

Geographic distribution of *Microtus arvalis* and *Microtus rossiaemeridionalis* in Eastern Europe

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ABSTRACT. We studied a sample of occurrence localities of two sibling species: the common *Microtus arvalis* and the East-European vole *M. rossiaemeridionalis*, identified genetically or cytogenetically, by species distribution modelling (MaxEnt) methods for the territory of Eastern Europe. Climate data and remote sensing data were used as predictors. Despite of some difference in modern distribution of the species, we did not find any significant difference between ecological preferences of the common and East-European voles. Thus, we have tried to explain modern differences in distribution without ecological arguments. Such difference can be caused by historical reasons, when one of the species holds the territory on the basis of the founder principle or density-dependent spatial structuring. Another possibility is a segregating based on the behavioral or physiological peculiarities of the vole species. The low AUC values of our spatial models can be explained taking into account the dynamic change of landscapes of the Russian Plain, where the zone of sympatry of the sibling species is located, as well as by poor knowledge of species distribution details.

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Распространение *Microtus arvalis* и *Microtus rossiaemeridionalis* в Восточной Европе

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РЕЗЮМЕ. Выборка точек находок на территории Восточной Европы двух видов-двойников серых полевков: обыкновенной *Microtus arvalis* и восточноевропейской *M. rossiaemeridionalis*, определенных методами молекулярной генетики или цитогенетики, была исследована методами экологического моделирования (species distribution modelling, MaxEnt). В качестве предикторов использованы данные по климату и дистанционному зондированию земли. Несмотря на некоторые различия в современном распространении двух видов, показано, что экологические предпочтения обыкновенной и восточноевропейской полевки достоверно не отличаются. Поэтому предпринята попытка объяснить современное расхождение ареалов и особенностей распространения без привлечения экологических различий видов. Это может быть обусловлено историей расселения, при которой один из двух видов удерживает территорию за счет принципа основателя и плотно-зависимого пространственного разделения, а также поведенческими и физиологическими особенностями полевков. Невысокие значения AUC полученных моделей может быть связано с динамическими процессами смены ландшафтов на Русской равнине, где находится зона симпатрии видов-двойников, а также слабой изученностью деталей их распространения.

КЛЮЧЕВЫЕ СЛОВА: *Microtus arvalis*, *Microtus rossiaemeridionalis*, экологическое моделирование ареалов.

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Introduction

Voies of *Microtus arvalis* sensu lato group include two sibling species that dominate in communities of small mammals of grassy habitats in temperate zone of Eurasia, including agricultural ecosystems. These are common vole *Microtus arvalis* Pallas, 1779 and East-European vole *Microtus rossiaemeridionalis* Ognev, 1924. We consider common vole as a taxon that includes two parapatric chromosome races «arvalis» sensu stricto and «obscurus», following Musser & Carleton (2005), Abramson & Lissovsky (2012), Lissovsky *et al.* (2019). Having vast distribution and high density, common and East-European voles are of important biocoenotic and economic value. The species participate in circulation of a number of zoonoan-throponosis agents, playing a role of the primary host in some cases (Shekhanov, 1979; Dobrohotov *et al.*, 1985; Mikhailova *et al.*, 2008).

Modern geographic distribution of the common and East-European voles is presumably conditioned by both prehistoric processes of natural dispersion and range transformation during agricultural period, including extensive ploughing of Eastern Europe in XX century. Recent, relative to the time of species evolution, croplands appearance led to drastic changes in the species distribution. The voles spread from second in area meadow habitats and occupied agrocenoses. The arable lands became dominating in area in forest-steppe (presumable initial distribution optimum of the sibling species) as well as in irrigated steppe and in deforestation northern areas. The processes of enlargement of agrocenoses led to notable increasing of distribution area and number of the two vole species in Eastern Europe (Tupikova *et al.*, 2000; Neronov *et al.*, 2001; Khlyap & Warshavsky, 2010; Malygin *et al.*, 2020).

Despite the fact that more than 50 years have passed since the discovery of the hidden taxonomic diversity in *Microtus arvalis* sensu lato, our knowledge of the distribution and ecological preferences of the sibling species remains incomplete. The peculiarity of the pair of sibling species is a lack of morphological features suitable for species identification; therefore, one should provide special expensive and time-consuming investigation for identification of every specimen. As a result, the number of geographic localities, where specimens were identified properly, still remains too small compared to the entire known distribution area of both species.

The distribution maps of the common and East-European voles were published for the first time by Malygin (1983). The maps demonstrated wide distribution of *M. arvalis* and a narrower distribution of *M. rossiaemeridionalis*. Later, Shenbrot & Krasnov (2005) published distribution maps of these voles, constructed on the basis of previous studies (Malygin, 1983; Baranovsky *et al.*, 1994; Sokolov & Bashenina, 1994; Meyer *et al.*, 1996), which included information on properly identified specimens using karyology or protein electrophoresis, as the only methods avail-

able at that time. After the development of genetic methods in zoological studies in the last decades, the new data on distribution of the sibling species of the common voles have been collected. Recent invasions of these species into remote regions, sometimes located thousands kilometres away from the previously known range, have been found (review in Malygin *et al.*, 2020). The main goal of this study is interpolating of modern information on occurrences of the common and East-European voles on the territory of the Eastern Europe and allied territories using species distribution modelling technique.

Materials and methods

We used information on voles occurrences from the database "Mammals of Russia" (<https://rusman.ru> — Lissovsky *et al.*, 2018) that includes museum specimens, data from literature as well as unpublished information for a long period. Only specimens identified by genetic, cytogenetic or protein electrophoresis methods which accuracy of geographic coordinates < 2 km were included in the study. Initial dataset for the whole Russia included 713 records of *M. arvalis* and 601 of *M. rossiaemeridionalis*. The whole dataset is available at https://rusman.ru/sample/records?id=s_2_c0b69d62ed. The training sample was selected from the territory of European Russia: it included 637 records in 100 localities (exact geographic points) of *M. arvalis* and 530 in 70 localities of *M. rossiaemeridionalis* (Fig. 1). These localities formed notable spatial aggregations. We selected one occurrence point per 50×50 km square (100 and 70 localities, respectively), and then filtered points by between-points distance (with step of 5 km) until Moran I < 0.15. The final occurrences dataset included 85 records of *M. arvalis* and 35 of *M. rossiaemeridionalis*.

We had the best and quite homogenous occurrences data coverage for European part of Russia only, so we made all calculations on the basis of this territory and projected the model to the whole climate temperate zone of Eurasia. The spatial frame of the analysis included a grid with 2 km resolution in geographic Mollweide projection. We used 62 variables in the main analysis: CHELSA 19 "bioclimatic" variables (<https://chelsa-climate.org/downloads/>; Karger *et al.*, 2017), altitude and 42 MODIS generalised average monthly data layers (six months of 2004 per seven spectral bands; <http://glcf.umd.edu/data>, Eastern Hemisphere only) as environmental data. Alternatively we tested spatial distribution on the basis of "bioclimatic" variables only. We used principal components (explaining 0.999 of total variance) of the environmental variables as predictors for analyses.

Species distribution modelling was carried out in R (R Core Team, 2020) using original script (Supplement) based on ENMeval (Muscarella *et al.*, 2014; Kass *et al.*, 2021), maxnet (Phillips *et al.*, 2019; Phillips, 2021) packages, using MaxEnt version 3.4.1 (Phillips *et al.*, 2019). The idea of calculations was in selecting the best

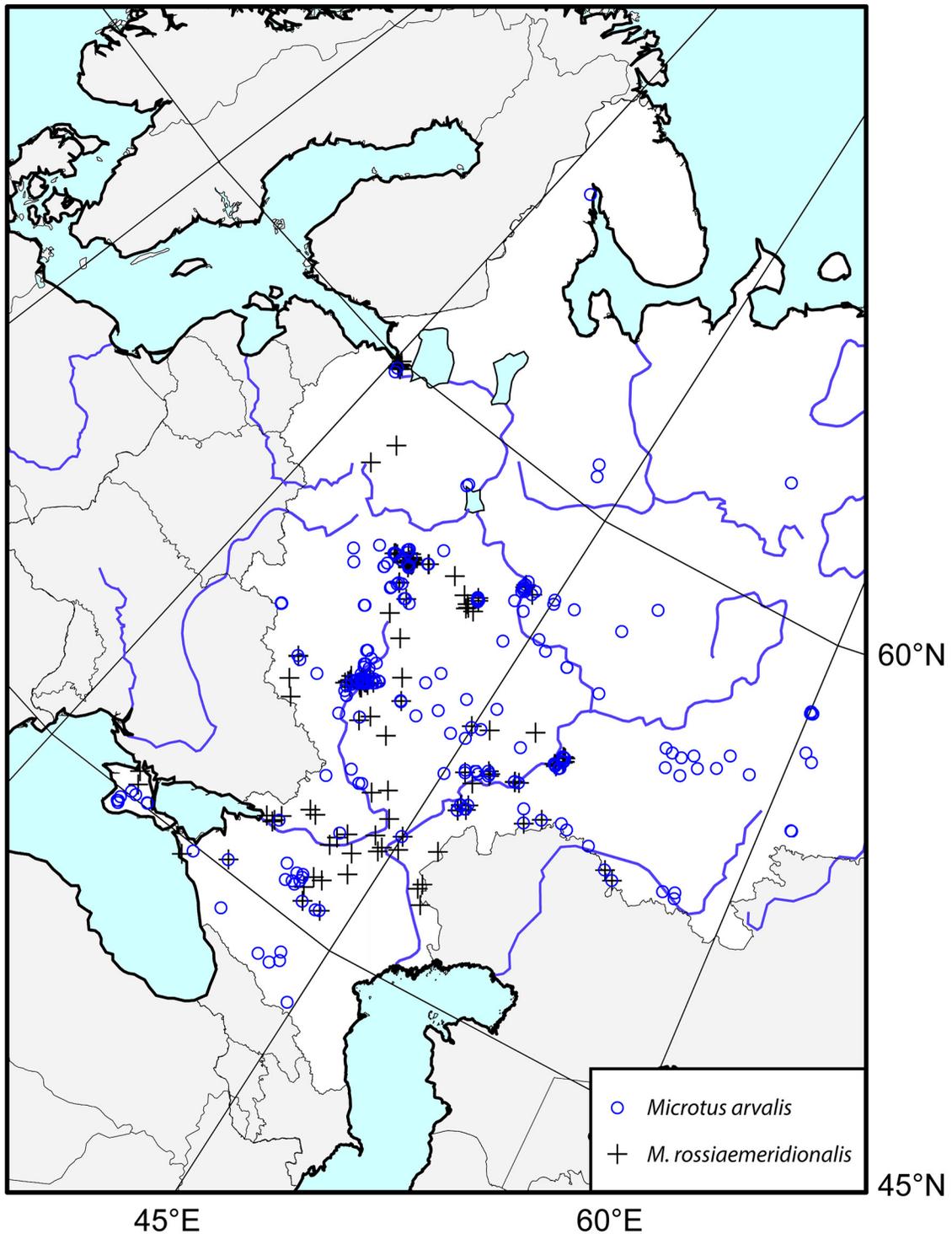


Fig. 1. Occurrence places of common *Microtus arvalis* and East-European *Microtus rossiaemeridionalis* voles, analysed in this study. Territory that was not included in the analysis is shaded.

model (on the basis of AICc values, evaluated on the basis of the test sample) among the set of models with different values of regularization multiplier (0.75, 1, 2,

3), different sets of feature types (linear — "L", linear + quadratic — "LQ", linear + quadratic + hinge — "LQH") (Muscarella *et al.*, 2014), and different sets

of background points. Selection of background points (BP) had a key role for the analyses. We constructed the surface with probability values for the BP selection. The "distribution range" (an area including 70 km buffers around occurrence points) had probability of selection of 1; other territory — 2. Occurrence points of ecologically similar species — with similar approach to detection (*Agricola agrestis*, *Alexandromys oeconomus*, *Microtus subterraneus*, *M. socialis*) surrounded by various buffers (2, 3.5, 5 km) outside of the "distribution range" got a value of 4 (the best studied areas). The exact values for these coefficients were selected in preliminary runs.

The best model for *M. arvalis* had regularization multiplier of 1, LQ (linear + quadratic) feature types and 3.5 km buffer for BP selection. The best model for *M. rossiaemeridionalis* had regularization multiplier of 3, LQH (linear + quadratic + hinge) feature types and 5 km buffer for BP selection.

The difference between two resulting models was calculated in the both G- (Warren *et al.*, 2010) and E-space (Brown & Carnaval, 2019). We compared two models (maps) in the case of G-space; and rasterized scatterplots of the two first principal components of values of environmental data in occurrence points in the case of E-space. Schoener's D was used for comparison (Schoener, 1968; Warren *et al.*, 2010). The sample of occurrence points was randomized 100 times, preserving sample size and all model parameters for both "species". The p-values were calculated comparing Schoener's D after inter-species comparison and the distribution of simulated D values. The background

tests and E-space correction (Brown & Carnaval, 2019) were not actual because of wide species sympatry.

Results

We found that only in 15 of 100 occurrence points of *M. arvalis*, voles were identified repeatedly more than after 5 years; 64 points were known after a single record. Fifteen occurrence points were known only before 2000, 35 were found or confirmed after 2010. In *M. rossiaemeridionalis* 11 of 70 occurrence points were identified repeatedly, 46 were known after a single record; 17 were known before 2000 only, and 27 were confirmed after 2010. The distribution of dates of the voles' registration was: $24.05.1998 \pm 6$ years 3 months (std dev); median 27.06.1998; min–max 1965–2021.

Distribution of suitable habitats for the two species in study is represented in Figs. 2 and 3. Models with different parameters differed notably. Similarity (Schoener's D) between various models of *M. arvalis* was 0.79–0.85; in *M. rossiaemeridionalis* — 0.75–0.82. The final model for *M. arvalis* had an AUC value of 0.84; *M. rossiaemeridionalis* — 0.86. Models constructed on the basis of climate data only had AUC values 0.78 for *M. arvalis* and 0.86 for *M. rossiaemeridionalis*. The overlap between two species in the space of the two first principal components of ecological predictors was notable (Fig. 4)

Despite of some difference in the distribution of occurrence points (Fig. 1), there was no significant difference between models of two species. For geographical comparison D was 0.72 (*p*-value 0.096); comparison in ecological axes resulted in D of 0.26 (*p*-value 0.275).

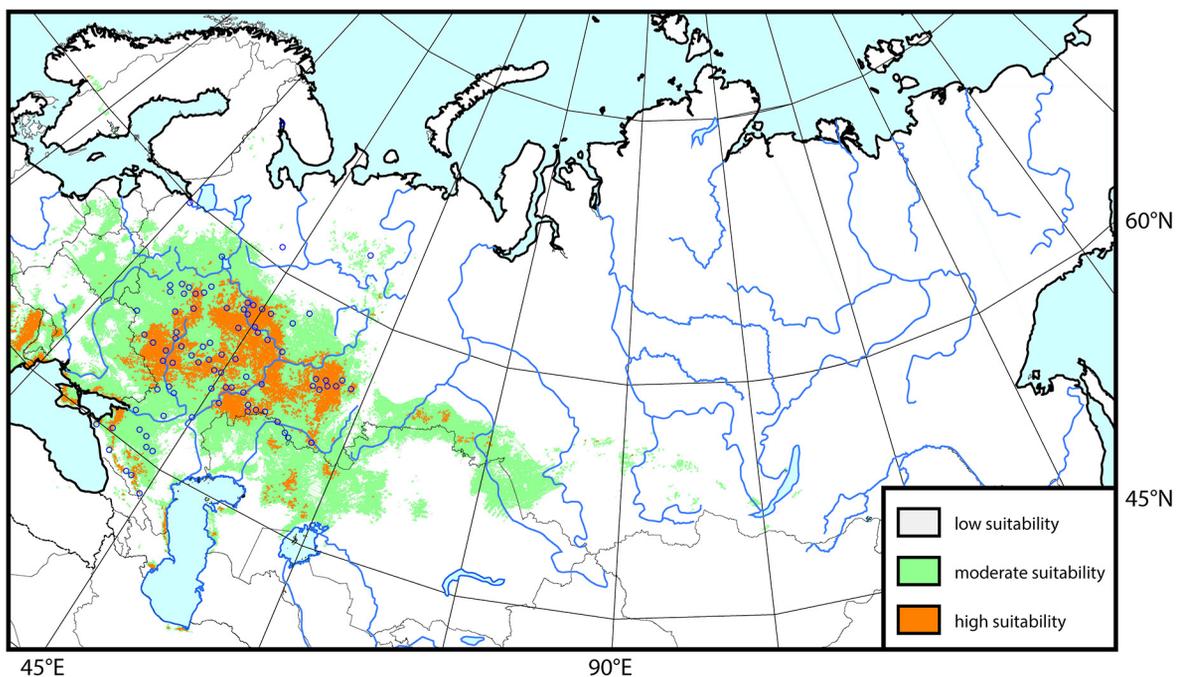


Fig. 2. Distribution of suitable habitats for *Microtus arvalis* after species distribution modelling. Localities used in training sample are shown.

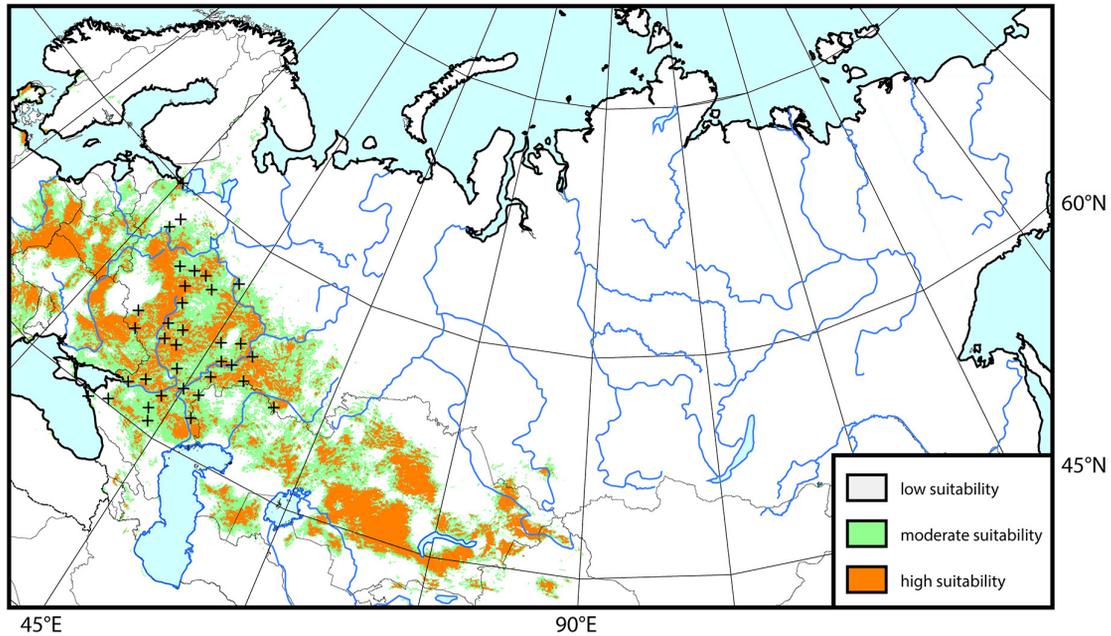


Fig. 3. Distribution of suitable habitats for *Microtus rossiaemeridionalis* after species distribution modelling. Localities used in training sample are shown.

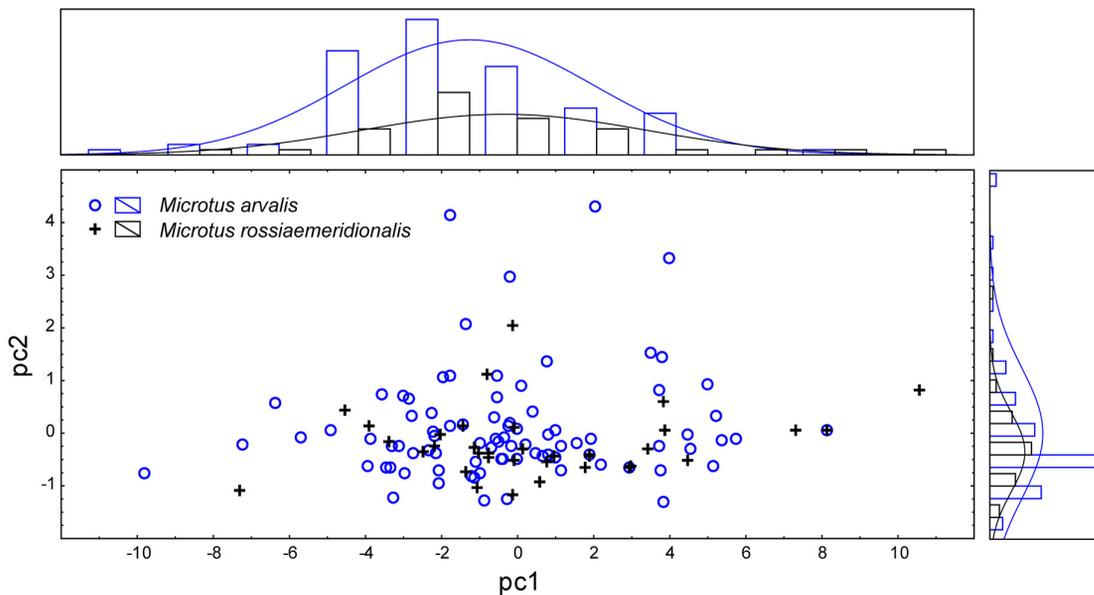


Fig. 4. Distribution of occurrence places of common and East-European voles in ecological hyperspace. Axes are the two first principal components of climatic and earth remote sensing data.

Discussion

Outlines of our species distribution models match previous information in general (Malygin, 1983; Meyer *et al.*, 1996; Shenbrot & Krasnov, 2005), including wide overlap of the ranges in Eastern Europe and decreasing of the northern latitude of the distribution

in the eastern direction. Nevertheless, the absence of significant difference between ecological niches of the two species allows us to discuss a new interpretation of the main mechanisms of their spatial segregation.

It was previously known (Shenbrot & Krasnov, 2005; Malygin *et al.*, 2020) that there are some regions, where only one of the sibling species was found. For

example, *M. rossiaemeridionalis* was only recorded at the south of the Eastern Europe: steppes of interfluvium of lower Don and Volga Rivers, northern part of Nizhneye Povolzh'ye (Lower Volga) region, steppes of Trans-Volga and Cis-Ural regions in Russia. Common vole only was found in the majority of the West European countries (Zima, 1999), in mountains of Crimea, Caucasus and Transcaucasia, at the south of Cis-Ural region and Western Siberia, at the south-east of the range east to Altai and Zailiyskiy Alatau Mountains (Meyer & Yatsenko, 1980). Since we did not find differences between ecological preferences in the common and East-European voles, the existence of such regions should be explained without causing discussion on ecological differences. One of the possible ways is historical dispersion, when one of the species (races etc.) keeps the territory according to the founder principle or density-dependent spatial structuring (Waters *et al.*, 2013; Vodá *et al.*, 2015; Shchipanov & Pavlova, 2019). Such scenario was probably realised at the south of Volga-Dnieper interfluvium that was not affected by Dnieper glaciation (Malygin *et al.*, 2020).

The possibility of multiple translocations of each of the two species should not be ruled out. Such translocations have created (or create now) the mosaic of the vole settlements, in addition to natural dispersion. In such case, the behavioral peculiarities of the species can play an important role in the formation of distribution mosaic (Canestrelli *et al.*, 2016). According to studies (Malygin & Deulin, 1979; Tikhonov *et al.*, 2009 a, b) the common vole is more aggressive both towards the conspecifics and the East-European vole. Additionally this species is adapted to feeding on low-calorie forage, in contrast to the East-European vole (Mokeeva & Chentsova, 1981; Bashenina *et al.*, 1988).

In contrast, *M. rossiaemeridionalis* has higher fertility and stress resistance, lower aggression, better adaptation to high densities (Malygin & Deulin, 1979; Zorenko, 1980; Malygin, 1983; Sokolov & Bashenina, 1994; Tikhonova *et al.*, 2005, 2007). Better adaptation of the species to high daily temperature amplitude comparing to *M. arvalis* allows *M. rossiaemeridionalis* to survive in arid conditions (Bashenina *et al.*, 1988). For the same reasons, the East-European vole shows a higher tendency to synanthropy (Karaseva *et al.*, 1999; Tikhonova *et al.*, 2012) and is more often associated with meadow-shrub habitats or sparse forests in the temperate zone, while the common vole prefers open meadows and fields (Malygin, 1974; Okulova *et al.*, 2008).

Nevertheless the bigger part of the voles distribution is covered by sympatry zone, where the two vole species were found to be symbiotopic (Malygin, 1983; Baranovsky & Okhotsky, 1988; Karaseva *et al.*, 1994; Tikhonova *et al.*, 1999; Bobrov *et al.*, 2008; Mikhailova *et al.*, 2008). This phenomenon agrees with our results. It was found (Bobrov *et al.*, 2008) that the major part of the sympatry zone in the late XX century coincides with the area of extensive ploughing. Ploughed fields dominate over other landscapes in such areas. The process of ploughed fields settling by voles can

be (with some reservations) compared with settling of lands after a glacier retreat. In both cases, lands are not occupied by any other species and competition is quite low. The competition between both vole species was probably further reduced by the high ecological capacity of the agrocenoses. Besides, the traditional way of straw storing in large stacks provided an additional shelter during winter time. Existence of such shelter allowed winter breeding that was previously impossible in the temperate zone (Kulik, 1951; Kucheruk & Rubina, 1953; Malygin *et al.*, 2020).

The cases of occurrence of the vole species far from the main distribution range (Malygin *et al.*, 2020) unambiguously point to ongoing anthropogenic translocation of the species in question. Known cases of remote *M. rossiaemeridionalis* findings are characteristic by long dispersion distances. Such cases are Spitsbergen Island (Bol'shakov & Shubnikova, 1988; Fredga *et al.*, 1990), Komi Republic (Bashlykova & Korolev, 2014), Russian Far East (Kartavtseva *et al.*, 2012; Markova *et al.*, 2016). *Microtus arvalis* was found in local patches of suitable habitats situated to the north of the main range. Such sites were Voroniy Island in the White Sea, Kandalakshskiy Nature Reserve (Boyko, 2003), the south of Arkhangelsk Region of Russia (Bulatova *et al.*, 2010; Bulatova & Emel'yanova, 2018), Komi Republic (Bashlykova & Korolev, 2014). The sites of remote occurrence of the sibling species are rarely agree.

Our discussion of distribution and formation of the voles' ranges cannot answer all arising questions, and is more a formulation of the problem. One of the obvious reasons of the uncertainty is a lack of data on voles' distribution. The sibling species were separated by methods of karyology in the second half of 1960s (Meyer, 1968; Meyer *et al.*, 1969, 1972; Orlov, 1969). Thus, specimens collected before this date and lacking data on karyotype were not identified. Specimens collected later, but those who were not analysed by karyology or genetics are useless for distribution study also. Voles without exact geolocation of catching location cannot be used in our study as well. Unfortunately, tradition of printing exact geolocation on museum labels or in publications is also quite new. As a result, we found only about a hundred of not-aggregated localities for each of these two wide spread species (see Methods). Data obtained on the basis of repeated captures (see Results) during five years or longer period represent 15% of localities only. Information collected on the basis of single capture comprises 64–70% of localities. Apparently we should admit that our modest data can be a reason of errors in distribution description. It is quite probable that one of the species was not found in 64–70% of localities due to asynchronous population dynamics or, on contrary, was captured in unsuitable habitats after human translocation or natural dispersion.

Species distribution modelling aims to compensate the lack of occurrence data, and we have enough localities to expect models of high quality (big AUC values for example). Lower AUC values and notable difference between spatial models with different parameter

values indicate a lower quality of our resulting calculations. The low quality of the model is also indicated by the predicted model of *M. rossiaemeridionalis*, which displays area of high suitability in the arid regions of Middle Asia (Fig. 3). The low suitability area in Central Europe for *M. arvalis* (Fig. 2) is also erroneous. Such a model bias is occurred usually when "some entry points does not fit the model".

The low quality of the models can be explained in different ways. Besides probable biased set of occurrence points discussed above, change of natural habitats of Russian Plain could play a role. After the collapse of the USSR (end of 1991), there were significant changes in the agricultural sector. The areas of arable land and hayfields have significantly decreased. Agroecosystems and meadows, especially in the forest zones of European Russia, began to overgrow with forests. And although most of the vole occurrence points in our dataset were collected after 2000 (see Results), predictors data of points collected during previous years could be read incorrectly. The analysis of climatic data only (that is, the complete exclusion of mosaic landscapes) did not improve the results, although climate change in the Russian Plain also took place. It cannot be ruled out that the reduction in the area of arable land, as well as changed harvesting and storage technologies, which reduced the possibility of winter breeding of "arvalis" group voles, and hence the number (Trankvilevsky & Kvasov, 2018; Malygin *et al.*, 2020) have changed the character of spatial distribution of voles. Their distribution changed from almost continuous to inhabiting isolated local areas of meadow-field habitats, which are not detectable on the scale of our study. This leads to a distortion of the suitability distribution and a bias in the results of the analysis.

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Supplementary data. The following Supplement is available online.

Supplement Script in R for distribution modeling in *Microtus arvalis*.

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