INTERSPECIFIC INTERACTIONS AS A FACTOR OF LIMITATION OF GEOGRAPHICAL DISTRIBUTION: EVIDENCE OBTAINED BY MODELING HOME RANGES OF VOLE TWIN SPECIES *MICROTUS ARVALIS* — *M. LEVIS* (RODENTIA, MICROTIDAE)

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Interspecific Interactions as a Factor of Limitation of Geographical Distribution: Evidence Obtained by Modeling Home Ranges of Vole Twin Species *Microtus arvalis* — *M. levis* (Rodentia, Microtidae). Mezhzherin, S. V., Lashkova, E. I., Kozinenko, I. I., Rashevskaya, A. V., Tytar, V. M. — Based on the maximum entropy modeling algorithm and using 12 environmental variables, we modeled the distribution of the vole twin species *Microtus arvalis* and *M. levis*, with particular attention to regions where the species overlap. For both species models performances were considered "excellent" (AUC > 0.9), although some occurrences appeared in areas of low habitat suitability, whereas in some areas of predicted high habitat suitability there were no occurrences. Apparently, both species do not fully occupy areas predicted to be favorable in terms of habitat suitability and persistence. The cause for such restriction are not the considered factors (including bioclimatic), but competitive interactions that prevent individuals of one species from expanding within the home range of the other. Contributions of the considered environmental variables for generating the potential distribution prediction were distinguished: for *M. arvalis* net primary production alone made the largest contribution (42 %), whereas for *M. levis* there was a cumulative effect of a number of factors.

K e y   w o r d s : *Microtus*, species distribution modeling, home range, interspecific interactions.

One of the issues at the forefront of modern evolutionary biology is the interaction of vicarial species in places of parapatry (Barton, Hewitt, 1985, 1989; Helbig, 2005; Jiggis, Mallet, 2000). As a rule, extensive introgressive hybridization occurs in places of contacts of closely related species. As a consequence, in the joint areas there are practically no specimens of parental species, but only hybrids with different proportions of

genetic material. The phenomenon is interesting because the spread of alien genes usually does not go beyond the narrow hybrid zone, which is believed to be due to genetic factors and landscape-climatic restrictions on the mutual immigration of individuals of parental species. However, there are cases when close, but reproductively isolated species interact on the boundaries of their home ranges. In this case, the stabilization of their home ranges is most likely associated with competitive interactions of different species, although the influence of natural and climatic factors is also not excluded.

One example of situations in which the restriction of species distribution, at a first glance, is not related to the effect of environmental factors, can be the situation involving two twin species of vole: the Common vole *Microtus arvalis* (Pallas, 1778) and the East European vole (*M. levis* Miller, 1908). These species cannot be diagnosed by morphological traits, but nevertheless are reproductively isolated (Malygin, 1983). Individuals of both species occur in the same habitats, which are open landscapes with meadow or steppe vegetation or fields of perennial grasses. In overlapping areas, the species form mixed populations. At the same time *M. arvalis* on the eastern limit of its range, in particular, in Ukraine, is restricted moving further to the east approximately along a line connecting Kharkiv and Odesa, while for *M. levis* the limit of advance in the western direction is a conventional straight line between Chernobyl and Vilkovo (Teslenko, Zagorodnyuk, 1986; Zagorodnyuk, Teslenko, 1986). Limitations in the distribution of these species, at a first glance, are not related to any obvious landscape or habitat differences, since these species occupy very close niches and are not characterized by pronounced ecological segregation. Therefore, the question arises as to what causes the restrictions of the expansion of *M. arvalis* range towards the east, and *M. levis* in the western direction: competitive interactions of species or, nevertheless, some environmental factors.

In order to obtain an answer to this question, computer modeling was carried out of the spatial distribution of these two species with the subsequent extrapolation of their potential distribution using available points of occurrences.

For most of species, the possibility of occurrence in a certain area can be predicted by species distribution models (SDMs). SDMs are becoming an important method and have been widely used (Franklin, 2009). SDMs are techniques that use the relationship between species occurrence and environmental conditions to model the geographical ranges of suitable-habitat for the certain species (Peterson, 2006; Miller, 2010).

A variety of distribution modeling methods is available for predicting the potential geographical range of a species. *Maxent* (Phillips et al., 2006) stands out because it has been found to perform best among many different modeling methods (Elith et al., 2006) and may remain effective despite small sample sizes. *Maxent* is a maximum entropy based machine learning program that estimates the probability distribution for a species' occurrence based on environmental constraints (Phillips et al., 2006). It requires only species presence data (not absence) and environmental variable (continuous or categorical) layers for the study area. The modeling results in a map of habitat suitability of the species ranging from zero to 1 per grid cell.

Material and methods

For building the model, an original database containing 397 *M. arvalis* and 298 *M. levis* georeferenced locations was used. Each individual was genetically identified; therefore their affiliation to one or the other species did not raise doubts. Particular attention when drawing up the list of occurrences was given to the regions where the species are met together.

The sources of information were unpublished results of our field investigations, as well as data from the literature (Malygin, 1983; Teslenko, Zagorodnyuk, 1986; Zagorodnyuk, Teslenko, 1986; Zagorodnyuk et al., 1994; Zima et al., 1991). Raster information from the Global Agro-Ecological Zones (GAEZ) database (IIASA/ FAO, 2012), which includes components of climate, soil, relief, land cover, etc., was used as environmental parameters. Amongst the climatic variables we used the mean annual precipitation, annual temperature range and the duration of the frost-free period. The ratio of seasonal precipitation (P) over reference evapotranspiration (PET) for the periods between April–September and October–March was used as a measure of the potential stress from lack of water (or "dryness"), a condition that can severely affect ecosystem performance and individual survival. The relief was characterized by the median altitude and terrain slope index. Anthropogenic factors were represented by human population density and accessibility (i. e., estimated travel time to nearest market/ city with 50,000 or more inhabitants), partially by the dominant land cover pattern. Other characteristics from the GAEZ database included dominant soils types and net primary production.

The *Maxent* software (version 3.3.3e) was utilized for modeling (http://www.cs.princeton.edu/schapire/ maxent/), using the autofeatures and setting the regularization parameter to 2. Logistic output format was used to describe the probability of presence (Phillips, Dudik, 2008), which is a continuous habitat suitability range between zero (unsuitable) and 1 (the most suitable). *Maxent* was run 25 times (using all predictor variables) for each species in order to get average prediction. A bootstrapping replication technique was applied to the dataset which uses all occurrence data to build the model. The outputs in ASCII format were processed and visualized using SAGA GIS (Conrad et al., 2015). The Jackknife analysis was used to indicate the most informative variables (in corresponding percentages > 10 %). The accuracy and performance of species distribution models were evaluated using threshold-independent receiver operation characteristic (ROC) analysis (Elith et al., 2006;

Phillips et al., 2006). The area under the ROC curve (AUC) ranges between zero and 1. Models with an AUC value higher than 0.7 are considered acceptable (Swets, 1988).

We used the 10 percentile training presence threshold as suggested by (Phillips, Dudik, 2008). This threshold value provides a better ecologically significant result when compared with more restricted thresholds values.

Results and discussion

Based on the maximum entropy modeling algorithm and using 12 environmental variables, we obtained 25 raster outputs modeling the distribution of the considered species. All the distribution models were better than random (AUC > 0.5). For both species, models performances were considered "excellent" (AUC > 0.9): 0.923 ± 0.001 for *M. arvalis* and 0.954 ± 0.001 for *M. levis*.

In the case of *M. arvalis*, the species was also found in a number of places featured by low habitat suitability (i. e., below the 10 percentile training presence value of 0.28) (fig. 1). This applies to both the southern (Northern Balkans and foothills of the Pyrenees), and the northern limits of its home range (Central Russia). In addition, there are zones optimal for the habitation of the species, but in which there are no genetically identified findings. In the west, they coincide with the territories of Germany, the Netherlands, Belgium and the British Isles, where, in fact, *M. arvalis* is a common species, and the absence of points on the map (fig. 1) is due to a deficit of genetic studies of the species. In the east, the regions of the Forest-Steppe and steppes (i. e., grasslands) of the Left-bank Ukraine, as well as the North Caucasus, are predicted to be optimal from the point of view of the modeling exercise. In all these places *M. arvalis* is unequivocally absent (Malygin, 1983; Teslenko, Zagorodniuk, 1986). This means that in the case of *M. arvalis*, the cause limiting the expansion of the species eastward from the conventional Kharkiv-Odesa line is not linked to bioclimatic factors or any other of those used in the modeling.
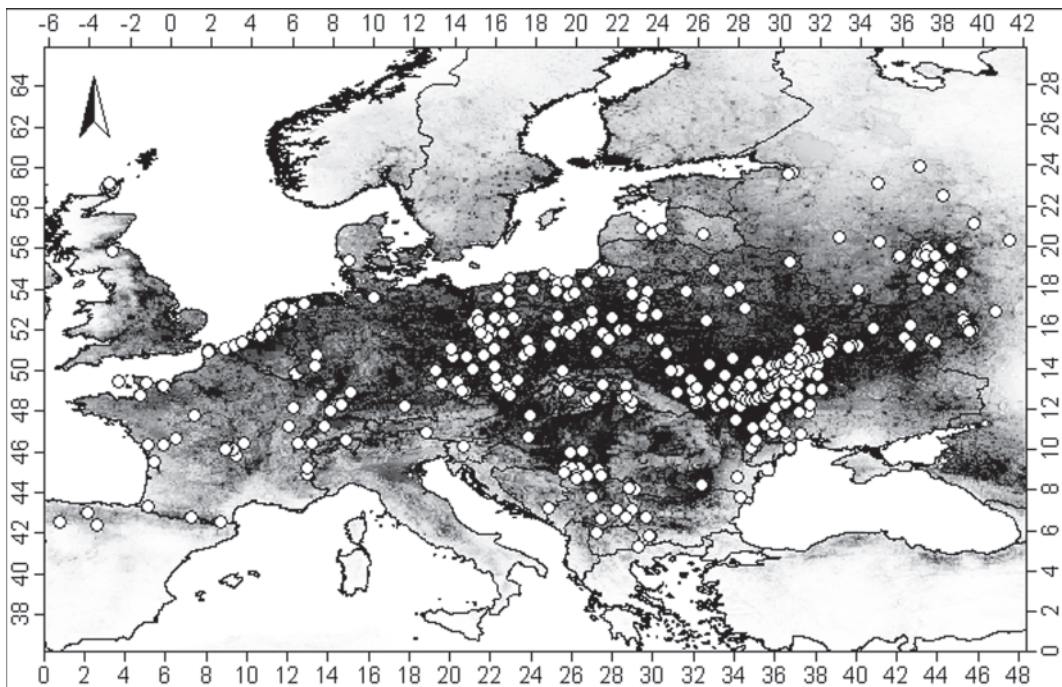

Fig. 1. Potential distribution of the Common vole *Microtus arvalis*. White circles are georeferenced occurrences of genetically identified individuals; black indicates areas of maximum habitat suitability, white are areas of lowest suitability.
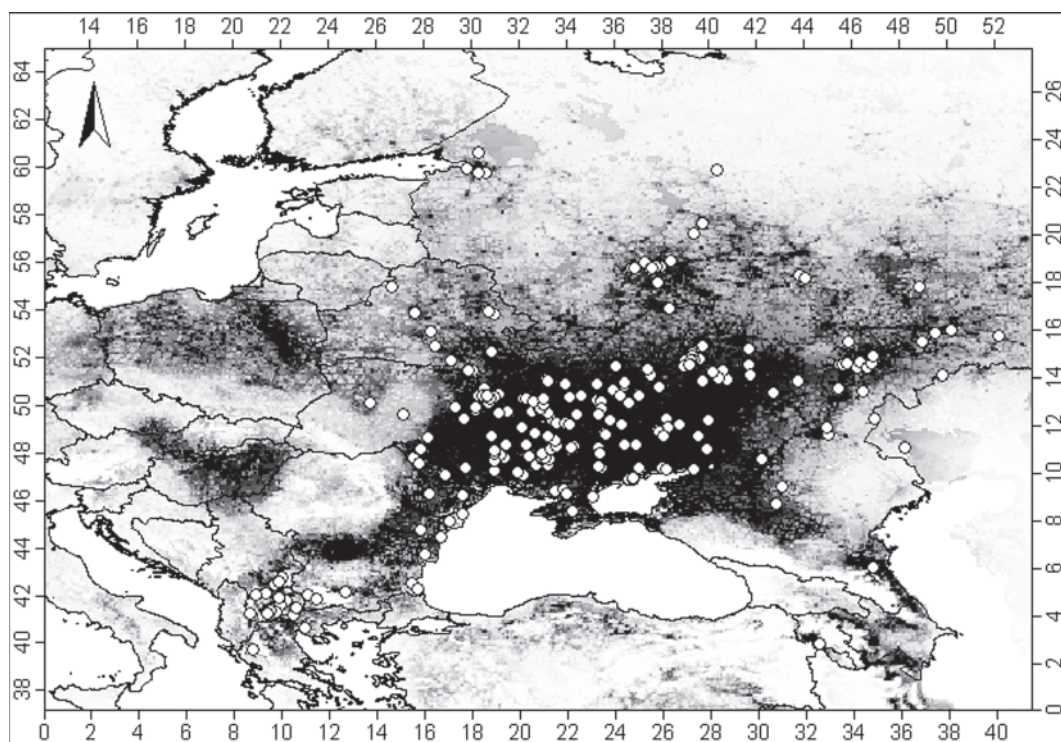
Fig. 2. Potential distribution of the East European vole (*Microtus levis*). Captions as in fig.1.

The situation is similar for the East European vole (*M. levis*) — most of its home range is within the zone with the optimal habitation conditions (i. e., above the 10 percentile training presence value of 0.29) (fig. 2). Differences between the actual home range and the one predicted by the model are as follows. Firstly, in the north, the species is fairly common in regions of the north of the Baltic, where conditions seem to be tolerable for it. Secondly, in the south the species is found in Asia Minor and Transcaucasia (fig. 2), where habitat suitability is predicted to be low. On the other hand, *M. levis* is absent in Poland, Slovakia and Hungary, although, as predicted, the combination of bioclimatic factors and other factors used in the modeling should favor the species within these countries. The map does not show any occurrence points in places with satisfactory conditions in the east of the home range: in the Don steppes and in the Northern Caucasus. However, it should be noted that in this case the contradiction between the predicted habitat suitability and the presence of a species in the region is false. In fact, the East European vole inhabits these areas, and the reason for the absence of occurrence points is that voles of the region remain unexplored in terms of their genetic identity. Thus, in the situation with *M. levis*, as in the case of *M. arvalis*, there are areas outside the actual home range that seem to be optimal for habitation of the vole, but they appear to be unoccupied.

T a b l e 1. **The most informative variables (in corresponding percentages > 10 %) for generating the potential distribution prediction for the Common vole *Microtus arvalis***

Variable	Contribution, %
Net primary production	42.6
Annual temperature range	12.3
Ratio of seasonal precipitation (P) over reference evapotranspiration (PET) for the period between April–September	10.2
Human population density	9.9

T a b l e 2. The most informative variables (in corresponding percentages > 10 %) for generating the potential distribution prediction for the East European vole *M. levis*

Variable	Contribution, %
Annual temperature range	22.2
Accessibility	18.8
Dominant soils types	17.7
Duration of the frost-free period	15
Human population density	13.6

Thus, it can be argued that for the two considered species there are large unoccupied areas of favorable habitat suitability, which can not be considered strictly isolated from areas of the actual home ranges. In the case of *M. arvalis*, these unoccupied areas are located to the southeast of the actual home range of the species, and in the case of *M. levis* — strictly to the west.

Another result of this study is the assessment of the contribution of various considered factors in the formation of the contemporary home range of both species (tables 1, 2). In this respect four main parameters are distinguished for *M. arvalis*, accounting for about 75 % of the total effect of all factors. The key contribution to generating the potential distribution prediction is made by the net primary production, which accounts for 42 % of the total effect. As for *M. levis*, there is no clearly indicated leading factor shaping the home range of the species. The annual temperature range has the greatest weight, however its contribution is only 22.2 %. In all, five significant factors have been distinguished, totaling an effect of 87.3 %. The analysis of the contribution of specific factors has a definite meaning in the context of this study, since, for example, *M. levis* shows that it is difficult to explain the patterns of spatial distribution of a species by using a few unambiguous environmental factors.

Summing up this research, we can formulate the following trends: both species do not fully occupy areas optimal in terms of habitat suitability and persistence. These areas are within the home range of the other species, and therefore the most likely cause preventing corresponding areas being occupied are antagonistic interactions of similar species, in which one species does not allow the expansion of another species into its home range.

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