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Distribution patterns of the Baraba buzzing grasshopper *Angaracris barabensis* (Pallas) (Orthoptera: Acrididae)

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Abstract
Aim. *Angaracris barabensis* is widely distributed across the Asian grasslands. It is often qualified as one of the important pests. The aim of the paper is to estimate possible shifts of its distribution relative to global warming.
The geographic coordinates of 384 localities were determined for the species. Two different approaches to species distribution modelling (maximum entropy and multidimensional ellipsoid envelope) were used.
The general patterns of distribution were described. Several models of the species distribution were generated and compared. The main factors of its distribution are revealed. Ecological modelling predicts opportunity of possible northward shifts of the species range in Central and East Siberia and persistence of areas of possible harmfulness in South Siberia, Mongolia and North China.
Our predictions show two opposite trends. In the western and south-eastern parts of the species range, suitability of conditions will decrease. In the central and north-eastern parts, the suitability will remain almost the same or even increase.
The comparative analysis shows there are no evident contemporary shifts of range boundaries of *A. barabensis* associated with global warming per se or this tendency is extremely weak. However, the distribution of suitable conditions can change significantly during the next several decades.

Key Words
Inner Asia, Acrididae, grasslands, steppe, range, population, modelling, plant protection, forecast.

Закономерности распространения барабинской трещотки *Angaracris barabensis* (Pallas) (Orthoptera: Acrididae)

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Резюме
Цель. *Angaracris barabensis* — вид, широко распространенный в злаковниках Азии. Часто он считается одним из важнейших вредителей. Цель статьи – оценить возможные изменения его распространения в условиях глобального потепления.
Определены географические координаты 384 точек находок вида. Использованы два разных подхода к моделированию распространения (максимальной энтропии и эллипсоидальных многомерных экологических ниш).
Описаны общие закономерности распространения. Сгенерированы и сопоставлены несколько моделей распределения вида. Выявлены основные факторы его распространения. Экологическое моделирование демонстрирует возможность сдвига его ареала на север в Средней и Восточной Сибири и сохранение районов возможной вредоносности вида на юге Сибири, в Монголии и Северном Китае.
Выявлены два противоположных тренда. В западной и юго-западной частях ареала вида вероятно снижение пригодности местообитаний. В центральной и северо-восточной частях уровни пригодности либо не изменятся, либо возрастут.
Сравнительный анализ показывает отсутствие очевидных смещений границ ареала *A. barabensis*, которые можно было бы связать с глобальным потеплением как таковым либо этот тренд почти не прослеживается. Вместе с тем распределение подходящих для вида условий может существенно изменится в ближайшие десятилетия.

Ключевые слова
Внутренняя Азия, Acrididae, злаковники, степи, ареал, популяция, моделирование, защита растений, прогноз.

INTRODUCTION

The Baraba buzzing grasshopper, *Angaracris barabensis* (Pallas), is the only species of the genus *Angaracris* Bey-Bienko from the tribe Bryodemini [1–3]. This tribe includes several genera mainly associated with the steppes, semi-deserts and arid mountains of Inner Asia [3–5]. The only species distributed across almost all Palaearctic Region is *Bryodemella tuberculata* (Fabricius) [3; 5; 6]. Adults of this group (in many species, both females and males) are able to fly very well and can stay in the air during several minutes and more, but these flights are not typically associated with active dispersal. The flying Bryodemini adults commonly produce sounds by wing crepitation [7; 8].

The Baraba buzzing grasshopper is widely distributed across grasslands of the temperate parts of Asia, from the Ural Mts. up to the northeastern parts of China and from the forest-steppes up to the semi-deserts and the arid mountains of the Tibetan Plateau. It prefers different variants of the steppes and the northern semi-deserts. Both grasses and dicots are its favorable food [9; 10]. Its abundance is usually relatively low, especially in the western and northern parts of its range. It may rarely damage agricultural fields and rangelands. However, local populations of the species can be very dense in the arid mountains of South Siberia and over grasslands of Mongolia and adjacent parts of China. In the beginning of the 21st century, over these territories, *A. barabensis* became one of the important pests [11–14]. The actual problem is how the species distribution and the areas of its possible harmfulness may change in the future, especially relative to global warming. The aim of the paper is to estimate some possible shifts of the *A. barabensis* distribution as a potential pest species across its whole range.

MATERIALS AND METHODS

Study territory

Field data were collected from 1977 until 2023 in the southern parts of Siberia and in the northern parts of Kazakhstan. The Ural Mts. mainly borders this area on the west, and the Da Hinggan (Great Khingan) Mts. — on the east. Its northern boundary is approximately defined by the southern border of the taiga life zone (about 56°N), and the southern one — by the deserts (about 40°N). Some populations of the species are known from the arid mountains of south Mongolia and the Tibetan Plateau as well [3; 4; 15]. Originally, these territories were covered by forest-steppes, steppes and semi-deserts, but many local landscapes were converted to agricultural lands (fields and pastures) [16; 17]. Across the local plains, average temperatures are relatively moderate (mean temperatures of the warmest month are between 16 °C to 24 °C, the same for the coldest month may be from –4 °C to –34 °C), and average annual precipitation amounts vary between 125 to 610 mm [16; 18].

Field studies

The species distribution was characterized by collecting in natural, semi-natural and transformed ecosystems, usually in July and August when adults were dominated [19]. Three different quantitative methods were used. First, sampling during a fixed period of time was done in each site investigated [20; 21]. Orthopterans were collected with a standard net (commonly 40 cm diameter) over a period of 10–30 minutes. Results for each habitat have been recomputed to an hour. Second, the standard sweep nettings were done (from 50 to 200 sweep numbers). Results have been recalculated to 100 sweeps. Third, we estimated insects' densities on randomly placed plots 0.25 x 0.25 m^2 (in some cases — 0.5 x 0.5 m^2 or 1 x 1 m^2). Two or three methods were frequently used in the same time. After 1998, the Glonass/GPS navigation devices were used to determine geographic coordinates. Some possibilities of Google Earth Pro (©Google 2022) were also handled to ascertain the same parameters for habitats studied before 2000. The main part of studied specimens is 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).

Data analysis

Besides our field data, we examined some old data as well, especially collected during the expeditions 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 [3; 19; 22–39] and data from the collections of Zoological Institute (Saint Petersburg, Russia), including materials of the so-called Soviet-Mongolian expeditions, Novosibirsk State University, and the Institute of Systematics and Ecology of Animals. Our set includes the geographic coordinates of 384 localities.

We used two different approaches to produce the species distribution models over the whole range: first, Maxent 3.4.4 based on the machine learning, maximum entropy modelling [40–43], and, second, 'ellipsenm' producing a multidimensional ellipsoid envelope model of an ecological niche [44]. Both have some limitations. They are based only on presence data, depend on the number of points, selected options of modelling and selected sets of variables [40–45]. Besides, the last one is very sensitive to correlation between variables. To create the Maxent models we exploited the full sets of the applicable bioclimatic variables to equate results for the same territory, but for different periods. Accuracy of these models was rated 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 rated by their predictive contributions and Jackknife tests. The maximum entropy models were generated with following options: features — auto, output format — cloglog, regularization multiplier = 1 [40]. To produce the 'ellipsenm' models we selected only 6 variables from the 19 standard annually averaged bioclimatic ones [46; 47], namely the annual mean temperature (bioval1), maximal temperature of the warmest month (5), minimal temperature of the coldest month (6), annual precipitation (12), precipitation of the warmest quarter (18), and precipitation of the coldest quarter (19). In this case, 25 replicates were counted as well, the method was covmat and the level used to produce the ellipsoids was 99%. The resources of WorldClim 2 [46; 47] were used, such as "Historical climate data" (19 standard annually averaged bioclimatic variables at the 30 arcsecond spatial resolution) and "Future climate data" (19 standard averaged bioclimatic variables) for 2021–2040 and 2041–2060 downscaled from the global climate model [46] CNRM-ESM2-1 (Centre National de Recherches Météorologiques and Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique, France) [48] at the 30 arcsecond spatial resolution and for the three Shared Socioeconomic Pathways (1–2.6, 2–4.5, 3–7.0) [49]. Maps of species distribution were produced on the basis of geographic coordinates with QGIS 3.18.3. A Lambert conformal conic projection was chosen as the basic map. We also used the Map Comparison Kit 3.2.3 [50] to compare maps for different periods.

RESULTS

General distribution and bionomics of Angaracris barabensis

The range of *Angaracris barabensis* is mainly associated with the Asian grasslands (Fig. 1). It is bordered by the northern limits of the Siberian forest-steppes (56–57°N) on the north and by the southern areas of the semi-deserts (about 48–49°N in the western part of the range, and about 40°N near the northern and north-eastern limits of the extreme areas of the Gobi Desert) on the south (except its mountain parts). In Inner Mongolia, the species range loops southwards, crosses the Loess Plateau and stretches to the northern and northeastern ranges of the Tibetan Plateau. On the west, the range is almost limited by the Ural Mts., and on the east, by the Great Khingan Mts. However, some populations are found on the plains of Heilongjiang (NE China) as well. *A. barabensis* is not known from mountains of Tarbagatai and Tien Shan (Kazakhstan and NW China), but occurs in the arid mountains of south Mongolia (e.g. Noyon, Gurvan Saikhan, Khanbogd) and in the northern, eastern and south-eastern parts of the Tibetan Plateau. The upper altitudinal limit of the Baraba buzzing grasshopper is elevated southwards from 1300 m in the northern parts of the Altai-Sayan Mts. to 1900 m in their southern parts [51; 52] and up to 3200–3800 m in the Tibetan Plateau [37; 38]. In the western parts of the species range, there is no significant difference between the species distribution until the 1960s [3; 19] and in the second half of the 20th century and in the beginning of the 21st century.

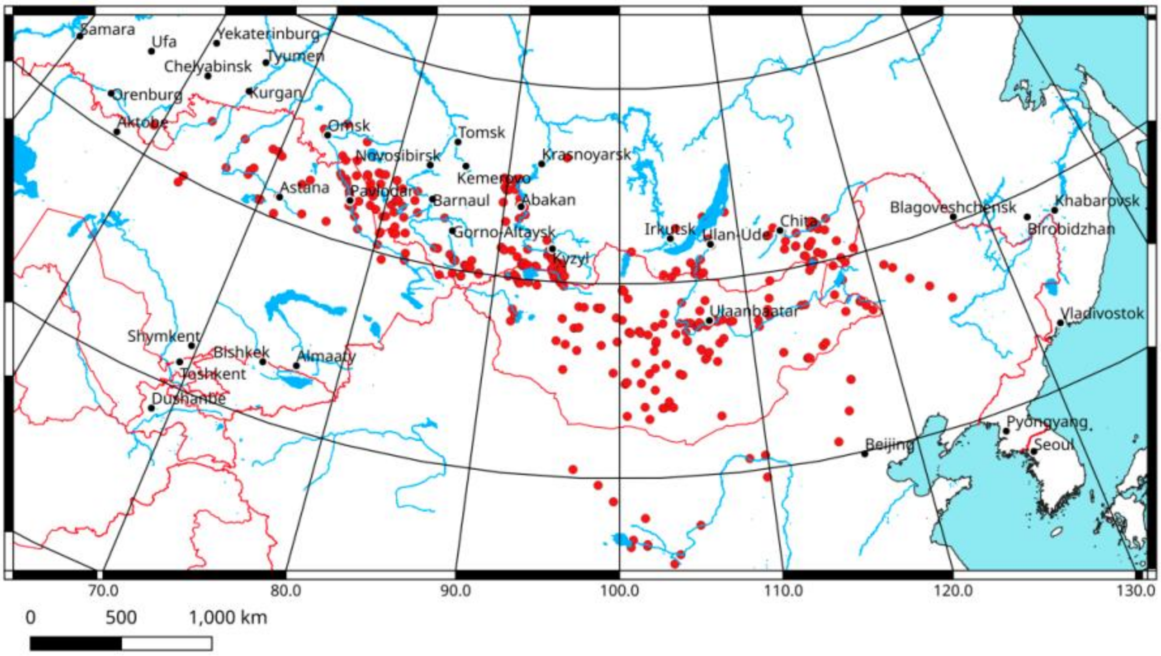


Figure 1. General distribution of *Angaracris barabensis* over its range
Рисунок 1. Общее распространение *Angaracris barabensis* в границах ареала

In the northern part of the range, *A.barabensis* inhabits the forest-steppes. However, its distribution is extremely localized. Its populations may be usually observed in the overgrazed steppe pasturelands. The species abundance is commonly low (as a rule, less than 10 grasshoppers per hour). In the steppes, its populations are associated with either the local watershed plains or the droughty habitats of upper flood plains and lower terraces, and the stony southern slopes of hills. Near the western boundary of the range, its abundance is low [32; 53]. In the southern part of West Siberia, its abundance is not very high as well (commonly between 4 and 60 per hour or between 10 and 600 per ha), but population densities may vary significantly from year to year. The geographic range of *A.barabensis* occupies also the semi-deserts of the central and eastern parts of Kazakhstan, but its local colonies are insular and its density is very low. In the steppes of south West Siberia and Kazakhstan, the Baraba buzzing grasshopper can also occupy local transformed habitats [53; 54], especially old abandoned agricultural fields and dry ditches along roads.

In the semi-arid mountains of South Siberia, the species prefers the typical and dry steppes, often rocky. Its populations may be relatively large (with abundance more than 100 per hour or 1–2 per sq m). For instance, in 2018, in the typical steppes of the central parts of Tuva, the abundance of the Baraba buzzing grasshopper varied between 250 and 612 per hour and the average density was about 3 per sq m. Besides, in the region, *A. barabensis* actively penetrates into transformed landscapes and occupies different crop and abandoned fields, canal and road sides. *A. barabensis* is common in the steppes of the Loess Plateau [55] and in different grasslands of the Qilian Mts. (NE Tibetan Plateau) as well [38].

It is a univoltine form with overwintering eggs [19; 37; 56]. Its supercooling point is very low (–32.7 °C) [56]. Adults are common during the second half of summer [19; 56]. In the steppes of the Korgalzhyn Biosphere Reserve (Kazakhstan: Akmola region), *A. barabensis* feeds mainly on different forbs, such as *Dodartia orientalis* Linnaeus, *Artemisia* spp., *Limonium gmelini* (Willdenow) Kuntze, *Salsola* sp., *Trifolium hybridum* Linnaeus. Besides, it actively consumes local lichens, namely *Xanthoparmelia vagans* (Nylander) Hale [2]. In the steppes of Altai-Sayan Mts., the species prefers to consume different groups of plants: some dicots (*Caragana pygmaea* (Linnaeus) de Candolle, *Bassia prostrata* (Linnaeus) Beck, *Artemisia frigida* Willdenow) and grasses (*Agropyron cristatum* (Linnaeus)) [9]. The similar pattern is described for the steppes of Inner Mongolia [12; 57; 58]: in the region, *A.barabensis* feeds mainly on sagebrushes (*Artemisia* spp.), cinquefoils (*Potentilla* spp.), and *Allium bidentatum* Fischer. ex Prokhanov & Ikonnikov-Galitzky. In the alpine grasslands (Gansu, NW China), it commonly eats the plant species from Polygonaceae and Asteracea [37].

In South Siberia, the species was mentioned as possible pest only in Transbaikalia (Dauria) [19]. Later, its harmfulness was noted for almost all steppes of South Siberia and Kazakhstan [59; 60]. In the end of the 20th century and in the beginning of the 21st century, it was mentioned as the important pest across the easternmost parts of its range, namely in Mongolia [14] and China (Inner Mongolia and the Tibetan Plateau) [12; 13; 61].

Ecological models of the species distribution

The analysis of the predicted distribution of *A. barabensis* established on its occurrence and two modelling approaches (Fig. 2 and 3) shows all steppes and semi-deserts between the Ural Mts. on the west and the Great Khingan Mts. on the east are very suitable for the species. Besides, very suitable conditions for this species are in the mountains of Tien Shan (NW China and Kyrgyzstan), Tarbagatai (Kazakhstan and NW China), Barlyk (Birlik), Maili and Jair (NW China) where *A. barabensis* is not found. Elevated levels of habitat suitability in the eastern part of the species range show opportunities of its upsurges (cf. [14]). Besides, the territories of the forest-steppes and the south taiga in south Siberia (e.g. along the Angara River) may be very applicable for this grasshopper. The ellipsoid envelope model (Fig. 3) shows the similar pattern, but with relatively low levels of condition suitability than the maximum entropy one (Fig. 2).

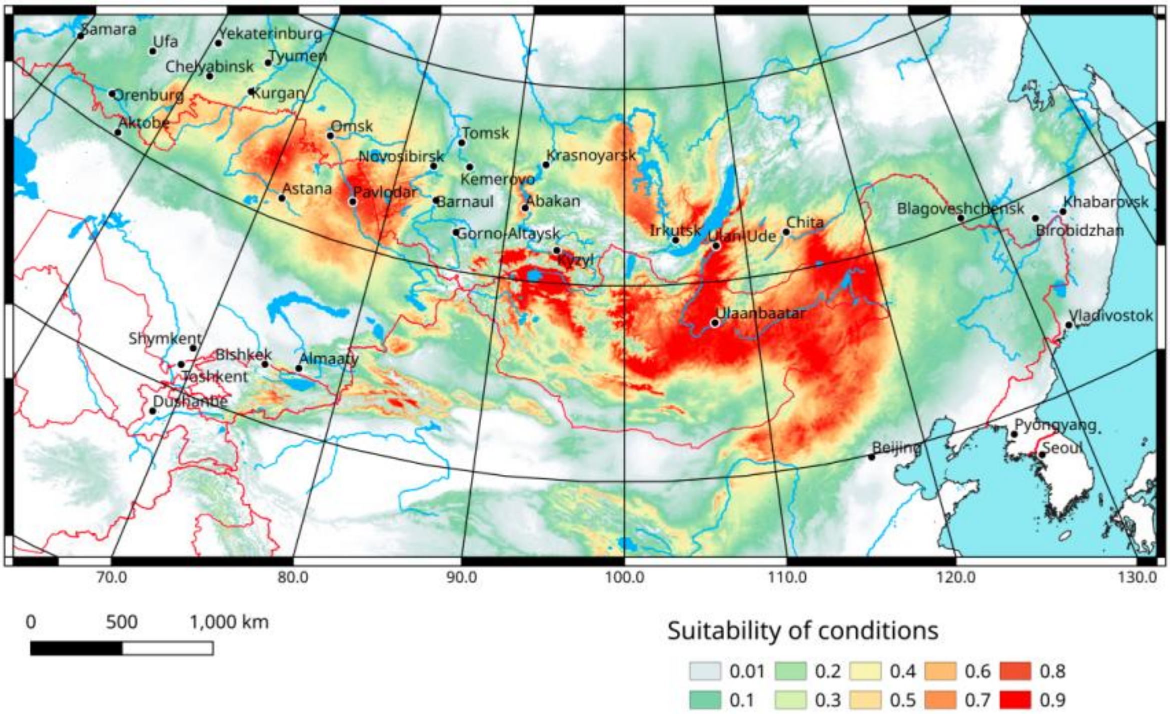


Figure 2. Predicted probabilities of suitable conditions for *Angaracris barabensis* (all bioclimatic variables for 1970–2000; point-wise means for 25 replicates) (Maxent model)
Рисунок 2. Оценка пригодности местообитаний *Angaracris barabensis* по модели максимальной энтропии (все биоклиматические переменные для периода 1970–2000 гг.; средние по пикселям по 25 повторностям)

The Maxent models are well supported (Fig. 4 and 5). The most significant variables for all data are the annual mean temperatures, annual precipitation, isothermality, temperature seasonality, and precipitation of the coldest quarter (Table 1), and precipitation of the warmest quarter, and minimal temperature of the coldest month as well (Fig. 5).

Ecologico-geographic modelling of *Angaracris barabensis* distribution in 2021–2040 and 2041–2060 predicated on the climatic model CNRM-ESM2-1 for several Shared Socioeconomic Pathways (1–2.6, 2–4.5, 3–7.0) displays that the local parts of the range may shift northwards and northeastwards (Fig. 6). However, these shifts will be relatively weak (especially in comparison with the forecasted shifts for the *Oedaleus decorus* (Germ.) distribution in West Siberia [62]. In any case, the main areas with suitable conditions for *A. barabensis* remains almost the same, but in the western and the southeastern parts of its range, the level of their applicability may significantly decrease relative to the modern situation.

As may be expected, the forecasted shifts become more significant if the level of greenhouse emissions increases (from the 1–2.6 to 3–7.0 Pathways). They also increase from now until 2041–2060. Almost all possible shifts are predicted for East and Central Siberia. The local parts of the species range will be able to move northwards and northeastwards to the modern forest-steppes and south taiga. As a result (especially after 2041 and if greenhouse gas emission will remain high), *A. barabensis* will be able to penetrate into several new regions, namely the Irkutsk Region (north-western parts) and the Republic of Sakha (Yakutia) (central parts). Besides, some areas where the species will be able to occur are in the mountains of Tien Shan (mainly in NW China and Kyrgyzstan). However, these mountain areas are far away from the real southern boundaries of the species range.

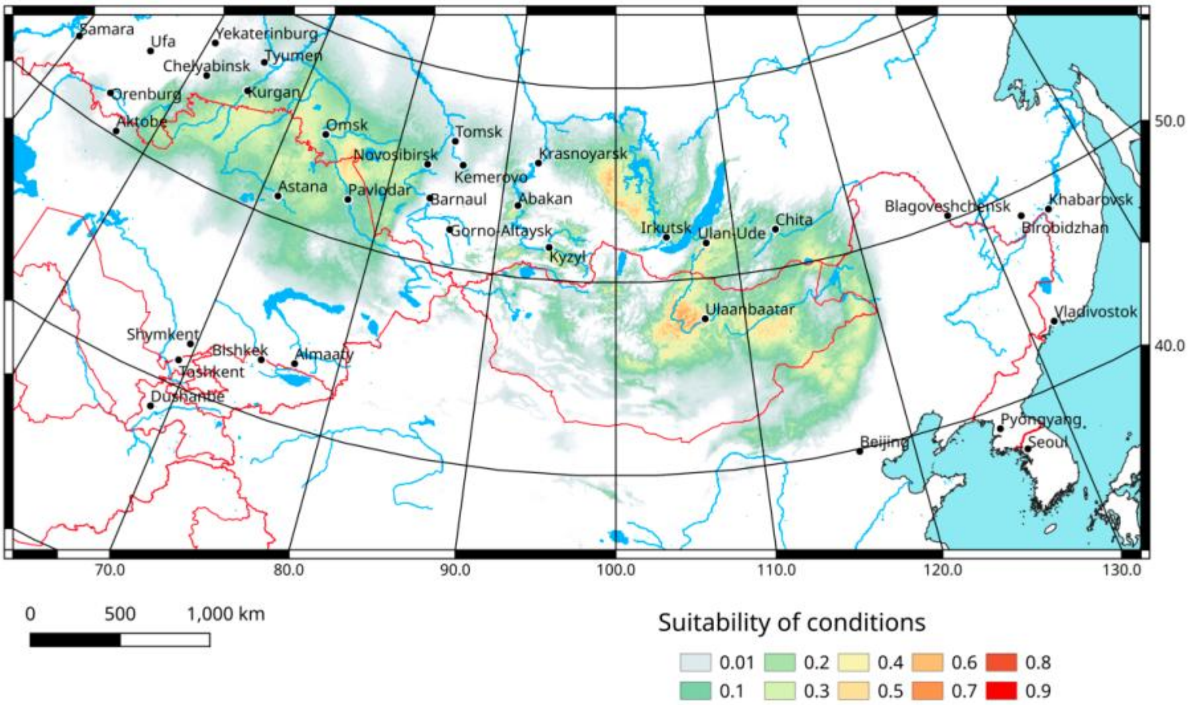


Figure 3. Predicted probabilities of suitable conditions for *Angaracris barabensis* (selected bioclimatic variables for 1970–2000; point-wise means for 25 replicates) (ellipsoid model)

Рисунок 3. Оценка пригодности местообитаний *Angaracris barabensis* по модели эллипсоидной многомерной экологической ниши (отобранные биоклиматические переменные для периода 1970–2000 гг.; средние по пикселям по 25 повторностям)

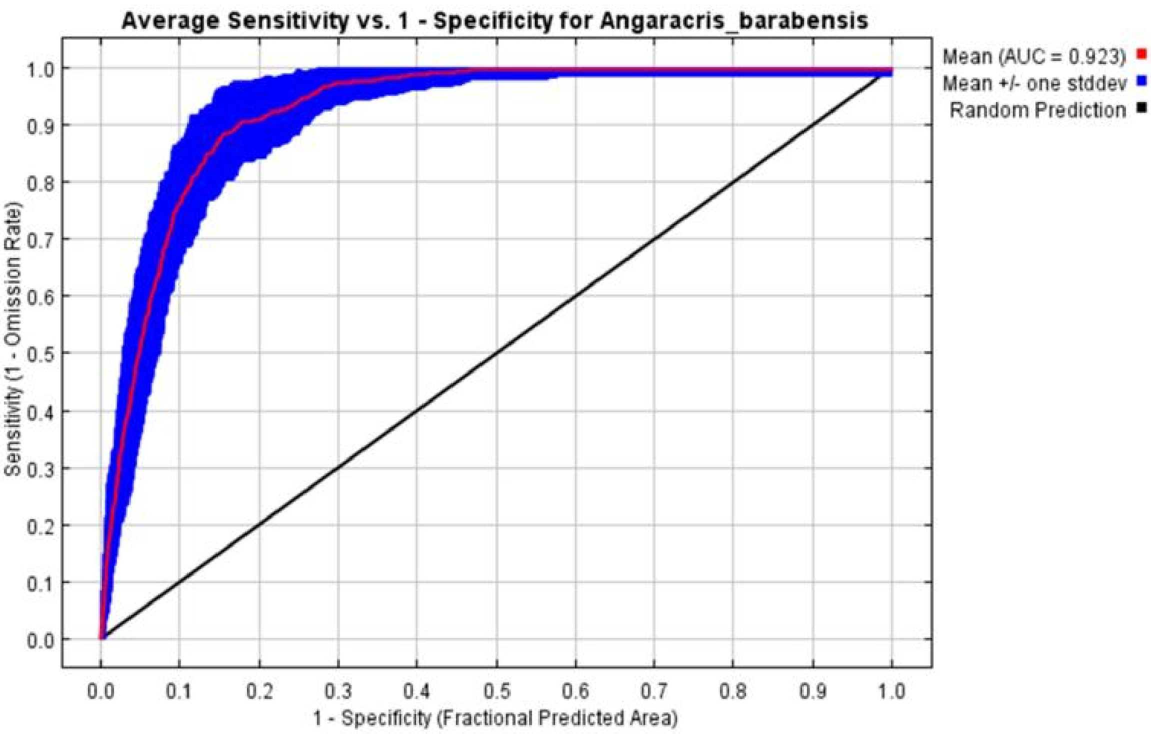


Figure 4. Reliability test for the *Angaracris barabensis* distribution model (bioclimatic variables for 1970–2000; 25 replicates with cross-validation)

Рисунок 4. Проверка надежности модели распространения *Angaracris barabensis* (биоклиматические данные за 1970–2000 гг.; 25 повторностей с кросс-валидацией)

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

Bioclimatic variable Биоклиматическая переменная	**Percent contribution** Процентный вклад переменной	**Permutation importance** Важность перестановки
1 — Annual mean temperature Среднегодовая температура	16,1	35,5
2 — Mean diurnal range Средний суточный диапазон температур (помесячно)	1,4	4,2
3 — Isothermality Изотермичность	12,3	4,4
4 — Temperature seasonality Сезонное варьирование температуры	10,8	2,4
5 — Max temperature of warmest month Максимальная температура самого теплого месяца	0,1	1,3
6 — Min temperature of coldest month Минимальная температура самого холодного месяца	6,5	1,2
7 — Temperature annual range Абсолютная амплитуда температур	0,5	0,9
8 — Mean temperature of wettest quarter Средняя температура самого влажного квартала	1,5	1,1
9 — Mean temperature of driest quarter Средняя температура самого сухого квартала	0,6	5,8
10 — Mean temperature of warmest quarter Средняя температура самого теплого квартала	0,2	0,3
11 — Mean temperature of coldest quarter Средняя температура самого холодного квартала	0,3	6,7
12 — Annual precipitation Годовая сумма осадков	13,6	24,7
13 — Precipitation of wettest month Осадки самого влажного месяца	1,3	8,6
14 — Precipitation of driest month Осадки самого сухого месяца	4	1,1
15 — Precipitation seasonality Сезонное варьирование осадков	0,9	0,6
16 — Precipitation of wettest quarter Осадки самого влажного квартала	0	0
17 — Precipitation of driest quarter Осадки самого сухого квартала	0,2	0,2
18 — Precipitation of warmest quarter Осадки самого теплого квартала	19	0,9
19 — Precipitation of coldest quarter Осадки самого холодного квартала	10,8	0

Note: In highlighted green—five most significant variables
Примечание: Зеленым выделены 5 наиболее значимых переменных

DISCUSSION

The ecologo-geographic modelling of the species distribution demonstrates that both models for climatic conditions of 1970–2000 almost coincide with the real data on the *A. barabensis* distribution over its range, but the maximum entropy model demonstrates higher levels of suitability than the ellipsoid envelope one. The recent finding of this species near the westernmost segment of its geographic range on the European slope of the Ural Mts. validates partly our prediction [63].

The first maximum entropy model of the species distribution was published in 2018 [14], but it was limited to the territory of Mongolia. If one compares our model and the model for Mongolia some evident similarity would be observed, however, our model shows the wider distribution of the areas suitable for *A. barabensis* across all territory of the country. These differences may be explained by both the limited set of the original data concerning Mongolia and some disagreements in the climatic variables, because the authors used the set of local data for the country [14]. The similarity remains almost the same for forecasted shifts based on increasing greenhouse gas emissions.

Our predictions, especially based on the high levels of greenhouse gas emissions, show two opposite trends. In the western and south-eastern parts of the species range, suitability of conditions will decrease, and one may forecast that *A. barabensis* will become relatively rare and its abundance will decline (Fig. 7). In the central and north-eastern parts of the range, especially in the intermountain basins of the Altai-Sayan Mts., in Mongolia, and in the southern parts of East Siberia, the suitability will remain almost the same or even increase. This means the Baraba buzzing grasshopper may remain one of the main pests across these territories.

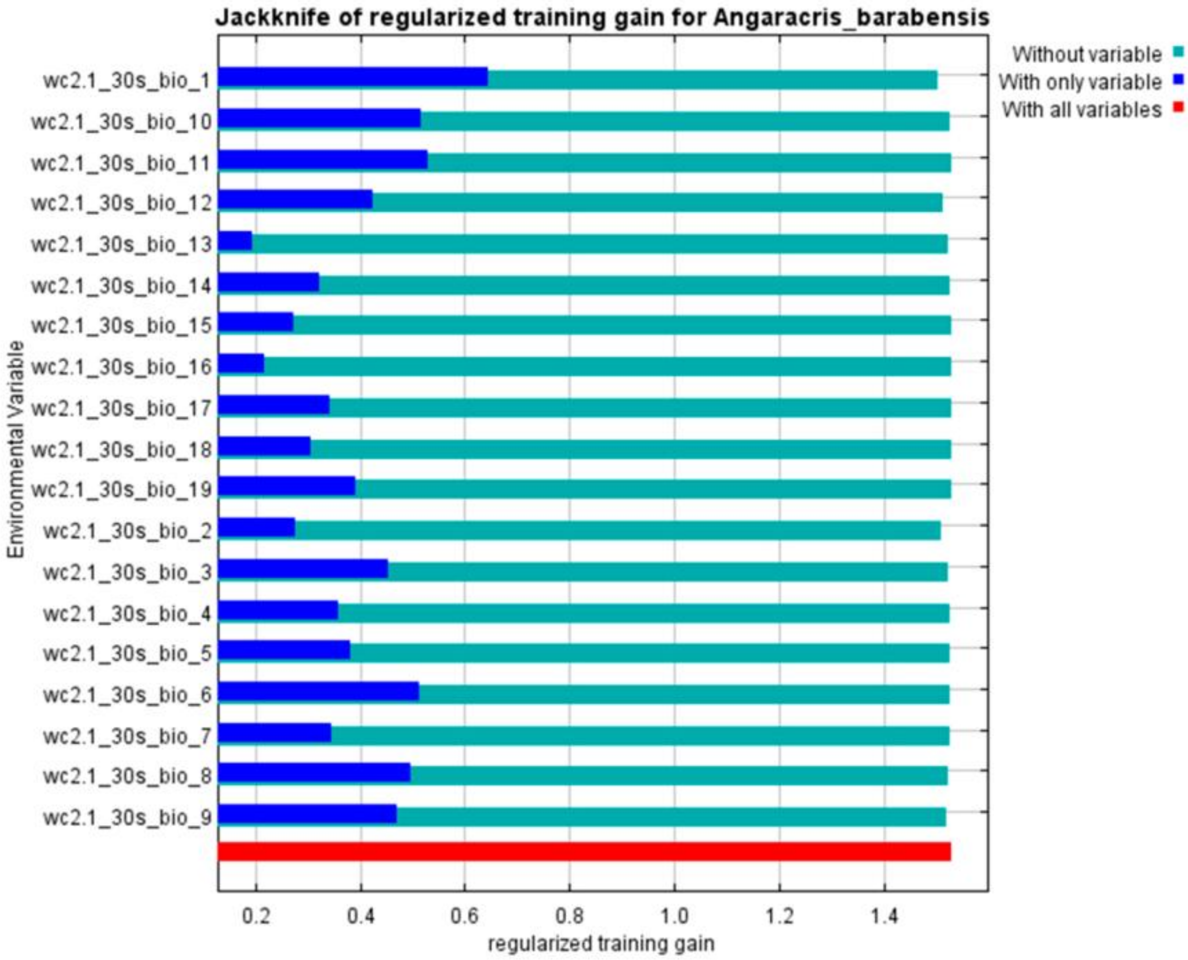
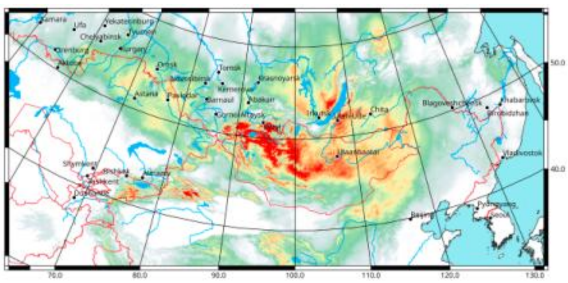
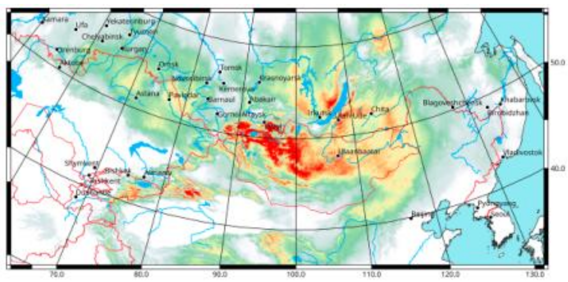


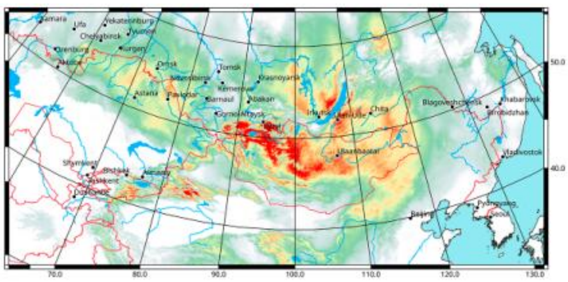
Figure 5. Jackknife of regularized training gain for the *Angaracris barabensis* distribution model
(all bioclimatic variables for 1970–2000; 25 replicates with cross-validation)
Рисунок 5. Тест складного ножа для модели распространения *Angaracris barabensis*
(все биоклиматические переменные для периода 1970–2000 гг.; 25 повторностей с кросс-валидацией)



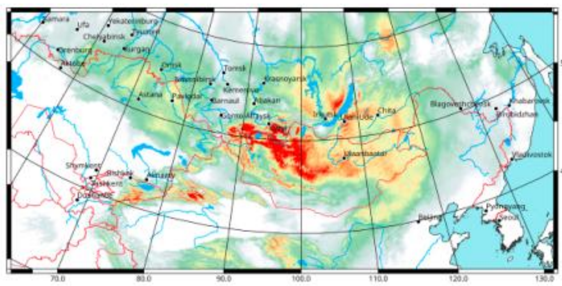
A



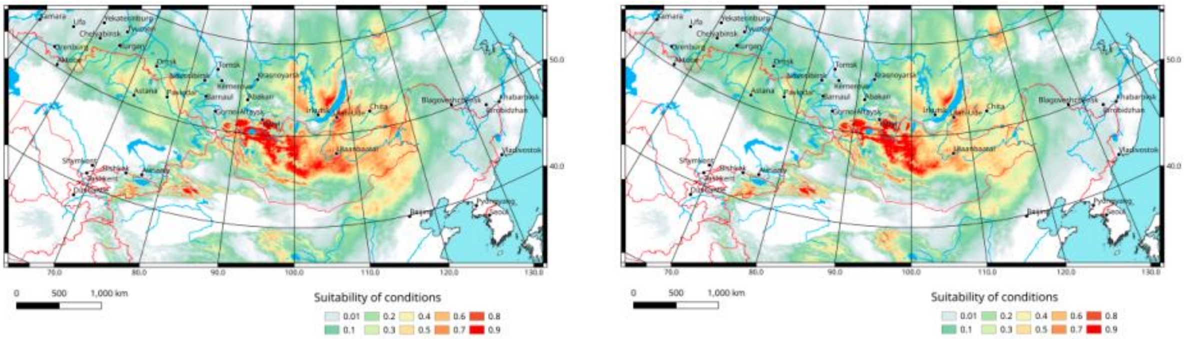
B



C



D



E F

Figure 6. Predicted probabilities of suitable conditions for *Angaracris barabensis* (forecasts of bioclimatic variables for 2021–2040 and 2041–2060 according the global climate model CNRM-ESM2-1 [48]; point-wise means for 25 replicates): (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; (C), (D) — the 2–4.5 Shared Socioeconomic Pathway based on intermediate greenhouse gas emissions; (E), (F) — the 3–7.0 Shared Socioeconomic Pathway based on high greenhouse gas emissions [49]

Рисунок 6. Прогнозируемые вероятности распределения подходящих условий для *Angaracris barabensis* (прогнозы биоклиматических переменных за 2021–2040 гг. и 2041–2060 гг. в соответствии с глобальной климатической моделью CNRM-ESM2-1 [48]; средние по пикселям для 25 повторностей): (A), (C), (E) — 2021–2040 гг.; (B), (D), (F) — 2041–2060 гг.; (A), (B) — сценарий изменения концентрации парниковых газов в атмосфере 1–2.6, основанный на низких уровнях эмиссии парниковых газов; (C), (D) — сценарий изменения концентрации парниковых газов в атмосфере 2–4.5, основанный на средних уровнях эмиссии парниковых газов; (E), (F) — сценарий изменения концентрации парниковых газов в атмосфере 3–7.0, основанный на высоких уровнях эмиссии парниковых газов [49]

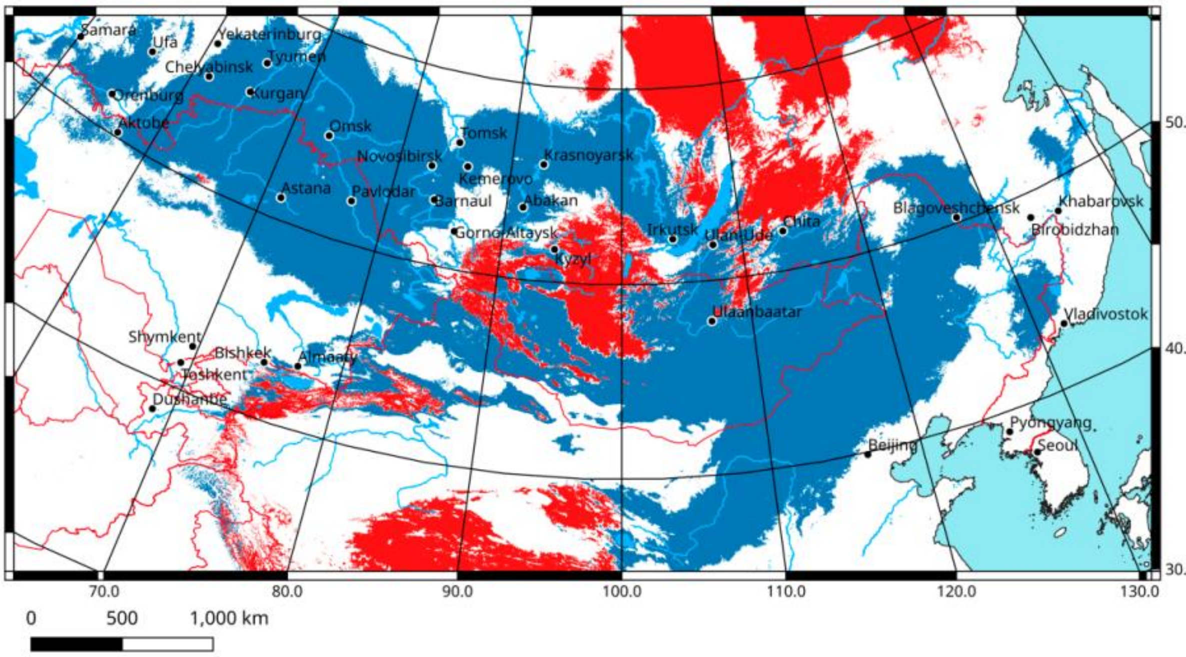


Figure 7. Forecasted trends in the *Angaracris barabensis* distributions: Predicted suitability for current conditions versus for 2041–2060 and the 3–7.0 Shared Socioeconomic Pathway based on high greenhouse gas emissions (cf. Fig. 2 and 6, F). *Positive trend in red, negative one in blue*

Рисунок 7. Прогнозируемые изменения распределения *Angaracris barabensis:* Сопоставление оценок пригодности местообитаний для современного периода и для 2041–2060 гг. по сценарию изменения концентрации парниковых газов в атмосфере 3–7.0, основанному на высоких уровнях эмиссии парниковых газов (ср. Рис. 2 и 6, F). *Улучшение условий выделено красным, ухудшение — синим*

CONCLUSIONS

Examination of the published and unpublished data concerning the latitudinal, longitudinal and altitudinal distribution patterns of *Angaracris barabensis* shows there are no evident contemporary shifts of its range boundaries associated with global warming per se or this tendency is extremely weak. Main changes look like very limited and may be explained by changes of annual precipitation levels and/or their rhythms. Besides, they may be determined by local transformations of ecosystems resulted from increasing human activity, for instance, agriculture field abandoning, overgrazing, development of irrigation systems. However, the distribution of suitable conditions can change significantly during the next several decades. Ecological modelling predicts opportunities of possible northward and northeastward shifts of applicable habitats in Central and East Siberia and persistence of areas of feasible harmfulness in South Siberia, Mongolia and China (mainly across the Tibetan Plateau). However, in this huge area, there are very sparse monitoring systems. In this context, integration of ecologo-geographic modelling and data of remote sensing [64; 65] on the basis of the GIS looks like very prospective and important [66; 67].

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