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MODELLING THE BIOCLIMATIC NICHE AND DISTRIBUTION OF THE STEPPE MOUSE, *MUS SPICILEGUS* (RODENTIA, MURIDAE), IN UKRAINE

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Modelling the Bioclimatic Niche and Distribution of the Steppe Mouse, *Mus spicilegus* (Rodentia, Muridae), in Ukraine. Tytar, V. M., Kozinenko, I. I., Mezhzherin, S. V. — The Steppe mouse, *Mus spicilegus*, is endemic to Europe and found to be expanding its home range in recent years. In Ukraine there are indications a north- and eastwards expansion and/or reestablishment of *M. spicilegus*. We suggest that climatic conditions may be the primary factors that foster or limit the range expansion of *M. spicilegus* in Eastern Europe. Our objective was to complement the knowledge about the distribution of the species with an estimation of the potential distribution of the species in Ukraine using known occurrence sites (in Ukraine and neighbouring areas) and environmental variables in an ecological niche modelling algorithm. After accounting for sampling bias and spatial autocorrelation, we retained 73 occurrence records. The algorithm used in this paper, Maxent (Phillips et al., 2006), is a machine learning algorithm and only needs presence data, besides the environmental layers. Using this approach, we have highlighted the importance and significance of a number of bioclimatic variables, particularly those characterizing wintering conditions, under which higher mean temperatures enhance habitat suitability, whereas increased precipitation leads to an opposite effect. The broadly northwards shift of the home range of the species in Ukraine could generally be due to the increasing (since the 1980s) mean temperature of the winter season. We expect this expansion process will continue together with the changing climate and new records of locations of the species may be used for monitoring such change.

Key words: Steppe mouse, *Mus spicilegus*, bioclimatic niche, Maxent, climate change.

Introduction

The Hillock, or Mound-building, or Steppe mouse, *Mus spicilegus*, is endemic to Europe, found from Lake Neusiedl on the Austro-Hungarian border expanding through Slovakia, Hungary, Serbia, Montenegro, Bulgaria, Moldova, and Ukraine, reaching as far as the Rostov-on-Don region in the utmost south-west of Russia (Coroiu et al., 2016). It is unique among mice in its habit of building earthen mounds constructed between about mid-August and mid-November. The construction is done by juveniles, three to four weeks

old, and the mound is their winter home, with adults occasionally cohabiting (Sokolov et al., 2008), however by spring adults have died, leaving only the off-spring to found the following generation (Sokolov et al., 1990). The mouse occurs in a variety of habitats including grassland, steppe, cultivated land, orchards, clearings and woodland borders (Coroiu et al., 2016).

The Steppe mouse is a common species with a wide range, and the International Union for Conservation of Nature (IUCN) has rated its conservation status as being of “least concern” (LC) while noting that the intensification of agriculture and destruction of grassy steppe may be a future threat. However, in Slovakia the range appears to be expanding (Coroiu et al., 2016). The same seems to be occurring in Ukraine and Russia. Recent records are indicating a north- and eastwards expansion of the species’ range and/or reestablishment of *M. spicilegus* in places from which the species had disappeared since the first half of the XXth century. For instance, a thorough search of the species in the Ukrainian steppe reserve of Askania-Nova found no trace of *M. spicilegus* until 1999 (Polishchuk, 2012), despite having records published early as 1928 (Brauner, 1928), and the same relates to the Rostov-on-Don region of Russia, where the species reappeared in 1999–2004 in seven locations (Lipkovich, 2005). On the other hand, *M. spicilegus* had never previously been recorded from the Kaniv Nature Reserve (49.74444° N, 31.45583° E), a location nearby the northern boundary of the species’ home range, so the findings made here in 2000–2004 (Ruzhilenko, 2005) could be evidence of range expansion, which, in the opinion of the author, are due to climate change.

According to I. V. Zagorodnuik, the range of the species in Ukraine is split into parts by at least four large rivers, the Prut, Dnister, Southern Boug and Dnipro, as well as by an extensive number of smaller ones, whose sources are located considerably further to the north beyond the contemporary range of *M. spicilegus*. Despite this, in all cases the northernmost findings of the species are located on the same line; see figure 2 in Zagorodnuik, Berezovsky (1994). Because winter migrations of the animals are hardly possible, obviously there are specific external factors that determine the character of the species’ geographical distribution. Obvious biogeographic barriers, as noted above, are absent. There are also no obvious differences in the habitat (moisture, biotope spectrum and their feeding capacity) within the distribution area of the species in more northern areas. Therefore, as I. V. Zagorodnuik concludes, there is a need to search for other reasons, among which there may be wintering conditions for the species, primarily the temperature and depth of soil freezing (Zagorodnuik, Berezovsky, 1994). Earlier an assumption had been made that Steppe mouse population reductions are largely due to adult deaths occurring during the winter (Berry, 1981). Later on the main factors responsible for mouse deaths were concretized as low temperature and frequent thaws, leading to drenched food and nest chambers (Muntyanu, 1990).

Under the current knowledge, we in our turn suggest that climatic conditions may be the primary factors that foster or limit the range expansion of *M. spicilegus* in Eastern Europe. Our objective was to complement the knowledge about the distribution of the species with an estimation of the potential distribution of the species in Ukraine using known occurrence sites (in Ukraine and neighbouring areas) and environmental variables in an ecological niche modeling algorithm. Ecological niche models (ENMs) have been widely used for predicting potential distributions of species and exploring their habitat suitability requirements (Franklin, 2009; Miller, 2010). This methodology can be particularly useful to predict the potential distribution of *M. spicilegus* because climatic conditions are likely to play an important role in limiting the distribution of this species.

Traditionally, determining such driving factors would require laborious field measurements of the key environmental variables in natural populations. However, the advent of GIS and the increased availability of global environmental data in recent years have favoured the proliferation of diverse kinds of ENMs intended to answer a wide range of applied ecological questions (Peterson et al., 2011). Because these models seek to identify the features that characterize a species’ known distribution (their “bioclimatic envelope”), ENM can provide basic quantitative information about species’ apparent habitat preferences (Nakazato et al., 2010).

Material and methods

Occurrences from the known range of the species in Ukraine, Moldova, the Rostov-on-Don and Belgorod regions of Russia were obtained from the literature (Lyalyukhina et al., 1989; Zagorodnuik, Berezovsky, 1994; Kondratenko, 1998; Ruzhilenko, 2005; Lipkovich, 2005; Tsvelykh, 2009; Smirnov, 2009; Tokarsky et al., 2011; Polishchuk, 2012; Evstafiev, 2015; Partolin, 2016; etc.). Field trips undertaken in 2017 to Cherkasy Region yielded additional, previously unknown records of the species. In total our dataset contained 269 georeferenced occurrences (fig. 1); occurrences that lacked latitude and longitude coordinates were georeferenced using Google Maps (<http://maps.google.com.ua>).

These occurrence points varied in spatial density due to variable sampling intensity over geography. As a result, and to avoid overemphasizing heavily on sampled area, we selected points for model calibration using a subsampling regime to reduce sampling bias and spatial autocorrelation, which would produce models of lower rather than higher quality (Beck et al., 2013). Following M. A. Nuñez and K. A. Medley (Nuñez, Medley, 2011), we generated models using all available occurrence points and measured spatial autocorrelation among model pseudo-residuals ($1 - \text{probability of occurrence generated by model}$) by calculating Moran’s I at multiple distance classes using the SAM v4.0 software (Rangel et al., 2006). Significance was determined using

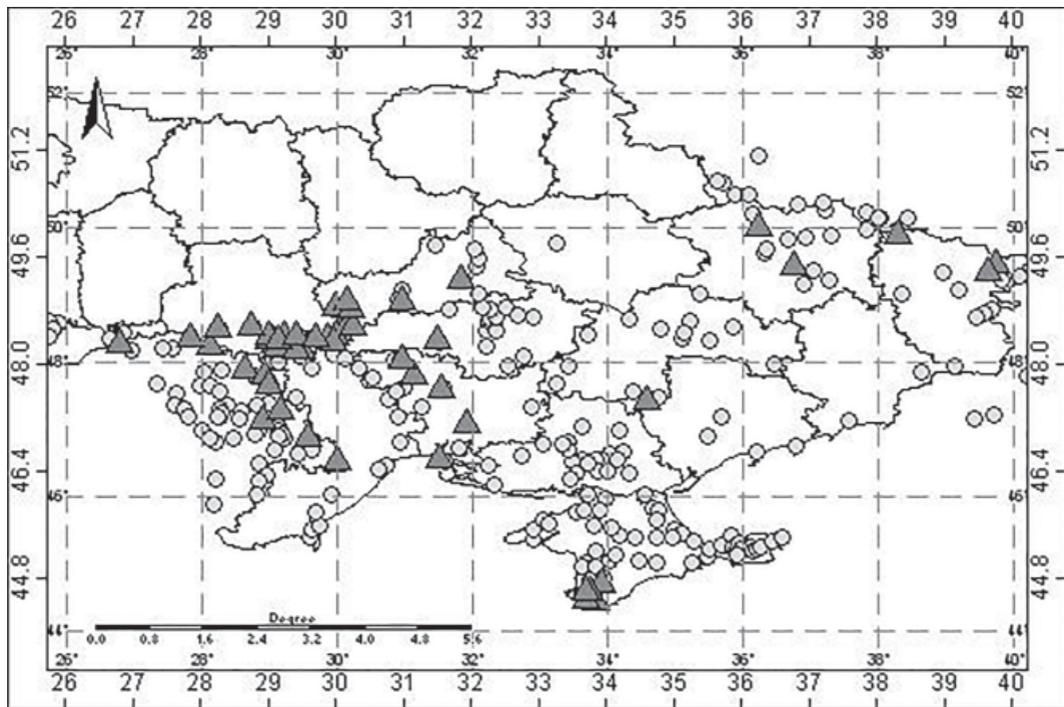


Fig. 1. Occurrences of *Mus spicilegus* in Ukraine and neighbouring areas used for creating the ENM. [Data collected before (triangles) and after (circles) 1990.]

permutation tests ($n = 999$). Moran's I is a widely used measure of spatial autocorrelation, ranging from 0 to 1, with values > 0.3 considered relatively large (Lichstein et al., 2002). A minimum distance of 53.6 km, at which Moran's $I < 0.3$, $p = 0.001$, was detected.

Next we used the spThin package in R (Aiello-Lammens et al., 2015) to subsample our dataset such that all occurrence records were separated by this minimum distance. The procedure greatly reduced sampling bias and spatial autocorrelation, resulting in evenly distributed occurrence points across space. In the end, we retained 73 occurrence records after thinning. This number of occurrence records is considered more than sufficient to generate robust species distribution models (Hernandez et al., 2006).

The algorithm used in this paper, Maxent (Phillips et al., 2006), has proven good performance and accuracy for such studies (Elith et al., 2011). Maxent (Version 3.3.3k) is a machine learning algorithm. The main advantage of applying Maxent to the modeling of geographical species distributions in comparison with other methods is that it only needs presence data, besides the environmental layers. Pseudo-absence points (used instead of true absences) were randomly generated (using the default option) within a bounding box encompassing *M. spicilegus* presence points.

As part of its output, Maxent ranks the environmental layers used to train the ENM based on their relative importance in model formulation. To do so, it employs two metrics: (1) percent contribution, and (2) permutation importance. The latter is considered to provide a much more accurate ranking than percent contribution (Searcy, Shaffer, 2016). In the permutation importance option the contribution for each variable can be determined by randomly permuting the values of that variable and measuring the resulting model performance. Values are normalized to give percentages; we considered percentages exceeding a 10 % threshold. The second option to determine the importance of environmental variables uses a jackknife test and the regularized gain change during each iteration of the training algorithm. The environmental variable with the highest gain is considered to have the most useful information by itself, whereas the variable causing the largest decrease in the model's gain contains the most information not found in the other environmental variables.

Importantly, Maxent also allows the construction of response curves to illustrate the effect of selected variables on habitat suitability. These response curves consist of the specific environmental variable as the x -axis and, on the y -axis, the predicted probability of suitable conditions as defined by the logistic output. Upward trends for variables indicate a positive relationship; downward movements represent a negative relationship (Baldwin, 2009).

The Maxent general-purpose machine learning technique is prone to over-fitting, therefore uses "regularization" (a beta parameter) to avoid over-fitting data. Higher values of beta increase the "smoothness"

of species' responses to the environment. There is also a choice of an expanded set of transformations of the original covariates (termed features), which are helpful in making predictions about the outcome. MaxEnt fits models using linear, product, quadratic, hinge and threshold functions, therefore enhancing the flexibility for modelling non-linear species-habitat responses. Because MaxEnt's default regularization parameter and feature classes have profound impacts on model performance (Merow et al., 2013), we used ENMeval (Muscarella et al., 2014) to build a series of models with all possible combinations of these parameters. We selected a model with a combination of feature class and regularization multiplier that provided the best trade-off between model goodness of fit and complexity using the corrected Akaike information criterion, AICc (Akaike, 1974; Warren, Seifert, 2011). Replicated runs ($n = 25$) of bootstrap type were completed to build the model.

We used the 10th percentile training presence logistic threshold value to generate binary maps (Liu et al., 2005). This threshold value provides a better ecologically significant result when compared with more restricted threshold values (Phillips, Dudík, 2008). Based on the probability value, we divided the habitat areas into three classes: unsuitable and/or marginal area (below the threshold value), median area (threshold value — 0.6), and core area (0.6–1.0).

Maps of habitat suitability in the ASCII format were processed and visualized in SAGA GIS (Conrad et al., 2015). Statistical data was analyzed using the PAST software package (Hammer et al., 2001).

Environmental variables

For bioclimatic modeling we used the CliMond archive, a set of free climate data products (Kriticos et al., 2012). The climate data includes interpolated surfaces at 10' and 30' for recent historical climate and relevant future climate scenarios, available in a variety of formats, including Bioclim variables. These are derived from the monthly temperature and rainfall values in order to generate biologically meaningful variables, which are often used in species distribution modeling and related ecological modeling techniques. The bioclimatic variables (Bio01–Bio19) represent annual trends (e. g., mean annual temperature, annual precipitation) seasonality (e. g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e. g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). For future climate assessments we used the climate model of 2030 generated for the A1B scenario for emissions of greenhouse gases and sulphate aerosols. For tracking retrospective climate change the MERRAclim global set of satellite-based bioclimatic variable that have been built for each of the last three decades (1980s, 1990s and 2000s) was employed (Vega et al., 2017). Grids were presented in a 10 arcmin resolution.

Co-linearity between predictors may lead to overfitting and impeded predictive performance (Guisan, Thuiller, 2005), therefore variable selection analyses was employed by retaining only variables with a Spearman's pair-wise rank correlation coefficient $\rho < |0.9|$. When two variables were highly correlated we chose the one least correlated to others, leading to a total of thirteen selected climatic variables (table 1).

Table 1. Selected climatic variables

Variable Code	Variable
Bio02	Mean diurnal temperature range (mean(period max–min)) (°C)
Bio03	Isothermality (Bio02÷Bio07)
Bio05	Max temperature of warmest week (°C)
Bio06	Min temperature of coldest week (°C)
Bio07	Temperature annual range (Bio05–Bio06) (°C)
Bio08	Mean temperature of wettest quarter (°C)
Bio09	Mean temperature of driest quarter (°C)
Bio12	Annual precipitation (mm)
Bio14	Precipitation of driest week (mm)
Bio15	Precipitation seasonality (C of V)
Bio17	Precipitation of driest quarter (mm)
Bio18	Precipitation of warmest quarter (mm)
Bio19	Precipitation of coldest quarter (mm)

Results

The final model was selected based on the fine tuning using the AICc value and the best model only used hinge features with a regularization multiplier value of 2.0. The performance of the Maxent model is usually evaluated by the threshold-independent receiver operating characteristic (ROC) approach, where the calculated area under the ROC curve (AUC) is

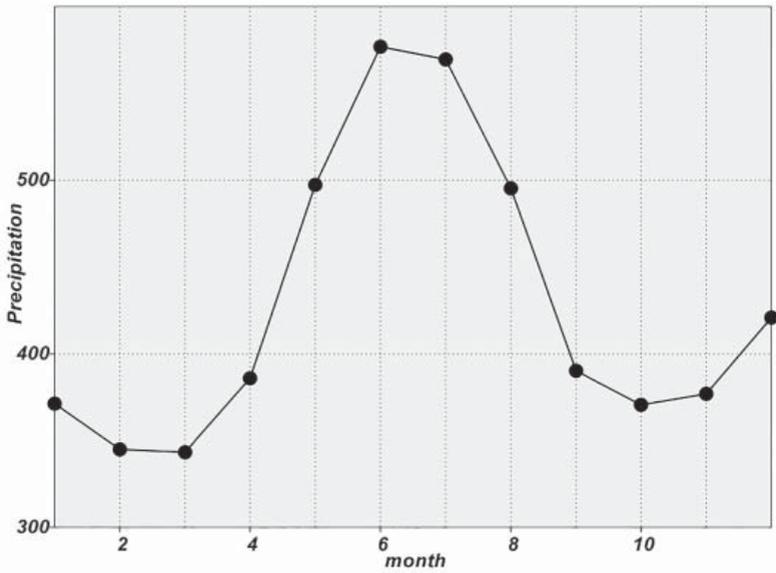


Fig. 2. Monthly precipitation (mm) change throughout the year.

considered as a measure of prediction success. The ROC curve is a graphical method that represents the relationship between the false-positive fraction (one minus the specificity) and the sensitivity for a range of thresholds. It has a range of 0–1, with a value greater than 0.5 indicating a better-than-random performance event (Fielding, Bell, 1997). A rough classification guide is the traditional academic point system (Swets, 1988): poor (0.5–0.6), fair (0.6–0.7), good (0.7–0.8), very good (0.8–0.9) and excellent (0.9–1.0). The ROC curve of the final model shows a ‘good’ predictive power with an average training AUC score of 0.733 and standard deviation of 0.023.

Based on permutation importance, Bio09 (Mean temperature of driest quarter) was the most significant variable (36.0 %) followed by Bio14 (Precipitation of driest week) contributing 24.1 %; the contribution of Bio12 (Annual precipitation), 9.4 %, was close to

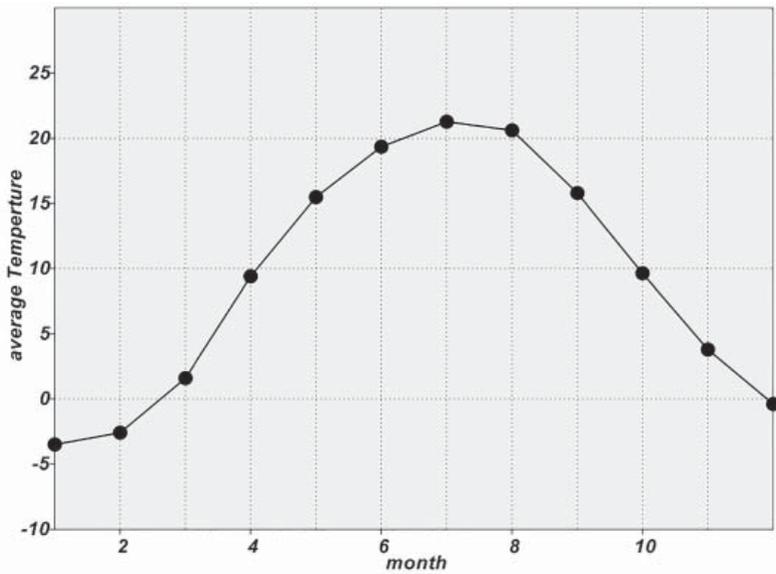


Fig. 3. Monthly temperature (°C) change throughout the year.

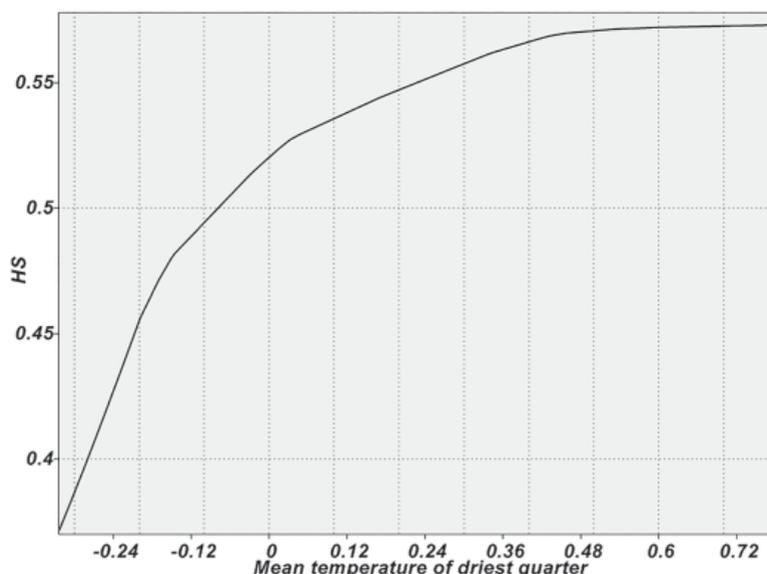


Fig. 4. The marginal response curve for the explanatory variable Bio09 (Mean temperature of driest quarter). (HS — habitat suitability).

the accepted threshold. Among the thirteen selected environmental variables, the first two mentioned above accounted for around 60 % of the model prediction.

The results of the Maxent model's internal jackknife test of factor importance were mostly consistent with the permutation importance. The environmental variable with highest gain when used in isolation is Bio12 (Annual precipitation), which therefore appears to have the most useful information by itself, and the environmental variable that decreases the gain the most when it is omitted is Bio09 (Mean temperature of driest quarter), which therefore appears to have the most information that isn't present in the other variables.

In terms of the bioclimatic niche of the Steppe mouse two of the emphasized above variables seem to play a key role in shaping the ecology and distribution of the species:

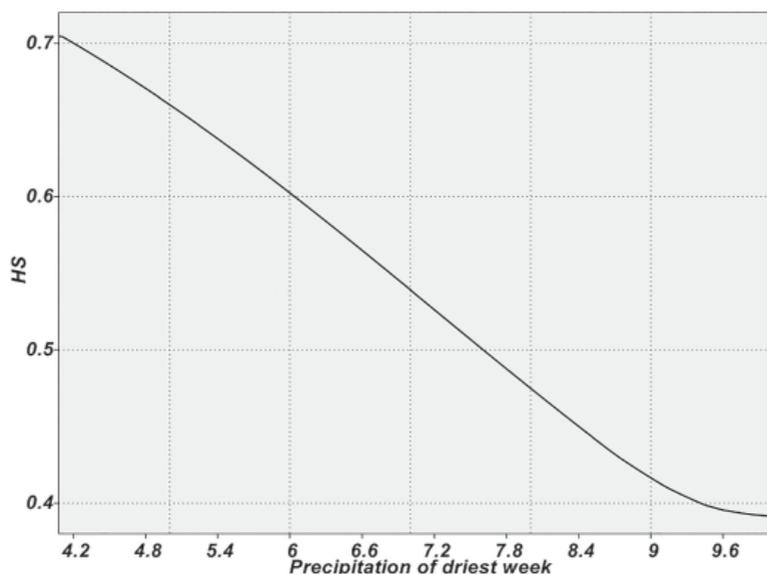


Fig. 5. The marginal response curve for the explanatory variable Bio14 (Precipitation of driest week). (HS — habitat suitability).

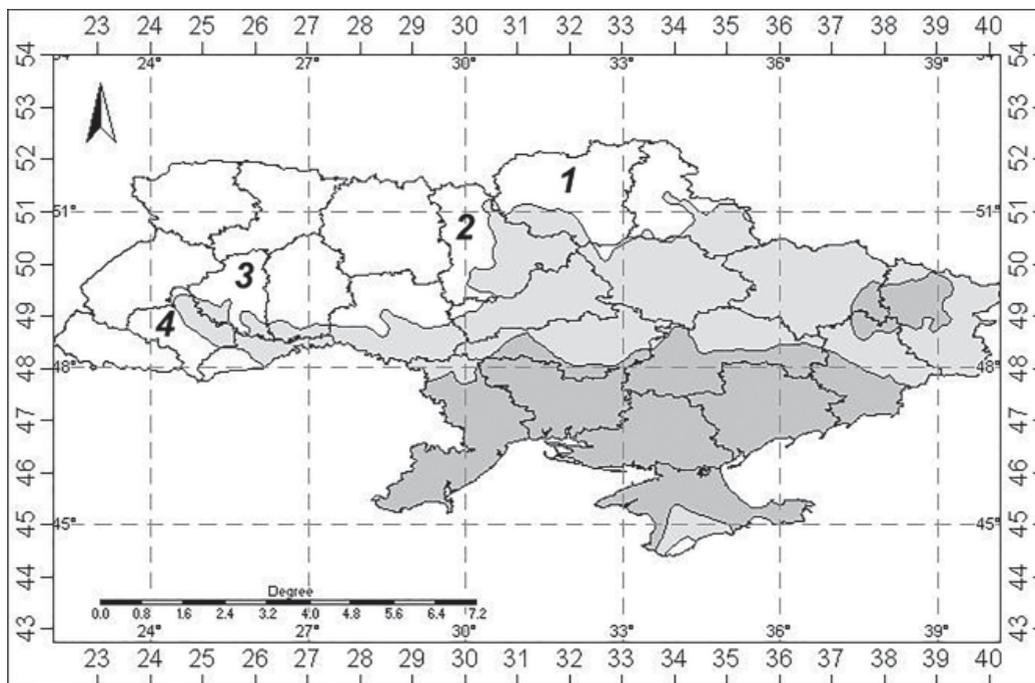


Fig. 6. A current climate habitat suitability map for the Steppe mouse (*Mus spicilegus*) in Ukraine. Darker shades of gray denote areas of higher predicted habitat suitability probabilities (≥ 0.5) and lighter shades correspond to lower (≥ 0.311 and < 0.5). [Administrative regions in Ukraine: 1 — Chernihiv Region; 2 — Kyiv Region; 3 — Ternopil Region; 4 — Ivano-Frankivsk Region.]

namely Bio09 (Mean temperature of driest quarter) and Bio14 (Precipitation of driest week). Both in conjunction can be considered as proxies for describing wintering conditions as far as the driest season in the study area falls on January-March when temperatures by large exhibit their lowest levels (figs 2 and 3, respectively; the graph in fig. 2 has been smoothed using the three-point moving average).

Habitat preference is interpreted from the response of the predicted habitat suitability to a marginal change in each variable, all other variables set to their average value. Values giving a high habitat suitability (≥ 0.5) can be considered as preferable for the species, although they may also be found in areas with lower habitat suitability (Wangen et al., 2016). The response curves for Bio09 (Mean temperature of driest quarter) and Bio14 (Precipitation of driest week) are presented in fig. 4 and fig. 5, respectively. Because Bio12 (Annual precipitation) and Bio14 (Precipitation of driest week) are loosely correlated (Spearman's $\rho = 0.76$, $p = 0.00$) their effects on habitat suitability appear in a similar fashion, therefore the graph for the former variable is not shown. The y -axis baseline in the graphs is set to the 10th percentile training presence logistic threshold value of 0.3708.

The response to Bio09 (Mean temperature of driest quarter) shows a threshold increase from low to high habitat suitability as the mean temperature increases from -0.32 °C and reaches a plateau of 0.57 at the point of 0.78 °C; high habitat suitability (≥ 0.5) can be considered to occur in areas where temperatures are above -0.08 °C. On the contrary, Bio14 (Precipitation of driest week) demonstrates a downward and close to linear trend, suggesting that increasingly wetter conditions lead to lower habitat suitability. Using a linear regression model for approximation, we can assume that habitat suitability will reach the 10th percentile training presence logistic threshold at around the point of 9.9 mm

of precipitation; high habitat suitability (≥ 0.5) can be considered to occur in areas where there is 7.7 or less millimeters of precipitation/driest week in the year.

Current Distribution

The probability maps obtained from the 25 replicated runs were averaged to obtain a habitat suitability map for the Steppe mouse corresponding to current climate (fig. 6). The choice of the cut-off really depends upon the purpose of modelling exercise. For creating a range map the threshold defined in the minimum training presence statistics ensures that the model captures all training data. This is effectively a species potential distribution: everywhere the species could survive in the environment based on the samples (Jobe, Zank, 2008). For the mean of the 25 minimum training presence thresholds we computed lower and upper limits for 95 % confidence intervals, using 9999 bootstrap replicates, and picked from there a value of that best suited our purpose in terms of capturing the training data. In this respect a threshold value of 0.311 captured 98.6 % of our data.

Discussion

In this study we made an attempt to highlight important variables of the current bioclimatic niche of the Steppe mouse, realizing that the persistence of populations of the species is affected by a combination of physical, biological factors, and anthropogenic drivers, which interact in a complex manner. Nevertheless, our coarse scale modeling exercise has shown the importance and significance of bioclimatic variables, particularly those characterizing wintering conditions, in shaping the niche of the species, although model performance (based on the AUC) reaches at the best only 'good' predictive power. However, such models are considered useful and acceptable for the purpose they are intended for (Rykiel, 1996). This occurs when ecological parameters are omitted from the modelling framework and lead to the insufficient description of the species' distribution and niche (Hanspach et al., 2010). In our case this was expected because intentionally only bioclimatic parameters were used. Of course, it is reasonable to suggest that factors other than climate shape the distributions and niche of the species.

Climatic factors, which normally underlie population change, are expected to exert their influence most strongly during certain critical for the survival of the species seasons (e. g., the summer dry period or the winter cold period). Over-winter survival is a crucial factor in temperate regions, especially for small mammals (Aars, Ims, 2002). Among the ecological factors, low ambient temperatures seem to be especially important (Jackson et al., 2001). Unlike house mice, mound-building mice live in agricultural fields and are found in the steppe zone in Central and Eastern Europe, which have extremely cold but dry winters (Simeonovska-Nikolova, 2000). Consequently temperature should be an important factor, and the modelling exercise confirms this. In this respect it can be suggested that mounds have an insulating role and indeed they reduce temperature variation of the soil (Szenczi et al., 2011)

On the other hand, winters with mild weather seem to be particularly detrimental by causing flooding during periods of spring thaw (Aars, Ims, 2002). Similar critical weather episodes in winter and early spring have also been suggested to dramatically reduce winter survival in small mammals. For instance, deer mouse (*Peromyscus maniculatus*) populations in Colorado responded favourably to rainfall during warm periods, but crashed when high rainfall occurred during cold periods (Calisher et al., 2005; Luis et al., 2010). In our case winter survival of the species most likely depends on the combination of temperature and precipitation, when the ambient temperature is not too low (to avoid freezing), but not too high (to perhaps trigger snow melting), and less precipitation the better. This echoes with A. I. Muntyanu's view on main factors responsible for mouse deaths: low temperature and frequent thaws, leading to drenched food and nest chambers (Muntyanu, 1990); from the ENM we can now say

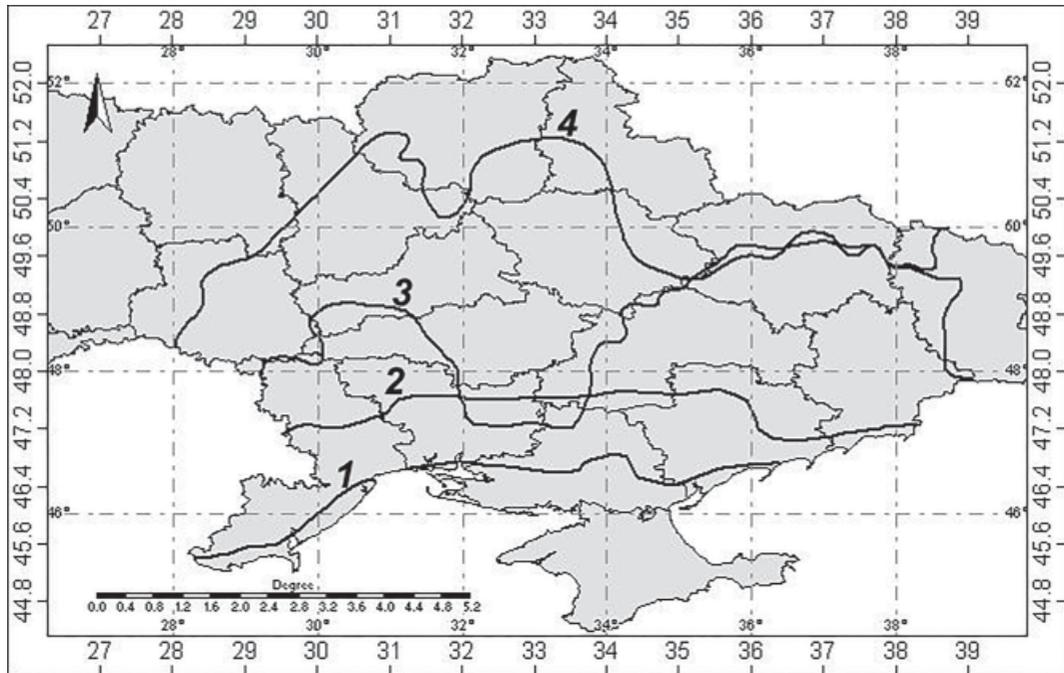


Fig. 7. 0.5 °C isotherms for Bio9 (Mean temperature of driest quarter) for different time periods: 1 — 1980s; 2 — 2000s; 3 — contemporary; 4 — predicted for 2030.

that this is most likely to happen if there are provisions for a considerable source of melt water and/or rain.

Overwintering structures of the Steppe mouse (mounds) are built from soil and a considerable amount of plant material. Recent studies presume that the stored vegetable matter is not, or not exclusively, serving as food and indicate that the mounds have not only an insulating role, but also waterproofing properties (Hölzl et al., 2011; Szenczi et al., 2011). On this item we tend to agree with the authors, because once winter precipitation is so important it seems reasonable to suggest the development of such waterproofing properties. In this case the stored vegetable matter could function as a “thatched roof” and help to keep the mound and animals inside in a dry condition.

Interestingly, areas of *M. spicilegus* habitat suitability are predicted to occur in the north beyond the known home range limits of the species, namely in Kyiv and Chernihiv Regions (marked 1 and 2 in fig. 6), from where up to now no presences have been recorded. In terms of inventory the model presented here may be useful for guiding search for new populations of the Steppe mouse and identifying candidate areas for ground validation of the model. Similarly, areas of habitat suitability are predicted to occur in the west, also beyond the known home range limits of the species. These are located in Ternopil and Ivano-Frankivsk Regions (3 and 4 in fig. 6) and appear to occur alongside the Dnister River, which may play a role of an ecological corridor for the spread of the species in a westward direction.

Although factors other than climate can be responsible for shaping the distributions of the considered species, most likely it is climate change that has triggered the recent expansion of the home range of the Steppe mouse in Ukraine and neighbouring Russia. If so, this expansion process will continue together with the changing climate and new records of locations of the species may be used for monitoring such change. To describe the pace of climate change that the species should track we mapped for different time periods the 0.5 °C isotherm for Bio9 (Mean temperature of driest quarter), which was distinguished as the most influential variable forming the bioclimatic niche of the Steppe mouse (fig. 7).

Since the 1980s there has been a significant shift towards the north, which by and large could have favoured the expansion of the species.

Conclusion

Climatic conditions have been suggested to be the primary factors that limit the range expansion of *M. spicilegus* in Eastern Europe. Using an ENM approach, we have shown in this respect the importance and significance of a number of bioclimatic variables, particularly those characterizing wintering conditions, under which higher mean temperatures enhance habitat suitability, whereas more precipitation leads to an opposite effect. The broadly northwards shift of the home range of the species in Ukraine could generally be due to the increasing (since the 1980s) mean temperature of the winter season. We expect this expansion process will continue together with the changing climate and new records of locations of the species may be used for monitoring such change.

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