



## SPECIES DISTRIBUTION MODELLING OF THE YELLOW-NECKED MOUSE, *SYLVAEMUS TAURICUS*, WITH SPECIAL REFERENCE TO UKRAINE

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### Abstract

Rodents are essential components of many terrestrial ecosystems and have several beneficial activities in nature, such as soil aeration and insect control, however, rodents are also sources of zoonotic pathogens. As pests they are known to be reservoirs of tick-borne zoonotic infections of viral, bacterial and protozoan origin, and are important hosts of the immature stages of *Ixodes* ticks. Recent studies in Europe have demonstrated the role of rodents, especially *Sylvaemus* mice and *Myodes* voles, in the epidemiology of tick-borne bacterial zoonoses, such as Lyme borreliosis and anaplasmosis. In particular, the yellow-necked mouse, *Sylvaemus tauricus* (Pallas, 1811; syn.: *Apodemus flavicollis* (Melchior, 1834)), supports the transmission of the most important pathogens carried by the castor bean tick, *Ixodes ricinus*. Using a species distribution modelling approach, an assessment was carried out of the probability of presence of the yellow-necked mouse in different parts of Ukraine and a search accomplished to find effective environmental factors that play roles in its distribution. We considered this task important given the ecological and epidemiological significance of this particular rodent species and the urgency of the problem exacerbated by Russia's armed aggression in Ukraine. Results showed a broad potential for the distribution of the species in the western and central parts of Ukraine, and in the Crimea. Areas predominantly in western and central Ukraine, and in the Crimea, are highly favourable for the mouse, whereas in the south and, to a smaller scale, in the easternmost part of the country they are the least favourable. Amongst the bioclimatic environmental factors that play roles in shaping the species' niche are the ones that are fully or mostly temperature-related (for instance, annual mean temperature, continentality, etc.). Other factors in a declining order of their roles are associated with soil and land cover features, cloud frequency and standardised human impact. A moderate, though statistically significant, correlation has been found between the distribution of the Lyme disease agent *Borrelia burgdorferi* s. l. and predicted habitat suitability values for *S. tauricus*.

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## Моделювання видового поширення мишака жовтогрудого, *Sylvaemus tauricus*, з особливою увагою до України

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Резюме. Гризуни є важливими компонентами багатьох наземних екосистем і відіграють ряд корисних для людей ролей в природі, таких як аерація ґрунту та боротьба з комахами, однак гризуни також є джерелами зоонозних патогенів. Як відомо, вони є резервуарами кліщової зоонозної інфекції вірусного, бактеріального та протозойного походження та є важливими господарями незрілих стадій іксодових кліщів. Недавні дослідження в Європі продемонстрували роль гризунів, особливо мишей *Sylvaemus* і полівок *Myodes*, в епідеміології бактеріальних зоонозів, що передаються кліщами, таких як Лайм-бореліоз і анаплазмоз. Зокрема, мишак жовтогрудий, *Sylvaemus tauricus* (Pallas, 1811; син.: *Apodemus flavicollis* (Melchior, 1834)), підтримує передачу найважливіших патогенів, які переносяться кліщем собачим, *Ixodes ricinus*. Використовуючи методи моделювання поширення видів, було проведено оцінку ймовірності присутності цього гризуна в різних частинах України та здійснено пошук ефективних екологічних факторів, які відіграють роль у його поширенні. Ми вважали це завдання важливим, зважаючи на еколого-медичну значимість цього виду гризунів та актуальність проблеми, яка загострюється фактом збройної агресії Росії в Україні. Результати показали широкий потенціал для поширення мишака жовтогрудого у західній і центральній частинах України та Криму. Території переважно Західної та Центральної України та Криму є дуже сприятливими для цього гризуна, тоді як на півдні та в менших масштабах на крайньому сході країни вони є найменш сприятливими. Серед біокліматичних факторів навколишнього середовища, які відіграють роль у формуванні ніші виду, є ті, які повністю або переважно пов'язані з температурою (наприклад, середньорічна температура, континентальність тощо). Інші фактори в порядку зменшення їхньої ролі пов'язані з особливостями ґрунту та наземного покриву, хмарністю і стандартизованим впливом людини. Було виявлено помірну, хоча статистично значущу, кореляцію між поширенням збудника хвороби Лайма *Borrelia burgdorferi* s.l. і прогнозованими значеннями придатності середовища існування для *S. tauricus*.

Ключові слова: *Sylvaemus tauricus*, моделювання видових ареалів, Україна.

### Introduction

Rodentia is one of the most diversified mammalian order in the world [Wilson & Reeder 2005] and its members are essential components of many terrestrial ecosystems. These animals have several beneficial activities in nature, such as soil aeration and insect control, however, rodents are also sources of zoonotic pathogens [Meerburg *et al.* 2009]. Rodents as pests are known to be reservoirs of tick-borne zoonotic infections of viral, bacterial and protozoan origin, and are important hosts of the immature stages of *Ixodes* ticks. Recent studies in Europe have demonstrated the role of rodents, especially *Sylvaemus* mice and *Myodes* voles, in the epidemiology of tick-borne bacterial zoonoses, such as Lyme borreliosis and anaplasmosis [Król *et al.* 2022]. In particular, the yellow-necked mouse, *Sylvaemus tauricus* (Pallas, 1811; syn.: *Apodemus flavicollis* (Melchior, 1834)), supports the transmission of the most important pathogens carried by *I. ricinus* [Levytska *et al.* 2020].

The yellow-necked mouse, with its subspecies, is a rodent widespread throughout continental Europe, from Spain to the Urals, as well as in England and Wales and the Middle East, namely Syria and Israel [Amori *et al.* 2016]. Its habitat is closely linked to forest ecosystems; it is, in fact, present in all woods of a certain extent, both coniferous and broad-leaved, where it mainly prefers areas with a more mature stand [Pucek *et al.* 1993]. Although its presence is reported from sea level up to the limit of forest vegetation, the species is clearly more common in hilly and mountainous areas than in lowlands. In general, it is a ground-dwelling species with a high capacity for climbing trees [Borowski 1962]. They are nocturnal and travel large distances in trees and the forest floor in search of buds, seeds or small insects, which make up their broad food niche [Drożdż 1996; Ketten *et al.* 2016].

Rodent-borne diseases, including those indirectly transmitted by vectors, represent an increasing threat for public health. The provisioning of early warning indicators of the changing hazard is of great utility for the improvement of prevention and control strategies [Marini *et al.* 2022]. In this respect, understanding and modelling the ecological niche, also referred to as ‘species distribution modelling, or SDM’ [Elith & Leathwick 2009], of the vertebrate host species can, therefore, be a powerful predictor of the risk of exposure to the pathogens they transmit. Indeed, SDMs are increasingly used to estimate species’ ranges, but with an implicit assumption that areas of high suitability will result in higher probability of persistence and/or abundance [Bean *et al.* 2014]. Species are expected to have higher probability of occupancy in geographic areas with environmental conditions at the centre of a species’ niche than at the edges [Pearson & Fraterrigo 2011]. Simultaneously, it is frequently assumed that the same should be expected for habitat quality: quality should be the highest in areas with environments that most closely match the centre of a species’ niche and decline towards the edges. Fortunately for our purpose, research into the relationship between habitat quality and SDMs has generally found positive correlations between SDM values and population abundance [Pearce & Ferrier 2001; Van Der Wal *et al.* 2009] and confirmed that SDMs can be effective proxies for some measures of habitat quality or features, including correlations of SDM values with long-term trends in abundance, and support the hypothesis that habitat suitability indices obtained from SDMs can reflect the local abundance potentialities of a species [Bean *et al.* 2014; Monnier-Corbel *et al.* 2023]. Under such circumstances hantavirus infections, for instance, which are transmitted to humans by direct biting but mainly indirectly by inhaling aerosolised urine and faeces of infected rodents [Kallio *et al.* 2006], are logically more likely to occur in areas of high habitat suitability predicted by an SDM. In another exemplifying case, *Sylvaemus* mice appear to be the most effective hosts for co-feeding transmission of tick-borne encephalitis virus (TBEV) to occur [Labuda *et al.* 1993], and for that reason TBEV is primarily associated with suitable habitat, namely deciduous woodlands, that supports large numbers of these small mammals. Previous studies have additionally shown that in woodland habitats of Central Europe, infection with *Borrelia burgdorferi* s. l. is carried by natural populations of a number of species of small rodents, including the yellow-necked mouse [Siński *et al.* 2006]. These rodents serve as reservoirs of the Lyme borreliosis agent, and since their relative and absolute population densities can be expected to vary with changing habitat suitability, this should have consequences for tick infestations and for the dynamics of transmission of tick-borne agents of the disease.

Therefore, considering the ecological and epidemiological importance of the yellow-necked mouse, this study is aimed to determine the probability of presence of the species in different parts of Ukraine and to find the effective environmental factors that play roles in its distribution by using SDMs. The results of this study will particularly be useful in finding areas with high potential for transmission of relevant pathogens, which can be used in planning mitigation strategies for the respective diseases in the study area.

The urgency of the problem is exacerbated by the fact that Russia’s armed aggression forced millions of Ukrainians to flee their homes in search of security, either in other regions of the country or abroad. While the war continues, the pace of migration remains high. According to the Ministry of Social Policy, by December of 2022, 4 893 079 people have been registered as internally displaced persons in Ukraine and temporarily relocated mainly to the western and central regions of the country, further away from the war zone. While refugee movement itself is associated with an increase in infectious disease transmission and is likely to affect zoonotic disease risks, it yet remains unclear how forced migration affects disease dynamics [Tarnas *et al.* 2021]. Human susceptibility to disease during forced migration might increase due to exhaustion, malnutrition and stress arising from displacement, magnified by crowded and substandard living conditions [Hammer *et al.* 2018].

## Material and Methods

The first type of data needed for building SDMs is a list of locations where the studied species has been found. The study area comprised a clipped around Ukraine portion of the native geographic range of the species in Europe and Western Asia (lower left corner: 17°E, 40°N, upper right corner:

43°E, 57°N) for which the corresponding data were extracted from the Global Biodiversity Information Facility [GBIF.org (11 July 2023) GBIF Occurrence Download <https://doi.org/10.15468/dl.422t3x>]. For Ukraine, supplemental presence data sets of the yellow-necked mouse originated from various national sources and from the own material of the Institute of Zoology located in Kyiv, Ukraine, as well as published records [Mezhzherin *et al.* 2002; Gashchak *et al.* 2008; Mezhzherin & Lashkova 2013; Materials 2021; etc.] and the Ukrainian Biodiversity Information Network (<https://ukrbn.com>). The species of most of the collected individuals in Ukraine was determined by employing cranial and odontological features [Mezhzherin & Lashkova 1992; Lashkova & Dzeverin 2002], and/or using allozyme-based genetic methods [Mezhzherin 1990; Mezhzherin & Zykov 1991].

SDMs were generated by employing Bayesian additive regression trees (BART), a cutting-edge technique in this field. Running SDMs with BARTs has been substantially facilitated by the development of an R package, ‘embarcadero’ [Carlson 2020], being highly effective at identifying informative subsets of predictors. The algorithm computes habitat suitability values ranging from 0, for fully non-suitable habitat, to 1, for fully suitable habitat. The package includes methods for generating and plotting response curves, illustrating 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 model output. Upward trends for variables indicate a positive relationship; downward movements represent a negative relationship [Baldwin 2009].

Models were evaluated using the area under the receiver operating characteristic curve (AUC) [Metz 1978] and the true skill statistic (TSS) [Allouche *et al.* 2006]. AUC scores range from 0 to 1, with 0 for systematically wrong model predictions and 1 for systematically perfect model predictions; AUC values 0.7 to 0.8 are considered acceptable, values >0.8 are considered to be good to excellent. TSS values range from -1 to +1, with -1 corresponding to systematically wrong predictions and +1 to systematically correct predictions; TSS values < 0.4 are considered poor, 0.4–0.8 are useful, and > 0.8 are good to excellent.

Because of habitat complexity it is often difficult to single out which factors play a crucial role in controlling a species’ distribution. SDMs are primarily climate-driven, meaning that the variables used to develop them typically portray climatic factors [Kriticos 2012]. This makes sense because climate is a chief driver of environmental suitability [Schrodt *et al.* 2019]. Information on the bioclimatic parameters was collected as raster layers at a 2.5' resolution from three primarily climatic data bases and used separately for building the anticipated SDMs and checking their performances. From the WorldClim website (<http://www.worldclim.com/version2>), 19 bioclimatic variables were downloaded, which indicate general trends in precipitation and temperature, including extremes and the seasonality of temperature [Fick & Hijmans 2017].

Secondly, we used for modelling purposes a set of 16 climatic and 2 topographic variables (the ENVIREM dataset, downloaded from <http://envirem.github.io>; accessed 26.11.2022), which are likely to have direct relevance to ecological or physiological processes determining species distributions [Title & Bemmels 2018]. The included topographic variables are potentially important too, because they have the capability to modify the effects of climate descriptors. Thirdly, related to climate is cloud cover, which can influence numerous important ecological processes (Global 1-km Cloud Cover dataset, downloaded from <https://www.earthenv.org/cloud>; accessed 12.07.2023). Surprisingly enough, the assessment of its importance has remained remarkably limited, although cloud cover dynamics may provide key information for delineating a variety of habitat types and predicting species distributions [Wilson & Jetz 2016].

For many applications in biodiversity and ecology, existing remote sensing-derived land-cover products are used. Land cover information offers a powerful first-order proxy for locally expected biodiversity and ecological processes [Pearson *et al.* 2004]. Land cover is also considered relevant in models aimed at predicting species distributions because it adds realistic information on habitat fragmentation and human influence, which are not represented in more commonly used sets of cli-

matic variables. Here we apply a global product that provides scale-integrated and accuracy-weighted consensus land-cover information on an approximately continuous scale (Global 1-km Consensus Land Cover dataset; downloaded from <https://www.earthenv.org/landcover>) [Tuanmu & Jetz 2014].

The distribution and abundance of organisms is influenced by the soils associated with particular ecosystems [Erick & Reeder 2003]. In this respect, burrowing animals usually take a benefit from some edaphic factors in their habitats, which means that those factors can possibly play a vital role in their geographical distribution [Jones *et al.* 1994; Khedher & Khalaf 2019]. Soil grids were obtained using the ‘geodata’ R package [Hijmans *et al.* 2023] allowing to download geographic soil data derived from the SoilGRIDS database [Poggio *et al.* 2021].

Finally, we employed Human Footprint maps as proxies for human disturbance of natural systems [Sanderson *et al.* 2002; Venter *et al.* 2016]. These were developed for a variety of human pressures, including the extent of built environments, population density, electric infrastructure, crop lands, pasture lands, roads, etc., and to facilitate comparisons placed within a 0–100 scale. The resulting standardised pressures are then summed together to create a standardised Human Footprint.

In the end, to achieve a single prediction, a consensus (i.e. ensemble) model was created by using weighted averages [Dormann *et al.* 2018], where the weight was derived from predictive performance (AUC). 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]. Then the ensemble SDM was reclassified to areas of low potential habitat suitability, medium and high potential habitat suitability. We defined these thresholds based on Jenks natural breaks, which maximises the similarity of numbers in groups by minimizing each class average deviation from the class mean, while maximizing each class deviation from the means of the other groups. The Jenks natural break provides a uniform interface to finding class intervals for continuous numerical variables [Jenks & Caspall 1971].

To check the assumption that predicted habitat suitability for the yellow-necked mouse, which serves as a reservoir of the Lyme borreliosis agent [Gern *et al.* 1994], and strongly contributes to both the density and the infection rate of the corresponding tick nymphs responsible for transmitting the disease [Tälleklint, Jaenson 1997], correlates with the distribution of the disease agent itself we analysed the relationship between the obtained habitat suitability values and reported incidence of Lyme disease. The latter is calculated as the number of reported cases per 100 000 people and is provided up-to-date by the Johns Hopkins Lyme and Tick-Borne Disease Dashboard (<https://www.hopkinslymetracker.org>). For this purpose, we used the R package ‘trafo’ [Medina *et al.* 2019] to help select suitable transformations, if any, depending on statistical requirements and the data being analysed. To control for spatial non-independence, we used a modified t-test to calculate the statistical significance of the correlation coefficient (a corrected Pearson’s correlation) based on geographically effective degrees of freedom as implemented in the ‘SpatialPack’ R package [Osorio & Vallejos 2014].

Maps of habitat suitability in the GeoTIFF format were processed and visualised in SAGA GIS [Conrad *et al.* 2015], statistical data was analysed using the PAST software package [Hammer *et al.* 2001] and/or the R environment [R Core Team 2020].

## Results and Discussion

The conducted search for occurrence data yielded a total of 269 non-duplicate georeferenced records of the yellow-necked mouse across the denoted study area. We generated models using all available occurrence points because the measured spatial autocorrelation among model pseudo-residuals by calculating Moran’s I at multiple distance classes using the GeoDa software tool [Anselin *et al.* 2006] was below 0.3, which for our purpose is considered acceptable [Lichstein *et al.* 2002]. Otherwise a special subsampling regime would be necessary to reduce sampling bias and spatial autocorrelation [Aiello-Lammens *et al.* 2015].



Table 1. Evaluation metrics for SDMs built using various sets of predictors

Таблиця 1. Показники оцінювання моделей поширення, побудованих з використанням різних наборів предикторів

Predictor dataset	AUC*	TSS**
ENVIREM	0.890	0.636
WorldClim v.2	0.864	0.572
SoilGRIDS	0.848	0.541
Global 1-km Consensus Land Cover dataset	0.812	0.491
Global 1-km Cloud Cover dataset	0.796	0.479
Human Footprint	0.746	0.380

\* Area under the receiver operating characteristic (ROC) curve; \*\* True skill statistic.

From the figures in Table 1 it is evident that SDMs built using various selected subsets of predictors, particularly from the ENVIREM and WorldClim v.2, datasets performed highly efficiently, with AUC values considered mostly to correspond to good and excellent, and predominantly useful TSS values. As part of its output, BART ranks the environmental layers used to train the SDM based on their relative importance in model construction.

As already stated, the best performing SDM was achieved using the ENVIREM dataset. Based on variable importance, the most contributing to the model were the ‘mean monthly potential evapotranspiration (PET) of the coldest quarter’ and ‘continentality’ (Fig. 1), jointly accounting for around 36% of the model prediction. In terms of the WorldClim v.2 dataset, prime importance was attributed to ‘annual mean temperature’ (Bio1) (Fig. 2) and ‘mean temperature of the driest quarter’ (Bio9), contributing together of around 41% of the variance. It is worth to note here that these predictors found by the software to be highly responsible for shaping the bioclimatic niche of the yellow-necked mouse are either directly temperature-related or by implication. For instance, Bio9 characterises the cold season (December–February) when precipitation in the study area drops to its lowest long-term average (47.2 mm), compared to the warmest months, specifically June–August (75.5 mm).

With regard to soil, predictors ‘bulk density of the fine earth fraction’ (Fig. 3) and ‘volumetric fraction of coarse fragments (> 2 mm)’ showed the highest importance, making up together 25.9%. The considered bulk density indicant is linked to soil functionality, including the formation of macro- and microporosity [Pacini *et al.* 2023] and reflects soil compaction [Orgiazzi *et al.* 2017].

Then on, soils with higher amounts of coarse fragments also impact total porosity [Chow *et al.* 2011] and consequently effect soil compaction too. Generally speaking, compaction occurs when soil particles are pressed together reducing the pore space, which increases bulk density [Fu *et al.* 2019], so these features are largely reciprocal. Interestingly, the corresponding response curve shows that rising values of ‘bulk density of the fine earth fraction’ are accompanied by a sharp increase in predicted for the yellow-necked mouse habitat suitability, which levels off at around 60% after reaching the value of approximately 1.2 Mg/m<sup>3</sup>. In Europe, this figure is well above the mean for woodland, the species' preferred biotope (see below), accordingly 0.71 Mg/m<sup>3</sup>, however lower than the recorded maximum (1.73 Mg/m<sup>3</sup>) [Pacini *et al.* 2023]. Not necessarily related, but soil compactness is prominent for burrowing mammals, since their burrows easily collapse in poorly consolidated soils [Carotenuto *et al.* 2020], meaning that in this respect there should be some sort of trade-off between soil compaction and the specifics of burrowing activity. Likely such trade-off, or close to it, has been found in the course of our modelling effort.

Next in terms of performance are land cover predictors. As expected, ‘Evergreen/Deciduous Needleleaf Trees’, ‘Deciduous Broadleaf Trees’ and ‘Mixed/Other Trees’ categories collectively accounted for around a half (49.3%) of the model prediction. However, less counted upon ‘Cultivated and Managed Vegetation’ and ‘Urban/Built-up’ land cover categories too are turning out to be reasonably important in determining the nature of the species' niche, 17.3 and 17.2%, respectively. Indeed, this species sometimes spreads to habitats modified by human activity, such as agroecosys-

tems [Hoffmeyer 1973; Popov 1993] and urban areas; for example, in Vienna, the yellow-necked mouse has been reported to occur in parks and green spaces [Mitter *et al.* 2015; Pieniżek *et al.* 2017]. During density peaks caused by oak mast years, the species also migrates to arable land and orchards [Gryz *et al.* 2019; Gryz & Krauze-Gryz 2019]. In wooded areas of peri-urban zones of Warsaw, the yellow-necked mouse has shown a marked increase in population densities starting at the verge of the 20th and 21st centuries [Lesiński *et al.* 2021]. Accordingly, it can be assumed that a number of habitats, other than woodlands, in the meantime in tune with growing human impact are increasingly being occupied by the rodent.

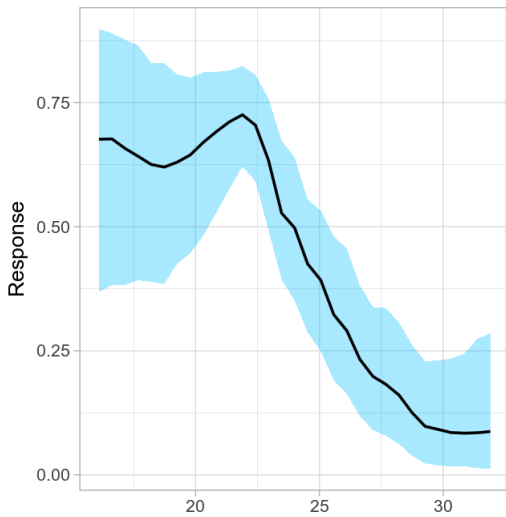


Fig. 1. Partial response curve for 'continentality' (°C). Response = habitat suitability.

Рис. 1. Парціальна крива відгуку для «континентальності». Response = прогнозована придатність середовища.

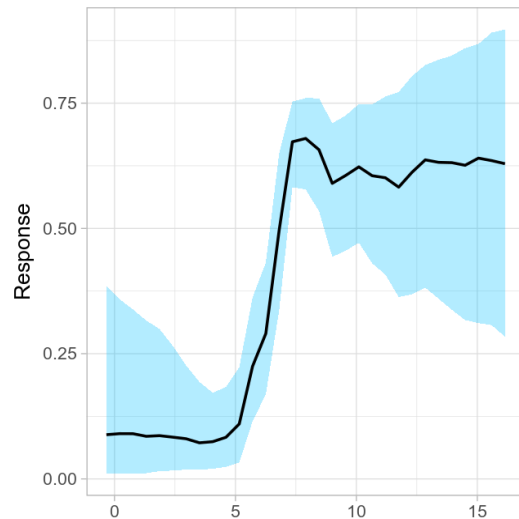


Fig. 2. Partial response curve for 'annual mean temperature' (°C).

Рис. 2. Парціальна крива відгуку для «середньорічної температури» (°C).

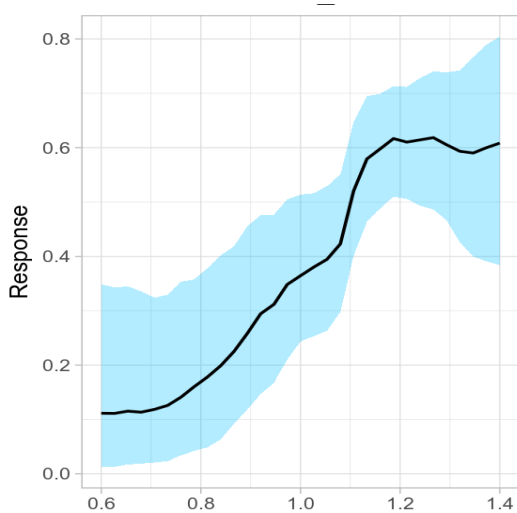


Fig. 3. Partial response curve for the 'bulk density of the fine earth fraction' (Mg/m<sup>3</sup>).

Рис. 3. Парціальна крива відгуку для «об'ємної щільності дрібноземної фракції» (Mg/m<sup>3</sup>).

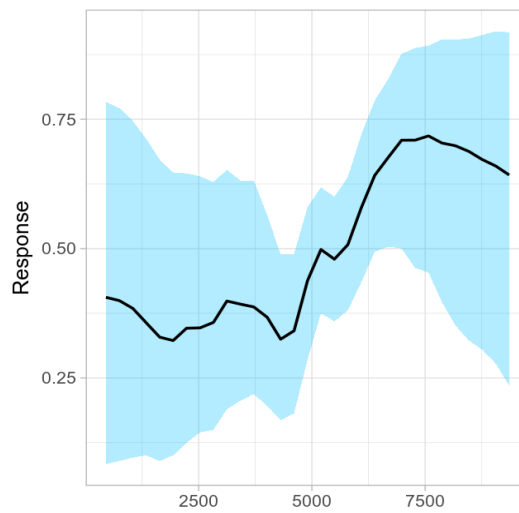


Fig. 4. Partial response curve for 'cloud frequency in July' (× 0.01).

Рис. 4. Парціальна крива відгуку для «частоти хмарності в липні» (× 0.01).

Today, cloud climatology offers another tool for predicting the geographic range of species than analysis of temperature and precipitation patterns. Cloud cover influences factors such as rain, sunlight, surface temperature and leaf wetness, and also plays an important role in establishing microclimate [Wilson & Jetz 2016]. Most contributing to the model were the monthly means through May to August, jointly explaining about 60% of the variance. Uniformly increasing cloud cover over the summer months noticeably boosts predicted habitat suitability; for example, based on the corresponding response curve for July (Fig. 4), both are strongly correlated, Spearman's  $\rho = 0.87$ ,  $p < 0.05$ . Curiously, increased cloud cover has been shown to enhance the activity of yellow-necked mice [Wróbel & Bogdziewicz 2015]. As previously discussed in the literature, cloud cover appears to be an important indirect clue for rodents, which allows to estimate the potential predation risk better than direct clues, such as urine (scent) of predators [Orrock *et al.* 2004]. In contrast to scent, cloud cover offers information on different danger types, that is, various types of predators that rely on vision when hunting, not on one specific species [Orrock *et al.* 2004; Orrock & Danielson 2009].

Further on, A. Wróbel and M. Bogdziewicz [2015] showed higher capture rates of *S. tauricus* during rainfall. One previous study revealed that the activity of the yellow-necked mouse increased during warm, cloudy nights, especially in the presence of light rain [Sidorowicz 1960]. Some researchers suggest that rain helps to mask the sound of movements and the odours emitted by rodents [Vickery & Bider 1981]. Additionally, mammalian predators, such as weasels, may reduce activity when rains to avoid the thermoregulatory cost of a wet coat combined with cool temperatures [Brandt & Lambin 2005]. Predictably enough, there is a strong statistical relationship between mean monthly cloud frequency and mean monthly precipitation pointing to the utility of cloud information itself for precipitation estimation [Behrangi *et al.* 2009]. Consequently, enhanced habitat suitability under raised cloudiness can also suggest the appearance of stronger advantages for the mice under wetter conditions during the considered months, a notion supported with field evidence.

Finally, the standardised Human Footprint showed a dome-shaped response when moderate human disturbance seems to benefit the rodent species by providing favourable conditions to trigger habitat suitability increases. However, over-disturbance by human activities reverses its positive effects on rodents and ends up in declining habitat suitability falling in our case from 57% to 43%. A similar trend recently has been documented for a substantial number of rodent species across China [Wan *et al.* 2022].

Summing up, a consensus habitat suitability map for *S. tauricus* in Ukraine has been created (Fig. 5), showing a broad potential distribution of the species in western and central Ukraine, and in the Crimea, particularly the elevated south. Next the SDM was reclassified to areas of low potential habitat suitability (0.19–0.38), medium (0.38–0.66) and high (0.66–0.88) potential habitat suitability (Fig. 6). Once again, predominantly western and central Ukraine, and the Crimea, are highly favourable areas for the mouse, whereas large portions of arid and semi-arid steppe in the south and, to a lesser extent, in the easternmost part of the country are the least suitable.

In terms of the assumption that the ensemble habitat suitability model of *S. tauricus*, a rodent involved in the transmission of Lyme disease, can serve as a proxy for the potential distribution of the disease agent itself, a correlation was checked between the obtained habitat suitability values with the recorded incidence of Lyme disease at reported locations. Unfortunately, such records of Lyme disease incidences in Ukraine are yet scarce and insufficient for a proper statistical analysis, therefore we used data from a neighbouring country, Romania, which in terms of climate similarity is fairly close to Ukraine, especially if accounting for warm season temperatures when tick activity is the highest [Qviller *et al.* 2014].

For instance, the highest daytime temperatures in Romania are reached in July with an average of 28.2°C, whereas in Ukraine August is the warmest month, with 27.9°C. Regarding night time lows, the warmest nights in both Romania and Ukraine occur in July reaching 15.9 and 16.2°C, respectively. For more comparisons see <https://www.worlddata.info/>. From the Johns Hopkins Lyme and Tick-Borne Disease Dashboard annual incidences of Lyme disease were downloaded for 41 counties and Bucharest Municipality for a five year period (from 2017 to 2021) and averaged.



Corresponding averaged habitat suitability values for each administrative entity, represented by a polygon shape file, were obtained using the 'grid statistics for polygons' module in SAGA GIS.

Firstly, using the R package 'trafo' suitable transformations depending on statistical requirements and the data being analysed were assessed by checking assumptions of normality, homoscedasticity, and linearity. All specified assumptions were shown to be acceptable ( $p > 0.05$ ) and there was no need in data transformation.

Secondly, using these incidences and the averaged habitat suitability values regarding each considered administrative unit in Romania, corrected Pearson's correlation coefficient ( $r$ ) controlling for spatial non-independence was calculated. The result showed a moderate statistically significant correlation [Moore *et al.* 2011] of 0.506 ( $p < 0.05$ ).

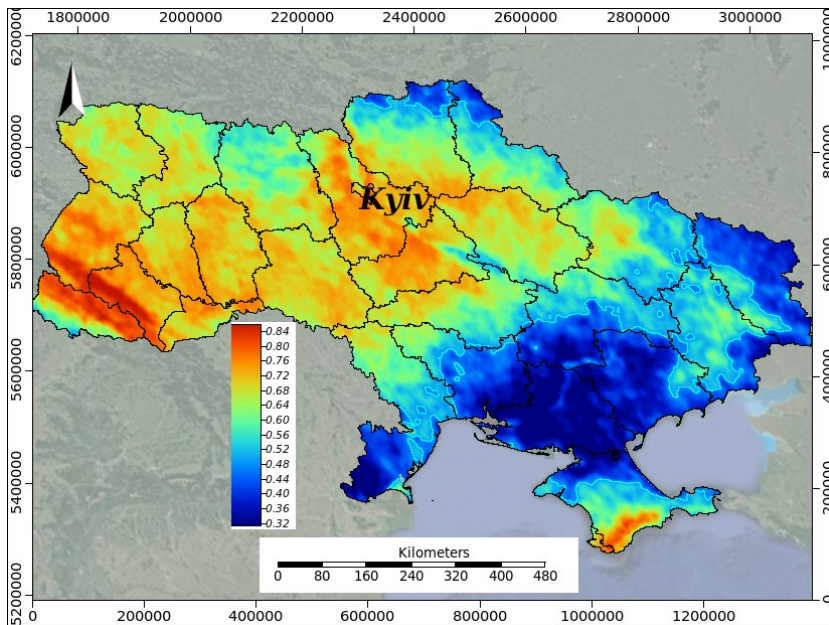


Fig. 5. Consensus habitat suitability map for *S. tauricus* in Ukraine; the legend shows potential habitat suitability ranging from high (red) to low (blue); the azure line represents the 10th percentile training presence logistic threshold.

Рис. 5. Консенсусна карта придатності місць перебування *S. tauricus* в Україні; легенда показує потенційну придатність середовища існування в діапазоні від високого (червоний) до низького (синій); блакитна лінія представляє 10-й процентиль логістичного порогу присутності по тренувальним точкам.

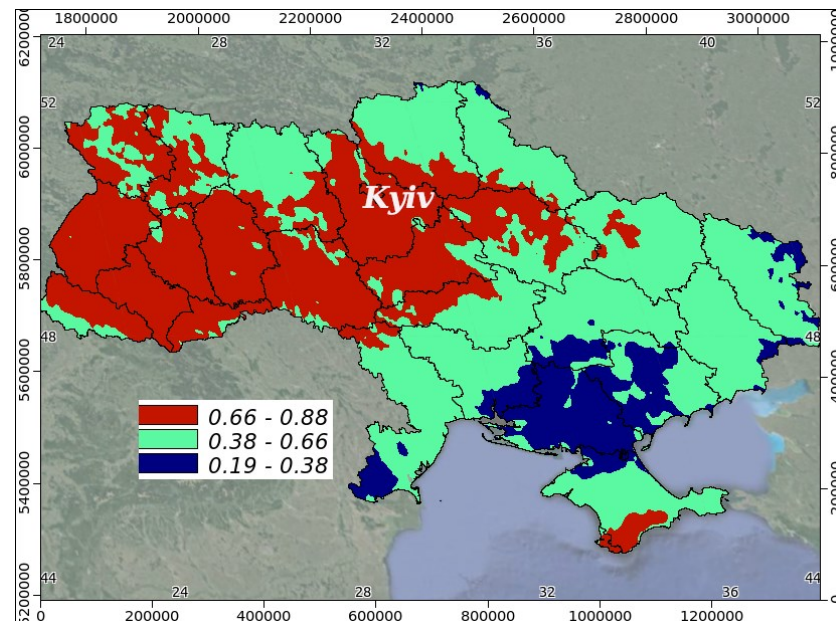


Fig. 6. Consensus map of habitat suitability for *S. tauricus* in Ukraine categorised into three classes: low (navy blue), moderate (green), and high (red); the corresponding ranges of habitat suitability are presented in the legend.

Рис. 6. Консенсусна карта придатності середовища існування для *Sylvaemus tauricus* в Україні класифікована на три класи: низький (темно-синій), помірний (зелений) і високий (червоний); відповідні діапазони придатності місць перебування представлені в легенді.

Thus, there is a sizeable potential for transmission of relevant pathogens which can be used in quick planning of the prevention of zoonotic diseases requiring coordinated actions by government authorities responsible for human and animal health, especially under wartime circumstances.

## Conclusion

Using an SDM approach [Elith & Leathwick 2009], an assessment was carried out of the probability of presence of the yellow-necked mouse in different parts of Ukraine and a search accomplished to find effective environmental factors that play roles in its distribution. We considered this task important considering the coenotic and epidemiological significance of this particular rodent species. Results showed a broad potential for the distribution of the species in western and central Ukraine and the Crimea. Areas predominantly in western and central Ukraine and the Crimea are highly favourable for the mouse, whereas in the south and, to a smaller scale, in the easternmost part of the country they are the least favourable. Amongst the bioclimatic environmental factors that play roles in shaping the species' niche are the ones that are mostly temperature-related.

Other factors in a softly declining order of their roles are associated with soil and land cover features, cloud frequency, and human impact. A moderate, though statistically significant, correlation has been found between the distribution of the Lyme disease agent and predicted habitat suitability values for *Sylviaemus tauricus*.

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## References

- Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, [et al.] 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, **38** (5): 541–545. [CrossRef](#)
- Allouche, O., A. Tsoar, R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43** (6): 1223–1232. [CrossRef](#)
- Anselin, L., I. Syabri, Y. Kho. 2006. GeoDa: an introduction to spatial data analysis. *Geographical Analysis*, **38** (1): 5–22. [CrossRef](#)
- Baldwin, R. A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy*, **11** (4): 854–866. [CrossRef](#)
- Bean, W. T., L. R. Prugh, R. Stafford, [et al.] 2014. Species distribution models of an endangered rodent offer conflicting measures of habitat quality at multiple scales. *Journal of Applied Ecology*, **51** (4): 1116–1125. [CrossRef](#)
- Behrangi, A., K. B. Hsu, S. Imam, [et al.] 2009. PERSIANN-MSA: A precipitation estimation method from satellite-based multispectral analysis. *Journal of Hydrometeorology*, **10** (6): 1414–1429. [CrossRef](#)
- Borowski, S. 1962. *Apodemus flavicollis* (Melchior, 1834) in the top of tall trees. *Acta Theriologica*, **6** (11): 314. [CrossRef](#)
- Brandt, M. J., X. Lambin. 2005. Summertime activity patterns of common weasels *Mustela nivalis vulgaris* under differing prey abundances in grassland habitats. *Acta Theriologica*, **50** (1): 67–79. [CrossRef](#)
- Carlson, C. J. 2020. 'embarcadero': Species distribution modeling with Bayesian additive regression trees in R. *Methods in Ecology and Evolution*, **11** (7):1–9. [CrossRef](#)
- Carotenuto, A., F. Guarracino, R. Šumbera, R. [et al.] 2020. Burying below ground: Interaction between soil mechanics and evolution of subterranean mammals. *Journal of the Royal Society, Interface* **17**: 20190521. [CrossRef](#)
- Chow, T. L., H. W. Rees, J. O. Monteith, [et al.] 2011. Effects of coarse fragment content on soil physical properties, soil erosion and potato production. *Canadian Journal of Soil Science*, **87** (5): 565–577. [CrossRef](#)
- Conrad, O., B. Bechtel, M. Bock, [et al.] 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. *Geoscientific Model Development Discussions*, **8**: 2271–2312. [CrossRef](#)
- Dormann, C. F., J. M. Calabrese, G. Guillera-Arroita, [et al.] 2018. Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. *Ecological Monographs*, **88** (4): 485–504. [CrossRef](#)
- Drożdż, A. 1966. Food habits and food supply of rodents in the beech forest. *Acta Theriologica*, **11** (15): 363–384. [CrossRef](#)
- Elith, J., J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40** (1): 677–697. [CrossRef](#)
- Erik, G. B., W. I. Robinson. 2003. *Wildlife ecology and management*. 5th ed. Upper Saddle River, N.J., Prentice Hall, 1–634.
- Fick, S. E., R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37** (2): 4302–4315. [CrossRef](#)
- Fu, Y., Z. Tian, A. Amoozegar, [et al.] 2019. Measuring dynamic changes of soil porosity during compaction. *Soil and Tillage Research*, **193**: 114–121. [CrossRef](#)
- Gaschak, S., S. Hufer, Yu. Maklyuk [et al.] 2008. On the species diversity of mice of the genus *Sylviaemus* in Ukraine. *Proceedings of the Theriological School*, **9**: 80–92. [In Russian]
- Gern, L., M. Siegenthaler, C. M. Hu, [et al.] 1994. *Borrelia*

- burgdorferi in rodents (*Apodemus flavicollis* and *A. sylvaticus*): duration and enhancement of infectivity for *Ixodes ricinus* ticks. *European Journal of Epidemiology*, **10** (1): 75–80. [CrossRef](#)
- Gryz, J., D. Krauze-Gryz. 2019. The common buzzard *Buteo buteo* population in a changing environment, Central Poland as a case study. *Diversity*, **11** (3): 35. [CrossRef](#)
- Gryz, J., L. Ozga, D. Krauze-Gryz. 2019. Long-term stability of tawny owl (*Strix aluco*) population despite varying environmental conditions — a case study from Central Poland. *Polish Journal of Ecology*, **67** (1): 75–83. [CrossRef](#)
- Hammer, C. C., J. Brainard, P.R. Hunter. 2018. Risk factors and risk factor cascades for communicable disease outbreaks in complex humanitarian emergencies: a qualitative systematic review. *BMJ Global Health*, **3** (4): e000647. [CrossRef](#)
- Hammer, Ø., D. A. Harper, P. D. Ryan. 2001. PAST: Paleontological statistics soft ware package for education and data analysis. *Palaeontologia Electronica*, **4** (1): 1–9.
- Hijmans, R. J., M. Barbosa, A. Ghosh [et al.] 2023. *Geodata: Download Geographic Data*. URL
- Hoffmeyer, I. 1973. Interaction and habitat selection in the mice *Apodemus flavicollis* and *A. sylvaticus*. *Oikos*, **24** (1): 108–116. [CrossRef](#)
- Jenks, G. F., F. C. Caspall. 1971. Error on choroplethic maps: definition, measurement, reduction. *Annals of the American Association of Geographers*, **61** (2): 217–244. [CrossRef](#)
- Jones, C. G., J. H. Lawton, M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos*, **69** (3): 373–386. [CrossRef](#)
- Kallio, E., J. Klingstrom, E. Gustafsson [et al.] 2006. Prolonged survival of Puumala hantavirus outside the host: evidence for indirect transmission via the environment. *Journal of General Virology*, **87** (8): 2127–2134. [CrossRef](#)
- Keten, A., V. Beskardes, E. Makineci [et al.] 2016. Abundance of *Apodemus* spp. varies by stand age in coppice-originated oak forest, Thrace, Turkey. *Bosque*, **37** (2): 425–429. [CrossRef](#)
- Khedher, A. A., A. A. Khalaf. 2019. Effect of some edaphic factors and the distribution of yellow-necked field mouse (*Apodemus flavicollis argyropuli*) in field crop biotopes. *The Journal of Duhok University. Section: Agriculture and Veterinary*, **22** (2): 9–24. [CrossRef](#)
- Kriticós, D. J. 2012. Regional climate-matching to estimate current and future sources of biosecurity threats. *Biological Invasions*, **14** (8): 1533–1544. [CrossRef](#)
- Król, N., A. Obiegala, C. Imholt, [et al.] 2022. Diversity of *Borrelia burgdorferi* sensu lato in ticks and small mammals from different habitats. *Parasites & Vectors*, **15**, Article number 195. [CrossRef](#)
- Labuda, M., P.A. Nuttall, O. Kozuch, [et al.] 1993. Non-viraemic transmission of tick-borne encephalitis virus: a mechanism for arbovirus survival in nature. *Experientia*, **49** (9): 802–805. [CrossRef](#)
- Lashkova, E. I., I. I. Dzeverin. 2002. Odontometric variability and identification of species of wood mice, *Sylvaemus* (Muridae, Rodentia), fauna of Ukraine. *Vestnik zoologii*, **36** (3): 25–33. [In Russian]
- Lesiński, G., J. Gryz, D. Krauze-Gryz [et al.] 2021. Population increase and synurbization of the yellow-necked mouse *Apodemus flavicollis* in some wooded areas of Warsaw agglomeration, Poland, in the years 1983–2018. *Urban Ecosystems*, **24** (3): 481–489. [CrossRef](#)
- Levytska, V., A. Mushynskiy, A. Berezovskyi. 2020. Rodents as a persistent source of tick-borne diseases. *Scientific Horizons*, **07** (92): 59–64. [CrossRef](#)
- Lichstein, J. W., T. R. Simons, S.A. Shriner, [et al.] 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, **72** (3): 445–463. [CrossRef](#)
- Liu, C., P. Berry, T. Dawson, R. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28** (3): 385–393. [CrossRef](#)
- Marini, G., A. Rizzoli, V. Tagliapietra. 2022. Predicting rodent population dynamics as early warning for zoonotic disease transmission. *International Journal of Infectious Diseases*, **116**, Supplement, page S70. [CrossRef](#)
- Materials... 2021. *Materials for the Mammal Atlas of Ukraine*. Kyiv, 1–240. (Series: Conservation Biology in Ukraine; Issue 20). [In Ukrainian]
- Medina, L., A.-K. Kreutzmann, N. Rojas-Perilla, [et al.] 2019. The R Package 'trafo' for transforming linear regression models. *R Journal*, **9** (2): 99–123. [CrossRef](#)
- Meerburg, B. G., G. R. Singleton, A. Kijlstra. 2009. Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology*, **35** (3): 221–270. [CrossRef](#)
- Metz, C. E. 1978. Basic principles of ROC analysis. *Seminars in Nuclear Medicine*, **8** (4): 283–298. [CrossRef](#)
- Mezhzherin, S. V., E. I. Lashkova, N. N. Tovpinets. 2002. Geographical distribution, abundance and biotopic distribution of wood mice of the genus *Sylvaemus* (Rodentia, Muridae) on the territory of Ukraine. *Vestnik zoologii*, **36** (6): 39–49. [In Russian]
- Mezhzherin, S. V., E. I. Lashkova. 1992. Diagnosis, geographical variability and distribution of two closely related species of mice *Sylvaemus sylvaticus* and *S. flavicollis* (Rodentia, Muridae) in the area of their cohabitation. *Vestnik zoologii*, No. 3: 33–41. [In Russian]
- Mezhzherin, S. V., O. I. Lashkova. 2013. *Mammals of Ukraine (a reference guide)*. Naukova Dumka, Kyiv, 1–358. [In Ukrainian]
- Mezhzherin, S. V. 1990. Allozyme variability and genetic divergence in mice of the subgenus *Sylvaemus* (Ognev et Vorobiev). *Genetika*, **26** (6): 1046–1054. [In Russian]
- Mezhzherin, S. V., A. E. Zykov. 1991. Genetic divergence and allozyme variability in mice of the genus *Apodemus* s. lato (Muridae, Rodentia). *Tsitologia i Genetika*, **25** (4): 51–59. [In Russian]
- Mitter, G., P. Sumasgutner, A. Gamauf. 2015. Niche-partitioning of three *Apodemus* species (Mammalia: Murinae) in an urban environment. *Annalen Des Naturhistorischen Museums in Wien. Serie B Für Botanik Und Zoologie*, **117**: 37–46.
- Monnier-Corbel, A., A. Robert, Y. Hingrat, [et al.] 2023. Species distribution models predict abundance and its temporal variation in a steppe bird population. *Global Ecology and Conservation*, **43** (9): e02442. [CrossRef](#)
- Moore, D. S., W. I. Notz, M. A. Flinger. 2011. The basic practice of statistics (6th ed.). W. H. Freeman and Company, New York, 1–745.
- Orgiazzi, A., C. Ballabio, P. Panagos [et al.] 2017. LUCAS Soil, the largest expandable soil dataset for Europe: a review. *European Journal of Soil Science*, **69** (1): 140–153. [CrossRef](#)
- Orrock, J. L., B. J. Danielson, R.J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology*, **15** (3): 433–437. [CrossRef](#)
- Orrock, J. L., B. J. Danielson. 2009. Temperature and cloud cover, but not predator urine, affect winter foraging of mice. *Ethology*, **115** (7): 641–648. [CrossRef](#)
- Osorio, F., R. Vallejos. 2014. SpatialPack: package for analysis of spatial data. R package version 0.2-3. URL
- Pacini, L., F. Yunta, A. Jones [et al.] 2023. Fine earth soil bulk density at 0.2 m depth from Land Use and Coverage Area Frame Survey (LUCAS) soil 2018. *European Journal of Soil Science*, **74** (4): e13391. [CrossRef](#)
- Pearson, R. G., T. P. Dawson, C. Liu. 2004. Modelling species distributions in Britain: A hierarchical integration of climate and land-cover data. *Ecography*, **27** (3): 285–298. [CrossRef](#)
- Pearson, S., J. Fraterrigo. 2011. Habitat quality, niche breadth, temporal stochasticity, and the persistence of populations in



- heterogeneous landscapes. In: J. Liu, V. Hull, A. Morzillo, & J. Wiens (Eds), *Sources, Sinks and Sustainability* (Cambridge Studies in Landscape Ecology). Cambridge: Cambridge University Press, 115–138. [CrossRef](#)
- Phillips, S. J., M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31** (2): 161–175. [CrossRef](#)
- Pieniżek, A., P. Boguszewski, R. Meronka. 2017. The impact of urban noise on the behavior of two mouse species belonging to the genus *Apodemus*. *Natural Resources*, **8**: 55–68. [CrossRef](#)
- Poggio, L., L. M. de Sousa, N. H. Batjes, [et al.] 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. *Soil*, **7** (1): 217–240. [CrossRef](#)
- Popov, V.V. 1993. Discriminant criteria and comparative study on morphology and habitat selection of *Apodemus sylvaticus* (Linnaeus, 1758) and *Apodemus flavicollis* (Melchior, 1834) (Mammalia, Rodentia, Muridae) in Bulgaria. *Acta Zoologica Bulgarica*, **46** (1): 100–111.
- Pucek, Z., W. Jędrzejewski, B. Jędrzejewska, [et al.] 1993. Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. *Acta Theriologica*, **38** (2): 199–232. [CrossRef](#)
- Qviller, L., L. Grøva, H. Viljugrein [et al.] 2014. Temporal pattern of questing tick *Ixodes ricinus* density at differing elevations in the coastal region of western Norway. *Parasites & Vectors* **7**, Article number 179. [CrossRef](#)
- R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: [URL](#)
- Sanderson, E. W., M. Jaitheh, M. A. Levy [et al.] 2002. The Human Footprint and the Last of the Wild. *BioScience*, **52** (10): 891–904. [CrossRef](#)
- Schrodt, F., M. J. Santos, J. J. Bailey, R. Field. 2019. Challenges and opportunities for biogeography—What can we still learn from von Humboldt? *Journal of Biogeography*, **46** (8): 1631–1642. [CrossRef](#)
- Sidorowicz, J. 1960. Influence of the weather on capture of micro-mammalia, I. Rodents. *Acta Theriologica*, **4**: 139–158. [CrossRef](#)
- Siński, E., A. Pawełczyk, A. Bajer, [et al.] 2006. Abundance of wild rodents, ticks and environmental risk of Lyme borreliosis: a longitudinal study in an area of Mazury Lakes district of Poland. *Annals of Agricultural and Environmental Medicine*, **13** (2): 295–300.
- Tällekliint, L., T. G. Jaenson. 1997. Infestation of mammals by *Ixodes ricinus* ticks (Acari: Ixodidae) in South-Central Sweden. *Experimental and Applied Acarology*, **21** (12): 755–771. [CrossRef](#)
- Tarnas, M. C., N. Angel, A. N. Desai [et al.] 2021. Increase in vector-borne disease reporting affecting humans and animals in Syria and neighboring countries after the onset of conflict: A ProMED analysis 2003–2018. *International Journal of Infectious Diseases*, **102**: 103–109. [CrossRef](#)
- Title, P. O., J. B. Bemmels. 2018. ENVIREM: An expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, **41** (2): 291–307. [CrossRef](#)
- Tuanmu, M.-N., W. Jetz. 2014. A global 1-km consensus land-cover product for biodiversity and ecosystem modeling. *Global Ecology and Biogeography*, **23** (9): 1031–1045. [CrossRef](#)
- Van Der Wal, J., L. P. Shoo, C. N. Johnson [et al.] 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *American Naturalist*, **174** (2): 282–291. [CrossRef](#)
- Venter, O., E. Sanderson, A. Magrach [et al.] 2016. Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific Data* **3**, 160067. [CrossRef](#)
- Vickery, W., J. Bider. 1981. The influence of weather on rodent activity. *Journal of Mammalogy*, **62** (1): 140–145. [CrossRef](#)
- Wan, X., C. Yan, Z. Wang [et al.] 2022. Sustained population decline of rodents is linked to accelerated climate warming and human disturbance. *BMC Ecology and Evolution*, **22**, Article number: 102. [CrossRef](#)
- Wilson, A.M., W. Jetz. 2016. Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. *PLoS Biology*, **14** (3): e1002415.
- Wilson, D. E., D. M. Reeder (eds). 2005. *Mammal Species of the World. A Taxonomic and Geographic Reference* (3rd ed.). Johns Hopkins University Press, **2**, 1–142. [CrossRef](#)
- Wróbel, A., M. Bogdziewicz. 2015. It is raining mice and voles: which weather conditions influence the activity of *Apodemus flavicollis* and *Myodes glareolus*? *European Journal of Wildlife Research*, **61**: 475–478. [CrossRef](#)