



UDC 598.1:591.9 (447.43/.44)

USING ECOLOGICAL NICHE MODELING FOR BIODIVERSITY CONSERVATION GUIDANCE IN THE WESTERN PODILLYA (UKRAINE): AMPHIBIANS

V. Tytar¹, S. Mezhzherin¹, L. Sobolenko²,

¹Schmalhausen Institute of Zoology NAS of Ukraine,
vul. B. Khmelnytskogo, 15, Kiev, 01601 Ukraine

E-mail: mezh@izan.kiev.ua, vtytar@gmail.com

²Pavlo Tychyna Uman State Pedagogical University,
Sadova str., 2, Uman, 20300 Ukraine

E-mail: sobolenko@ukr.net

Using Ecological Niche Modeling for Biodiversity Conservation Guidance in the Western Podillya (Ukraine): Amphibians. Tytar, V., Mezhzherin, S., Sobolenko, L. — Maximum entropy niche modeling was employed as a tool to assess potential habitat suitability for 13 amphibian species and to map their potential distribution in the Western Podillya (Ukraine). The predictor variables used were of climate, topography and human impact (assessed by the Human Footprint). The “mean temperature of coldest quarter” and “isothermality” were two of the most important factors in predicting habitat suitability and distribution. Another profound contribution has been displayed by the Human Footprint, meaning that human infrastructure may benefit amphibians, a phenomenon that perhaps is much more widespread than thought. Areas have been distinguished that in the first place should be of interest to nature conservationists targeting amphibians (exemplified by *Bombina variegata*) and a map summarizing species richness was produced.

Key words: Maxent, niche modeling, species distribution modeling, amphibians, Ukraine.

Моделирование экологической ниши как инструмент для планирования мероприятий, направленных на сохранение биоразнообразия Западного Подолья (Украина): амфибии. Титар В., Межжерин С., Соболенко Л. — Моделирование экологической ниши методом максимальной энтропии было использовано для оценки условий пребывания 13 видов амфибий и картирования их распространения на территории Западного Подолья (Украина). Среди предикторов были использованы показатели климата, рельефа и антропогенного воздействия (оценивается по интегрированному индексу «человеческий след»). Среди важнейших факторов, которые определяют пригодность и распределение мест обитания амфибий, были «средняя температура самого холодного квартала» и «изотермичность». Другой существенный вклад вносит индекс «человеческого следа». Это может означать, что инфраструктура, созданная человеком, формирует благоприятные условия для амфибий и, возможно, это явление более распространено, чем представлялось ранее. Отмечены территории, которые в первую очередь должны представлять интерес для охраны амфибий (вид *Bombina variegata* взят в качестве примера) и создана карта, которая обобщает видовое богатство исследованного региона.

Ключевые слова: Maxent, моделирование экологической ниши, модели распространения видов, амфибии, Украина.

Introduction

Amphibians are among the most threatened taxonomic groups worldwide. Numerous studies have documented declines in amphibian species abundance across the globe. Habitat fragmentation, degradation and loss, together with climate change are probably the most important drivers of population decline (Billeter et al., 2008). A report on the status of amphibians globally (Stuart et al., 2004) stated that about 32 % of amphibians are clearly threatened with extinction of which 22.5 % are poorly studied. The report also noted that over 100 amphibians are thought to have become extinct in very recent decades and that about 43 % of all described species are currently experiencing population declines. Therefore amphibians represent an exceptional group of species that are highly sensitive to both habitat and climate change, including other factors impacting the environment (Beebe, Griffiths, 2005).

To protect amphibian species, we need a better understanding of what constitutes suitable habitat and where such habitats exist. Habitat suitability mapping can identify areas in need of restoration or preservation (Gibson et al., 2004) and guide conservation plans (Gaston, Williams, 1996). However, data on species' distributions are often sparse, so one option to cope with this problem is to use habitat modeling approaches (Tytar, 2011). These models describe the environmental requirements of species and use it to produce distribution maps that are a pivotal stage in targeting conservation and recovery efforts (Elith et al., 2006; Peterson, 2006). Modeling can be used for revealing species ecological requirements and relationships between the distribution of species and predictive variables, as well as the importance of each variable in model building (Araújo, Guisan, 2006).

A variety of distribution modeling methods are now available for predicting the potential geographical range of a species. Unfortunately, the performances of most species distribution modeling methods are poor when sample size is small (for instance, < 10). Under these circumstances maximum entropy distribution (Maxent) modeling may be a good choice. Maxent, unlike other distributional modeling techniques, uses only presence and background data instead of presence and absence data. This method has been shown to perform well in comparison with alternative approaches (Elith et al., 2006).

In this study, we employed maximum entropy niche modeling as a tool to assess potential habitat suitability for amphibians and to map the potential distribution of this group for the area of the Western Podillya in Ukraine. More specifically, our objectives were to (1) identify the factors associated with (species) habitat distribution; (2) predict potential distributions of the species using known presence observations; and ultimately (as the primary goal) 3) produce a regional map of amphibian species richness for guidance of conservation measures.

Study region

The Western Podillya is part of the vast Eastern European Plain, bordered by the Dniester River and the Carpathians in the southwest. More specifically, the region of our interest is confined to a bounding box: Xmin = 24.73326, Xmax = 26.79984, Ymin = 48.43340, Ymax = 50.04167 (figures in decimal degrees) and covers an area of about 27 thousand sq. km. The average altitude is 320–350 m. The climate is Atlantic-continental with the annual mean temperature varying around 7.54 °C and receiving annual precipitation of the average of 650 mm. Western Podillya is occupied by the West Forest-Steppe Zone of Ukraine and belongs to the Continental Biogeographical Region as defined by the European Commission and the Council of Europe for evaluation and assessment of nature conservation (European Environmental Agency, 2002). According to the global land cover database GLC2000 (Bartholome, Belward, 2005), above 84 % of the area can be classified under the category “cultivated and managed areas”, leading to continuously increasing fragmentation of habitats. Only little remains of natural forests stands: “tree cover” (including “broadleaved, deciduous, closed”, “needle-leaved, evergreen” and “mixed leaf type”) occupy just 6.2 % of the study region. However, despite the seemingly large human pressure on the ecosystems, the region yet retains a certain amount of “wilderness”, as evidenced by the Human Footprint (HF). HF has been produced through an overlay of a number of global data layers that represent the location of various factors presumed to exert an influence on ecosystems: human population distribution, urban areas, roads, navigable rivers, and various agricultural land uses. The combined influence of these factors yields the Human Influence Index (HII) (Sanderson et al., 2002). The HII, in turn, is normalized by global biomes to create the HF dataset, having values ranging from 1 to 100. For the study region the average HF is 40.8, wherein 71 % of the area has values below 40 and 7.2 % — below 20, meaning there may be some good chances for successful nature conservation ventures in the region.

Methods

Occurrence Data Collection and Processing

We digitized presence survey data from Sobolenko (2010) to generate the occurrence data used in the modeling. Georeferencing (in OziExplorer v. 3.95.4 m) was accomplished for 413 point data obtained for 13 species: *Bombina bombina* (70), *B. variegata* (11), *Bufo bufo* (19), *B. viridis* (18), *Hyla arborea* (71), *Pelobates fuscus* (16), *Pelophylax esculentus* (15), *P. lessonae* (20), *P. ridibunda* (70), *Rana arvalis* (23), *R. temporaria* (29), *Lissotriton vulgaris* (29) and *Triturus cristatus* (22). Sources for taxonomy are from the IUCN Red List of Threatened Species, version 2013.2 (<http://www.iucnredlist.org>).

Environmental Data Collection and Processing

In most cases environmental predictors are selected based on the availability and experience that the variables show correlation with the species distribution (Guisan, Zimmerman, 2000). Biotic factors, which are challenging to model explicitly, may nonetheless be implicitly represented in the model because they strongly correlate with abiotic factors (Soberón, Nakamura, 2009; Tytar, 2011). In such circumstances it is reasonable to assume that biotic processes that lead to the species realized distribution may be captured by the relationship between the environmental predictor variables of abiotic character and the modeled species' occurrence patterns and it is reasonable to consider modeling the distribution only with selected environmental variables and meaningful climatic factors identified to be of most importance to amphibians (Girardello et al., 2009) and topographic features considered important for shaping amphibian communities (Ford et al., 2002). In this work,

we used climatic predictor data, sourced from the Worldclim dataset (Hijmans et al., 2005). The 19 Worldclim variables represent annual trends (e. g. mean annual temperature, annual precipitation) and extreme limiting environmental factors (e.g. temperature of the coldest and warmest months, precipitation of the wettest or driest quarter) and are known to influence species distributions. The topography predictor variables selected were: elevation, topographical wetness index (TWI) and aspect. These predictor variables were derived from a digital elevation model (DEM) distributed from the SRTM 90m Database (Jarvis et al., 2008). Using SAGA-GIS software (<http://www.saga-gis.org>), 2 layers were calculated from the DEM: aspect (a proxy for the amount of solar radiation on the ground surface) and the topographical wetness index (TWI), because of the important role played by moisture in habitat selection by amphibians (Wyman 1988). The TWI combines a measure of the upslope area and slope to predict the hydrology of a given location (Sorenson et al., 2005). Small values represent upper catenary positions (dry), and high values represent lower catenary (wet) positions. Finally, as a measure of anthropogenic impact, the Human Footprint (HF) data set, already mentioned above, has been included to the suite of variables for creating the models. All environmental data layers were spatial resolution rasters (~1 km) with the same extent and cell alignment, as required by most modeling software.

Due to the high levels of correlations between many environmental variables, we filtered the initial variable set of 23 predictors based on the results of multi-collinearity analysis. High correlations among variables may result in highly unstable performance of the Least Squares Estimator (LSE), which will lead to problems for running species distribution models. Multi-collinearity can be detected by calculating the Variance Inflation Factor (VIF): $VIF = 1/(1-R^2)$, where R^2 is the coefficient of determination. The rule of the thumb is that $VIF > 10$ means multi-collinearity may influence the LSE. Multi-collinearity was analyzed by using the Multiple Regression Tool in Statistica v.8.0. Removal of the variable with the highest values from the variable-list was followed by re-running collinearity diagnostics, till all the remaining values are below 10 (table 1).

Model building and evaluation

The Maxent software (version 3.3.3e) was utilized for modeling (<http://www.cs.princeton.edu/schapiro/maxent/>), using the default settings. Logistic output format was used to describe the probability of presence (Phillips and Dudík 2008), which is a continuous habitat suitability range between 0 (unsuitable) and 1 (the most suitable). Maxent was run ten times (using all predictor variables) for each species in order to get average prediction. A bootstrapping replication technique was applied to the dataset which uses all occurrence data to build the model. This method is optimal for dataset with few occurrences such as, for instance, *B. variegata*. The outputs in ASCII format were processed and visualized using DIVA GIS 7.5. The Jackknife analysis was used to indicate the most informative variables (in corresponding percentages $> 10\%$) and a look at the response curves from Maxent helps to establish the relative importance of each variable. The accuracy and performance of species distribution models were evaluated using threshold-independent receiver operation characteristic (ROC) analysis (Elith et al., 2006; Phillips et al., 2006). The area under the ROC curve (AUC) ranges between 0 and 1. Models with an AUC value higher than 0.7 are considered acceptable (Swets, 1988).

The logistic probabilities provide a relative indication of the likelihood of occurrence by the species, but they do not define predicted occurrence in the binary, presence/absence manner typically required by managers. Therefore, we applied three thresholds to the logistic output of each model to produce a four-category model, ranging from “Very Low” to “High” predicted probability of occurrence. The “Very Low” category contained logistical values ranging between 0 and the “Minimum Training Presence” (i. e., the logistic prediction for the training presence point with the lowest logistic prediction value). The “Low” category represented logistical values ranging from the “Minimum Training Presence” value to the “Maximum Training Sensitivity Plus Specificity” threshold (i. e., that threshold which maximizes the sum of sensitivity and specificity for the training

Table 1. Remaining predictors after multi-collinearity analysis

Таблица 1. Предикторы, остающиеся после проведения мультиколлинеарного анализа

Predictor	VIF
<i>Bio 2</i> : Mean Diurnal Range (Mean (period max-min)) (°C x 10)	8.3
<i>Bio 3</i> : Isothermality (<i>Bio 2/Bio 7</i>)	6.0
<i>Bio 8</i> : Mean Temperature of Wettest Quarter (°C x 10)	4.6
<i>Bio 11</i> : Mean Temperature of Coldest Quarter (°C x 10)	7.0
<i>Bio 14</i> : Precipitation of Driest Period (mm)	4.0
<i>Bio 15</i> : Precipitation Seasonality (Coefficient of Variation)	4.4
<i>Bio 19</i> : Precipitation of Coldest Quarter (mm)	4.9
<i>Aspect</i>	1.0
<i>Elevation</i>	5.4
<i>Human Footprint (HF)</i>	1.1
<i>Topographical wetness index (TWI)</i>	1.2
¹ <i>Bio 7</i> : Temperature Annual Range (°C x 10)	

data). The “Moderate” category contained values ranging from the “Maximum Training Sensitivity Plus Specificity” threshold to the “50th Percentile Training Presence” (i. e., the threshold representing the median logistic prediction value for all training presences). Finally, the “High” category contained values ranging from the “50th Percentile Training Presence” value to 1. Binary predictions were considered choosing the “minimum training presence” threshold (i. e., the logistic prediction for the training presence point with the lowest logistic prediction value) (Liu et al., 2005). Final versions of maps were considered to benefit by a simple smoothing filter as one of the means for coping with observation bias (Home et al., 2007) and generalizing raster outputs: 3 x 3 neighborhood filtering implemented in DIVA GIS was applied for this purpose.

Results and discussion

Factors associated with (species) habitat distribution

The Jackknife test of variable importance showed that Bio 11 (the mean temperature of coldest quarter) was one of the most important factors in habitat distribution prediction for amphibians in the region (table 2): 12 species out of 13, particularly *B. variegata* (fig. 1), have ecological requirements dependent on Bio 11, obviously having a negative impact on winter survival. The only exception is *P. esculentus*: the modeling suggests precipitation on the coldest quarter (Bio19) has greater significance for the species — lower levels (around 90–95 mm) favor predicted presence probability, whereas levels around 125–130 mm force the probability down to almost zero.

The other bioclimatic variable widely affecting habitat distribution prediction for amphibians in the region is Bio 3 (isothermality). For at least 6 species (*B. bombina*, *H. arborea*, *P. fuscus*, *P. lessonae*, *L. vulgaris* and *T. cristatus*; the percent contribution of Bio 3 > 20 %) optimality (according to the response curves) is reached at values around 26.5–27.5 and below these there is an exclusively sharp drop of predicted presence probability towards zero, clearly indicating the negative influence of “temperature unevenness” over the course of a year (fig. 2; *P. fuscus* taken for an example). On the other hand, excessive isothermality too negatively influences the predicted presence probability, but the effect is somewhat smoother (in the case of *P. fuscus* the predicted presence probability drops to about 0.2).

Table 2. The percent contribution of environmental variables (factors) in predicting the species geographic distribution models

Таблица 2. Процентный вклад различных параметров окружающей среды (факторов), использованных для построения прогностических моделей распространения видов

Species	Factors associated with (species) habitat distribution > 10 %										
	Bio 2	Bio 3	Bio 8	Bio 11	Bio 14	Bio 15	Bio 19	Aspect	Elevation	HF	TWI
<i>Bombina bombina</i>	–	23.9	–	11.1	–	–	16.9	–	10.1	13.5	–
<i>B. variegata</i>	26.2	11.4	–	30.0	–	–	–	–	–	–	–
<i>Bufo bufo</i>	–	–	–	16.6	–	–	–	11.2	19.6	15.7	–
<i>B. viridis</i>	–	–	–	18.3	–	–	–	14	–	27.2	–
<i>Hyla arborea</i>	–	21.5	–	10.1	–	–	15.7	–	10.2	14.2	–
<i>Pelobates fuscus</i>	12.4	25.0	–	14.3	–	–	–	–	–	20.4	–
<i>Pelophylax esculentus</i>	–	14.0	–	–	–	–	38.4	–	–	22.4	–
<i>P. lessonae</i>	–	23.4	–	16.6	–	–	13.2	–	–	15.5	17.0
<i>P. ridibunda</i>	–	18.7	–	16.0	–	–	14.4	–	–	12.8	10.2
<i>Rana arvalis</i>	–	15.0	–	14.1	–	–	–	–	18.3	12.4	–
<i>R. temporaria</i>	–	13.0	–	12.6	10.1	–	–	–	28.2	–	–
<i>Lissotriton vulgaris</i>	–	21.4	–	12.9	–	–	–	–	–	12.9	19.4
<i>Triturus cristatus</i>	–	24	–	14.2	–	–	15.6	–	–	26.3	–
Importance for <i>n</i> species:	2	11	0	12	1	0	6	2	5	11	3

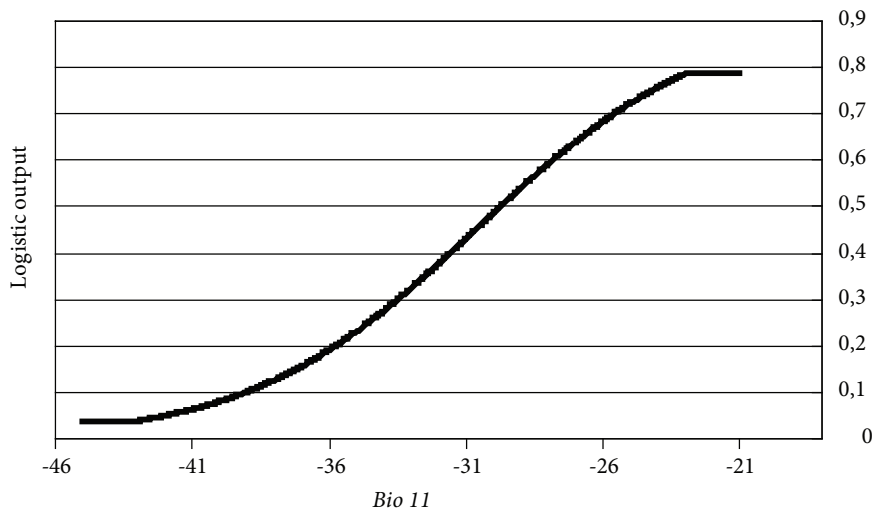


Fig. 1. Response of *Bombina variegata* to Bio 11: x-axis — mean temperature of coldest quarter ($^{\circ}\text{C} \times 10$); y-axis— logistic output (probability of presence).

Рис. 1. Реакция *Bombina variegata* на воздействие Bio 11: ось x — средняя температура наиболее холодного квартала ($^{\circ}\text{C} \times 10$); ось y — логистический формата значений модели (вероятность присутствия).

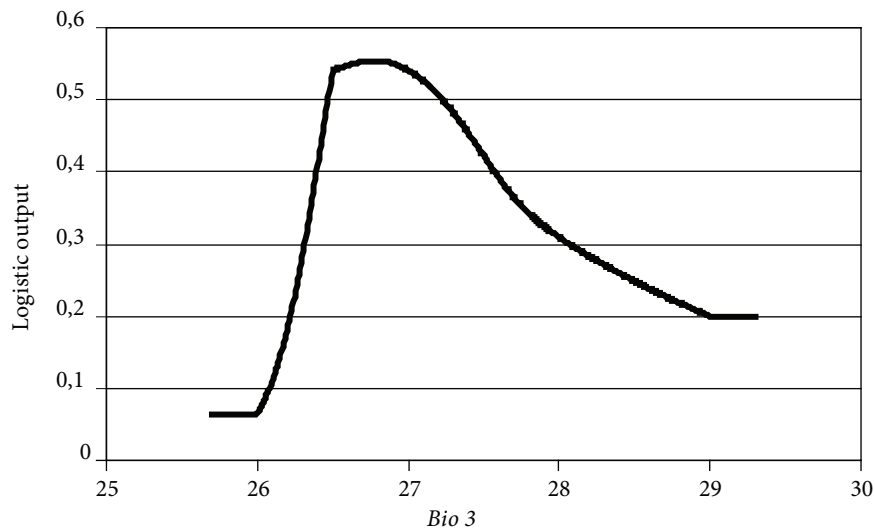


Fig. 2. Response of *Pelobates fuscus* to Bio 3: x-axis — isothermality; y-axis — logistic output (probability of presence).

Рис. 2. Реакция *Pelobates fuscus* на воздействие Bio 3: ось x — изотермичность; ось y — логистический формата значений модели (вероятность присутствия).

Of the non-bioclimatic variables a profound contribution in predicting the species geographic distribution models for 11 species has been displayed by the Human Footprint. The HF percent contribution reaches values ranging from 12.4 % (for *R. arvalis*) to 27.2 % (for *B. viridis*). Surprisingly (or not), the HF positively affects predicted presence probability (fig. 3; *T. cristatus* taken for an example). This is a highly interesting finding. Indeed, the relationships between human factors and biodiversity are important to assess the risk of extinction as human pressures are often related to large changes in biological diversity. However, the literature shows contradictory results. Previous studies report that human influence may affect species' spatial distribution both negatively and positively (Young et

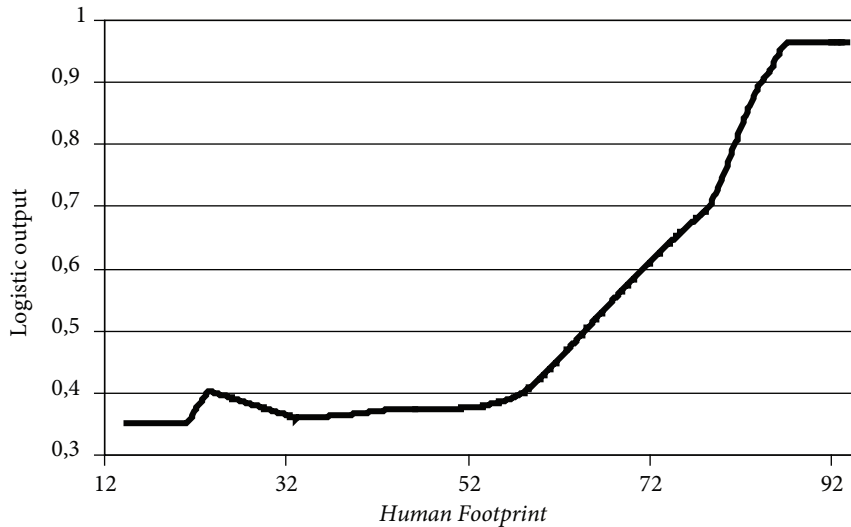


Fig. 3. Response of *Triturus cristatus* to the Human Footprint: x-axis — Human Footprint; y-axis — logistic output (probability of presence).

Рис. 3. Реакция *Triturus cristatus* на воздействие фактора «человеческого следа»: ось x — индекс «человеческого следа»; ось y — логистический формат значений модели (вероятность присутствия).

al., 2005). On one hand, human factors, such as human activities and, in particular, the alteration of habitats (Kiesecker et al., 2001) are major causes of biodiversity loss (Brooks et al., 2002). On the other hand, several studies have shown a positive relationship between human density and biodiversity, indicating that species-rich areas and human enterprises quite often co-occur (Luck, 2007). One reason may be that though human population is concentrated in regions critical for amphibians, there is still a substantial amount of intact habitat in many of these regions. Nevertheless, amphibians have been found breeding in a variety of habitats that are substantially different from their former pristine breeding habitats (Rubbo, Kiesecker, 2005), so native wildlife can often adapt to novel and altered habitats, given suitable conditions. In North America and in Australia, for instance, human infrastructure provided beneficial environments to some amphibian species (Tyler et al., 2007). Our assumption too is that human-constructed habitats such as ponds, fish farming facilities etc. have realized (or are on their way to realizing?) their potential to provide habitat for most of the amphibian species in the study area, a phenomenon that perhaps is much more widespread than thought. Beyond this general trend are only 2 species: *B. variegata* and *R. temporaria*, but this is just because the HF percent contribution to the predicted presence probability of these species is not so profound — 2.4 % and 7.8 %, respectively.

Potential distributions of the species

Based on the maximum entropy modeling algorithm and using 11 environmental variables ($VIF < 10$), we obtained 13 raster outputs modeling the distribution of the corresponding study species. Models providing an excellent prediction have an $AUC > 0.9$ (these are models for 7 species, see table 3) and fair models having an AUC between 0.7 and 0.9 (in fact, > 0.8) have been produced for the remaining species. Models with $AUC < 0.7$ are considered poor (Swets, 1988).

The resulting models contain four categories indicating the relative likelihood of occurrence for each species. These categories may be used to determine whether site-specific surveys are needed if a management action (e. g., establishing a protected area) is being planned. Areas categorized as “Very Low” are the most unlikely to host populations

Table 3. Summary statistics for Maxent habitat suitability models

Таблица 3. Итоговые статистики моделей пригодности местообитаний, построенных в программе Maxent

Species	Suitable Habitat (% of study area)				AUC ± SD ¹
	Very Low	Low	Moderate	High	
<i>Bombina bombina</i>	72.5	9.7	11.4	6.4	0.873 ± 0.015
<i>B. variegata</i>	26.9	53.8	11.2	8.1	0.902 ± 0.019
<i>Bufo bufo</i>	61.8	22.8	5.5	9.9	0.898 ± 0.036
<i>B. viridis</i>	44.3	43.0	1.7	11.0	0.896 ± 0.021
<i>Hyla arborea</i>	17.9	61.8	11.4	9.0	0.866 ± 0.022
<i>Pelobates fuscus</i>	68.5	17.7	7.3	6.5	0.941 ± 0.016
<i>Pelophylax esculentus</i>	55.6	26.6	6.9	10.9	0.941 ± 0.015
<i>P. lessonae</i>	67.2	23.5	5.4	3.9	0.941 ± 0.017
<i>P. ridibunda</i>	31.3	51.7	9.5	7.6	0.870 ± 0.020
<i>Rana arvalis</i>	36.1	54.6	2.3	6.9	0.884 ± 0.030
<i>R. temporaria</i>	45.4	45.5	3.5	5.6	0.913 ± 0.023
<i>Lissotriton vulgaris</i>	45.7	42.6	7.3	4.3	0.917 ± 0.017
<i>Triturus cristatus</i>	71.4	13.5	10.9	4.1	0.937 ± 0.020

SD¹ — standard deviationFig. 4. Two upper categories ("Moderate" and "High") collapsed to identify areas of predicted presence (dark gray shading) for *B. variegata* in the study area.Рис. 4. Две верхние категории («Умеренный» и «Высокий») объединены в целях выявления областей прогнозируемого присутствия (тёмно-серый оттенок) для *B. variegata* в исследуемом районе.

of the species, and may suggest that site surveys for the species are not warranted within an area prior to management activities. Conversely, areas mapped as “Moderate” or “High” are likely very suitable for the species and suggest that surveys should be conducted prior to management actions to determine whether the species is present and the degree to which it may be impacted. The case of *B. variegata* can exemplify this approach. This toad has been considered as far as the northern margin of the home range of the species runs through the study area, meaning populations here are highly fragmented and more vulnerable to impact than elsewhere (Sobolenko, 2010). Results for *B. variegata* predict that only 8.1 % of the area is of “High” and 11.2 % of “Moderate” suitability for the species (table 3). Together these areas (likely to be very suitable for the species) are shaded in dark gray on the map (fig. 4.), and they in the first place should be of interest to nature conservationists targeting the species. For instance, in Ternopil Oblast the most promising areas for protection of the species are located alongside the Dniester River, particularly within the districts (rayons) of Zalischyky and Borshchiv.

By overlaying the binary maps derived for separate species that indicate either presence or absence, a summarizing species richness map was produced (fig. 5): light gray areas are predicted to accommodate 1 to 5 species, darker ones — from 6 to 10 species, and the darkest — 11 to 13 amphibian species. As seen, some of the richest areas in term of amphibian species composition are rayons of Chortkiv, Zalischyky, Borshchiv and Kamyanets-Podilskiy.

Together, in such a way predictive distribution models can be used to protect rare species and species’ assemblages, but as far as amphibians represent an exceptional group of species that are highly sensitive to environmental change it may be that protecting

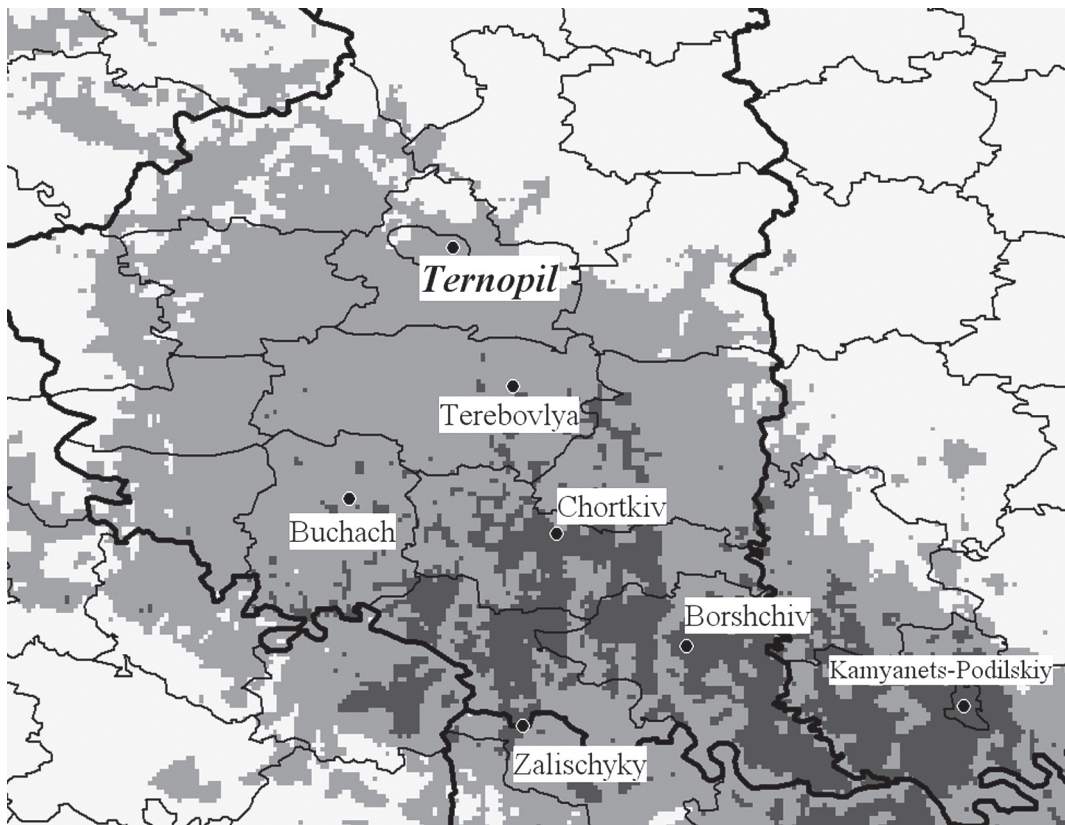


Fig. 5. Summarized species richness map (see text for explanation).

Рис. 5. Карта, обобщающая видовое богатство исследованного региона (см. текст для объяснения).

amphibians the human society can succeed in protecting itself from habitat degradation and the collapse of supporting ecosystems.

References

- Araújo, M. B., Guisan, A. Five (or so) challenges for species distribution modeling // *Journal of Biogeography*. — 2006. — **33**, N 10. — P. 1677–1688.
- Bartholome, E., Belward, A. S. GLC2000: A new approach to global land cover mapping from Earth observation data // *International Journal of Remote Sensing*. — 2005. — **26**, N 9. — P. 1959–1977.
- Beebee, T. J. C., Griffiths, R. A. The amphibian decline crisis: A watershed for conservation biology? // *Biological Conservation*. — 2005. — **125**, N 3. — P. 271–285.
- Billeter, R. J., Lira, D., Bailey, R. *et al.* Indicators for biodiversity in agricultural landscapes: a pan European study // *Journal of Applied Ecology*. — 2008. — **45**, N 1. — P. 141–150.
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G. *et al.* Habitat loss and extinction in the hotspots of biodiversity // *Conservation Biology*. — 2002. — **16**, N 4. — P. 909–923.
- Elith, J., Graham, C. H., Anderson, R. P. *et al.* Novel methods improve prediction of species' distributions from occurrence data // *Ecography*. — 2006. — **29**, N 2. — P. 129–151.
- European Environmental Agency (EEA). The Continental biogeographical region — agriculture, fragmentation and big rivers // EEA Report No 1/2002. Europe's biodiversity — biogeographical regions and seas. — 2002. — 52 p.
- Ford, W. M., Menzel, M. A., Odom, R. H. Elevation, aspect, and cove size effects on southern Appalachian salamanders // *Southeastern Naturalist*. — 2002. — **1**, N 4. — P. 315–324.
- Gaston, K. J., Williams, P. H. Spatial patterns in taxonomic diversity // *Biodiversity: A Biology of Numbers and Difference* / Ed. K. J. Gaston. — Oxford: Blackwell Science Ltd., 1996. — P. 202–229.
- Gibson, L., Wilson, B., Cahill, D. *et al.* Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS based approach // *Journal of Applied Ecology*. — 2004. — **41**, N 2. — P. 213–223.
- Girardello, M., Griggio, M., Whittingham, M. J. *et al.* Models of climate associations and distributions of amphibians in Italy // *Ecological Research*. — 2009. — **25**, N 1. — P. 103–111.
- Guisan, A., Zimmermann, N. E. Predictive habitats distribution models, in ecology // *Ecological Modelling*. — 2000. — **135**, N2. — P. 147–186.
- Hijmans, R. J., Cameron, S. E., Parra, J. L. *et al.* Very high resolution interpolated climate surfaces for global land areas // *International Journal of Climatology*. — 2005. — **25**, N 15. — P. 1965–1978.
- Home, J., Garton, E., Sager-Fradkin, K. Correcting home-range models for observation bias // *Journal of Wildlife Management*. — 2007. — **77**, N 3. — P. 996–1001.
- Jarvis, A., Reuter, H. I., Nelson, A. *et al.* Hole-filled SRTM for the globe. Version 4, 2008. — (Available from the CGIAR-CSI SRTM 90m Database: <http://srtm.csi.cgiar.org>).
- Kiesecker, J. M., Blaustein, A. R., Belden, L. K. Complex causes of amphibian population declines // *Nature*. — 2001. — **410**, N 6829. — P. 681–684.
- Liu, C. R., Berry, P. M., Dawson, T. P. *et al.* Selecting thresholds of occurrence in the prediction of species distributions // *Ecography*. — 2005. — **23**, N 3. — P. 385–393.
- Luck, G. W. A review of the relationships between human population density and biodiversity // *Biological Reviews*. — 2007. — **82**, N 4. — P. 607–645.
- Peterson, A. T. Uses and requirements of ecological niche models and related distributional models // *Biodiversity Informatics*. — 2006. — **3**. — P. 59–72.
- Phillips, S. J., Anderson, R. P., Schapire, R. E. Maximum entropy modeling of species geographic distributions // *Journal of Ecological Modelling*. — 2006. — **190**, N 3–4. — P. 231–256.
- Phillips, S. J., Dudik, M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation // *Journal of Ecography*. — 2008. — **31**, N 2. — P. 161–175.
- Rubbo, M. J., Kiesecker, J. M. Amphibian breeding distribution in an urbanized landscape // *Conservation Biology*. — 2005. — **19**, N 2. — P. 504–511.
- Sanderson, E. W., Jaiteh, M., Levy, M. A. *et al.* The Human Footprint and the Last of the Wild // *BioScience*. — 2002. — **52**, N 10. — P. 891–904.
- Soberón, J., Nakamura, M. Niches and distributional areas: concepts, methods and assumptions // *Proceedings of the National Academy of Sciences USA*. — 2009. — **106**, Supplement 2. — P. 19644–19650.
- Sobolenko, L. Yu. Amphibians and reptiles of Western Podillya: fauna, ecology and distribution of species : Abstract of Ph. D. thesis. — Kiev, 2010. — 24 p. — Ukrainian : Соболенько Л. Ю. Амфібії та рептилії Західного Поділля: фауна, екологія і поширення видів.
- Stuart, S. N., Chanson, J. S., Cox, N. A. *et al.* Status and trends of amphibian declines and extinctions worldwide // *Science*. — 2004. — **306**, N 5702. — P. 1783.
- Swets, J. A. Measuring the accuracy of diagnostic systems // *Science*. — 1988. — **240**, N 4857. — P. 1285–1293.
- Tyler, M. J., Wassersug, R., Smith B. How frogs and humans interact: Influences beyond habitat destruction, epidemics and global warming // *Applied Herpetology*. — 2007. — **4**, N 1. — P. 1–18.

- Tytar, V. M. Analysis of home ranges in species: an approach based on modeling the ecological niche // *Vestnik zoologii*. — 2011. — Supplement N 25. — 96 p. — Ukrainian : *Титар В. М. Аналіз ареалів у видів: підхід, заснований на моделюванні екологічної ніші*.
- Wyman, R. L. Soil acidity and moisture and the distribution of amphibians in five forests of southcentral New York // *Copeia*. — 1988. — N 2. — P. 394–399.
- Young, J., Watt, A., Nowicki, P. *et al.* Towards sustainable land use: identifying and managing the conflicts between human activities and biodiversity conservation in Europe // *Biodiversity and Conservation*. — 2005. — 14, N 7. — P. 1641–1661.

Received 27 October 2014

Accepted 24 March 2015