1.7
10 — Mean temperature of warmest quarter	2.3	9
11 — Mean temperature of coldest quarter	0.3	4.1
12 — Annual precipitation	1.5	0.1
13 — Precipitation of wettest month	0.4	4.7
14 — Precipitation of driest month	**10.8**	0.2
15 — Precipitation seasonality	2.9	3.9
16 — Precipitation of wettest quarter	3.5	4.2
17 — Precipitation of driest quarter	0.1	1.3
18 — Precipitation of warmest quarter	**12.5**	2.9
19 — Precipitation of coldest quarter	2.3	7.9

In bold —four most significant variables steppes [Dobrolyubova, Yakushov, 2013; Kristín *et al*., 2020 etc.], but it is rare near the northern boundary of the species range [Kindwall, 1995; Ozerski, 2009]. In some populations, macropterous adults could be very abundant [Nadig, 1986]. However, flight possibilities of the macropterous form are under question [Heidinger *et al*., 2018]. In any case, *B. bicolor* can passively migrate with hay [Wagner, 2004].

In Asia, the species range covers a vast territory from the Ural Mts. to Sakhalin Island and containing the southern parts of the forest life zone (including coniferous forests), all forest-steppes and steppes (except the steppes of North China) (Fig. 1). *B. bicolor* is widely but locally distributed across the Republic of Sakha (Yakutia), except its north-western and northern parts [Ermakova, 2014]. It also occurs in Saryarka (Kazakh Uplands), Tarbagatai and the Tien Shan Mts. The species was also mentioned for the desert areas of Ustyurt Plateau in Uzbekistan [Bazarbaeva *et al*., 2022], but this mention is evidently based on misidentification of the specimen from the genus *Bergiola* which is widely distributed across Turan Plain.

In the Asian parts of its range, *B. bicolor* is also associated with different meadows and steppes. For instance, in the forest-steppes of the south-western parts of West Siberian Plain, it occupies almost all applicable habitats from wet meadows up to relatively dry steppe plots and its abundance is relatively high [Nefedov, Miram, 1939]. The similar pattern was described for the south-eastern parts of this Plain [Sergeev, 2019, 2021; Sergeev, Efremova, 2020]. In the North Tien Shan Mts., the species occurs over the mountain steppes and meadows as well [Myrzaliev, 1988; our data]. It prefers altitudes between 900 and 2000 m.

The population distribution of *B. bicolor* looks like insular, because the species is absent or almost absent on both meadows with high vegetation and the typical and dry steppes. Its abundance is usually moderate and varies between 6 and 60 insects per hour. However, *B. bicolor* may be abundant in some meadow habitats. In the forest-steppes of the south-eastern part of West Siberian Plain, its maximal registered abundance was 120 per hour, in the Bayanaul Mts. (Kazakh Uplands) —

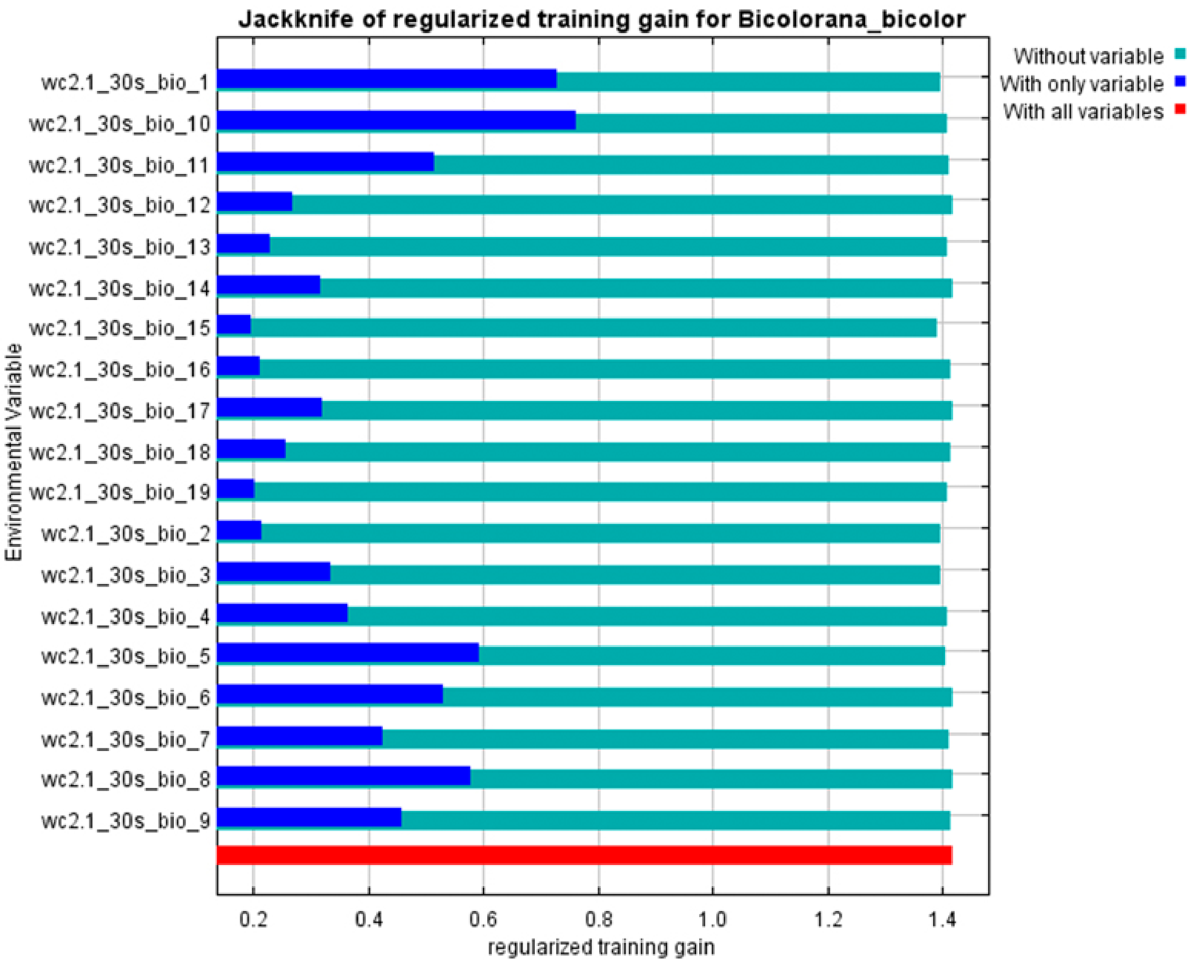


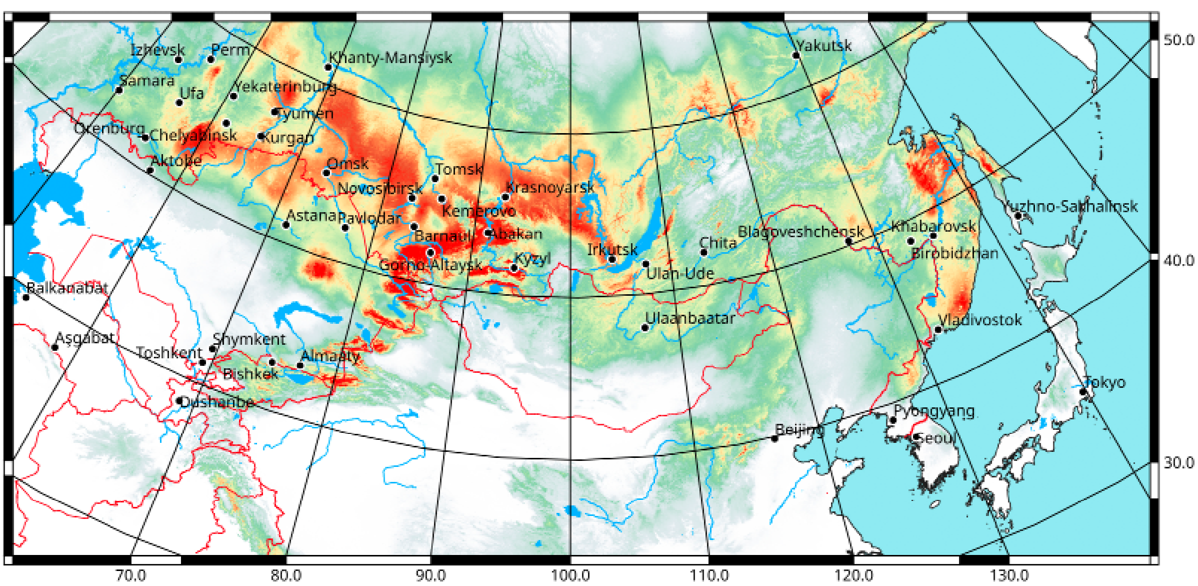
Fig. 4. Jackknife test for the *Bicolorana bicolor* distribution model (all bioclimatic variables for 1970–2000; 25 replicates with cross-validation).
Рис. 4. Тест складного ножа модели распространения *Bicolorana bicolor* (все биоклиматические переменные для периода 1970–2000 гг.; 25 повторностей с кроссвалидацией).

484 and, in different meadow habitats of North and Central Altai, it usually varied between 230 and 594 specimens per hour. The species is found across roadsides, irrigation channels, lawns, and forest clearings as well.

DISTRIBUTION MODELLING. The species distribution model for the contemporary period (Fig. 2) corresponds very well to the distribution of known localities (Fig. 1). However, it shows that some areas with very suitable conditions are distributed outside the known species range. Some of them are in the steppe territories of North China. The model is well supported with AUC = 0.911 (Fig. 3).

The annual mean temperatures are the most significant variable (Table 1 and Fig. 4). Besides, precipitations of the warmest quarter, the annual temperature ranges, and precipitations of the driest month are important as

a



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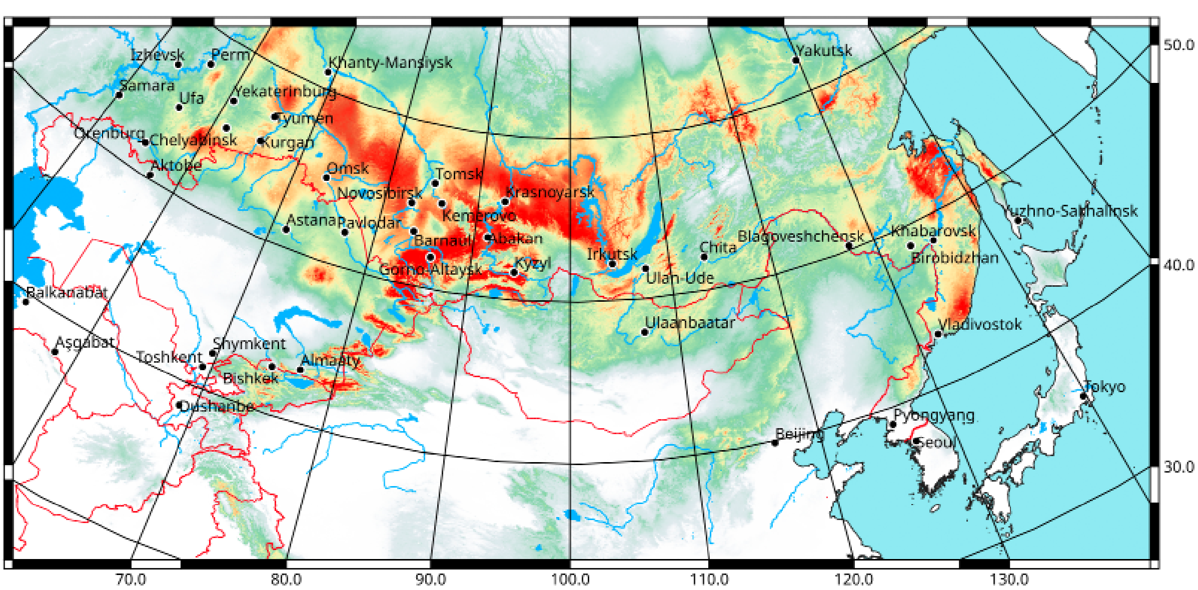


Fig. 5. Predicted probabilities of suitable conditions for *Bicolorana bicolor* (forecasts of bioclimatic variables for 2021–2040 and 2041–2060 according the global climate model CNRM-ESM2-1 [Séférian, 2018]; point-wise means for 25 replicates with cross-validation): a, c, e — 2021–2040; b, d, f — 2041–2060; a, b — the 1–2.6 Shared Socioeconomic Pathway based on low greenhouse gas emissions [Meinshausen *et al*., 2020].
Рис. 5. Оценка пригодности местообитаний *Bicolorana bicolor* по всем данным о распространении вида и прогнозным биоклиматическим переменным для периодов 2021–2040 и 2041–2060 гг. по глобальной климатической модели CNRM-ESM2-1 [Séférian, 2018] (средние по пикселям по 25 повторностям с кроссвалидацией): a, c, e — 2021–2040 гг.; b, d, f — 2041–2060 гг.; a, b — по сценарию социально-экономического развития 1–2,6 (невысокий уровень эмиссии парниковых газов) [Meinshausen *et al*., 2020].

well (Table 1). The Jackknife test allows to add several other variables as the important ones (Fig. 4): mean temperatures of the warmest quarter, maximal temperatures of the warmest month, mean temperatures of the wettest quarter, and minimal temperatures of the coldest month.

The comparative analysis of the species distribution models generated for the contemporary period and for two periods in the future (2021–2040 and 2041–2060) (Fig. 5) shows that the optimal areas for *B. bicolor* will shift northward and northeastward: in West and Central Siberia – up to Khanty-Mansiysk (61°N) near the confluence of the Ob and Irtysh Rivers and Yeniseysk (56°N) near the confluence of the Yenisei and Angara Rivers, and in the Far East — up to the northern parts of Khabarovsk Region (Krai) (58–59°N). Besides, the southern and central parts of the Republic of Sakha (Yakutia) may become relatively suitable for this bush-cricket. On the contrary, applicability of the central parts of Kazakhstan, North Mongolia and North China will decrease. These trends look like uniform and increase from now to 2041–2060 and from the scenarios of the low to the high levels of greenhouse gas emissions.

c, d

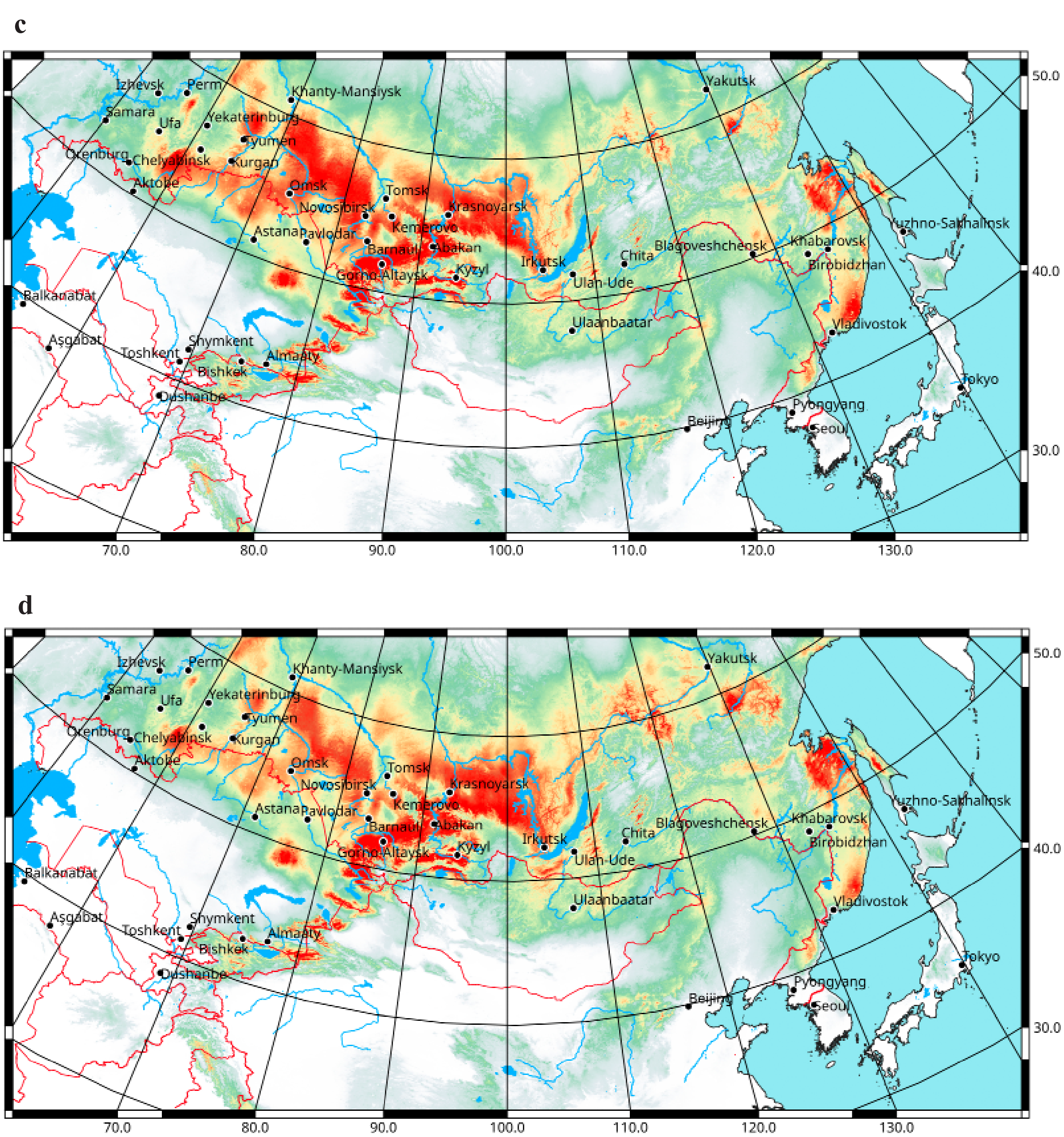
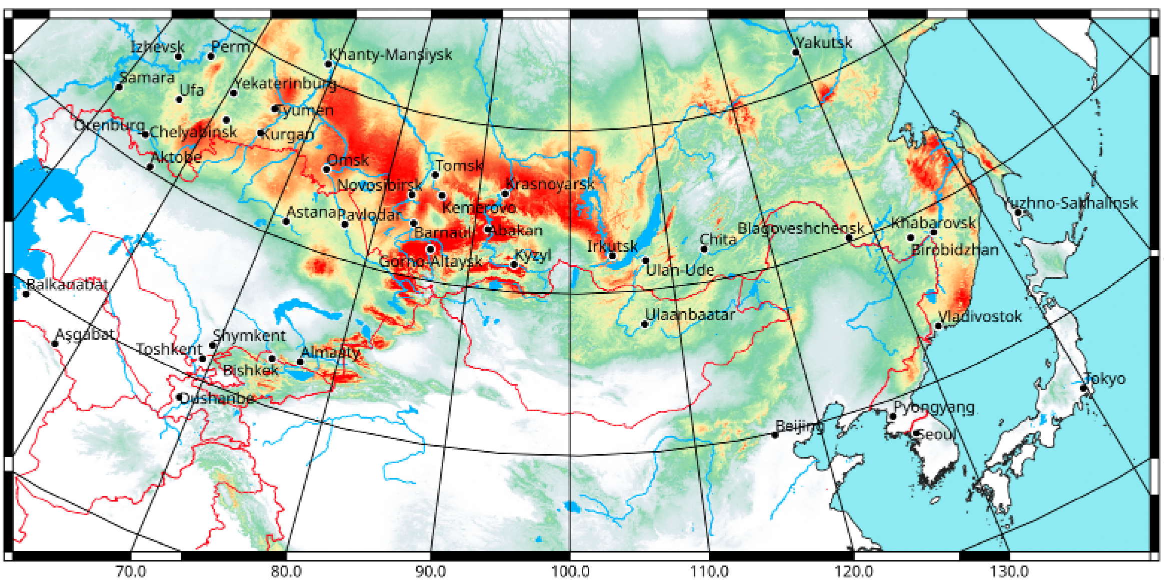


Fig. 5. c, d — the 2–4.5 Shared Socioeconomic Pathway based on intermediate greenhouse gas emissions [Meinshausen *et al*., 2020].
Рис. 5. c, d — по сценарию социально-экономического развития 2–4,5 (средний уровень эмиссии парниковых газов) [Meinshausen *et al*., 2020].

Discussion

The European populations of *B. bicolor* were assessed for the IUCN Red List of Threatened Species [Hochkirch *et al*., 2016]. It was listed as Least Concern, and, in Europe, its colonies remain more or less common. The species occurs in some natural reserves, e.g. in the Mordovia State Nature Reserve [Ruchin, Mikhailenko, 2018] and the Askaniya-Nova Biosphere Reserve [Medvedev, 1928]. Our data show that, in Asia, the species is widely distributed, its populations occur in many applicable habitats (especially in plain and mountain meadows and meadow steppes). In several areas of Kazakh Uplands and the Altai Mts., the species populations may be very abundant. *B. bicolor* is also known from the local natural reserves, such as the Ilmen State Reserve in the Ural Mts. [Lagunov, 2006], the Bayanaul National Park in Kazakh Uplands [Kadyrbekov *et al*., 2017; our data], the Troitsk Forest-Steppe Reserve (now the so-called zakaznik in the Chelyabinsk Oblast) [Nefedov, Miram, 1939], the Lazovsky and Kedrovaya Pad Nature Reserves in the Far East [Storozhenko, 2006, 2009].

e



f

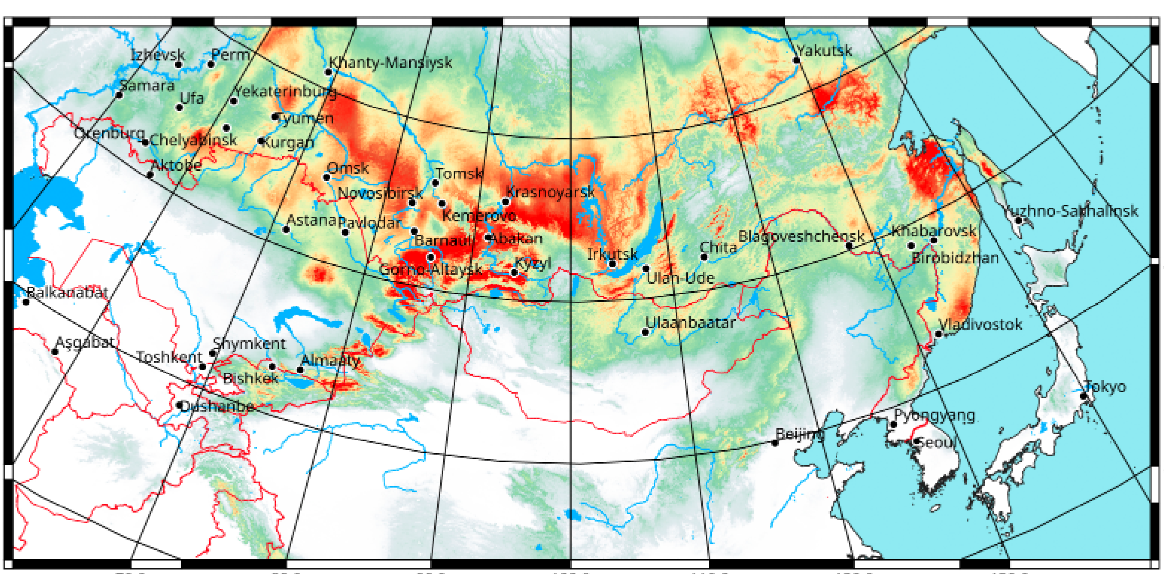


Fig. 5. e, f — the 3–7.0 Shared Socioeconomic Pathway based on high greenhouse gas emissions [Meinshausen *et al*., 2020].
Рис. 5. e, f — по сценарию социально-экономического развития 3–7,0 (высокий уровень эмиссии парниковых газов) [Meinshausen *et al*., 2020].

Comparisons between the models produced for several species of the long-horned Orthoptera from temperate Asia, namely *B. bicolor*, *Miramiola pusilla* (Miram) [Sergeev, Molotsov, 2024], and *Paracyphoderris erebeus* Storozhenko [Storozhenko *et al*., 2023] show quite different trends. Shifts forecasted for *P. erebeus* are very weak, almost unrecognizable. Some predicted changes in the distribution of *M. pusilla* look like discordant. However, the possible shifts in the distribution of *B. bicolor* are significant, relatively unidirectional and match to the global warming trends.

Conflict of interest

All authors declare no conflicts of interest.

Acknowledgments

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