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The Value of Forest Ecosystems in the Conservation of Amphibians Revealed by Predictive Mapping

Michał BEŁCIK and Krzysztof KLIMASZEWSKI

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Global amphibian populations have been experiencing a marked decline in recent years. While many studies in Europe focus on seeking correlations between waterbody features and amphibian species occurrence or on their abundance in agricultural landscapes, much less attention has been paid to other potentially suitable habitats such as forests. We used data stored in a Forest Numerical Map (FNM) for mapping and to find potential habitats of the most common amphibian species in the Sobibór forest district in Eastern Poland. Field records of amphibians occurring in study sites were combined with data on forest characteristics stored in the FNM. Based on these records, we used Generalized Linear Models and a Resource Selection Function to build ecological niche models for different anuran species as well as for total anuran abundance. Our results showed the differences between the habitat preferences of selected amphibian species. The model parameters for the common spadefoot toad (*Pelobates fuscus*) show a strong positive correlation with coniferous forest habitats, no trends were found for the water frog (*Pelophylax esculentus complex*), and model parameters predicting fire-bellied toad, (*Bombina bombina*) abundance revealed that the species had a strong affinity for sites that had previously been used for agriculture and possessed a higher soil humidity. The use of predictive mapping identified certain areas favorable for our studied species; the methodology has the potential to enhance the conservation of amphibians occurring in forests via appropriate management. An example would be the construction of ponds or the less frequent cleaning of drainage ditches in the proximity of stands preferred by amphibians.

Key words: Forest Numerical Map, GIS, amphibian habitats, conservation.

Michał BEŁCIK✉, Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland.
E-mail: belcik@iop.krakow.pl
Krzysztof KLIMASZEWSKI, Division of Zoology, Department of Animal Environment Biology, Faculty of Animal Sciences, Warsaw University of Life Sciences – SGGW, Ciszewskiego 8, 02-786 Warszawa, Poland.

In recent years, there has been growing attention directed towards the decline of amphibian populations both in Europe (ALLAIN & DUFFUS 2019; PABIJAN & OGIELSKA 2019) and across the world (COLLINS & CRUMP 2009; HEATWOLE & WILKINSON 2009; SILVA *et al.* 2009). Amphibians are considered to be one of the most threatened vertebrate groups (SILVA *et al.* 2009). Along with other causes for decline such as climate change (KIESECKER *et al.* 2001), infectious diseases (DASZAK *et al.* 2000), toxic chemicals, and UV radiation (BLAUSTEIN & WAKE 1995), the most significant one, habitat destruction, is caused by human activities. Due to the dual nature of the amphibian life cycle's requirements, changes in both aquatic (BRODMAN *et al.* 2006) and terrestrial (MARSH & TRENHAM 2001) habitats are crucial.

Many European studies have focused on the conservation of amphibians in agricultural landscapes (SUÁREZ *et al.* 2016; MITCHELL 2016) where these animals provide numerous ecosystem services such as pest control and nutrient cycling. Human alterations of the characteristics of waterbodies and the agricultural landscape composition around them were of major interest (Plăiaşu *et al.* 2012; Chester & Robson 2013). However, in our current Anthropocene setting, efficient conservation of amphibians requires understanding the importance of surrogate or supplementary habitats for these organisms because only part of their typical habitats will be spared.

One of the least understood phenomena is the occurrence and reproduction of European amphibians in forest ecosystems. Of course, there are some species typical for forested landscapes such as the European tree frog, *Hyla orientalis,* or the green toad, *Bufotes viridis,* and forest ecosystems are major habitat for amphibians in the tropics, but it is generally accepted that European amphibians prefer waterbodies within open landscapes. However, forests seem to be a potentially suitable habitat for amphibians for several reasons. Forest stands may buffer some environmental variability that is harmful for amphibians and forest ecosystems are much less impacted by human activity (low level of pollution and pesticide use, lower density of roads and traffic). In addition, forests may also provide favorable conditions for seasonal migrations (low exposure to sun, higher humidity, lower road traffic). Thus, it is possible that the role of forests in the conservation of European amphibians is underestimated. To predict the value of forest ecosystems for amphibians and to plan conservation measures, tools that take spatial context of the studied habitats are required. Geographical Information Systems (GIS) allowed for the development of various models of species occurrence (Wadsworth & Treweek 1999; Fortin *et al.* 2002; Hartel *et al.* 2010; Joly *et al.* 2001; Ray *et al.* 2002; Sillero 2011), but regardless of the method used, a landscape data source has to be available prior to such analyses (Sillero & Tarroso 2010).

The aim of our study was to develop ecological niche models for the most common anuran species found in Poland, and to use those models to predict the value of forest ecosystems for the conservation of those species.

Materials and Methods

Study area

Our research was conducted in a forest district located in the South-eastern region of Poland. It is situated next to the Bug river, which is the eastern border of Poland. The coordinates of our bounding box nodes were (in the WGS 84 coordinate system): 1st node (lat: 51.486897 long: 23.535264), 2nd node (lat: 51.483791 long: 23.659319), 3rd node (lat: 51.387959 long: 23.670241), 4th node (lat: 51.385728 long: 23.529963). Total territorial range was 50, 610 ha, with over 46% forest cover. This is a considerable amount, especially when compared to the mean forest cover of Poland (29.2%). The dominant tree species was scots pine (*Pinus sylvestris*), together with an abundance of black alder (*Alnus glutinosa*), English oak (*Quercus robur*), silver birch (*Betula pendula*), and Norway spruce (*Picea abies*).

The main reason for choosing this area for research was the great abundance of water features such as swamp forests, lakes, ponds, and bogs, making it a suitable habitat for amphibians. This made the local flora and fauna unique even on a nation-wide scale, with the probably the largest population of the European pond turtle (*Emys orbicularis*) in Poland (Mitrus 2009). Seventeen sites were chosen for this study. These represented a clearly defined location, at the bank of a pond or other type of water body, from which the observations were taken and amphibian presence and abundance index were noted. These sites were chosen to encompass a maximum diversity of analyzed characteristics, e.g. features of the forest surrounding the ponds, size, accessibility, and presence of amphibians.

Amphibian surveys

Amphibian occurrence and abundance index were noted during field studies carried out in the spring of 2012. For field recordings, a GPS Garmin 62s was used. Each site was visited twice – in early spring (March, April) and later in the season (May-June). It allowed us to record both early breeding species (the common toad (*Bufo bufo)*, moor frog (*Rana arvalis*), common frog (*Rana temporaria*), and common newt (*Triturus vulgaris*)) and late breeding ones (water frogs (*Pelophylax esculentus complex*), the European tree frog (*Hyla orientalis*), fire-bellied toad (*Bombina bombina*), natterjack toad (*Epidalea calamita*), green toad (*Bufotes viridis*), common spadefoot (*Pelobates fuscus*), and great crested newt (*Triturus cristatus*)). During each survey, two methods of amphibian recording were used: vocal and visual. First, a 20 min stop was performed by the observer to record anuran calls coming from a given site, during which every call coming from that site was recorded. After that, a slow walk was performed along the shore of every site in order to record occurrences of amphibians spotted visually, with the observer making a complete circle around the given site. While making a sound identification, males of the same species were grouped into four abundance classes (single – less than 5 individuals, few – 5-10, abundant – 10-50, very abundant – more than 50 individuals). Some of the species (the common newt, green toad, natterjack toad, and great crested newt) were observed only occasionally, and therefore were excluded from the species-specific analyses. Before implementing this vocal assessment of abundance, we tested it on ponds where male abundance could also be visually assessed. In our tests, we visited ponds where moor frog males were present. Males of this species can be distinguished by their bright blue color during mating season, which allowed for visual identification and an abundance assessment, hence creating an opportunity for us to test the accuracy of our method. Given the inaccessibility of most of the ponds (located in difficult, swampy terrain) for other forms of assessment, we had to rely on this method alone. However, other monitoring programs relying solely on auditory assessment have previously been successfully implemented, such as the USGS North American Amphibian Monitoring Program (www.pwrc.usgs.gov/naamp/).

Database of environmental variables

We used data from a Forest Numerical Map (FNM) designed for the Polish State Forests (https://www.bdl.lasy.gov.pl/portal/). The idea was to focus mostly on the various tree stand parameters contained in this database (such as stand age, height, density, etc.). These parameters are stored in a dataframe format and are easily available for every state-owned forest stand, therefore they can be widely used in large-scale habitat modelling and to determine variables linked with amphibian abundance in forest ecosystems.

As the main aim of the study was to create an ecological niche model for amphibians, only tree stand parameters relevant to amphibian biology were extracted from this database and used as explanatory variables. Those were: previous agricultural use (on a 0-1 scale, where 0 indicates that forest was always present on the site while 1 indicates that the land was previously used for agriculture), soil humidity (on a 0-4 scale where 0 indicates low humidity and 4 indicates high), age of the stand (in years), height of the stand (in meters), percentage of coniferous species, percentage of broad-leaved species, and the density of the stand (on a 0-10 scale with 0 indicating a clear cut and 10 indicating a very high density of trees). The median and range of those values for each pond are shown in Table 1. Characteristics were obtained from the forest compartments that every given water object lay within, or bordered with.

Table 1

Values for each stand parameter for every sample pond. Variables are: Previous agricultural use (0 – not used for agriculture, 1 – used), soil humidity (ranging from 0 to 2), age of the trees in the main forest story (in years), height of the trees in the main forest story (in meters), percentage of coniferous species in the main forest story (ranging from 0 to 10), percentage of broad-leaved species in the main forest story (ranging from 0 to 10), density of trees in the main forest story (ranging from 0 to 1)

Pond	Agricultural usage	Soil humidity	Stand age (in years)	Stand height (in meters)	Percent of coniferous species	Percent of broad-leaved species	Stand density
1	0	0	0	0	0	0	0
2	0	1	0	0	0	0	0
3	0	1	93	25	9	1	0.5
4	1	1	56	22	7	3	1
5	1	0	0	0	0	0	0.8
6	0	1	83	19	0	10	0.8
7	1	1	63	21	0	10	0.3
8	0	1	78	24	0	10	0.6
9	1	2	31	12	0	0	0
10	0	2	82	24	6	4	0.7
11	0	1	81	21	10	0	1
12	1	2	37	18	0	10	0.5
13	0	1	20	10	0	10	0.9
14	0	1	16	4	0	10	0.4
15	1	1	56	20	0	10	1
17	0	1	86	25	2	8	0.7
Mean	0.38	1.06	48.88	15.31	2.13	5.38	0.58
Median	0	1	48	15	2	6	0.6
Range	0-1	0-2	0-93	0-25	0-10	0-10	0-1
SE	0.48	0.56	30.63	8.34	3.52	4.43	0.33

Data processing and statistical analysis

The obtained data were elaborated with the use of ESRI ArcGIS ver. 10. For statistical analysis, the statistical software, R, was used (R CORE TEAM 2015). First, correlation analysis was used to identify highly correlated environmental variables (Table 2). Secondly, amphibian abundance index (summed across surveys) for a given site was correlated with each of the forest stand parameters in order to identify possible important variables linked with abundance. The variables that had a correlation value equal or higher than 0.3 with the abundance index were then used in the complex modeling and building of predictive maps. To find associations between amphibian abundance and various tree stand parameters, data obtained from the Forest Numerical Map was analyzed using the Generalized Linear Model (GLM) for the Poisson distribution and log-link function (BOURNE *et al.* 2007; BOLKER *et al.* 2009). For each GLM, we only used explanatory variables that were correlated with the response variable, but without collinearity among the explanatory variables. The GLMs were validated via the one-leave-out method (TORGO 2010). Moreover, model performance was checked using the 'model_performance' and 'model_check' functions from the "performance" R package (LÜDECKE *et al.* 2021). The models showed no signs of collinearity between explanatory variables in all of our models (with Variance Inflation Factors being lower than 5).

We decided to use GLMs since they have been proven to be a robust statistical tool when dealing with sites with sparse data (EDWARDS & CRONE 2021). Another reason behind our choice was that GLMs are flexible and well suited for analyzing ecological relationships (GUISAN *et al.* 2002). They are also one of the most widely used types of regression models used for analyzing ecological data with the straightforward interpretation of estimated parameters.

The Resource Selection Function (RSF) was used to estimate the abundance of a given amphibian species and to show it on our predictive maps (MCLOUGHLIN *et al.* 2010). The GLMs and RSFs were calculated for the total abundance of amphibians in the area and for each of the chosen anuran species.

The RSF is a transformed version of the GLM used:

$$Y = \exp\,(b_1X_1 + b_2X_2 + b_3X_3 + \ldots + b_nX_n)$$

where Y is the expected amount of individuals, and X is the different resources, (in this case these were forest stand parameters, obtained from the FNM database). The b's are the parameters describing the relation between X and Y, and were obtained from the GLM. The RSF was then applied to a raster calculator, which created ecological niche maps. Ecological niche models are popular among ecologists because they allow for an easy visualized version of the results of statistical modelling (HIRZEL *et al.* 2002; GARZON *et al.* 2006). The basic structural element of this map, is the forest compartment. There were 6,981 compartments all together in this district, with a mean area of 3.18 hectares. This was caused by the accuracy of the data from the Forest Numerical Map–it was the smallest spatial element for this data. All of the maps were created on a 1:120 000 scale.

We also analyzed the effect of environmental variables on amphibian species richness, but we did not include the results as no variable was significantly correlated with species richness which precluded the building a predictive map.

We performed a canonical correspondence analysis to test how different variables related to the forest environment affected species composition at different sites using Canoco 5 (LEPŠ & ŠMILAUER 2003). We estimated the impact of each explanatory variable to ordination by calculating pseudo F statistics with p-values given after the Bonferroni correction.

Table 2

Pearson's correlation matrix for environmental variables. Statistically significant correlations are these above the diagonal with r <0.500

	Previous agricultural use	Soil humidity	Stand age	Stand height	Percentage of coniferous species	Percentage of broad-leaved species	Stand density
Previous agricultural use	1	0.207	-0.176	0.007	-0.179	-0.024	0.069
Soil humidity		1	0.3523	0.409	0.172	0.088	-0.111
Stand age			1	0.937	0.568	0.222	0.421
Stand height				1	0.493	0.345	0.476
Percentage of coniferous species					1	-0.460	0.322
Percentage of broad-leaved species						1	0.341
Stand density							1

Results

Eleven amphibian species (including the *Pelophylax esculentus* complex group) were observed. Those were: the great crested newt (*Triturus cristatus*), common newt (*Triturus vulgaris*), common spadefoot (*Pelobates fuscus*), common toad (*Bufo bufo*), natterjack toad (*Epidalea calamita*), green toad (*Bufotes viridis*), fire-bellied toad (*Bombina bombina*), European tree frog (*Hyla orientalis*), common frog (*Rana temporaria*), moor frog (*Rana arvalis*), and water frogs (*Pelophylax esculentus* complex). Those species varied significantly in numbers, from single observations (natterjack toad and green toad) to the continuous observation of large groups (moor frog, European tree frog, and water frogs). Number of species and abundance varied between sites (mean number of species ± SE = 4±2, mean abundance ± SE = 455±319).

Total abundance

In order to build a model explaining species abundance, we used a GLM with three environmental variables – percentage of broad-leaved species, stand density, and previous agricultural use (Table 3, Fig. 1). Stand density had the biggest positive impact on amphibian abundance but previous agricultural use had the highest negative influence (Table 3). One-leave-out model validation indicated mean error to be 248.6312.

Abundance of individual species

Correlations between the occurrence of certain amphibian species and different environmental variables are shown in Table 3. Individual species response varied and the results of the GLMs are shown in Table 4. These models confirmed that previous agricultural land use, percentage of broad-leaved species, and stand density had a significant effect on species abundance estimates (Table 4). Specifically, the abundance of water frogs was positively associated with stand age and density but negatively associated with previous agricultural use of forest area (Table 4, Fig. 2). Model validation indicated a mean error of 187.4664. Abundance of the common spadefoot showed a positive association with previous agricultural use and

Table 3

Pearson's product-moment correlation between environmental variables and amphibian abundance

	Amphibian abundance		Common spadefoot		Fire-bellied toad	
	Correlation estimate	p-value	Correlation estimate	p-value	Correlation estimate	p-value
Stand density	0.376	0.137	-0.247	0.340	0.147	0.574
Stand age	0.262	0.310	-0.072	0.785	-0.241	0.353
Previous agricultural use	-0.311	0.225	0.168	0.522	-0.356	0.161
Percentage of coniferous trees	-0.050	0.849	-0.121	0.645	-0.307	0.230
Percentage of broad-leaved trees	0.414	0.098	-0.187	0.473	0.442	0.076
Stand height	0.238	0.359	-0.086	0.741	-0.142	0.586
Soil humidity	-0.259	0.316	-0.074	0.779	-0.263	0.308
Forest site type	-0.137	0.601	0.009	0.974	-0.237	0.360
	Common tree frog		Moor frog		Water frogs	
	Correlation estimate	p-value	Correlation estimate	p-value	Correlation estimate	p-value
Stand density	-0.127	0.628	0.378	0.135	0.475	0.054
Stand age	0.014	0.959	0.176	0.499	0.392	0.119
Previous agricultural use	-0.361	0.155	0.280	0.276	-0.339	0.183
Percentage of coniferous trees	-0.295	0.250	-0.131	0.616	0.351	0.168
Percentage of broad-leaved trees	0.308	0.230	0.368	0.146	0.097	0.712
Stand height	-0.052	0.843	0.311	0.225	0.290	0.259
Soil humidity	-0.365	0.149	-0.008	0.975	-0.056	0.830
Forest site type	-0.081	0.758	-0.024	0.927	-0.084	0.749

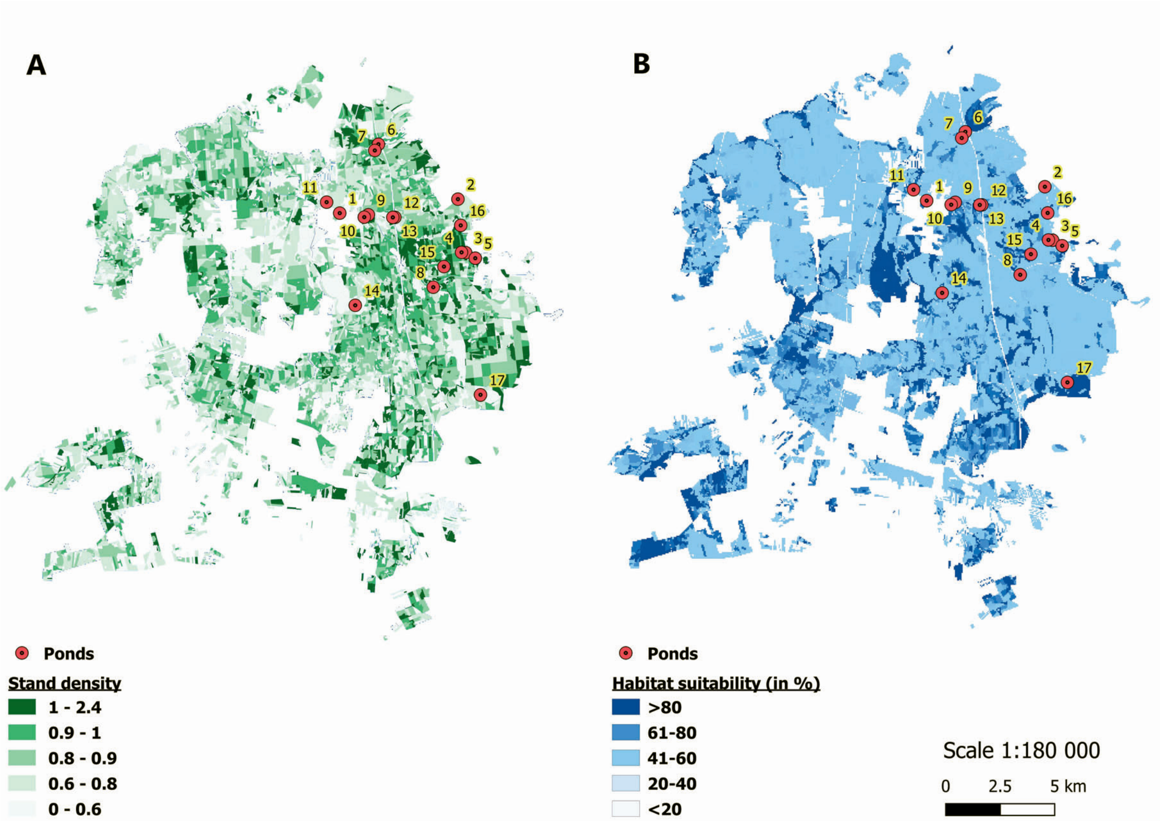

Fig. 1. Prediction map of the habitat suitability (part B) of the Sobibór forest district for all of the studied amphibian species compared to the most significant explanatory variable for this group – forest stand density (part A).

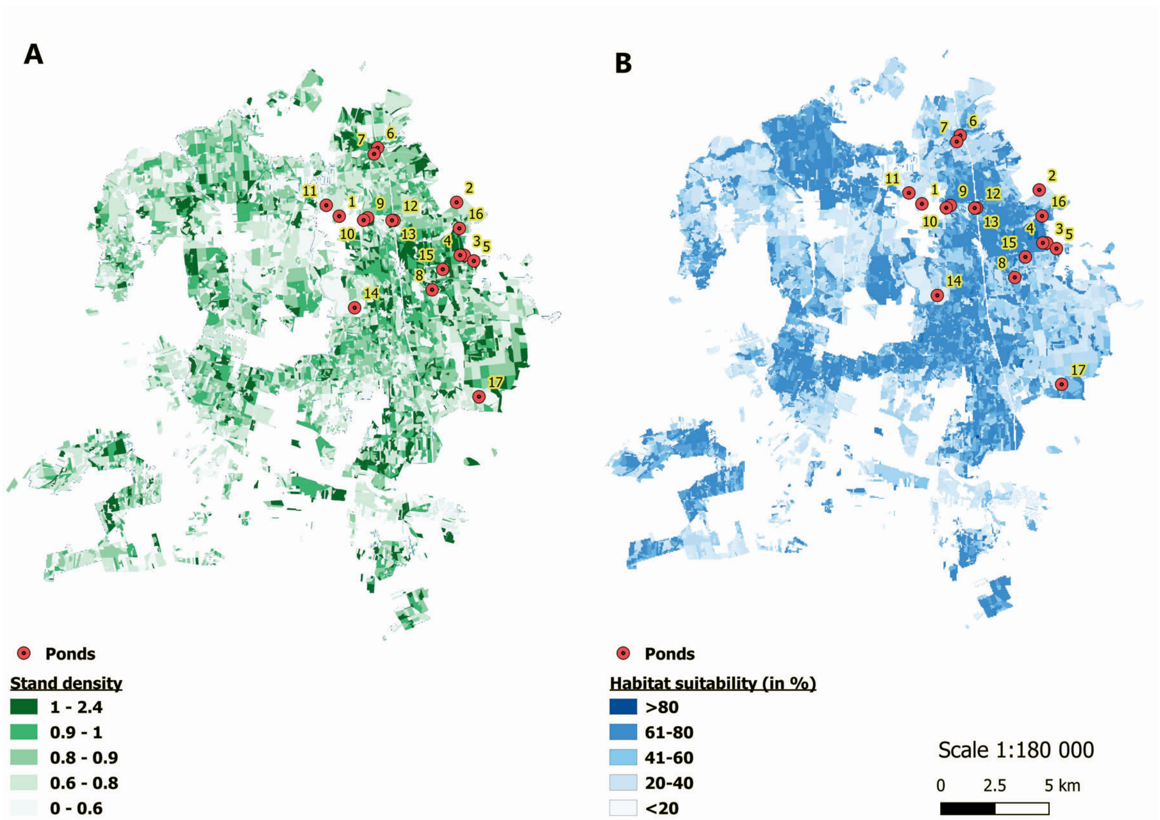

Fig. 2. Prediction map of the habitat suitability (part B) of the Sobibór forest district for water frogs compared to the most significant explanatory variable for this group – forest stand density (part A).

Table 4

Results for the GLM of amphibian abundance and the chosen amphibian species

	Estimate	SE	z value	p
Amphibian abundance				
(Intercept)	5.502	0.031	175.010	<0.001
Percentage of broad-leaved species	0.049	0.003	17.430	<0.001
Stand density	0.714	0.039	18.150	<0.001
Previous agricultural use	-0.520	0.027	-19.610	<0.001
Common spadefoot				
(Intercept)	2.692	0.145	18.612	<0.001
Previous agricultural use	0.456	0.152	3.003	0.003
Percentage of broad-leaved species	-0.030	0.018	-1.668	0.095
Stand density	-0.719	0.217	-3.318	0.001
Fire-bellied toad				
(Intercept)	2.762	0.155	17.870	<0.001
Previous agricultural use	-1.894	0.176	-10.740	<0.001
Percentage of broad-leaved species	0.243	0.016	15.360	<0.001
Stand age	-0.020	0.002	-11.850	<0.001
European tree frog				
(Intercept)	5.254	0.043	120.842	<0.001
Previous agricultural use	-1.354	0.070	-19.245	<0.001
Stand density	-0.424	0.067	-6.339	<0.001
Moor frog				
(Intercept)	-0.524	0.725	-0.722	0.470
Percentage of broad-leaved species	0.033	0.078	0.419	0.676
Stand height	0.009	0.042	0.216	0.829
Stand density	-0.591	1.089	-0.543	0.587
Water frogs				
(Intercept)	4.250	0.057	74.918	<0.001
Previous agricultural use	-0.830	0.046	-17.928	<0.001
Stand age	0.004	0.001	5.689	<0.001
Stand density	1.551	0.068	22.662	<0.001

negative associations with the percentage of broad-leaved species and stand density with a mean error estimation of 27.62313 (Table 4, Fig. 3). Abundance of the fire-bellied toad showed a negative association with previous agricultural use and stand age but a positive association with the percentage of broad-leaved species (Table 4, Fig. 4). Mean error of estimation was 42.73797. Abundance of the European tree frog was negatively linked with previous agricultural land use and stand density (Table 4, Fig. 5). Mean error of estimation was 228.7293. The model for abundance of the moor frog showed that no variables had a statistically significant effect (Table 4).

Species composition

CCA confirmed our species-level GLM modeling and showed that explanatory environmental variables explained 14% of species composition. The first ordination axis explained 5% of species composition ($F=4.4$, $p = 0.041$). The remaining three axes explained 3.66%, 2.39%, and 1.77% of variation ($F=2.0$, $p=0.001$), respectively. Among the explanatory variables, previous agricultural use appeared to be the most important one. Stand density, percentage of broad-leaved species, and soil humidity are also worth considering as meaningful variables differentiating amphibian assemblages (Table 5, Fig. 6).

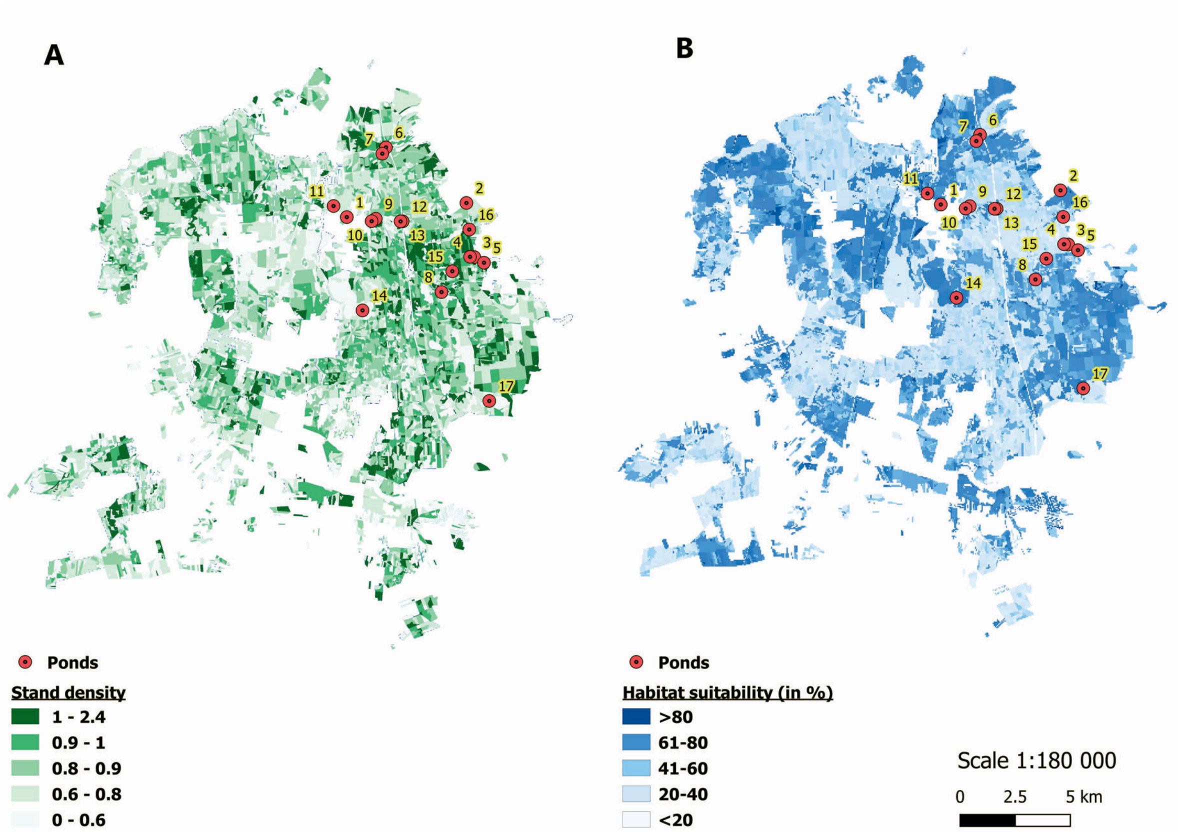

Fig. 3. Prediction map of the habitat suitability (part B) of the Sobibór forest district for the common spadefoot compared to the most significant explanatory variable for this species – forest stand density (part A)

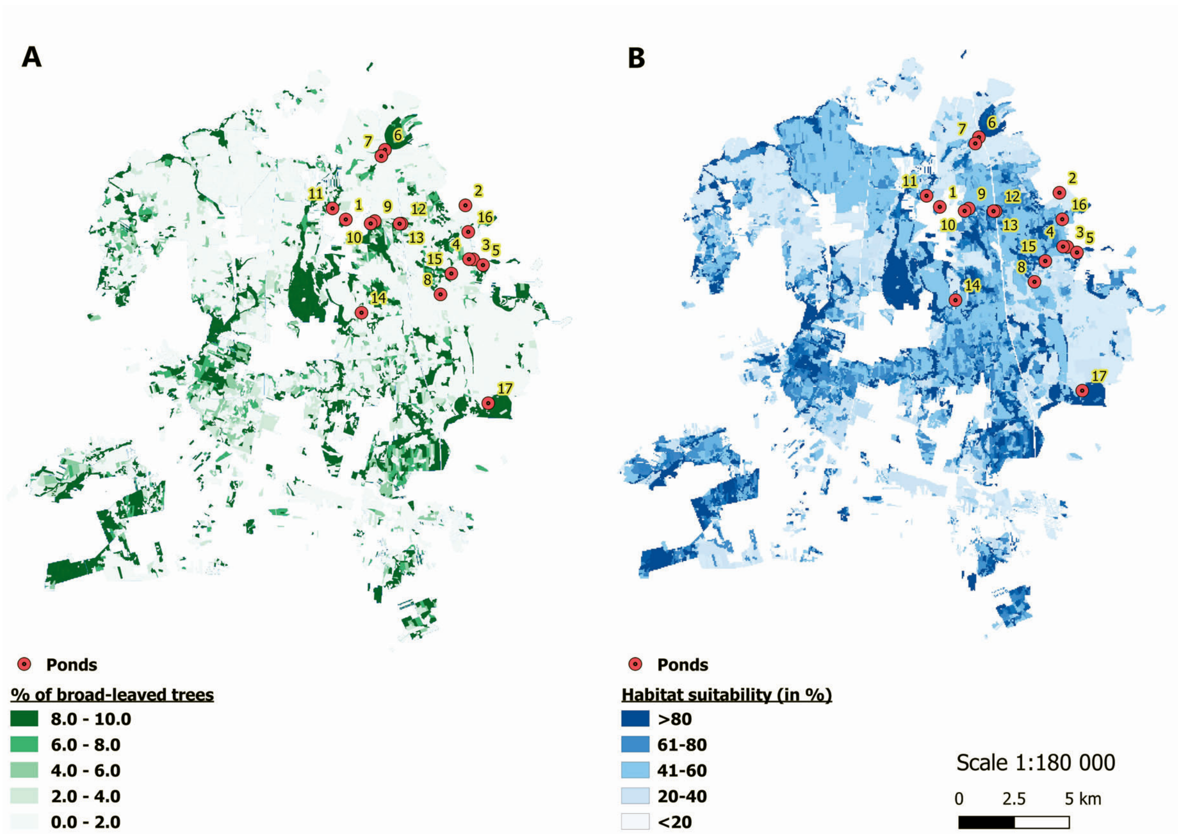

Fig. 4. Prediction map of habitat suitability (part B) of the Sobibór forest district for the fire-bellied toad compared to the most significant explanatory variable for this species – percentage of broad-leaved tree species (part A).

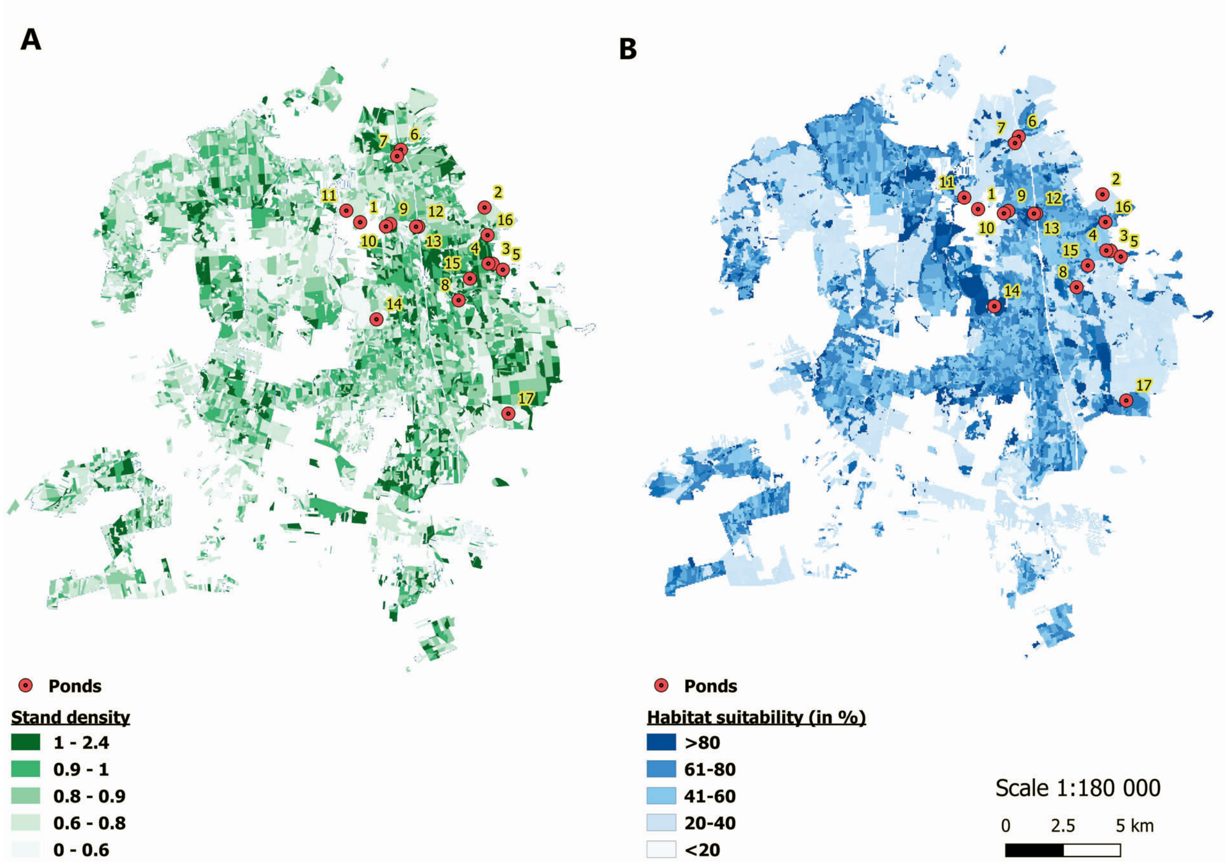

Fig. 5. Prediction map of the habitat suitability (part B) of the Sobibór forest district for the European tree frog compared to the most significant explanatory variable for this species – forest stand density (part A).

Table 5

Forest characteristics influencing the species composition of amphibians in forests. Results from the canonical correspondence analysis

Name	Explains %	pseudo-F	p
Previous agricultural use	2.9	2.8	0.005
Stand density	2.1	2.1	0.039
Percentage of broad-leaved species	2.1	2.0	0.048
Soil humidity	2.3	2.3	0.018
Age of the stand	1.4	1.4	0.208
Height of the stand	2.2	2.2	0.023
Percentage of coniferous species	1.0	1.0	0.379

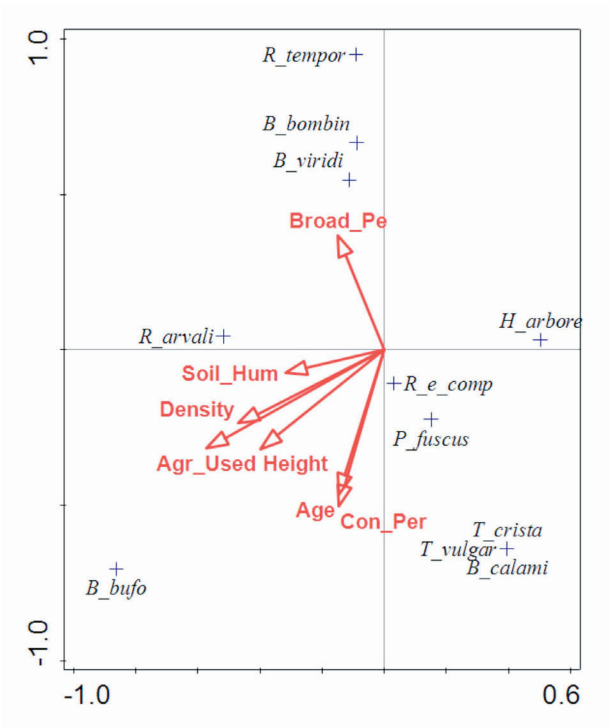

Fig. 6. Biplot representing the canonical correspondence of amphibian species and forest features.

Discussion

Our results demonstrated the suitability of forests as a habitat for amphibians. This is in contrast to general opinions that traditionally used open landscapes are ecologically optimal for amphibians (Hartel *et al.* 2010). For some species, like the moor frog (or groups of species, like water frogs), our ecological niche model shows a relatively high abundance in forests (Fig. 2). Of course, this is only under the assumption that there are plenty of small sized water bodies available in the area, as it is in the case of this particular forest district. Nevertheless, our study shows that forests should be looked at more carefully in the context of amphibian conservation, and that they might be a vital part of any conservation policy or effort. This study also emphasises the need for further studies of this subject – especially studies that include variables that describe amphibian microhabitats in their models.

Our model for total amphibian abundance (Table 4, Fig. 1.) showed that the entirety of the Sobibór forest district was well suited for amphibians. The factor most positively influencing their abundance was stand density. This can be explained by the fact that swamps and small water bodies are most commonly located in dense alder forests. That would also explain the positive correlation between amphibian abundance and percentage of broad-leaved species (Table 3). Overall, this underlines the main conclusion of the present study, i.e. that when water bodies are present (even small or a seasonal ones), amphibian diversity and abundance in forests might in fact be fairly high.

Interestingly, abundance of amphibians was strongly linked with land history. Previous agricultural use negatively affected overall abundance, which we found slightly surprising. There have been previous studies on the correlation between current plant diversity and historical land use (Foster *et al.* 1998; Kouba *et al.* 2015) which showed that historical land use had a significant impact on the composition of vegetation in forest stands. The relationship between historical land use and animal diversity was also studied (Culbert *et al.* 2017), showing an association between bird communities and previous agricultural use. This is the first study showing that abundance of amphibians can be affected by historical land use as well.

Analyses performed on the species level revealed some different responses of specific species to forest characteristics. First we will focus on the water frog species (or group of species, in this case) (Fig. 2) consisting of the marsh frog (*Pelophylax ridibundus*), edible frog (*Pelophylax esculentus*), and pool frog (*Pelophylax lessonae*). Different species from this group have different ecological preferences, but the whole group occupies almost all types of water features (Arnold & Ovenden 2004). This could explain why our prediction map showed us a rather uniform distribution for the species group over our whole study area, with a high abundance index (Fig. 2). The model parameters for these species seem to be similar to those of overall amphibian abundance. Water frogs showed a strong affinity towards stand density, which was expected for this group, considering their preference of dense vegetation in water bodies. This could also explain their positive relationship with stand age, as there was a greater abundance of understory vegetation. The group showed a negative relationship with previous agricultural use, which could be explained by the fact that Scots pine (*Pinus sylvestris)* are the species that has mostly been used for afforestation, and pine stands in this region tend to have a lower amount of understory vegetation.

Model parameters for the moor frog (Table 4) had no statistical significance, therefore no prediction map were made for this species.

Model parameters for the fire-bellied toad revealed a strong negative relationship with sites that has been previously used agriculturally (Table 4, Fig. 4), which could also be explained by the fact that afforestation has been done mostly with coniferous trees, as it is in the case of water frogs. Apart from that, the species was associated with sites having a higher percentage of broad-leaved species, which can be treated as a typical adaptation for this amphibian. There are two significant features about the prediction map for this species – the first one is patches of very high density, and the second is that they are located very close to each other, leaving other areas with a very low predicted value of habitat suitability.

Considering the European tree frog, a positive correlation with the percentage of broad-leaved species as well as with stand density, and a negative correlation towards stand age were observed. This corresponds with the species' preferred habitat, which is areas with shrubs and dense, broad-leaved forests. Our prediction map for this species showed that habitat suitability varies greatly, with the highest predicted density in the center of the forest district (Fig. 5).

The common spadefoot is representative of species that are difficult to detect in the field. It is a nocturnally active species, that hides in the ground burrows during the daytime. It is however partly diurnal during its breeding season when it is found in deep pools, ditches, ponds, and lakes, particularly nutrient-rich ones with a good growth of reeds and other plants at their edges, and sometimes even in rather brackish water (Arnold & Ovenden 2004). Model parameters seem to support this thesis, at least to some extent. There was a negative association between primarily broad-leaved forests, and the predicted abundance of this species. The most surprising correlation, however, was towards previous agricultural use which can be explained by the fact that afforestation is done with mostly coniferous trees, and this amphibian shows some affinity towards coniferous forests. Also, our prediction map clearly showed that the highest density of this amphibian was expected in the middle and South-western part of the forest complex. Another interesting finding is that the prediction map suggests that over the half the stands in the complex should be a good habitat for the common spadefoot.

Study limitations

Our study had some limitations that must be taken into account when interpreting results. First of all, our study does not contain any information about predator presence, which might be one of the most important predictors of amphibian occurrence and density (TARKHNISHVILI *et al.* 2009). Another important aspect is the limited amount of spatial information included in the vector layers of the FNM we used. For example, there is no information about water bodies that are smaller than lakes. Data describing pond characteristics, such as vegetation cover within a pond or bank slope can be important factors for determining amphibian presence (JOLY *et al.* 2001). The location of water bodies, along with data concerning their size, and the plants covering them would certainly help to increase the accuracy of models created. The lack of a relationship between variables and species richness may be due to the lack of variability in the variables or to a low number of species richness. However, anuran species richness in Poland is generally rather low. In the whole of Poland there are only 14, 11 of which were found during our data collection in Sobibór.

Despite of all of the limitations mentioned above, the data from Forest Numerical Maps can be a valuable asset in the creation of ecological models concerning the habitat preferences of different species. The use of FNMs in the prediction of amphibian habitat suitability should be a subject of further studies, as it may be a useful tool for the managing and protection of this group of organisms.

Practical guidelines

Our results may be useful in the conservation of amphibians in forest ecosystems in a number of ways. They might help in the selection of the optimal sites for fire-control pond construction or for ponds specifically meant for amphibians. Moreover, they might allow for the selection of forest stands where less intensive management of drainage ditches could be conducted (for example less frequent mowing and cleaning). Our results may also be used to allocate conservation actions in a cost-efficient way to sites preferred by amphibians. Thus, our method of predicting the potential habitats of amphibians may be a starting point to evaluate the suitability of forest stands for their potential in the conservation of amphibians in Poland and in other European countries.

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Author Contributions

Research concept and design: M.B., K.K.; Collection and/or assembly of data: M.B; Data analysis and interpretation: M.B; Writing the article: M.B, K.K.; Critical revision of the article: M.B, K.K.; Final approval of article: M.B, K.K.

Conflict of Interest

The authors declare no conflict of interest.

References

ARNOLD E.N., OVENDEN D.W. 2004. Field Guide to the Reptiles and Amphibians of Britain and Europe. Corrected 2nd edition. Harper Collins Publishers, London, 288 pp.

ALLAIN S.J.R., DUFFUS A.L.J. 2019. Emerging infectious disease threats to European herpetofauna. Herpetol. J. **29**: 189-206. https://doi.org/10.33256/hj29.4189-206

BLAUSTEIN A.R., WAKE D.B. 1995. The puzzle of declining amphibian populations. Sci. Am. **272**: 52-57.

BRODMAN R., PARRISH M., KRAUS H., CORTWRIGHT S. 2006. Amphibian biodiversity recovery in a large-scale ecosystem restoration. Herpetol. Conserv. Biol. **1**: 101-108.

BOLKER B.M., BROOKS M.E., CLARK C.J., GEANGE S.W., POULSEN J.R., STEVENS M.H.H., WHITE J-S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. **24**: 127-135. https://doi.org/10.1016/j.tree.2008.10.008

BOURNE C.M., REGULAR P.M., SUN B., THOMPSON S.P., TRANT A.J., WHEELER J.A. 2007. Generalized linear model analysis in ecology. Memorial University of Newfoundland and Labrador, St. Jonh's.

CULBERT P.D., DORRESTEIJN I., LOOS J., CLAYTON M.K., FISCHER J., KUEMMERLE T. 2017. Legacy effects of past land use on current biodiversity in a low-intensity farming landscape in Transylvania (Romania). Landsc. Ecol. **32**: 429-444. https://doi.org/10.1007/s10980-016-0441-3

CHESTER E.T., ROBSON B.J. 2013. Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. Biol. Conserv. **166**: 64-75. https://doi.org/10.1016/j.biocon.2013.06.016

COLLINS J.P., CRUMP M.L. 2009. Extinction in Our Times: Global Amphibian Decline. Oxford University Press. Oxford. https://doi.org/10.1371/journal.pbio.1000198

DASZAK P., CUNNINGHAM A.A., HYATT A. D. 2000. Emerging infectious diseases of wildlife: threats to biodiversity and human health. Science **287**: 443-449. https://doi.org/10.1126/science.287.5452.443

EDWARDS C.B., CRONE E.E. 2021. Estimating abundance and phenology from transect count data with GLMs. Oikos **130**: 1335-1345. https://doi.org/10.1111/oik.08368

Fortin M-J., Dale M.R.T., Ver Hoef J. 2002. Spatial analysis in ecology. Encyclopedia of Environmetrics **4**: 2051-2058. John Wiley & Sons, Ltd. Chichester. https://doi.org/10.1002/9781118445112.stat07766

Foster D.R., Motzkin G., Slater B. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems **1**: 96-119. https://doi.org/10.1007/s100219900008

Garzon M.B., Blazek R., Neteler M., Sanchez de DioS R., Ollero H.S., Furlanello C. 2006. Predicting habitat suitability with machine learning models: The potential area of *Pinus sylvestris* L. in the Iberian Peninsula. Ecol. Modell. **197**: 383-393. https://doi.org/10.1016/j.ecolmodel.2006.03.015

Guisan A., Edward T.C. Jr, Hastie T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Modell **157**: 89-100. https://doi.org/10.1016/S0304-3800(02)00204-1

Hartel T., Nemes S., Öllerer K., Cogalniceanu D., Moga C., Arntzen J.W. 2010. Using connectivity metrics and niche modelling to explore the occurrence of the northern crested newt Triturus cristatus (Amphibia, Caudata) in a traditionally managed landscape. Environ. Conserv. **37**: 195-200. https://www.jstor.org/stable/44520015

Heatwole H., Wilkinson J. W. 2009. Amphibian Biology. Volume 8. Amphibian Decline: Diseases, Parasites, Maladies and Pollution. Chipping Norton: Surrey Beatty & Sons Pty Ltd. https://doi.org/10.1017/CBO9781139095075.025

Hirzel A.H., Hausser J., Chessel D., Perrin N. 2002. Ecological-niche Factor Analysis: How to compute Habitat-Suitability Maps without Absence Data? Ecology **83**: 2027-2036.https://doi.org/10.2307/3071784

Joly P., Miaud C., Lehmann A., Grolet O. 2001. Habitat matrix effects on pond occupancy in newts. Conserv. Biol. **15**: 239-248. https://doi.org/10.1111/j.1523-1739.2001.99200.x

Kiesecker J.M., Blaustein A.R., Belden L.K. 2001. Complex causes of amphibian population declines. Nature **410**: 681-684. https://doi.org/10.1038/35070552

Kouba Y., Martínez-García F., de Frutos Á., Alados C.L. 2015. Effects of Previous Land-Use on Plant Species Composition and Diversity in Mediterranean Forests. PLoS ONE **10**: e0139031. https://doi.org/10.1371/journal.pone.0139031

Lepš J., Šmilauer P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press. 362 pp. https://doi.org/10.1017/CBO9780511615146

Lüdecke D., Ben-Shachar M., Patil I., Waggoner P., MAkowski D. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J. Open Source Software **6**(60): 3139. https://doi.org/10.21105/joss.03139

Marsh D.M., Trenham P.C. 2001. Metapopulation dynamics and amphibian conservation. Conserv. Biol. **15**: 40-49. https://doi.org/10.1111/j.1523-1739.2001.00129.x

McLoughlin P.D., Morris D.W., Fortin D., Vander Wal E., Contasti A.L. 2010. Considering ecological dynamics in resource selection function. J. Anim. Ecol. **79**: 4-12. https://doi.org/10.1111/j.1365-2656.2009.01613.x

Mitchell J.C. 2016. Restored wetlands in mid-atlantic agricultural landscapes enhance species richness of amphibian assemblages. J. Fish Wildl. Manag. **7**: 490-498. https://doi.org/10.3996/092015-JFWM-085

Mitrus S. 2009. The European pond turtle in Poland. 197-199. (In: Rogner M. (ed.) European Pond Turtles – *Emys orbicularis*. Chelonian Library 4. Edition Chimaira, Frankfurt am Main, 271 pp.)

Ray N., Lehmann A., Jolly P. 2002. Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. Biodivers. Conserv. **11**: 2143-2165. https://doi.org/10.1023/A:1021390527698

R Core Team. 2015. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Pabijan M., Ogielska M. 2019. Conservation and declines of amphibians in Poland. 26-45. (In: HEatwole H., Wilkinson J.W. (eds.) Amphibian Biology, Volume 11: Status of Conservation and Decline of Amphibians: Eastern Hemisphere, Part 5: Northern Europe. Exeter: Pelagic Publishing. 200 pp.)

Plăiaşu R., Bancila R., Samoila C., Hartel T., Cogalniceanu D. 2012. Waterbody availability and use by amphibian communities in a rural landscape. Herpetol. J. **22**: 13-21. https://doi.org/10.5167/uzh-88472

Sillero N., Tarroso P. 2010. Free GIS for herpetologists: free data sources on Internet and comparison analysis of proprietary and free/open source software. Acta Herpetol. **5**: 63-85. https://doi.org/10.13128/Acta_Herpetol-8535

Sillero N. 2011. What Does Ecological Modelling Model? A Proposed Classification of Ecological Niche Models Based on Their Underlying Methods. Ecol. Modell. **222**: 1343-1346. https://doi.org/10.1016/j.ecolmodel.2011.01.018

Silva J.P., Toland J., Jones W., Eldridge J., Hudson T., O'Hara E. 2009. LIFE and Europe's reptiles and amphibians: Conservation in practice. Office for Official Publications of the European Communities. Luxembourg.

Suárez R.P., Zaccagnini M.E., Babbitt K.J. 2016. Anuran responses to spatial patterns of agricultural landscapes in Argentina. Landsc. Ecol. **31**: 2485-2505. https://doi.org/10.1007/s10980-016-0426-2

Tarkhnishvili D., Serbinova I., Gavashelishvili A. 2009. Modeling range of Syrian spadefoot toad (*Pelobates syriacus*) with combination of GIS-based approaches. Amphibia-Reptilia **30**: 401-412. https://doi.org/10.1163/156853809788795137

Torgo L. 2010. Data Mining using R: learning with case studies, CRC Press. 426 pp.

Wadsworth R., Treweek J. 1999. Geographical Information Systems for Ecology: An Introduction. Addison Wesley Longman Ltd., Boston. 204 pp.