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АКАДЕМІЇ НАУК
УКРАЇНИ

БІОЛОГІЯ
BIOLOGY

https://doi.org/10.15407/dopovidi2023.05.066
UDC 599.323.45:591.9

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Ecological niche modeling and factors determining the range of the wood mouse *Sylvaemus sylvaticus* (Linnaeus, 1758)

Ecological niche modeling of the wood mouse Sylvaemus sylvaticus, using machine learning method and a space of 35 bioclimatic factors, revealed that the most favorable conditions for this species are found in Western Europe. The primary core distribution areas are concentrated there, with the probability of encountering this species in habitable landscapes reaching 60 %. In contrast, the bioclimatic conditions of Eastern Europe are pessimistic: the habitat of the species is significantly fragmented, the cores are absent, the probability of encounters does not exceed 40 %, most often being less than 10 percentiles. It is evident that among the bioclimatic factors, climate continentality plays a central role, indirectly influencing the eastern border of the S. s. sylvaticus range and shaping specific vegetation types. Direct effects of individual factors and interspecies relations are possible and do occur, limiting the species' eastern expansion, primarily in the southern part of its eastern range borde.

Key words: *modeling, Sylvaemus sylvaticus, ecological niche, habitat fragmentation.*

The wood mouse *Sylvaemus sylvaticus* (Linnaeus, 1758) is a widespread species with a large European range. Comprehensive studies have designated it as a model organism for evolutionary-geographic analyses. Karyotyping [1], allozyme analysis [2], and phylogeographic investigations [3-5] have provided a basis for classifying this species as polytypic, represented by two subspecies: *S. sylvaticus sylvaticus* and *S. s. dichrus*. This classification is attributed to the existence of two refugia during the last glacial maximum [4]: a western refugium covering the Pyrenees and Southern France, and an eastern refugium encompassing the Apennine-Balkan region. From these refugia, two cases of prochoresis were developed, forming the modern range of the species. Moreover, the

Citation: Mezhzherin S.V., Tytar V.M., Tereshchenko V.O. Ecological niche modeling and factors determining the range of the wood mouse *Sylvaemus sylvaticus* (Linnaeus, 1758). *Допов. Нац. акад. наук Укр.* 2023. № 5. С. 66—72. https://doi.org/10.15407/dopovidi2023.05.066

scale of the western prochoresis significantly exceeds the eastern. It extends along the Atlantic coast from the zone of subtropical dry forests of North Africa to the boreal forest zone of Norway and Iceland inclusively, and outreaches to the east up to the North of Ukraine. The territories of Austria, Romania, Southern and Central Ukraine lie beyond the Apennine-Balkan prochoresis. Consequently, the eastern border of the S. sylvaticus habitat spans from the Baltic Sea to the Black Sea, through the south of Lithuania, the center of Belarus, and adjacent regions of northeastern Ukraine, including the Russian Federation and eastern Ukraine [6, 7].

What restricts the species' eastward expansion? Landscape and biotope factors, which typically determine the stability of the range, are not apparent in this case. The eastern border crosses through relatively homogeneous habitats, which contrasts with the clear climatic differences between the northern and southern limits of the species' distribution.

In addition to bioclimatic factors, the expansion of the range to the east can be limited by competitive interactions with related species, such as voles of the *Microtus aravalis — M. levis* group [8].

The purpose of this study was to address the following questions: 1) whether bioclimatic factors limit the eastward distribution of *S. sylvaticus*; 2) whether their effect is direct or indirect; 3) can the interaction of *S. sylvaticus* with related species be considered a limiting factor for its distribution.

These questions can be answered by modeling the ecological niche of *S. sylvaticus* using bioclimatic variables. As a result, not only the most favorable zones for the existence of this species, but also the bioclimatic factors that limit its geographical distribution will be established.

The material for modeling were a number of individuals of *S. sylvaticus*, the species affiliation was established by the sequences of the cytb gene taken from GenBank, as well as a number of samples labeled at the allozyme level [2]. A total of 115 points were used, which evenly covered the species' range (Fig. 1).

The work uses the method of machine learning based on Bayesian additive regression trees (BART), and is implemented in the R software environment ("embarcadero" package [9]). A distribution map of predicted environmental suitability values for a species tied to geographic coordinates is simultaneously produced, varying from 0 to 100 %. The quality of the model was evaluated using ROC analysis. The quantitative interpretation of ROC is given by the AUC indicator — the area bounded by the ROC curve and the axis representing the share of false-positive classifications. The higher the AUC, the better the classifier. Models with an AUC value above 0.7 are considered acceptable. The program also automatically determines the contribution of each predictor to the construction of the final model and draws dependence curves describing the changes in the predictive values of environmental suitability as a function of individual predictors.

The predictors are retreived from the CliMond database [10], which contains bioclimatic indices taking into

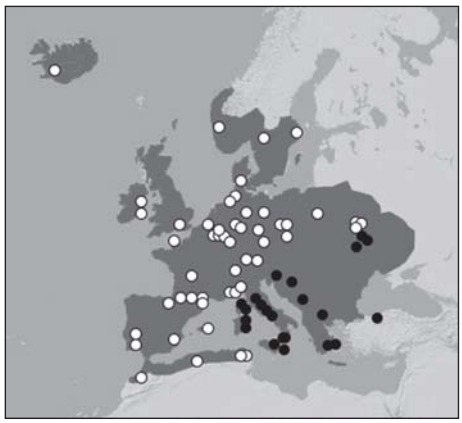

Fig. 1. Localization of samples involved in modeling: white circles are *S. s. sylvaticus*, black circles are *S. s. dichrus*. Habitat scheme according to [7]

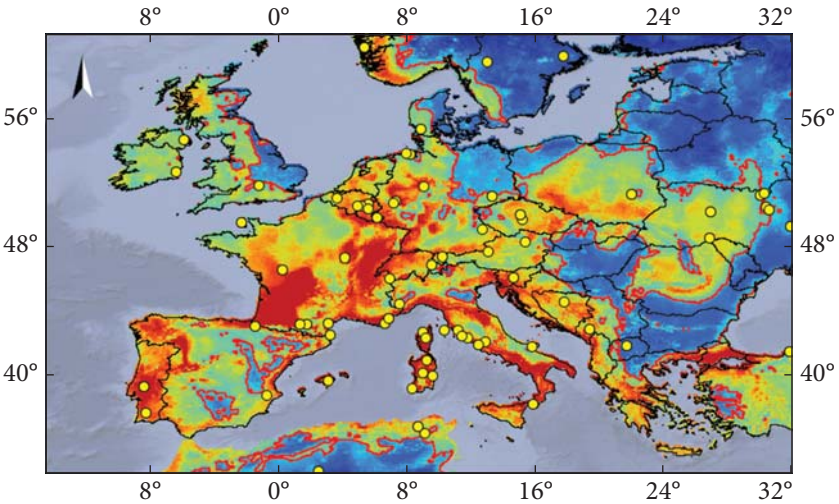

Fig. 2. Territories with a set of bioclimatic factors that are suitable to varying degrees for the habitat of *S. sylvaticus*. Detection probability: gradient from dark red to orange — 50-65 % and from yellow to light green — 35-50 %. The red contour line marks the 10th percentile threshold. Places of material collection are indicated by circles

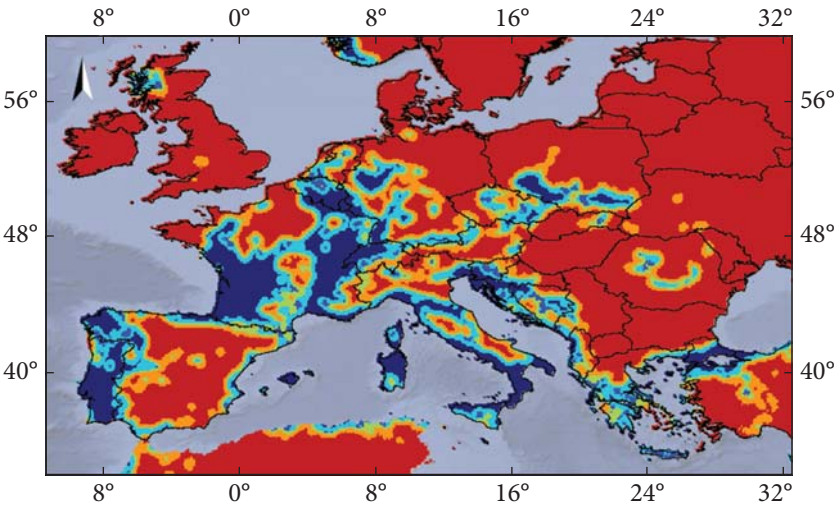

Fig. 3. Fragmentation degree of *S. sylvaticus* range. Cores (non-fragmented or slightly fragmented areas of the range) are shown in dark blue; the average level of fragmentation is depicted in blue; highly fragmented areas are is red

account temperature, humidity, and solar radiation indicators. A total of 35 parameters characterizing the modern climate are used.

Ecological niche modeling allowed to determine the optimal areas for the habitat of *S. sylvaticus* (Fig. 2). In this case, the AUC is 0.86. The most favorable area for the wood mouse is the territory of Western Europe, including France, Belgium, the Netherlands, and the western and southern parts of Germany and Switzerland. In these well-fitting landscapes, the probability of

detecting this species reaches 64 %. The mountain systems of the Alps and the Apennines belong to zones with a detection probability of less than 10 percentiles. Southern and Northern Europe are less favorable, with a probability of detection of 50 % occurring only in coastal areas. Eastern Europe is the least suitable for the wood mouse, with the probability of encounters, even in the most favorable places, being less than 50 %, and in most areas, the detection frequency of *S. sylvaticus* is up to 10 %.

The evaluation of the degree of fragmentation presented on the map yields similar results. Cores are non-fragmented or slightly fragmented areas that are not scattered by zones unsuitable for *S. sylvaticus* habitat. They make up at least 10 % of the area range (Fig. 3). Areas with an average level of fragmentation are usually adjacent to the cores, but they also occur in isolation. The rest of the distribution range is covered by fragmented territories, where areas suitable for the species give way to unsuitable areas. The main cores are within the nominative range of *S. s. sylvaticus*, explaining its extensive distribution area. The largest cores are concentrated in Western Europe, with one in the southwest of France, including the Pyrenees, and the second covering the Northeast of France, the western part of Germany, Belgium, Switzerland, and the western part of Austria. There are cores in the South (the western part of the Iberian Peninsula), the North (the southwestern part of the Scandinavian Peninsula, the northern part of Britain), and in the Center of Europe, where the core is formed in the south of Poland and the east of the Czech Republic. Smaller cores are concentrated within the distribution zone of *S. s. dichrurus*, located in the Mediterranean, including the north of the Apennine Peninsula (with adjacent islands), to a lesser extent the Western and Southern Balkans, and part of Asia Minor around the Sea of Marmara. There are small cores in Romania (Southern Carpathians and Transylvania). There are no cores in the territory of Eastern Europe.

The BART algorithm determined the likely impact of five climate predictors. These are temperature factors (Fig. 4): the difference between the highest and lowest temperatures per year (conditional climate continentality) (X5m_07); the maximum temperature of the warmest month (X5m_05), as well as humidity indicators (precipitation seasonality (X5m_15), precipitation levels during the driest (X5m_17) and most humid (X5m_16) months). It should be noted that the connection between the factors and the response to their actions is non-linear, and therefore, there are certain zones of optimal factor effects. Thus, regions with a fairly humid temperate climate

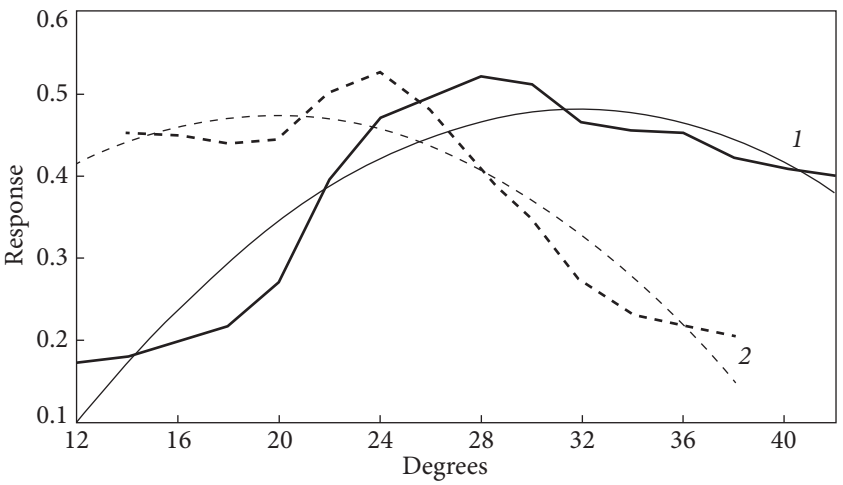

Fig. 4. Response curves of predictors on the gradation of bioclimatic factors: *1* — maximum temperature of the warmest month (X5m_05); *2* — the difference between the highest and lowest temperature of the year (X5m_07)

and high summer temperatures are the most favorable for the wood mouse. These regions include Western and Southern Europe and the southern part of Northern Europe. The continental and fairly dry climate of Eastern Europe does not favor this species.

The established bioclimatic factors do not directly affect the wood mouse population, limiting the species' distribution to the East. Most likely, these are mainly abiotic circumstances that form the type of vegetation. The wood mouse, whose prohoresis evolved from the Mediterranean, avoids both forests with dense canopies and bushy grassy vegetation. Therefore, in the territory of Eastern Europe, where the primary types of natural vegetation are coniferous forests, meadows and steppes, *S. sylvaticus* has a limited number of optimal stations. These are mainly areas with a dense soil surface, where it is easy to collect small seeds: low-growing shrubs and thickets of ruderal vegetation. Such places are concentrated in anthropogenically altered landscapes, which serve as corridors for the species' expansion to the East. In the north of the eastern border of the range, the influence of the vegetation factor is very evident since *S. sylvaticus* is present exclusively in agricultural lands. In the south, where open landscapes predominate, there are more plant communities suitable for the wood mouse. It is no coincidence that in this zone, the range extends much further to the east than in the north. An additional limiting factor here may be low winter temperatures and the presence of common species in eastern Ukraine, such as *S. uralensis*, which have a symbiotic interaction with *S. sylvaticus*.

A case of an ambiguous influence of climatic factors on the area is represented in subspecies of house mice *Mus musculus musculus* / *M. m. domesticus*, with their hybrid zone passing through the south of Denmark and further across Southern Germany, Western Czech Republic, Western Austria and Northern Balkans [11-13]. This division of Europe into two climatic zones is provided: a southwestern zone with a temperate climate and Mediterranean as *M. m. domesticus* habitat, and the northeastern part with a continental climate, belonging to *Mus musculus musculus* range. Intriguingly, these are synanthropic mice, which deal with adverse climatic factors by hibernating in buildings. This suggests that, as with the wood mouse, indirect circumstances play a decisive role. Apparently, the type of vegetation relevant in the summer, when house mice leave their human settlements, is significant.

Conclusion. As a result of the research, the questions posed in the work can be answered as follows. 1. The eastern limit of the range of *S. sylvaticus* is determined by bioclimatic factors. 2. Their effect is indirect and is linked to the formation of a certain type of vegetation. The factor that directly limits the expansion of the range to the east may be only the degree of continentality of the climate, which is influenced by low winter temperatures. 3. Competitive interactions with other species of mice may be present, but only at the southern border of the eastern limit of the range and are of secondary importance as a factor in restraining the distribution of the wood mouse to the East.

REFERENCES

1. Orlov, V. N., Bulatova, N. Sh., Nadjafova, R. S. & Kozlovsky, A. I. (1996). Evolutionary classification of European wood mice of the subgenus *Sylvaemus* based on allozyme and chromosome data. Bonn. zool. Beitr., 46, H. 1-4, pp. 191-202.
2. Gemmeke, H., Radkte, M. & Niethammaer, J. (1987). Zur innerartlichen Proteinvariation bei der Waldmaus (*Apodemus sylvaticus*). Z. Säugetierkunde, 52, pp. 242-247
3. Michaux, J. R., Filippucci, M.-G., Libois, R. M., Fons, R. & Matagne, R. F. (1996). Biogeography and taxonomy of *Apodemus sylvaticus* (the woodmouse) in the Tyrrhenian region: enzymatic variations and mitochondrial DNA restriction pattern analysis. Heredity, 76, Supl. 2, pp. 267-277. https://doi.org/10.1038/hdy.1996.40
4. Michaux, J. R., Libois, R. M. & Filippucci, M.-G. (2005). So close and so different: comparative phylogeography of two small mammal species, the Yellow-necked fieldmouse (*Apodemus flavicollis*) and the Woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. Heredity, 94, Supl. 1, pp. 52-63. https://doi.org/10.1038/sj.hdy.6800561
5. Michaux, J. R., Magnanou, E., Paradis, E., Nieberding, C. & Libois, R. (2003). Mitochondrial phylogeography of the Woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. Mol. Ecol., 12, No. 3, pp. 685-697. https://doi.org/10.1046/j.1365-294X.2003.01752.x
6. Mezhzherin, S. V. & Lashkova, E. I. (1992). Diagnostics, geographic variation amd distribution of two closely related mice species *Sylvaemus sylvaticus* and *S. flavicollis* (Rodentia, Muridae) in an area of their overlapping occurrence. Vestnik Zollogii, No. 3, pp. 33-41 (in Russian).
7. Schlitter, D., Van der Straeten, E., Amori, G., Hutterer, R., Kryštufek, B., Yigit, N. & Mitsainas, G. (2021). *Apodemus sylvaticus* (amended version of 2016 assessment). The IUCN Red List of Threatened Species 2021: e. T1904A197270811. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T1904A197270811.en
8. Mezhzherin, S. V., Lashkova, E. I., Kozinenko, I. I., Rashevskaya, A. V. & Tytar, V. M. (2017). Interspecies 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). Vestnik Zoologii, 51, No. 5, pp. 429-434. https://doi.org/10.1515/vzoo-2017-0051
9. Carlson, C. J. (2020). embarcadero: Species distribution modelling with Bayesian additive regression trees in R. Methods Ecol. Evol., 11, No. 7, pp. 850-858. https://doi.org/10.1111/2041-210X.13389
10. Kriticos, D. J., Webber, B. L., Leriche, A., Ota, N., Macadam, I., Bathols, J., Scott, J. K. (2012). CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. Methods Ecol. Evol., 3, No. 1, pp. 53-64. https://doi.org/10.1111/j.2041-210X.2011.00134.x
11. Thaler, L., Bonhomme, F. & Britton-Davidian, J. (1981). Processes of speciation and semi-speciation in the house mouse. In Berry, R. J. (Ed.). Biology of the house mouse. Symposia of the Zoological Society of London, No. 47 (pp. 27-41). London: Academic Press.
12. Mezhzherin, S. V., Kotenkova, E. I. & Mikhailenko, A. G. (1994). Hybrid zones. In House mouse: origin, distribution systematics, behavior (pp. 37-50). Moskow: Nauka (in Russian).
13. Macholán, M., Baird, S. J. E., Munclinger, P., Dufková, P., Bímová, B. & Piálek, J. (2008). Genetic conflict outweighs heterogametic incompatibility in the mouse hybrid zone? BMC Evol. Biol., 8, 271. https://doi.org/10.1186/1471-2148-8-271

Received 15.02.2023

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МОДЕЛЮВАННЯ ЕКОЛОГІЧНОЇ НІШІ І ФАКТОРИ, ЩО ВИЗНАЧАЮТЬ АРЕАЛ ЛІСОВОЇ МИШІ *SYLVAEMUS SYLVATICUS* (LINNAEUS, 1758)

Моделювання екологічної ніші лісової миші *Sylvaemus sylvaticus* методом машинного навчання в просторі 35 біокліматичних факторів показало, що найсприятливішими для виду є абіотичні умови Західної Європи, де зосереджені головні ядра ареалу і ймовірність знахідок у придатних ландшафтах сягає 60 %. Біокліматичні обставини Східної Європи є песимальними: зона перебування виду значно фрагментована, ядра відсутні, вірогідність стрівальності не перевищує 40 %, найчастіше менш ніж 10 процентилів. Очевидно, що серед біокліматичних чинників головне значення має континентальність клімату, що опосередковано впливає на розташування східної межі ареалу *S. s. sylvaticus* і формування певних типів рослинності. Безпосередня дія окремих факторів і міжвидові відносини можливі і мають місце, певним чином обмежуючи просування виду на схід, однак лише на південному фасі східної межі ареалу.

Ключові слова: *моделювання, Sylvaemus sylvaticus, екологічна ніша, фрагментація ареалу.*