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The Handsome Cross Grasshopper *Oedaleus decorus* (Germar) (Orthoptera: Acrididae) in the Asian Part of Its Range

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Abstract

The handsome cross grasshopper *Oedaleusdecorus* (Germar), which was a minor pest in the 19th and first half of the 20th century, in the late 20th and early 21st centuries, became one of the emerging regional pests in the Asian part of its range, especially across the intermountain basins of the mountains of South Siberia, Mongolia and North and Northeast China. This is why it is necessary to identify the main trends of possible changes in its distribution. Several sets of data on the species distribution (1895–1960, 1961–2023, and all data) are analysed and several various approaches to modelling (graphic, maximum entropy and multidimensional ellipsoid) are utilised. The models produced for modern conditions describe well the known geographical and ecological distributions of the species in the Asian part of its range. Graphic models characterising the species' distribution within a system of life zones and major ecosystem types show its general preference for dry steppes and semideserts. The models demonstrate apparent opportunities for this species to pierce northwards (at least up to 58° N in West Siberia, 62–63° N in East Siberia) in the future. This means that in the future, there is a certain probability that some individuals will migrate to these more northern regions. In the context of global warming, further northwards and northeastward shifts in the range boundaries of *O. decorus* can be predicted. In addition, there have been some changes in its population distribution and abundance, especially in the optimal parts of its population system where *O. decorus* normally colonises all applicable habitats; its average abundance is relatively high and it is common even during depressions. These shifts may be justified by both climatic changes (especially northwards) and some transformations of human activities (mainly for eastwards relocation).

Keywords: pest; plant protection; outbreak; steppes; semideserts; deserts; Asia; dispersal

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1. Introduction

The handsome cross grasshopper *Oedaleus decorus* (Germar, 1825) (taking into account the synonymy of *Oedaleus asiaticus* Bey-Bienko, 1941 [1]) is one of the most widely distributed acridid species in extratropical Eurasia. Its geographic range includes the semiarid

areas of temperate and subtropical Eurasia, mainly temperate grasslands, Mediterranean landscapes and mountain steppes, from several islands in the eastern Atlantic Ocean (Madeira Archipelago, Canary Islands) in the west to the Yellow Sea in the east [1–8]. *O. decorus* is also known from North Africa as well [1].

Although *O. decorus* may be very common and its abundance is often high, especially in dry grasslands [7–12], until the late 20th century, it was usually considered a minor pest [5,10,13–18]. For example, in "*The Locust and Grasshopper Agricultural Manual*" [19], the species is characterised as an occasional minor pest (G). Over the past decades, the situation for this grasshopper has begun to change. As a result, *O. decorus* can be considered an important pest across the Asian part of its range, especially in the local steppes [8,20–25]. Importantly, the upsurges of *O. decorus* are often associated with outbreaks of the Italian locust (*Calliptamus italicus* (Linnaeus)) in the West Siberian steppes [12] and *C. abbreviatus* Ikonnikov in the Altai-Sayan Mts [24].

The handsome cross grasshopper feeds mainly on different grasses and commonly avoids dicots [2,17,26–34], but can sometimes eat sagebrushes [26]. Notably, when the diversity of food plants narrows, the general trophic preferences of the species do not change and its preference for grasses is maintained [27]. Moreover, no significant differences in feeding preferences between the sexes were found as well [28]. Interestingly, in some regions, for example in the intermountain basins of the mountains of South Siberia, the range of food selectivity of nymphs can be significantly wider than that of adults while maintaining a clear preference for grasses [29]. However, this species can cause severe damage not only to cereals, but also to alfalfa, vegetables, tobacco, cotton and other agricultural crops [2,21,22,34–37]. Moreover, it may harm hayfields and pastures.

O. decorus is a univoltine species with overwintering eggs [38,39]. Hoppers start to hatch in late April near the southern edge of a species range and in late May and the beginning of June in the northern parts [30,38–40]. Hatching can be prolonged over time and last for a month or more. Adult insects usually emerge in early June in southern regions and a little later in northern parts of the range [7,30,38]. The last adults may be observed until the end of September [30,38].

Although its ability to actively disperse locally, especially in arid areas, has long been known [18,40,41], possible migrations of *O. decorus* over fairly large distances have only recently been described for the easternmost parts of the species range [42]. Furthermore, recent studies of mitochondrial genome diversity and distribution across Inner Mongolia confirmed the existence of active local interpopulation connections [43]. In addition, the species can colonise many dry transformed habitats across agricultural areas and cities, e.g., overgrazed meadow steppes, lawns, and verges, and use them to expand its range [12]. Moreover, *O. decorus* may use some passing vehicles to crossover uninhabitable territories [7,44]. This means that its adults are good migrants and, coupled with the extensive range, are capable of invading vast territories relatively quickly, migrating from one region to another and from one landscape to another (sometimes located at a considerable distance) [7,21,40,41]. In this respect, the species has begun to resemble another representative of the genus *Oedaleus* Fieber, namely the Senegalese grasshopper *O. senegalensis* Krauss, whose migratory movements associated with active flights are well known [45,46].

The aims of this study are to identify general patterns of distribution of *O. decorus* as a possible harmful species across the Asian part of its range, to assess how its distribution may shift in the future relative to global climate trends and local landscape transformation, and to discuss some forecasts for its future distribution.

2. Materials and Methods

2.1. Study Territory

The natural borders of the territory studied are the Ural Mts. and the Caspian Sea to the west and the Pacific coast of Eurasia to the east. The northern range limit almost coincides with the southern border of the taiga life zone (approximately 56–57° N). The southern boundary is determined by the southern border of the subtropical deserts. Across this area, the temperatures of the warmest month vary significantly—between 16 °C and 32 °C, the temperatures of the coldest month from −34 °C to 4 °C, and the annual precipitation between 125 and 700 mm [47,48]. Primarily, various types of ecosystems were distributed across the study area: forests (including taiga), grasslands, and deserts. However, later, especially in the 19–20th centuries, many ecosystems of this territory were converted into agricultural fields (including irrigated) and rangelands.

2.2. Field Studies

Studies of the species distribution have been based on both qualitative and quantitative survey data collected in natural and disturbed landscapes, usually in July and August, when imagoes are dominant [4,33]. Quantitative samples were obtained for a certain period of time at each sampling plot [4,49,50]. Insects were caught with a standard net (40 cm diameter nets were typically used) for 10–30 min. Afterward, the results for each count were recomputed per one hour. Often, especially during acridid outbreaks, we also value the density of these insects on randomly distributed squares of 0.25×0.25 m^2 (in some cases, 0.5×0.5 m^2 or 1×1 m^2), mainly in zonal habitats [50–52]. To reveal the geographic coordinates of the species observations, GLONASS/GPS gadgets were used.

2.3. Data Analysis

Original data were collected in China, Kazakhstan, Kyrgyzstan, Russia, Tajikistan, and Turkmenistan from 1976 until 2024. In addition, we analysed materials from collections of Novosibirsk State University (Russia), the Federal Scientific Center of the East Asia Terrestrial Biodiversity (Vladivostok, Russia), the Institute of Systematics and Ecology of Animals (Novosibirsk, Russia), the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia), the Berezhkov collections at Tomsk State University (Russia), Gorno-Altaisk State University (Russia), the Zoological Museum of Moscow State University (Russia), and published data on *O. decorus* distribution, especially across Mongolia and China [1,3,7,12,21,23,30,37,38,53–65].

The original dataset of species occurrence points included 412 localities. This set was manually rarefied to one location per grid cell of the climatic data (30 arcseconds) (cf. [66]), although some special studies have shown that the problem of thinning is exaggerated [67,68]. As a result, the input data consisted of two subsets: (1) 76 points of the species findings from 1895 to 1960, and (2) 290 points of the species occurrences from 1961 to 2023, for a total of 364 points (Table S1). For locations studied before 2000, we determined the geographic coordinates of the nearest human settlements via Google Earth Pro 7.3.3 (©Google, 2026, Mountain View, CA, USA). The geographic coordinates of localities were used to produce the maps of the species ranges in the Lambert conformal conic projection via QGIS 3.44. The extents with boundaries along the parallels of 30° N and 70° N and the meridians of 40° E and 152° E were prepared. The spatial autocorrelation for each set of points was assessed via two-sided Moran's I test using GeoDa 1.22.0.14 software.

To model the species distribution, two very different approaches were used. First, the maximum entropy models were created via MaxEnt 3.4.4 software [69–73]. Second, the

multidimensional ellipsoid characterising the species ecological niche was produced via the ellipsenm 0.3.5 R package [74].

We exploit WorldClim 2 resources [75,76], namely, the "Historical Climate Data" (19 standard annually averaged bioclimatic variables for 1970–2000 with a spatial resolution of 30 arcseconds), the "Future Climate Data" with the same resolution downscaled from the two global climate models, namely, CNRM-ESM2-1 (Centre National de Recherches Météorologiques and Centre Européen de Recherche et de Formation Avancéeen Calcul Scientifique, France) [77,78] and GISS-E2-1-G (NASA Goddard Institute for Space Studies, USA) [79,80] for the three Shared Socioeconomic Pathways (SSPs) (1–2.6, 2–4.5, 3–7.0) [81] and for two periods (2021–2040 and 2041–2060).

Several MaxEnt models were generated for three datasets (before 1961, from 1961 until 2023, and total), the contemporary climatic conditions (the full set of variables) and the total set of occurrences and the two coming periods and the three SSPs. The following options were used: features—auto, output format—cloglog, regularisation multiplier = 1, and background points (randomly selected) = 10,000 [69,72]. Standard sets of bioclimatic variables and modelling parameters were specifically used since the use of different approaches for the selection of collinear variables and the so-called parameter optimisation significantly limits the possibility of comparative interpretations of models generated for different species, especially for identifying their fundamental differences. Moreover, several specialised studies have demonstrated that the collinearity problem for complex modelling approaches, such as MaxEnt or Random Forest, is significantly exaggerated [68,82,83]. The AUC (the area under the receiver operating characteristic curve) values for sets of 25 replicates with cross-validation were used to assess the accuracy of these models. Omission rates were also analysed. The predictive contributions of the bioclimatic variables and Jackknife tests were also used to reveal their significance.

The ellipsoid model was produced on the basis of on the total set of occurrences, with only 6 variables, namely the annual mean temperature (bio_1), maximal temperatures of the warmest month (bio_5), minimal temperatures of the coldest month (bio_6), annual precipitation (bio_12), precipitation of the warmest quarter (bio_18), and precipitation of the coldest quarter (bio_19), and 25 replicates. The method was covmat and the level used to produce the ellipsoids was 99%. The ellipsenm package was also used to evaluate the overlapping levels of the ecological niches of *O. decorus* and two native locust species, namely the migratory *Locusta migratoria* (Linnaeus) [84] and the Italian locust *Calliptamus italicus* [85].

3. Results

3.1. Shifts in Species Distribution

Until the 1960s, the species distribution was usually associated with the steppes (mainly southern steppes) and semideserts (Figure 1). The species finds across the forest–steppes and the northern steppes were very rare and insular [9,38,86] (Figure 2). Despite the obvious uneven distributions of the data collection points, especially in the period before 1961, the analysis of the spatial autocorrelation of their locations revealed their similarity. For all three sets, the Moran's I index values are low, but positive and statistically significant (for the period before 1961, the index is 0.258, pseudo-p = 0.001, z = 7.441; for 1961–2023, the index equals 0.025, p = 0.049, z = 1.687; for all the data, the index is 0.139, p = 0.001, z = 22.186). Such low spatial autocorrelation can be determined both by the uneven distribution of areas suitable for the species, especially in mountainous regions with their pronounced altitudinal zonation, which is characteristic of most of the studied territory, and by unevenness in the distribution of data collection points, which, however, is largely determined by the noted complexity of the relief. An analysis of the locations

of the known extreme points of the species occurrence in the eastern part of its range demonstrated the absence of any noticeable changes in its distribution (given the obvious uneven distribution of collection points). Thus, in the period before 1961, the northernmost point was located at 54.7° N latitude, the southernmost point was located at 35.7° N, and the easternmost point was located at 123.43° E; in the period from 1961 to 2023, these points were 55.46° N, 37.31° N, and 119.36° E, respectively.



(**A**) (**B**)

Figure 1. Characteristic localities of *Oedaleus decorus* in South Siberia: (**A**)—northern steppe (near the Aleksandrovskij settlement, Kulunda steppe, Novosibirsk Region, 53.67° N 78.25° E); (**B**)—dry intermountain steppe (Shivelig River, Uvs-Nuur Basin, Republic of Tyva, 50.89° N 94.56° E).

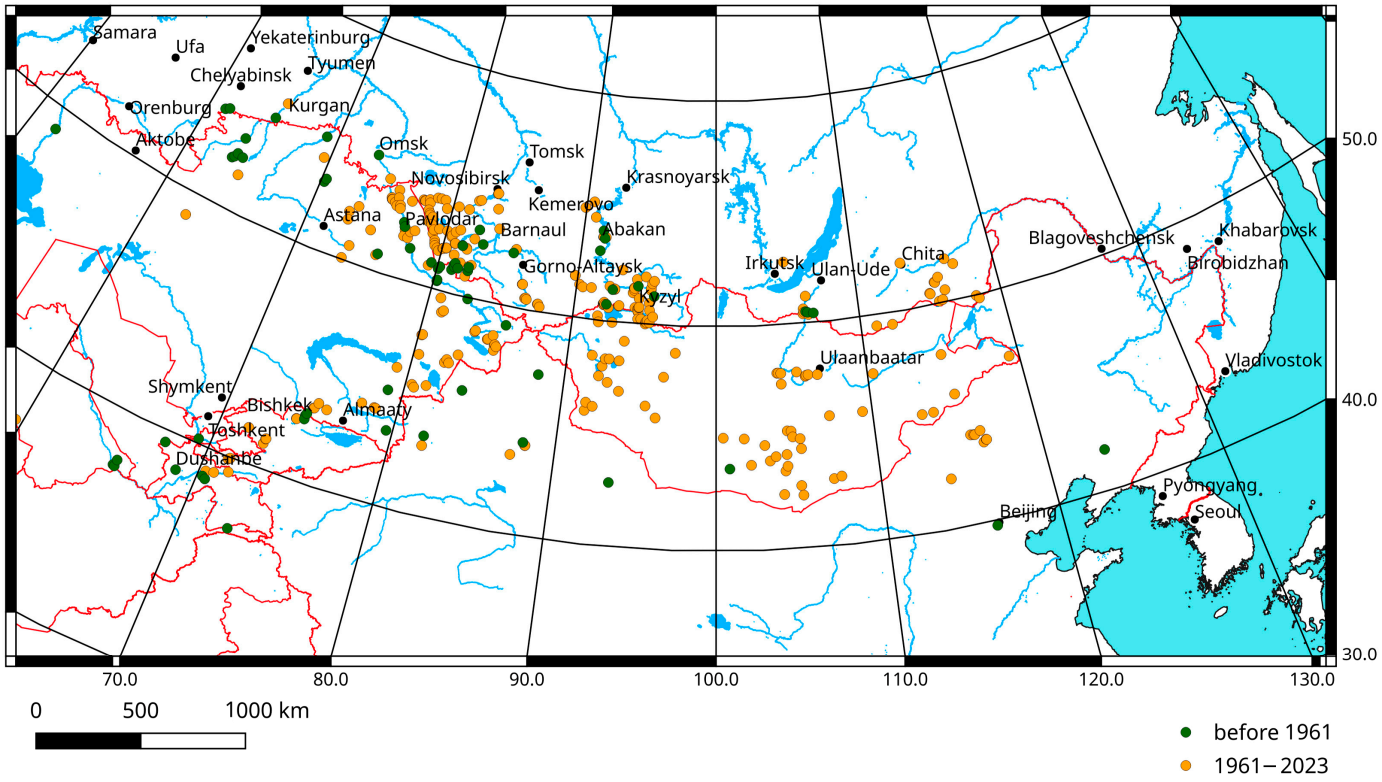


Figure 2. Distribution of *Oedaleus decorus* over the Asian parts of its range: location points for the period before 1961 in green; location points from 1961–2023 in yellow.

At the end of the 20th century, *O. decorus* became more or less common in many forest–steppe regions of southern Siberia, from the South Ural to the Yenisei River Basin. For example, *O. decorus* has become a very common and widespread species across the southern West Siberian Plain [12,87]. In addition, it also spreads across the forest–steppes between the Ob River and the northern ridges of the Altai-Sayan Mts. Most such populations were found in some local dry disturbed habitats, e.g., overgrazed meadow steppes, lawns, and roadsides. Similar changes have also been observed in the Yenisei River Basin, where the northernmost points of species occurrence in recent decades are located in the southern forest steppes of the Krasnoyarsk Krai (Territory). For Transbaikalia and Mongolia, the patterns of changes are not as obvious, since data on the distribution of *O. decorus* before the early 1960s are extremely sparse and limited mainly to the south of the region.

3.2. Distribution Patterns of the Handsome Cross Grasshopper in the Central Part of Its Range

An analysis of the species distribution across the main types of habitats in the near-central part of its range on the basis of abundance estimates (Figure 3) and between outbreaks revealed the insular nature of the occurrence of its populations in the forest–steppes and northern parts of the steppe life zone. In the periods between upsurges, *O. decorus* is quite frequent across both the typical and southern steppes and the semideserts. Its populations become local again in the northern deserts, and further south they are not found on the plains or in the lowlands. South of the 40th parallel, the species occurs almost exclusively in mountainous habitats. Its distribution is very similar to that of the Italian locust [51], but unlike the latter, it is characterised by limited penetration into local floodplains, especially the lower ones.

3.3. Ecological–Geographic Models of the Species Distribution

The MaxEnt model in the first half of the 20th century, which was based on climatic data from 1970 to 2000, revealed that vast territories favourable for the species were located in the steppe and semidesert regions of southern West Siberia and Central and East Kazakhstan, as well as across the dry foothills and lowlands of the main mountains of Central Asia (Tien Shan, Gissar (Hisar)-Alai Mts and the Hindu Kush) (Figure 4A). Several isolated areas were also revealed in the intermountain steppe valleys of the mountains of South Siberia and in two semiarid regions of North China. However, the presence of vast, unfavourable areas for the species in Mongolia and adjacent parts of China is also apparently largely due to the small number of observation points in this region before the early 1960s (cf. Figure 2).

The model produced for 1961–2023 looks different (Figure 4B). In the grassland areas of West Siberia and Kazakhstan, the suitable areas are distributed similarly. However, some minor shifts to the north and northeast can be traced (cf. [12]). Further south, the optimal areas for the species are significantly reduced and obviously become confined to low- and middle-mountain areas (see also Section 3.2). In contrast, the steppes and semideserts of the dry intermountain valleys of the mountains of South Siberia, and some areas near Baikal Lake, Mongolia, and Inner Mongolia in China are completely or almost favourable for *O. decorus*.

The model generated for the full set of data (Figure 4C) is similar to the model for 1961–2023, but there is a relatively small area around Beijing. The ellipsoid model shows an analogous pattern of distribution of optimal areas for *O. decorus* (Figure 4D), but the suitability levels are significantly lower than those of the models generated via the MaxEnt methodology (cf. [88]), which may depend on both the narrow set of variables used and the linear distribution of the pixelwise habitat suitability estimates.

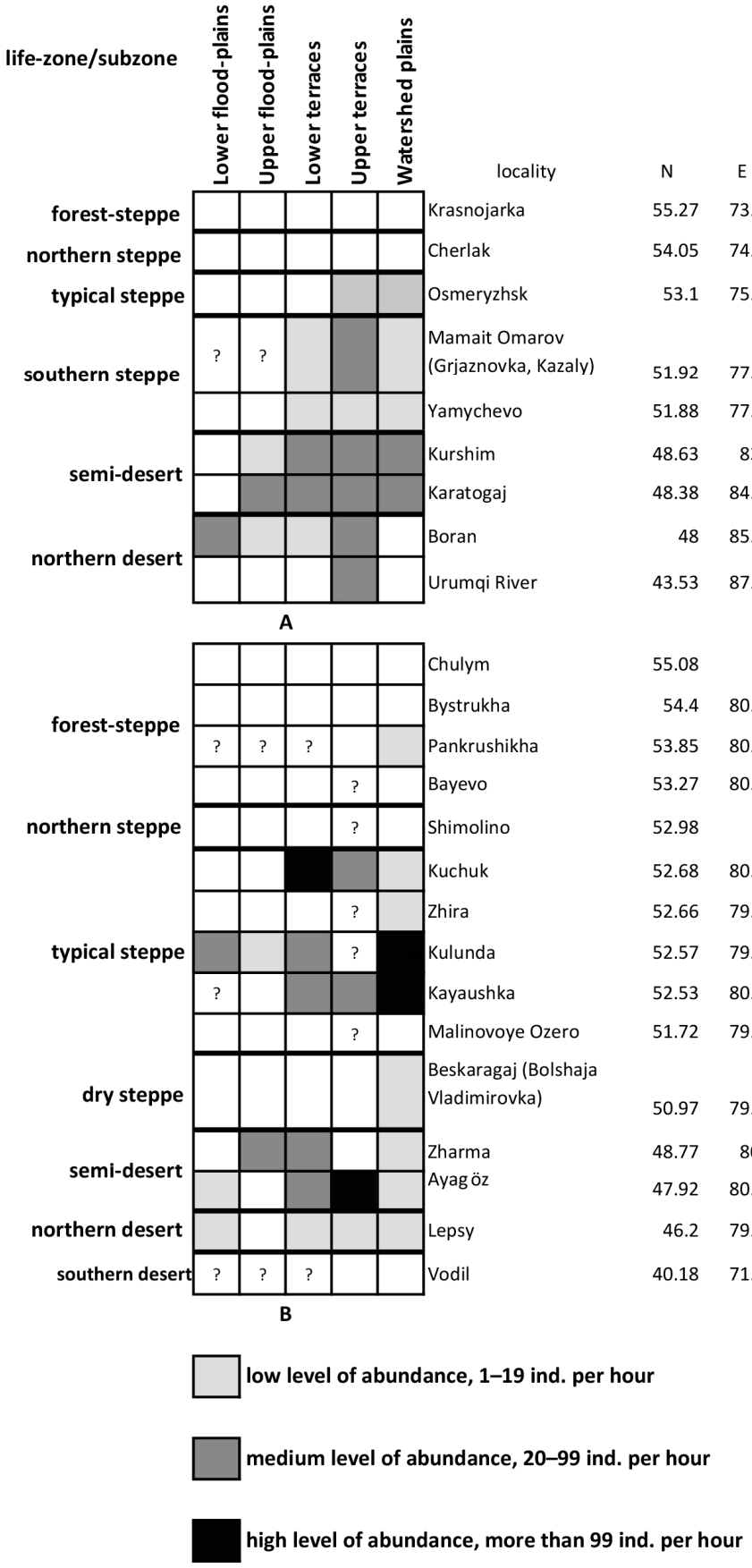


Figure 3. Population distribution of *Oedaleus decorus* along two gradients on the basis of survey data collected along transects (transzonal) crossing the central part of its range (West Siberian Plain, East and Southeast Kazakhstan, Xinjiang, and the Ferghana Valley) along mainly the Irtysh River (**A**) and near the 80th meridian east (**B**): ?—unsurveyed habitats.

For each of the analysed datasets, three main bioclimatic variables remained significant: annual mean temperatures (bio_1), mean diurnal ranges of temperatures (bio_2), and precipitation of warmest quarters (bio_18) (Table 1). Together they explain approximately half of the variations. All these factors are important for the development of grasshoppers during summer and for grass growth as well. Several other variables can also be significant (temperature seasonality (bio_4) and annual precipitation (bio_12) for 1961–2023; mean temperatures of warmest quarters (bio_10) for all data and the period before 1961; precipitation of wettest month (bio_13) for the period before 1961). The Jackknife tests allow adding the maximal temperatures of the warmest month (bio_5) and the mean temperatures of the wettest quarter (bio_8) (Figure 5). These additional variables may be important for influencing the postembryonic development of the species as well. The performance of the model for the three periods is high (Figure 6) (the AUC value for the period before 1961 is 0.899 (standard deviation = 0.102), that for 1961–2023 is 0.931 (0.021), and that for all the data is 0.916 (0.024)). The analysis of the omission values reveals that the average omission rates for 25 replicates with cross-validation are in good agreement with the predicted rates (the diagonals from 0,0 to 1,1) (Figure 7). The mean minimum training presence (MTP) thresholds (for cloglog output) are 0.0674 (for the period before 1961), 0.011 (1961–2023), and 0.0112 (for all the data). However, as expected, for the period before 1961, the average omission varies more noticeably (Figure 7A).

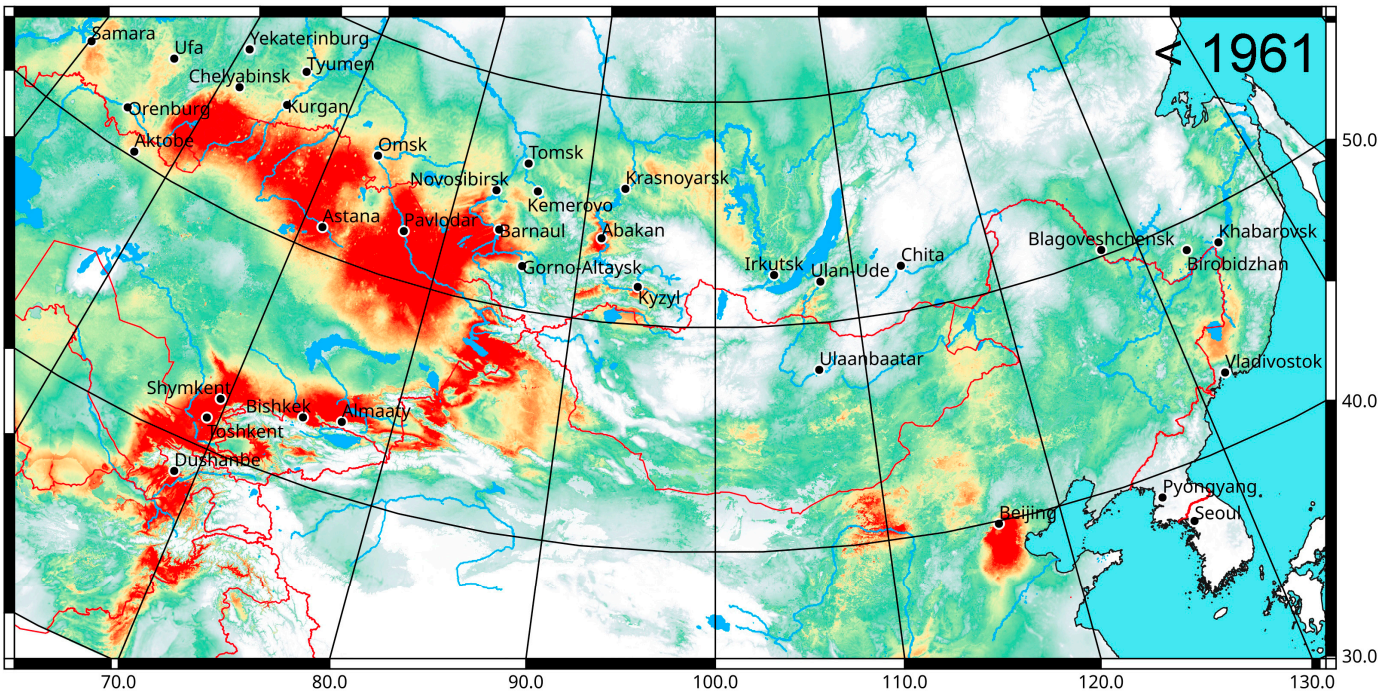
Table 1. Significance of bioclimatic parameters for the two periods (before 1961, 1961–2023) and for the full dataset.

Variable	Variable Explanation	Distribution Before 1961		Distribution 1961–2023		All Data	
		Percent Contribution	Permutation Importance	Percent Contribution	Permutation Importance	Percent Contribution	Permutation Importance
bio_1	annual mean temperature	29.8	18.3	16.9	22.8	16.2	28
bio_2	mean diurnal range (mean of monthly (max temp—min temp))	16.7	3.1	11.2	3.9	15.5	7.4
bio_3	isothermality (bio2/bio7) (×100)	5.3	11.6	9.3	6.6	10.4	4.4
bio_4	temperature seasonality (standard deviation ×100)	1.4	5.4	11	23.2	7.9	13.3
bio_5	max temperature of warmest month	0	0	0.1	1.3	0.3	2.7
bio_6	min temperature of coldest month	0.4	0.2	0.5	1.3	0.6	2.6
bio_7	temperature annual range (bio5-bio6)	0.3	0.4	0.5	2.7	0.5	1.1
bio_8	mean temperature of wettest quarter	1.5	0.2	1	0.2	0.6	0.2
bio_9	mean temperature of driest quarter	1.1	2.3	0.6	0.4	0	0
bio_10	mean temperature of warmest quarter	9	11.4	6.1	1.2	10.2	4.2
bio_11	mean temperature of coldest quarter	0.4	0.3	0.2	2.1	0.2	2.6
bio_12	annual precipitation	0.8	4.6	10.4	1.5	5	0.8
bio_13	precipitation of wettest month	8.5	14.6	5	1	6.9	0.6
bio_14	precipitation of driest month	3.8	1.9	0.9	0.8	3.3	1.3
bio_15	precipitation seasonality (coefficient of variation)	4	2.6	4.3	8.7	4.1	8.8
bio_16	precipitation of wettest quarter	0.2	0.1	2.1	0.3	0.9	0.5
bio_17	precipitation of driest quarter	3.2	1.2	0.5	4.2	1.2	7.2
bio_18	precipitation of warmest quarter	9.2	19.4	16.8	17.6	15.6	14.3
bio_19	precipitation of coldest quarter	4.8	2.4	2.6	0.2	0.6	0.1

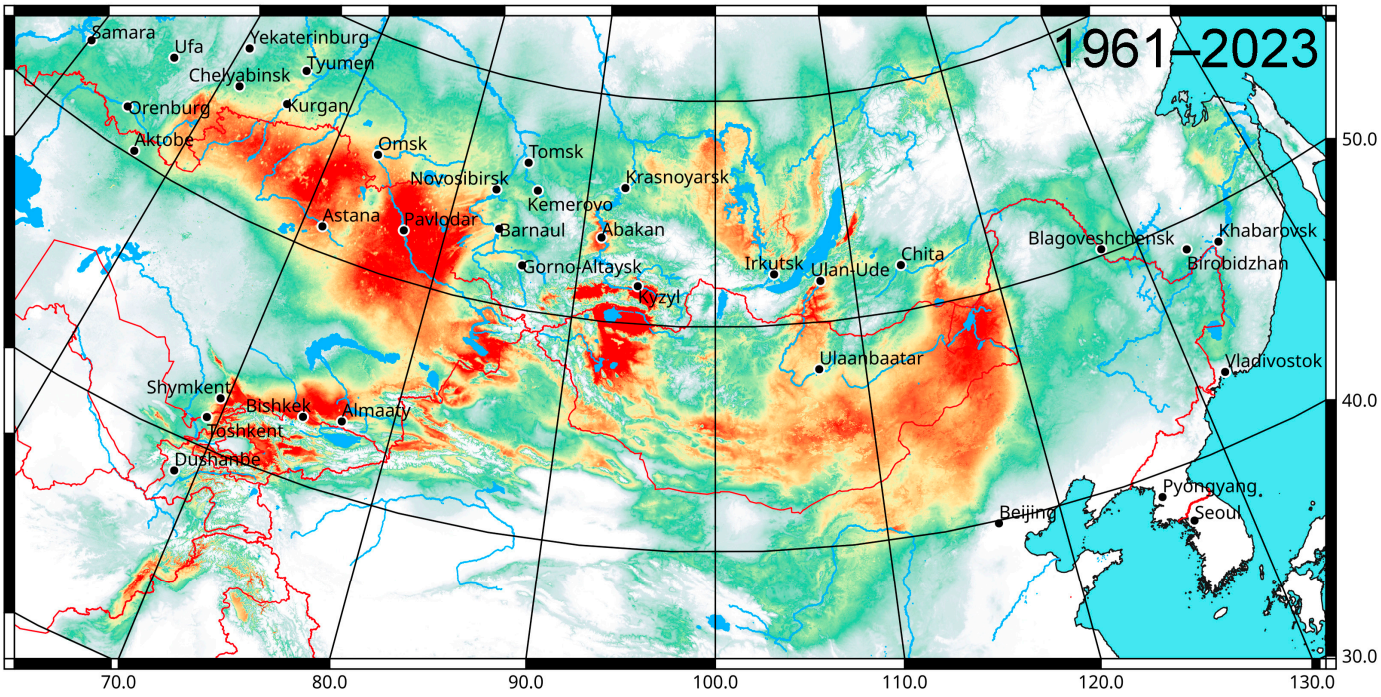
Highlighted green—five most significant variables for each group.

Modelling of the *O. decorus* distribution for the two periods (2021–2040 and 2041–2060) on the basis of the CNRM-ESM2-1 global climatic model for the three SSPs (Figure 8) revealed divergent trends in different parts of the range. In the grassland areas of West Siberia and the Kazakh Uplands (Saryarka), the territories with optimal conditions will shift moderately to the north and northeast (cf. [12]) but at the same time, they will become

somewhat less favourable, especially from 2041 to 2060, given the significant increase in greenhouse gas release.



(**A**)



(**B**)

Figure 4. *Cont.*

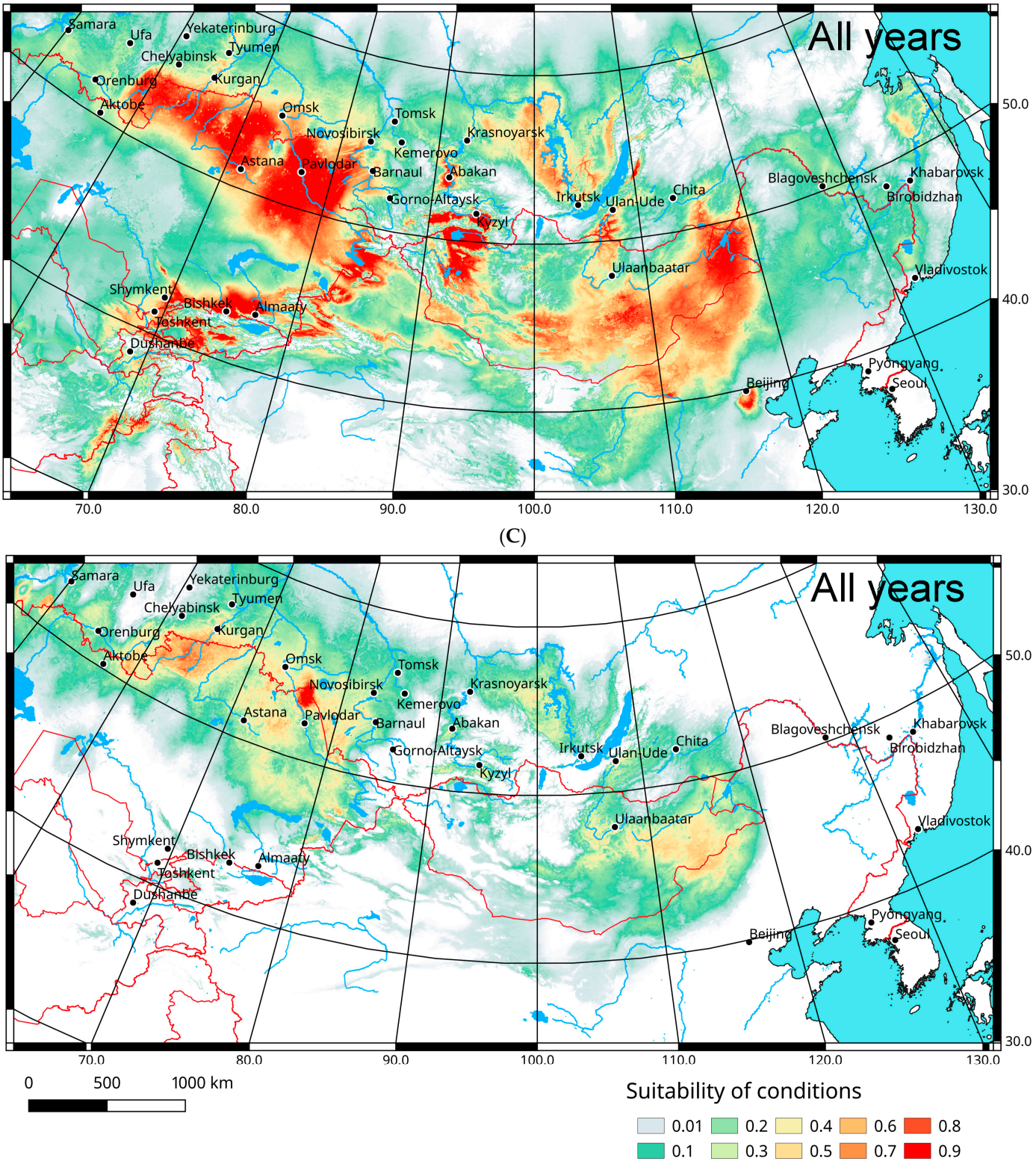


Figure 4. Spatial models of the *Oedaleusdecorus* possible distributions across the Asian part of its range according to bioclimatic variables from 1970 to 2000: (**A**)—MaxEnt model for occurrence data before 1961; (**B**)—MaxEnt model for data (1961–2024); (**C**)—MaxEnt model for all distribution data; (**D**)—ellipsoid model for all distribution data and selected variables.

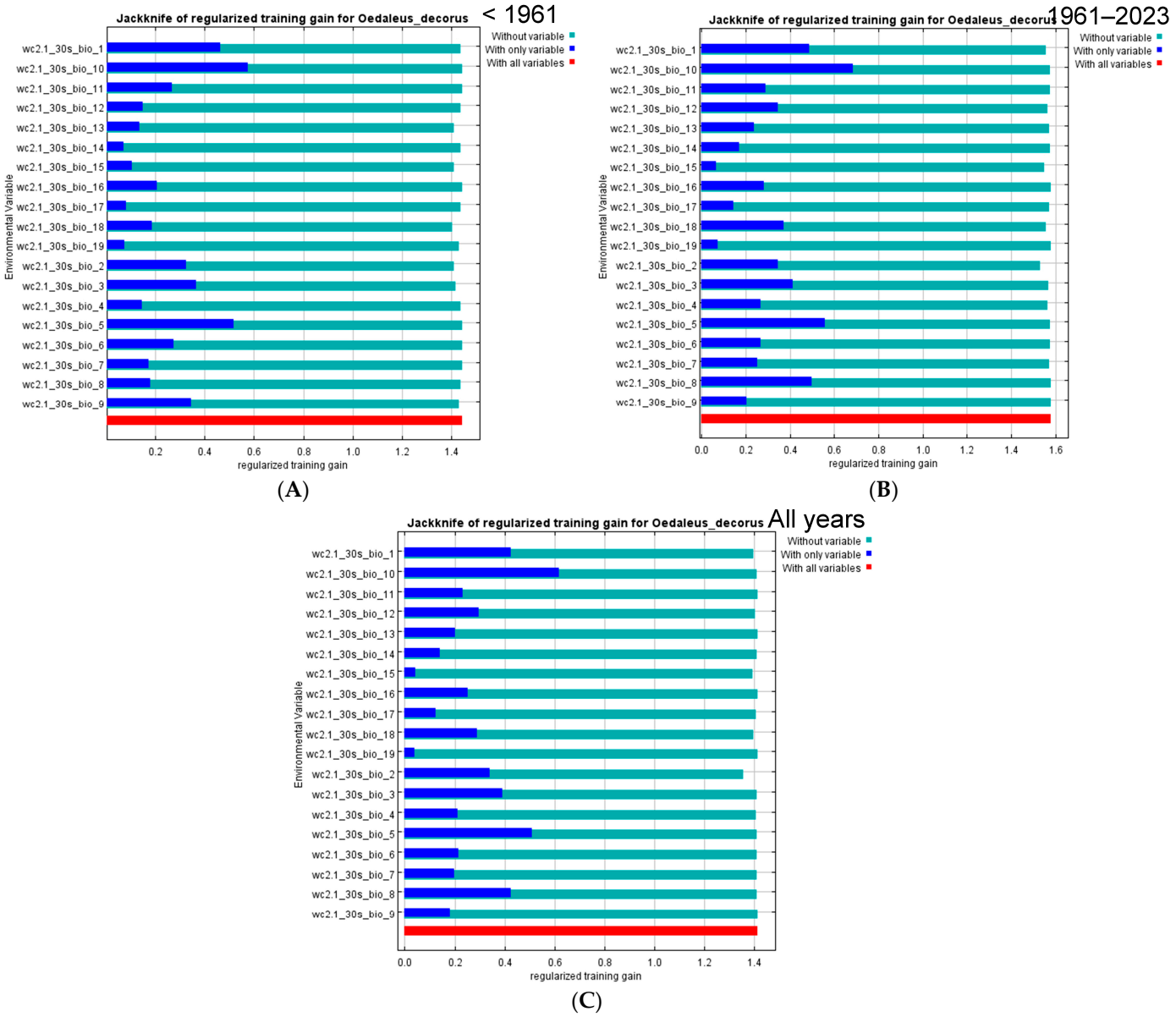


Figure 5. The Jackknife tests for spatial models of the *Oedaleus decorus* possible distributions across the Asian part of its range according to bioclimatic variables for 1970–2000: (**A**)—distribution data before 1961; (**B**)—distribution data from 1961 until 2023; (**C**)—all distribution data.

The areas in the Central Asian mountains (Tien Shan and Gissar-Alai) and in the grassland areas of the Altai-Sayan Mts and Northwest Mongolia will likely continue to be highly suitable for populations of the species. However, the suitability of areas in Transbaikalia (Dauria), the eastern parts of Mongolia and Inner Mongolia (China) may decrease somewhat, especially with significant temperature increases in the mid-21st century (Figure 8F). Notably, in the areas around Lake Baikal, including the Angara River region, as well as in the steppe-like parts of Central Sakha (Yakutia), new areas with very suitable conditions for the species may appear. In the region, until now, the species has been known only from the vicinities of Irkutsk (Figure 2).

When the global climate model GISS-E2-1-G is used, the models generated for two time periods and three SSPs (Figure 9) are very similar to the projections from theCNRM-ESM2-1 model (Figure 7). However, the overall predicted habitat suitability is somewhat higher.

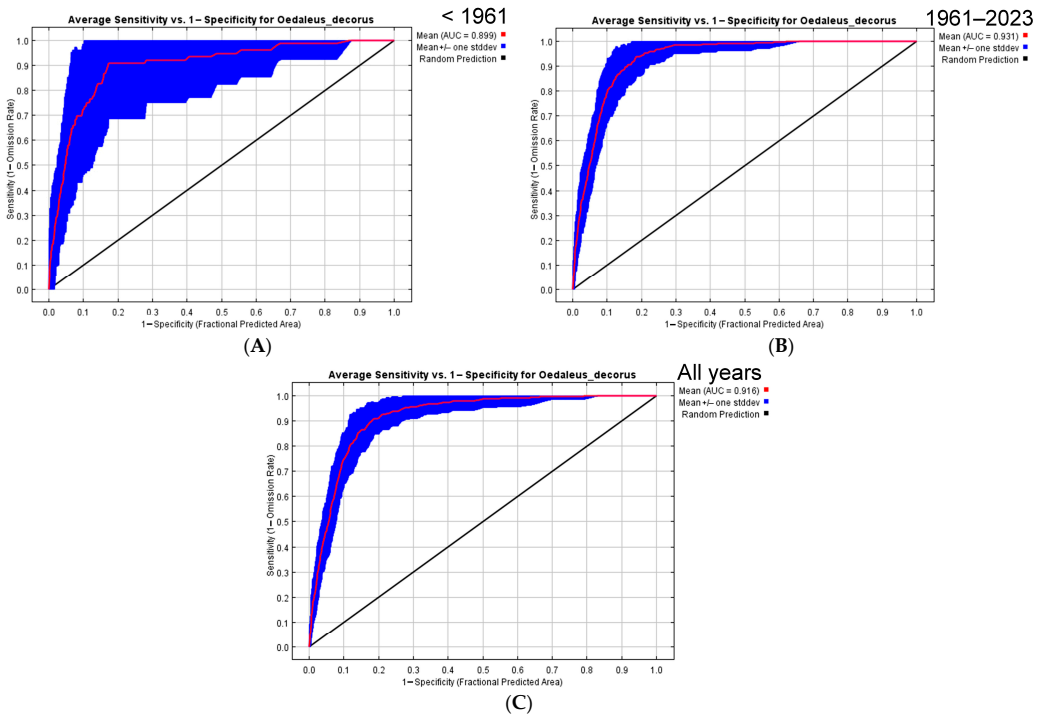


Figure 6. The reliability tests for spatial models of the *Oedaleus decorus* possible distributions across the Asian part of its range according to bioclimatic variables for 1970–2000: (**A**)—distribution data before 1961; (**B**)—distribution data from 1961 until 2023; (**C**)—all distribution data.

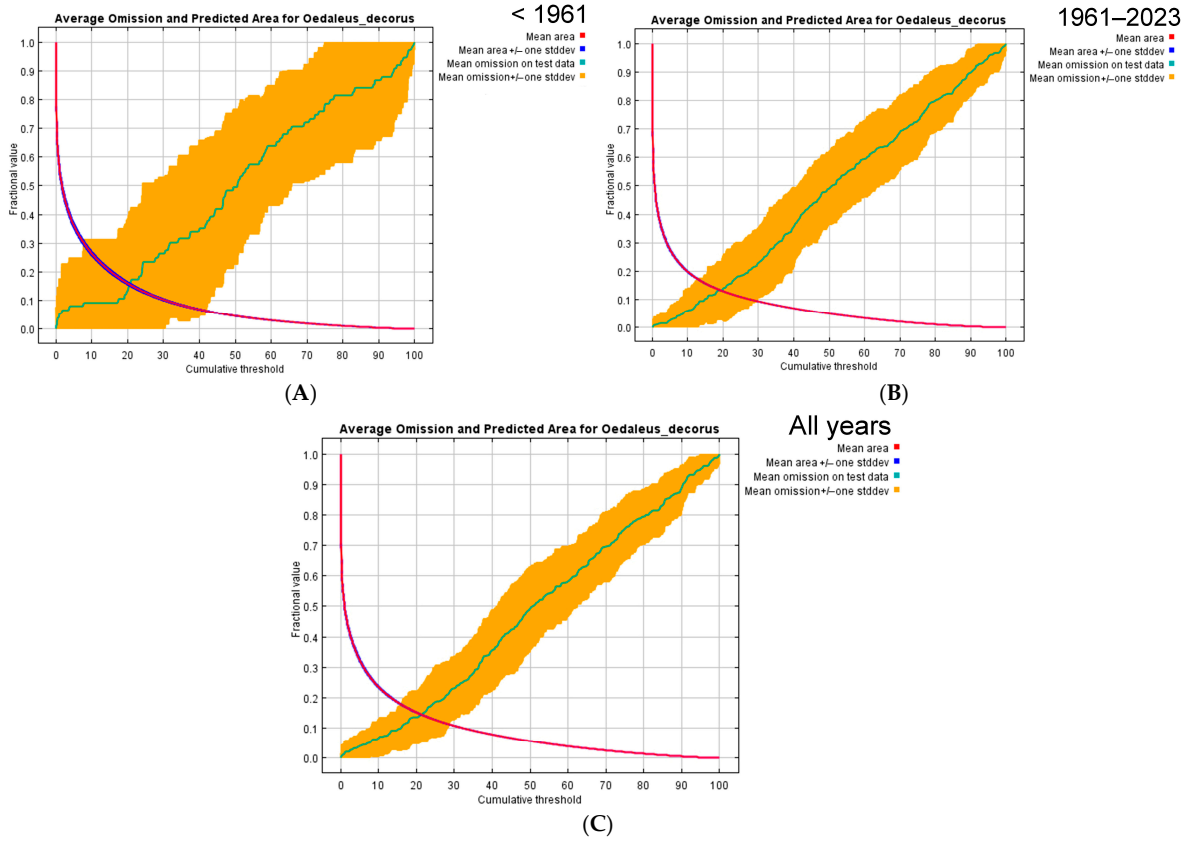


Figure 7. Average omissions and predicted areas for spatial models of the *Oedaleus decorus* possible distributions across the Asian part of its range according to bioclimatic variables for 1970–2000: (**A**)—distribution data before 1961; (**B**)—distribution data from 1961 until 2023; (**C**)—all distribution data.

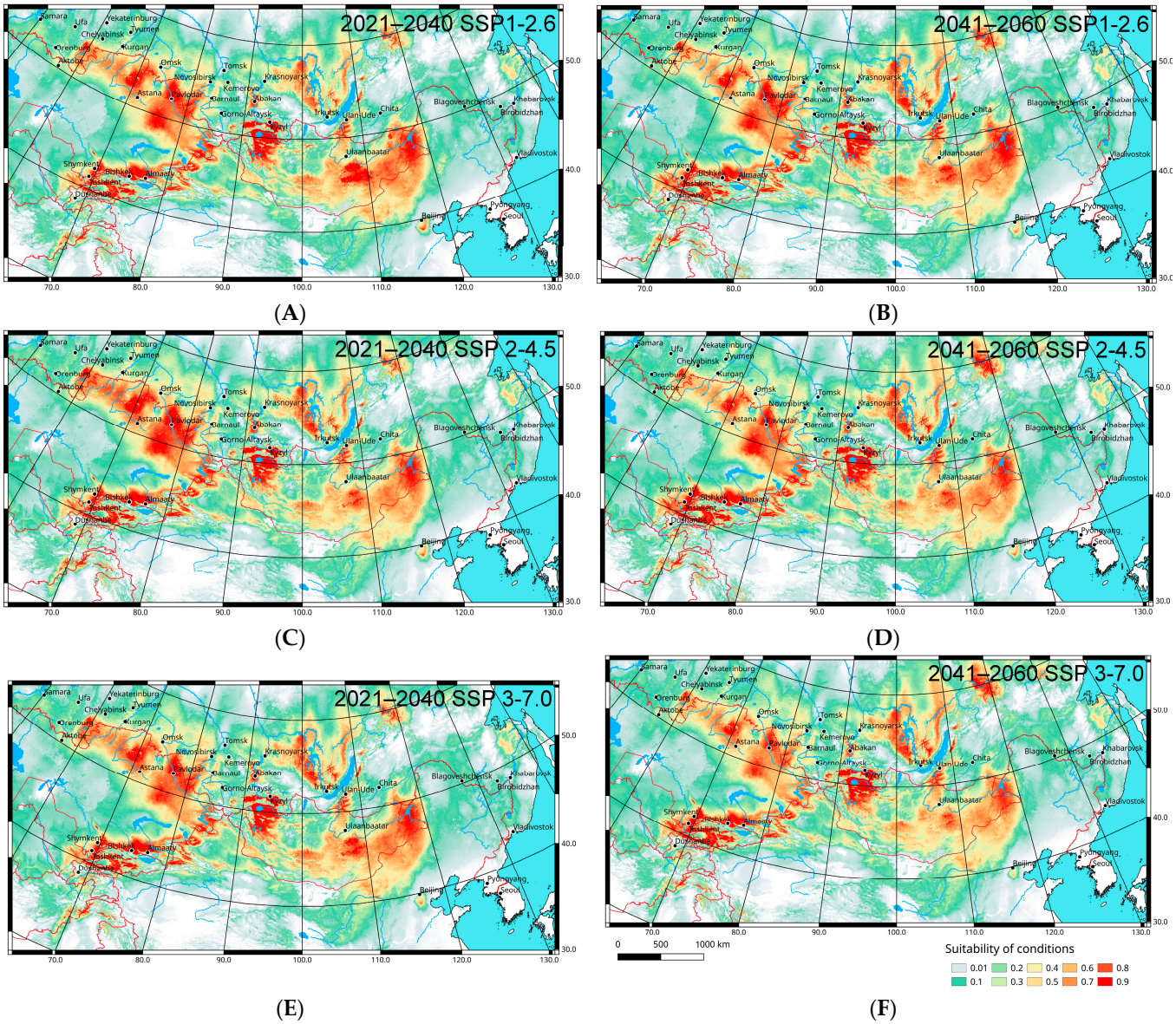


Figure 8. Spatial models of the *Oedaleus decorus* possible distributions across the Asian part of its range according to the global climate model CNRM-ESM2-1 for 2021–2040 and 2041–2060: (**A**,**C**,**E**)—2021–2040; (**B**,**D**,**F**)—2041–2060; (**A**,**B**)—the 1–2.6 SSP based on low greenhouse gas release; (**C**,**D**)—the 2–4.5 SSP based on intermediate greenhouse gas release; (**E**,**F**)—the 3–7.0 SSP based on high greenhouse gas release.

3.4. Are Local Populations of Oedaleus decorus Always Abundant Across the Territories with Very Suitable Conditions?

The geography of optimal habitat distributions for a particular species can be perceived as indicating that local populations of this species should live in such areas under suitable conditions and that their density should be significant. We specifically analysed several characteristics of the long-term dynamics of several local colonies of *O. decorus* associated with territories with very high levels of suitability (at least 0.8) (Figure 4). Although the data series in each case are different and contain significant gaps (Table 2), it is clear that even under optimal conditions, the species abundance can vary significantly, by orders of magnitude in some local populations.

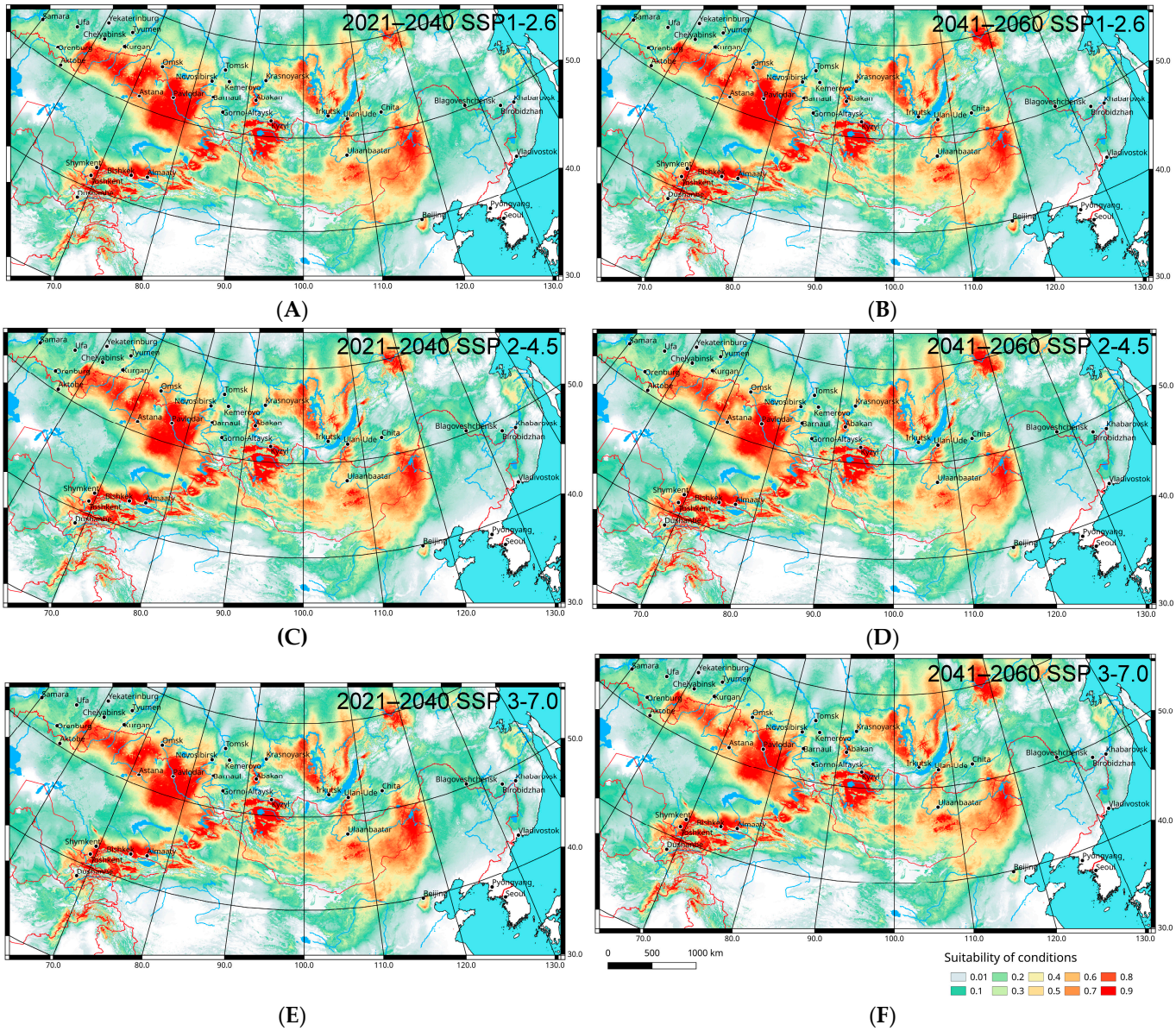


Figure 9. Spatial models of the *Oedaleus decorus* possible distributions across the Asian part of its range according to the global climate model GISS-E2-1-G for 2021–2040 and 2041–2060: (**A**,**C**,**E**)—2021–2040; (**B**,**D**,**F**)—2041–2060; (**A**,**B**)—the 1–2.6 SSP based on low greenhouse gas release; (**C**,**D**)—the 2–4.5 SSP based on intermediate greenhouse gas release; (**E**,**F**)—the 3–7.0 SSP based on high greenhouse gas release.

Table 2. Peculiarities of long-term population dynamics (abundance, ind. per hour) of *Oedaleus decorus* in the steppe habitats in the optimal areas of South Siberia.

Year	West Siberia (Kulunda Steppe)			South Tuva (Uvs-Nuur Basin)	Central Tuva (Ulug-Khem Basin)
	Aleksandrovskij (Figure 1A)	Yarovoe	Ust-Volchikha	Shivelig (Figure 1B)	Ust-Elegest/ Shagonar
	53.6° N 78.25° E	52.85° N 78.57° E–52.87° N 78.68° E	51.93° N 80.28° E	50.89° N 94.56° E	51.47° N 92.73° E/ 51.58° N 94.15° E
1962	?	?	?	*2*	*13*
1978	?	?	?	612	8

Table 2. *Cont.*

Year	West Siberia (Kulunda Steppe)			South Tuva (Uvs-Nuur Basin)	Central Tuva (Ulug-Khem Basin)
	Aleksandrovskij (Figure 1A)	Yarovoe	Ust-Volchikha	Shivelig (Figure 1B)	Ust-Elegest/ Shagonar
	53.6° N 78.25° E	52.85° N 78.57° E–52.87° N 78.68° E	51.93° N 80.28° E	50.89° N 94.56° E	51.47° N 92.73° E/ 51.58° N 94.15° E
1979	?	80	?	?	?
1992	?	18	?	?	?
1995	?	?	?	?	180
2000	**1146**	**252**	**474**	?	?
2001	**210**	**54**	**24**	?	?
2002	6	0	72	?	?
2003	6	0	6	48	44
2004	0	0	0	?	?
2005	0	54	0	?	?
2006	0	60	6	?	?
2007	18	150	20	?	?
2008	60	144	40	?	?
2015	+	4	204	?	?
2017	?	?	?	780	18
2018	+	?	17.2	?	?
2019	+	+	?	?	?

+—one or several specimens were collected or observed beyond counts, but in the same habitat; ?—no data; old data obtained by the team of Novosibirsk State University in 1962 are in italics; seasons with acridid outbreaks (together with the Italian locust in the Kulunda steppe) are in bold (cf. [51,52]).

For example, in 2000, *O. decorus* became extremely abundant in the steppes across the southeastern West Siberian Plain. This upsurge accompanied a more powerful outbreak of the Italian locust [12,51]. After that, the species abundance began to decline and in 2004, *O. decorus* was not found at any of the three sites, even outside the surveys. However, it can be found in neighbouring, drier or wetter habitats. Later, its abundance started to increase again. However, new peaks of abundance were registered in distinct populations in different years (2008—near the Aleksandrovskij settlement, in 2007 and 2008—in the vicinities of Bolshoye (Big) Yarovoe Lake, and in 2015—near the Ust-Volchikha settlement). A similar, although more vague, pattern can be seen in the dry steppes of Tuva and Inner Mongolia [11].

This reflects the characteristic features of most common acridid species—the generally unstable dynamics of their populations [89], the upsurges and depressions of which are often determined by a complex superposition of intrapopulation and external (relative to the population) processes [4,49,51,85]. Thus, for this species, we also see noticeable differences in the long-term dynamics of neighbouring local populations, which has already been demonstrated previously for the Italian locust [4,52].

3.5. To What Extent Do the Ecological Niches of the Main Potential Acridid Pests Overlap?

Overlapping of the multidimensional ellipsoids characterising the ecological niches of the most harmful acridids in the region is most significant for the pair *O. decorus* and the migratory locust (14.97%). Moreover, the degree of overlap between the niches of *O.*

decorus and the Italian locust is relatively small (5.37%), and for two locusts, it is even lower (3.64%).

4. Discussion

Grasshoppers, especially locusts, have long been well known as the most important pests of agricultural fields, pastures and hayfields. However, a comparison of historical data revealed that, in many regions, the ratio of different acridid species has changed significantly, and some potential pests have been replaced by others. Perhaps the most striking example is the fate of the only true locust in North America, namely, the Rocky Mountain locust *Melanoplus spretus* (Walsh) [90–92]. In the second half of the 19th century, the species was the most important pest across the prairies. This has caused enormous damage to many agricultural crops and has periodically resulted in huge swarms. However, this species completely disappeared more than a century ago [90,91].

Less impressive examples, but no less noticeable from the point of view of plant protection, are also known for other regions. For example, in the first half of the 20th century, the Siberian grasshopper *Gomphocerus sibiricus* (Linnaeus) was the main harmful acridid across the grasslands of the West Siberian Plain [13,16,38], but several decades later it became very rare [68]. Similar changes in the populations of this species have been observed in the Baikal region as well [93]. Many more complex patterns have been revealed for the Moroccan locust [94–96]. In some regions, its populations almost disappeared, after which their recovery began [95].

The exact opposite trend is observed for populations of the handsome cross grasshopper. Although a minor pest in the first half of the 20th century, at the end of the 20th and early 21st centuries, *O. decorus* became one of the emerging regional pests in the Asian part of its geographic range, particularly across the dry intermountain depressions of the South Siberian mountains, Mongolia and North and Northeast China [23,42,97–103]. These changes apparently began in the 1970s and 1980s [104,105] (cf. also Table 2). In Inner Mongolia, some local populations are characterised as gregarious [97–99,103]. Relatively long migrations are also assumed for the easternmost parts of the species range [42]. In the Kulunda steppe, which stretches from the Irtysh River to the Ob River, an outbreak of *O. decorus*, together with the Italian locust, occurred from 1999 to 2002 (with major peaks in 2000 and 2001) [12]. Moreover, the abundant local populations of *O. decorus* were observed together with populations of the Italian locust. Together, at high levels of abundance, both species can damage a wide range of agricultural crops, from wheat to sunflower, pastures, and hayfields. In the dry steppe regions of Kazakhstan, both species can cause significant damage to spring wheat crops at densities higher than one individual of each per square metre, and at a high density ($16/m^2$), almost all plants can be damaged by *O. decorus* only [104,105].

A comparative analysis of the new models and similar models created for a more limited area (southeast of the West Siberian Plain) and taking into account the variation in solar radiation flux revealed noticeable similarities [12]. However, overall, the new models show a greater level of suitability for *O. decorus* in this region, which is probably determined by the much larger number of points included in the analysis and, accordingly, a significantly larger territory, the use of these points in the actual models' generation of only so-called bioclimatic variables, or both together. However, random data partitioning may overestimate model performance because of spatial positive but low autocorrelation.

Models produced for modern conditions describe well the known geographical and ecological distributions of the species across Asian grassland areas. Graphic models characterising the distribution of *O. decorus* within a system of life zones and major ecosystem types, taking into account abundance estimates, show a general preference for dry steppes

and semideserts (Figure 3). A very similar pattern was previously described for the subspecies *O. decorus asiaticus* Bey-Bienko, which is presently a synonym of *O. decorus*, in the mountains of South Siberia [106]. Here, the species also prefers semideserts and dry steppes and rarely penetrates local floodplains. A similar pattern of zonal preferences has also been demonstrated for Inner Mongolia [103].

Analysing the ecological–geographic patterns of species distributions also makes it possible to recognise some main bioclimatic factors affecting the distributions of key pests. In the region studied, for *O.decorus*, as well as for the Italian [85] and the migratory locusts [84], these are primarily annual mean temperatures (bio_1).

The species distribution models, especially those generated via the MaxEnt algorithm, also match well with results from simulations of the distributions of suitable habitats for the *O. decorus* in the northern (mostly the steppe) parts of Inner Mongolia, China, which are based on the same algorithm (MaxEnt) but on a completely different set of variables (including soil types and characteristics of vegetation cover, NDVI, and absolute altitudes) [107]. Importantly, this study demonstrated the very important role of chestnut soils (kastanozems) (cf. [101]), which are typical for dry and desert steppes, as well as some steppe grass species, in the species distribution across this region. A similar model for *O. decorus* was also created for the so-called Hexi (Gansu) corridor (Northwestern China) [108]. In this case, the authors used the full set of bioclimatic variables and some additional parameters (e.g., NDVI, vegetation and soil types, absolute altitudes, etc.). Interestingly, in this desert area, the annual precipitation (bio_12) and soil available water content together with the NDVI are very significant for *O. decorus*.

Ecological–geographic modelling reveals some chances for *O. decorus* to pierce northwards (at least up to 58° N in West Siberia and 62–63° N in East Siberia) in the future. One of the intriguing results of the modelling is the possible emergence in the future of vast areas optimal for the existence of the species in the Lena River basin, particularly in the steppe landscapes of Central Yakutia. Although these territories are very far from the actual northern range limits of the species (mostly more than 1000 km), the possibility for adult individuals to fly with favourable air currents over fairly large distances (up to several hundred kilometres) are assumed for Northern China [42]. This means that in the future, there is a certain (although likely relatively small) probability that some individuals will migrate to these more northern regions. Furthermore, the species may be dispersed by road and rail transport (cf. [7,44]).

A large group of the studied species comprises Orthoptera, for which a shift in optimal areas to the north (and in some cases, to the northeast) is predicted [12,84,85]. However, there are few examples of possible significant changes in species distributions. Typically, shifts are limited and manifest themselves as a shift in the most favourable areas. This group includes the most important possible pests. The most significant northwards shifts are predicted for migratory locusts [84]. While in the mid-20th century, stable populations of this species were thought to be absent or extremely rare in the region, by the early 21st century, such populations have become quite common, with high numbers of the species in them, and in some cases, even signs of a gregarious phase are emerging. Accordingly, it can be concluded that a new area of mass reproduction for this species is forming. A northwards shift in optimal areas (albeit not insignificant) is also revealed for the Italian locust [66] and the handsome cross grasshopper (cf. [12]). Opposing trends are predicted for several potentially harmful grasshoppers in different parts of their ranges. For example, for *Angaracris barabensis* (Pallas) (Acrididae: Oedipodinae), there is a decrease in habitat suitability in the western part of its range and a general improvement in conditions in its central and northeastern parts [88].

If global warming continues, it may lead to more distant northward and northeastward shifts in the range limits of *O. decorus* and alteration in the disposition and abundance of its populations, particularly in the optimal parts of its population system within which the species normally inhabits all applicable habitats; its mean densities are rather high and its colonies may be found even during depressions [4,50]. These shifts may be justified by both climatic changes (especially northwards) and some changes in human activities (mainly for eastwards relocation).

Overlapping ecological niches often allows for the assessment of species similarity, including potential pests, which may be important for plant protection systems. However, the significant overlap in niches between the migratory locust and *O. decorus* is intriguing since the local ecological preferences of *O. decorus* and *L. migratoria* are quite different, although both species prefer to eat grasses. The first species clearly prefers dry steppes whereas the latter usually inhabits moist habitats with a noticeable presence of reeds [10,15,20,84]. However, parts of the ranges of these species within the study region almost coincide, which is what determines the significant overlap of ecological niches, the volume of which, in accordance with the approaches used, is determined by the distributions of only several bioclimatic parameters. In contrast, *O. decorus* and *C. italicus* are similar in their preferred habitats (although they usually feed on different groups of plants) [12,51,85], but since the first species widely inhabits the steppe and semidesert regions of the eastern part of Asia, while the second rarely penetrates them, the degree of overlap of their ecological niches in terms of bioclimatic variables is small.

5. Conclusions

South Siberia and the northern parts of Kazakhstan, Mongolia and China, which are mainly occupied by forest–steppes, steppes and semideserts and used for agricultural production, have been and remain regions where harmful acridids could and can reproduce en masse and cause significant damage to agriculture. However, while such problems became common in southern West Siberia and in Kazakhstan a century ago, in the dry intermountain valleys of the South Siberian mountains and across the steppe regions of Transbaikalia, the eastern parts of Mongolia and Inner Mongolia, where the abundance of acridids is usually high in natural habitats, the situation began to change only at the end of the last century, largely due to the expansion of agricultural crops and increased grazing. This regional differentiation is largely due to differences in the level of continentality and in the nature of the plain and mountain landscapes [47,109,110] and, in many cases, is well expressed in the distribution of acridid species [4,111,112] and even in the distribution of the biomass of these insects [113]. All this can be clearly seen in the distribution of *O. decorus*.

Across areas with continental climates, from the West Siberian to the Turanian Plain and the Junggar (Dzungarian) Basin, and including the Tien Shan and Pamiro-Alai Mts, the model species remained the minor and local pest until the late 20th century. At the beginning of the 21st century, *O. decorus* became an emerging harmful regional species together with the Italian locust [12,20,51,52,85]. In the regions with hypercontinental climates and relatively high altitudes (from Central Siberia to the Gobi Desert), the levels of acridid abundance were and remain high [24,113]. However, local grasshoppers were not generally considered very important pests [114]. In recent decades, the abundance of grasshoppers has increased significantly, primarily due to *O. decorus* and *C. abbreviatus* [24]. The areas stretching from Transbaikalia to the Inner Mongolian Plateau are also characterised by hypercontinental climates, but somewhat soften in summer due to monsoons. At the beginning of the 21st century, *O. decorus* was noted in these regions, especially in Inner Mongolia, as one of the emerging regional agricultural pests [21–23,97,98].

Overall, the ecological–geographical distribution models of *O. decorus* generated for the modern era clearly outline areas of potential mass reproduction. This allows plant protection services to watch areas less affected by population monitoring of the model species more closely and, accordingly, to form the basis for so-called spatial forecasting. Moreover, several uncertainties arise related to the predicted possible northwards shift in life zone boundaries in the future under global warming because such shifts are determined not only by climate changes but also by transformations of the structure of local ecosystems, particularly changes in soil cover, vegetation and inner ecosystem connections, e.g., changes in the place of the species in food webs (cf. [115]). In this context, the following question arises: how quickly can ecosystems be restructured and what will be the consequences of this restructuring? In any case, it is clear that these processes take decades and even centuries. Therefore, although climatic conditions have become favourable for *O. decorus* in the forest–steppe life zone of West Siberia, its distribution here, especially in the northern forest–steppes, remains local and is most often associated with ecosystems transformed by humans, such as verges and lawns.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy16151483/s1, Table S1: Geographic coordinates of known records of *Oedaleus decorus* in the Asian parts of its range.

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