

UDC 594.3: 591.54(477)

DISTRIBUTION OF THE FRESHWATER SNAIL SPECIES *FAGOTIA* (GASTROPODA, MELANOPSIDAE) IN UKRAINE ACCORDING TO CLIMATIC FACTORS. I. *FAGOTIA ESPERI*

V. Tytar¹, N. Makarova²,

¹*Schmalhausen Institute of Zoology, NAS of Ukraine,
vul. B. Khmelnytskogo, 15, Kiev, 01030 Ukraine
E-mail: vtytar@gmail.com*

²*Zhytomyr Ivan Franko State University
E-mail: natalya_stelmashchik@mail.ru*

Distribution of the Freshwater Snail Species *Fagotia* (Gastropoda, Melanopsidae) in Ukraine According to Climatic Factors. I. *Fagotia esperi*. Tytar, V., Makarova, N. — Maximum entropy niche modeling was employed as a tool to assess potential habitat suitability for the freshwater snail *F. esperi* (Férussac, 1823) in Ukraine for both contemporary climatic conditions and conditions projected for 2050. Of the 19 bioclimatic predictor variables used in the modeling, the “mean temperature seasonality” “mean temperature of driest quarter” and “precipitation of warmest quarter” were the three most important in predicting habitat suitability and distribution of this mollusk species.

Key words: Maxent, species distribution modeling, *Fagotia esperi*, climatic factors, Ukraine.

Распространение пресноводных моллюсков рода *Fagotia* (Gastropoda, Melanopsidae) на территории Украины в соответствии с климатическими условиями. I. *Fagotia esperi*. Титар В., Макарова Н. — Моделирование экологической ниши методом максимальной энтропии было использовано для выяснения роли климатических условий в формировании ареала пресноводных моллюсков *F. esperi* (Férussac, 1823) на территории Украины при современных и прогнозируемых на 2050 г. климатических условиях. Среди использованных в моделях 19 биоклиматических предикторов, наиболее важными оказались «температурная сезонность», «средняя температура наиболее сухого квартала» и «осадки наиболее теплого квартала», по которым проведена оценка пригодности среды обитания и потенциального распространения этого вида моллюсков.

Ключевые слова: Maxent, модель распространения видов, *Fagotia esperi*, климатические факторы, Украина.

Introduction

Inland waters make up only 0.01 % of the world's total water, yet they support an important part of global biodiversity (Dudgeon et al., 2006), but in the face of environmental change freshwater habitats are amongst the first to suffer. Human activities are responsible for habitat fragmentation and water pollution, increasing levels of greenhouse gases are causing worldwide climatic changes. In freshwater habitats, predicted climate change will mainly affect runoff regimes, the seasonality of water availability and the average temperature, as an increase in air temperature translates directly into warmer water temperature (Carpenter et al., 1992; Poff et al., 2002). Warmer waters hold less dissolved oxygen, which could have consequences for organisms requiring high oxygen levels. This in turn is likely to affect the life processes of many aquatic organisms, including freshwater gastropods. In particular this regards lithoreophilous species, such as prosobranch snails of the genus *Fagotia* Bourguignat, 1884.

These gastropods are a part of the subfamily *Melanopsinae*, which has about 10 other genera worldwide (Wenz, 1938). Initially Ferussac classified the two well known *F. acicularis* (Férussac, 1823) and *F. esperi* (Férussac, 1823) in the genus *Melanopsis*, but Bourguignat (1884) separated *F. esperi* together with 21 synonymous taxa into a new genus *Fagotia* and *F. acicularis* with further 18 synonyms into the genus *Microcolpia*. Later Wenz (1938) comprised both as subgenera of *Fagotia*. They originated simultaneously in the basin of the river Danube, and are nowadays widespread in central and eastern Europe, being native to Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Hungary, Montenegro, Romania, Serbia, Slovakia, Slovenia, Turkey and Ukraine.

In Ukraine both species, *F. esperi* and *F. acicularis*, are found in catchments of the Right-bank, namely the Danube, Dnister, Southern Buh, Dnipro (Anistratenko, Anistratenko, 2001; Starobogatov, 1970). Since their first discovery in Ukraine (Eichwald, 1830), population numbers and densities of both have suffered a sharp decline due to an array of anthropogenic impacts affecting the hydrology and hydrochemistry in habitats occupied by the two species. This trend might be aggravated by climate change in a way that in the near future these species may fall into the category of “critically endangered” and become a subject of the Red Data Book of Ukraine.

Research and development of conservation strategies for aquatic species such as *F. esperi* and *F. acicularis* is urgently needed to avoid the high probability of future extinctions and aquatic ecosystem change. In addition, as aquatic invertebrates they may be useful biological indicators of climate-induced changes in aquatic ecosystems because they are integral components of aquatic food webs and their distributions and abundances are strongly influenced by temperature and stream flow gradients dependent on precipitation. Loss of such species decrease stream habitat heterogeneity and may likely indicate an overall reduction in regional biodiversity.

Among the various tools used in conservation planning to protect biodiversity, species distribution models (SDMs), also known as climate envelope models, habitat suitability models, and ecological niche models provide a way to identify the potential habitat of a species in an ecoregion and their applications have increased exponentially (for an overview see Research..., 2014). SDMs are based on the concept of the “ecological niche” (Hutchinson, 1957), which can be defined as the sum of the environmental factors that a species needs for its survival and reproduction. When applied to species, all SDMs are based on the assumption of niche conservatism (Wiens, Graham, 2005) and rarely consider biotic interactions (Elith, Leathwick, 2009; Guisan, Thuiller, 2005). Moreover, these techniques are based on observed occurrence or abundance data and therefore estimate the realized niche or the potential niche (i. e. the realized niche assessed from a reduced number of ecological dimensions). Many niche models are based purely on climate variables because these data are readily available, covering large spatial scales. SDMs predict the potential distribution of a species by interpolating identified relationships between presence/absence or presence-only data of a species on one hand and environmental predictors on the other hand across an area of interest. From the array of various applications, *Maxent* (Phillips et al., 2006) stands out because it has been found to perform best among many different modeling methods (Elith et al., 2006) and may remain effective despite small sample sizes. *Maxent* is a maximum entropy based machine learning program that estimates the probability distribution for a species' occurrence based on environmental constraints (Phillips et al., 2006). It requires only species presence data (not absence) and environmental variable (continuous or categorical) layers for the study area.

In summary, our objectives are: (i) to describe in terms of climate and anthropogenic impact the ecological and geographical range of *F. esperi* in Ukraine, (ii) identify the environmental factors that constrain their distribution, (iii) estimate the species' responses to these environmental variables, (iv) map the nationwide potential distribution of the study species for present-day climate, (v) forecast the distribution in a future climate, based on a climate change projection model.

Material and methods

Species records. We gathered 168 records of *F. esperi* in Ukraine. The extracted points were manually georeferenced using *OziExplorer* v. 3.95.4 m. All the coordinates were collected in decimal degree and converted to a point vector file for modeling the distribution of the species. The georeferenced dataset was further trimmed to retain only spatially unique ones, corresponding to single environmental grid cells (all cells have a 10-minute horizontal and vertical resolution). Consequently, only 56 unique records were used to generate SDMs for the snail species.

Bioclimatic data. To relate the occurrence records of *F. esperi* with abiotic conditions, we downloaded 19 bioclimatic variables (see table 1 for names and acronyms) for the current climate and climate projected for 2050 from the *CliMond* database at a 10-minute resolution and WGS1984 projection (Kriticos et al., 2012). These variables represent annual trends (e. g., mean annual temperature, annual precipitation) seasonality (e. g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e. g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters).

Temperature has long been recognized as an important environmental factor in aquatic ecosystems in regard to its pivotal role over biological (development, growth and reproduction), chemical, and physical properties. Aquatic organisms all have a preferred temperature range and poikilothermic species must maintain a specific internal temperature or inhabit environments within a temperature range. Precipitation regimes and variation of precipitation events have broad effects on ecosystem productivity, habitat structure, and ultimately on species' distribution.

The bioclimatic temperature variables themselves are gained from ambient air temperatures, however they have been used in successful models of aquatic species (Kumar et al., 2009; Milanovich et al., 2010; Wenger et al., 2011; Blank, Blaustein, 2012) because the values typically correlate with water temperatures (Stefan, Preud'homme, 1993).

Statistical modeling. Factor analysis in *Statistica 8 Portable* was used to examine the contributions and the main patterns of inter-correlation among the potential environmental controls. Principal component (PC) was used as the extraction method. By rotating the factors a factor solution was found that is equal to that

Table 1. Summary of the bioclimatic profile of *F. esperi*

Bioclimatic variables	Acronym	Median	Minimum	Maximum
Annual Mean Temperature	<i>bio 1</i>	8.44	7.08	11.42
Mean Monthly Temperature Range	<i>bio 2</i>	8.48	6.43	9.69
Isothermality (<i>bio 2/bio 7</i>) (x 100)	<i>bio 3</i>	0.263	0.220	0.290
Temperature Seasonality (STD* x 100)	<i>bio 4</i>	0.030	0.027	0.032
Max Temperature of Warmest Month	<i>bio 5</i>	24.90	23.34	28.64
Min Temperature of Coldest Month	<i>bio 6</i>	-7.59	-8.80	-2.80
Temperature Annual Range (<i>bio 5/bio 6</i>)	<i>bio 7</i>	32.39	28.78	35.23
Mean Temperature of Wettest Quarter	<i>bio 8</i>	17.84	16.78	20.56
Mean Temperature of Driest Quarter	<i>bio 9</i>	-1.78	-2.98	11.91
Mean Temperature of Warmest Quarter	<i>bio 10</i>	18.62	17.23	21.36
Mean Temperature of Coldest Quarter	<i>bio 11</i>	-2.51	-4.05	1.24
Annual Precipitation	<i>bio 12</i>	596.5	356.0	700.0
Precipitation of Wettest Month	<i>bio 13</i>	19.2	9.4	23.2
Precipitation of Driest Month	<i>bio 14</i>	6.4	4.6	8.3
Precipitation Seasonality (CV)*	<i>bio 15</i>	0.342	0.152	0.431
Precipitation of Wettest Quarter	<i>bio 16</i>	224.8	110.0	271.7
Precipitation of Driest Quarter	<i>bio 17</i>	97.0	71.4	115.8
Precipitation of Warmest Quarter	<i>bio 18</i>	224.0	108.0	259.1
Precipitation of Coldest Quarter	<i>bio 19</i>	103.0	77.5	120.7

* STD — standard deviation; CV — coefficient of variation.

Absolute temperature values are in degrees Celsius (° C), precipitation in mm.

obtained in the initial extraction but which has the simplest interpretation, and for this purpose the Varimax normalized type of rotation was applied. Usually a solution that explains 75–80 % of the variance is considered sufficient.

Routine statistical processing was accomplished using the software *PAST* 2.13 (Hammer, et al., 2001).

Maxent distribution model. We used the freely available *Maxent* software, version 3.3. 3k, which generates an estimate of probability of presence of the species that varies from 0 to 1, where 0 being the lowest and 1 the highest probability. The default settings of *Maxent* were used in this study. We ran models with 25 bootstrap replicates, and assessed model performance using the average AUC (area under the receiver operating curve) score to compare model performance. AUC values > 0.9 are considered to have “very good”, > 0.8 “good” and > 0.7 “useful” discrimination abilities (Swets, 1988). The logistic output format was used, because it is easily interpretable with logistic suitability values ranging from 0 (lowest suitability) to 1 (highest suitability). Better interpretation is made in most cases by defining thresholds of habitat suitability. To establish which areas are climatically suitable for the snail, we used the 10 percentile training presence logistic threshold. This has the effect of conservatively identifying a region of highest fit that does not allow outlying points of presence to expand the predicted area of occupancy beyond a core region. Binary maps of species occurrence were created by reclassifying the integer raster datasets, where all values above the given threshold were assigned a value of 1 and all other values were assigned a value of 0.

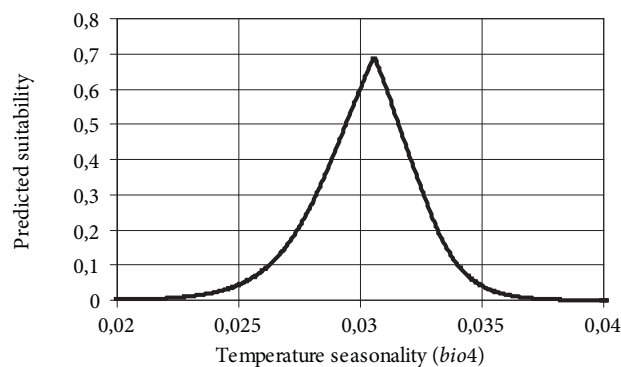


Fig. 1. Response curve of the temperature seasonality (*bio 4*).

Usually, researchers calculate correlation coefficients (e. g. Pearson coefficient) to avoid correlated variables and to reduce the effects of multi-colinearity in their models. However, from this type of analysis ecologically relevant variables could be excluded. Burnham and Anderson (1998) have made clear that applying correlation analysis in order to find a significant set of predictor variables will most probably expose false correlations. Fortunately, *Maxent* is able to incorporate complex dependencies between predictor variables and even in the presence of correlated variables, non-linearity, bimodality etc. *Maxent* performs better than most other modeling methods (Elith et al., 2011), though no single modeling method is thought to have the complete truth. Thus, all covariates were retained for the final model.

The jackknife variable importance feature in *Maxent* was used to assess the relative importance of the environmental predictors in the model. We determined the relative importance of variables remaining in the model with permutation of importance. Permutation of importance is a measure of the contribution of each variable quantified by the resulting decrease in training AUC when randomly permuting a variable. The values total to 100 % across all variables and larger decreases mean the model depends more heavily on that variable.

Maxent allows the construction of response curves to illustrate the effect of selected variables on probability of occurrence. If needed, a smoothing function (a regularization multiplier of 10) was used to smooth response curves of variables to prevent overfitting of the curve. Identification of the most important predictors, and the analysis of the relations between the predictors and (predicted) habitat suitability, allows the description of the autecology of a species (defined here as the biological relationship between a species and its environment). Using this methodology we analyze the autecology of *F. esperi*.

Results were processed and visualized in DIVA-GIS 7.5 and QGIS 2.6, free computer programs for mapping and geographic data analysis.

Results and discussion

Table 1 summarizes the bioclimatic profile of the species by indicating minimum, maximum, and medians for all 19 bioclimatic variables. As one could expect, this profile is clearly a narrower subset of the same variables extracted for 500 random points generated over a polygon layer representing the entire country. For instance, within places where *F. esperi* has been found in Ukraine annual mean temperatures (*bio 1*) range from 7.08 to 11.42 °C, whereas for the country these figures vary to a wider extent — from 3.69 to 11.93 °C; the mean values too show a difference: 8.65 ± 0.19 for *F. esperi* against 8.18 ± 0.06 °C for the entire country ($t = 2.58$, $p = 0.01$). One-way ANOVA shows a similar pattern for 9 other bioclimatic variables, addressed in this study: *bio 3*, *bio 4*, *bio 6*, *bio 7*, *bio 11*, *bio 14*, *bio 15*, *bio 17* and *bio 19*.

The PC analysis provided a comprehensive way to analyze the niche of *F. esperi* (table 2). The first three PCs accounted for close to 90 % of the variance in the data set covering all the bioclimatic variables extracted from the trimmed occurrence points within the home range of snail in Ukraine. The first component explained an overwhelming 62.8 % of the total variance and captures the positive significance of precipitation (*bio 12*, *bio 13*, *bio 15*, *bio 16*, *bio 18*), particularly in the warmest time of the year, and the inversely related importance of temperature variables (*bio 1*, *bio 5*, *bio 6*, *bio 8*, *bio 9*, *bio 10*, *bio 11*), indicated by their highly negative contribution. Both the second and third components (contributing to the total variance 15.5 and 11.3 %, respectively) are exclusively associated with variables expressing the homogeneity of temperatures throughout the year, but in a reverse manner. The second component negatively correlates with temperature seasonality (*bio 4*) and the temperature annual range (*bio 7*), whereas the third component displays a positive correlation with the mean monthly temperature range (*bio 2*) and isothermality (*bio 3*).

In general it can be argued that in terms of the abiotic niche, both water availability in the first place and temperature are the main drivers of the snail's life cycle, however the strong negative contribution of temperature variables featuring the thermal dimension of the niche of *F. esperi* raise concern on the future of the species under a scenario of a warming climate. Frequent or severe changes in temperature can also have negative effects on the discharge and depth of rivers and therefore habitat availability, and sharp changes in temperature seasonality reflect the likelihood of drought (death by desiccation) and flooding.

The *Maxent* model's internal jackknife test of variable importance showed that preci-

Table 2. Bioclimatic variables and their loadings on the first three axes of the Principal Components*

Variable acronym	PCA axis 1	PCA axis 2	PCA axis 3
<i>bio 1</i>	-0.94	0.22	0.09
<i>bio 2</i>	0.03	-0.38	0.92
<i>bio 3</i>	0.17	0.11	0.97
<i>bio 4</i>	-0.03	-0.99	-0.10
<i>bio 5</i>	-0.90	-0.28	0.22
<i>bio 6</i>	-0.87	0.44	-0.08
<i>bio 7</i>	-0.17	-0.90	0.39
<i>bio 8</i>	-0.92	-0.15	-0.11
<i>bio 9</i>	-0.78	-0.20	-0.39
<i>bio 10</i>	-0.96	-0.11	0.03
<i>bio 11</i>	-0.87	0.43	0.08
<i>bio 12</i>	0.87	0.12	0.09
<i>bio 13</i>	0.87	0.12	0.18
<i>bio 14</i>	0.57	0.15	0.14
<i>bio 15</i>	0.88	0.10	0.19
<i>bio 16</i>	0.88	0.12	0.15
<i>bio 17</i>	0.38	0.08	-0.03
<i>bio 18</i>	0.91	0.10	0.11
<i>bio 19</i>	0.27	-0.08	-0.22
Eigenvalue	11.9	2.9	2.1
% of total variance	62.8	15.5	11.3
% of cumulative variance	62.8	78.3	89.6

* Correlations marked in bold are > 0.70; values between 0 and 1 indicate a positive contribution to the axis, while values ranging between -1 and 0 indicate a negative contribution).

pitiation of warmest quarter (*bio 18*) and temperature seasonality (*bio 4*) were the two most important predictors of the snail's habitat distribution in terms of permutation importance (table 3). Variables *bio 9* (mean temperature of the driest quarter) and *bio 6* (minimum temperature of the coldest month) exhibited modest contributions to the model, thus indicating that contain information necessary for the model. The remaining variables contributed less to model development.

The environmental variable with highest gain when used in isolation is *bio 4*, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is *bio 9* (mean temperature of the driest quarter), which therefore appears to have the most information that isn't present in the other variables. Permutation importance of *bio 9* (13 %) too supports the significance of this variable for contributing to the *Maxent* model.

In summary, a multiple approach towards assessing the contribution of bioclimatic variables to the *Maxent* model, points out the greater importance of such variables as *bio 4*, *bio 9* and *bio 18*. Further on, response curves gave an indication of the dependence of the predicted probability of presence (i. e., predicted suitability) on each of these variables as well as the range under which they reach an optimum of suitability. These probabilities are calculated for the range values of one variable, with all other 19 variables set to their average value over the set of presence localities. Upward trends for variables indicate a positive relationship; downward movements represent a negative relationship; and the magnitude of these movements indicates the strength of the relationship (Baldwin, 2009), essentially they demonstrate biological tolerances.

The relationship between *bio 4* (temperature seasonality) and the presence probability of *F. esperi* is not linear (fig. 1). The presence probability increases exponentially from 0.019

Table 3. Different metrics* on the contribution of bioclimatic variables to the Maxent model

Variable acronym	Permutation importance	Jackknife training gain	
		with only variable	without this variable
<i>bio 1</i>	1.6	0.142	1.513
<i>bio 2</i>	1	0.119	1.518
<i>bio 3</i>	5.9	0.440	1.510
<i>bio 4</i>	10.9	0.564	1.485
<i>bio 5</i>	0.5	0.065	1.521
<i>bio 6</i>	9.8	0.283	1.510
<i>bio 7</i>	0.4	0.269	1.522
<i>bio 8</i>	1.6	0.139	1.512
<i>bio 9</i>	13	0.136	1.427
<i>bio 10</i>	0.3	0.186	1.522
<i>bio 11</i>	0.7	0.263	1.522
<i>bio 12</i>	3.2	0.276	1.515
<i>bio 13</i>	0.7	0.211	1.518
<i>bio 14</i>	7.3	0.321	1.496
<i>bio 15</i>	7.6	0.140	1.434
<i>bio 16</i>	0.2	0.251	1.521
<i>bio 17</i>	5.2	0.333	1.509
<i>bio 18</i>	23.3	0.328	1.454
<i>bio 19</i>	6.7	0.514	1.503

* All values are averages of the 25 replicates of the model. The relative contribution is obtained from the increase of the regularized gain when each variable is added to the model. The permutation importance is obtained by randomly permuting the values of that variable among the training points and measuring the decrease in training AUC produced by the permutation. The Jackknife training gain with only variable is the training gain that the model achieves when using only that variable, and the Jackknife training gain without this variable is the training gain that the model achieves when using the rest of variables except that one. Consequently, in the first two metrics larger values indicate higher contribution of variables to the model, while in the last one, the lower values indicate greater importance of variables to the model. Arbitrarily, permutation importance around 10 % and above, and only four highest contributions for the Jackknife training gain are considered (marked in bold).

and at 0.030 the presence probability reaches a peak (0.689), indicating the highest chances to find this snail. The probability decreases sharply from the peak to 0.040 after which there is no chance any more for this species to distribute. By using a threshold of 0.5, this species potentially occurs in the narrow temperature seasonality range of 0.029 to 0.031. If thermal tolerance is indeed strongly influenced by the seasonality in temperature an organism experiences (Janzen, 1967, Ghalambor et al., 2006), *F. esperi* in this context is most likely to be a thermal specialist with a relatively narrow tolerance. This is particularly important in the light of climate change as far as thermal specialists should have a greater cost associated with dispersal and adaptation to a changing environment, putting forward a threat to the species.

The relationship between *bio 9* (mean temperature of the driest quarter) and presence probability also is not linear (fig. 2). In this case the response curve can be characterized as “bell shaped”, indicating reduced suitability as the mean temperatures shift from the optimum of +1.20 °C. This is observable particularly in the range below zero, meaning that at a time of diminishing water supply (encompassing winter months, but not only) freezing temperatures have an enhanced negative effect on the snail response curves of variables are often broken, showing no specific trend in the climatic conditions required by the species. At a first sight this could be applied to the response curve for precipitation of the warmest quarter (*bio 18*), however the jackknife test of variable importance distinguished it as an essential predictor, so in this case regularization has been used as a smoothing parameter. The smoothed plots for *bio 18* are displayed in fig. 3, detecting a curve that could be bimo-

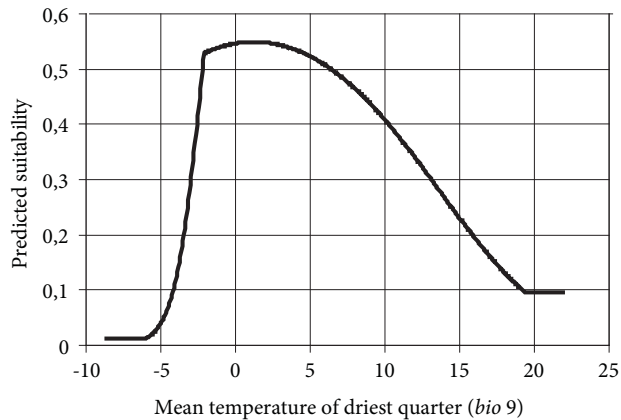


Fig. 2. Response curve of the mean temperature of the driest quarter (*bio 9*).

dal. One optimum of presence probability is not clear enough because the curve is “open ended”, whereas the other has an obvious peak centered around 256.4 mm of precipitation. At this certain time of the year this is, of course, rainfall, a sufficient amount of which is essential for the survival of the snails when ambient temperatures are at their height.

Bimodality (or irregularity) of the response curve indicates that there may be at least two or more spatial clusters of *F. esperi* in Ukraine: some greatly depending on rainfall of the warmest quarter of the year and could be from areas where rain is more infrequent, whereas others are not so much dependent on this particular dimension of the niche as far as rainfall is in plenty in places where they happen to occur. Interestingly, this assumption is supported by both conventional studies (Stelmashchuk, Stadnichenko, 2011) and the results of our species distribution modeling in *Maxent*, indicating a gap between “northern” and “southern” portions of the home range of *F. esperi* in Ukraine and smaller gaps elsewhere.

From the 25 model runs, the average AUC was 0.965 ± 0.001 , with little variation in AUC between runs. The averaged output from these 25 model runs is shown in fig. 4, a binary map showing presence above the 10 percentile training presence logistic threshold of 0.4042 for contemporary climatic conditions. From the map a “northern” cluster (*N*) can be assumed, and few more confined to the catchments of the Dnister (*Ds*), Danube (*Du*), Southern Buh (*Bu*) and lower reaches of the Dniro (*Dn*).

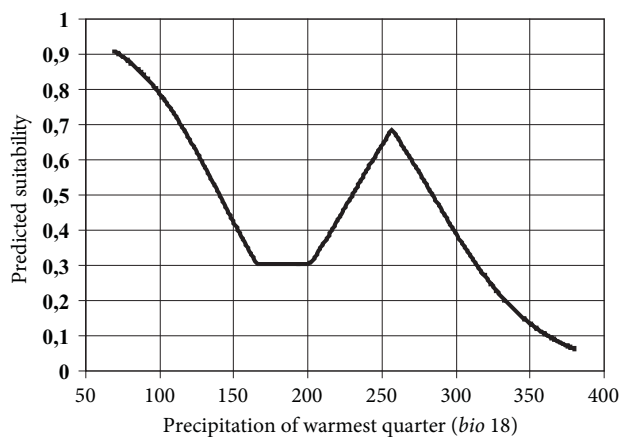


Fig. 3. Response curve of the precipitation of the warmest quarter (*bio 18*).

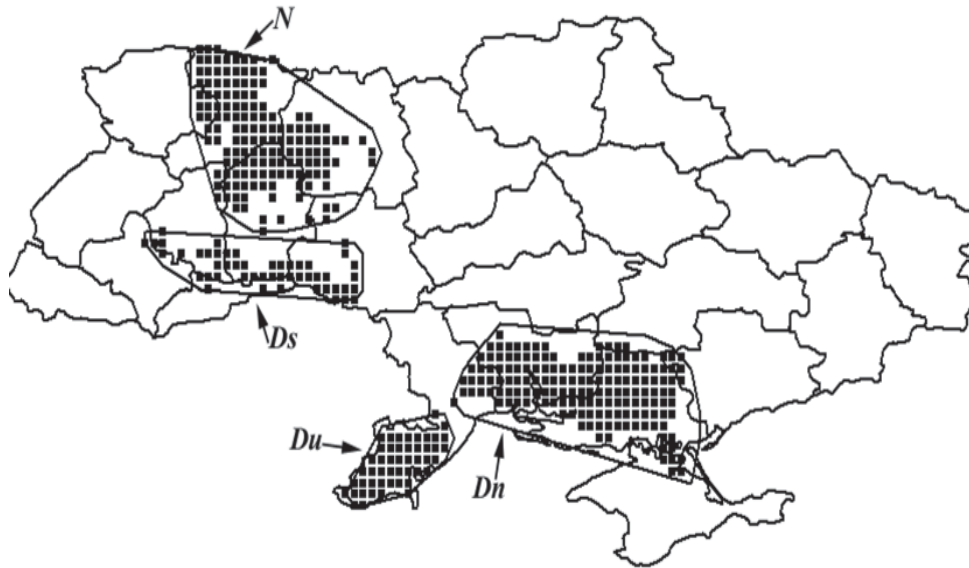


Fig. 4. The potential distribution map for *F. esperi* in Ukraine under contemporary climatic conditions (black squares represent pixels of 10-minute resolution, predicted to be suitable for the species). Convex polygons are drawn around assumed clusters: *N* — “northern”, *Ds* — “Dnister”, *Du* — “Danube”, *Dn* — “Dnipro”.

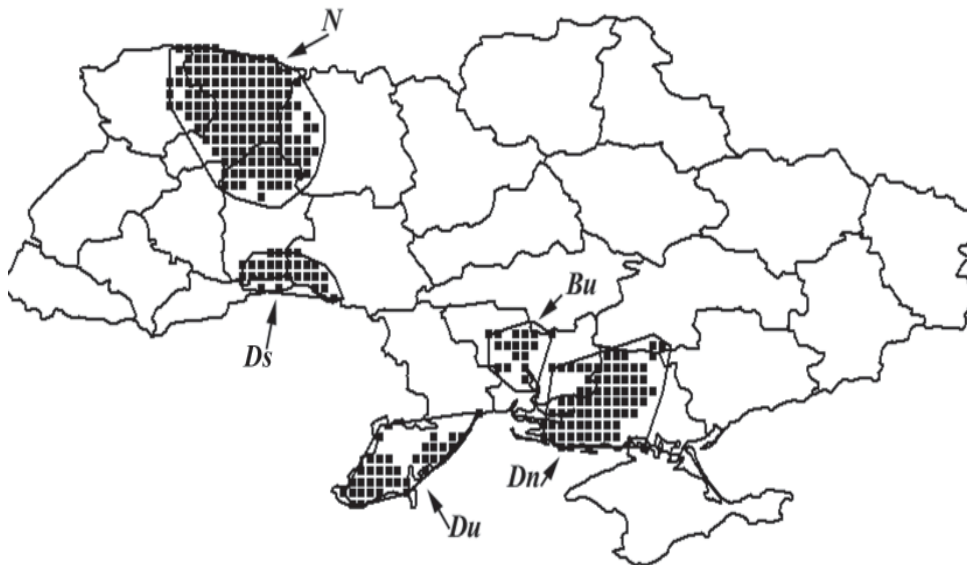


Fig. 5. The potential distribution map for *F. esperi* in Ukraine under climatic conditions projected for 2050. Captions as in fig. 4, *Bu* — “Southern Buh”.

Based on extensive field studies, N. Stel'mashchuk and A. Stadnychenko (Stel'mashchuk, Stadnychenko, 2011) also believe that there is a northern cluster of *F. esperi* in Ukraine, separated from the rest of the home range of the species roughly along the line Otaci–Mohyliv-Podilskiy–Pervomaysk–Archangelske–Antonivka. The modeled habitat suitability (i. e., probability of presence) in this gap achieves low values ranging between 0.1671–0.3341, whereas areas between the “southern” portions of the home range of *F. esperi* in Ukraine reach a higher suitability (from 0.3341 to 0.5012), and apparently are separated from one another to a lesser extent. In terms of the bioclimatic niche it is exactly the “northern” clus-

ter, where precipitation of the warmest quarter (*bio 18*) reaches 240.5 ± 2.7 mm, a figure quite close to the one predicted by the modeled response curve (see above).

Under a changing climate scenario, vulnerability of such specialist species as *F. esperi* may increase considering that climatic conditions, especially rising temperatures and variability of the temperature regime, can affect the snail. *Maxent*, as a SDM, has been used to project future distributions based on projected future climate of 2050. The averaged output binary map from 25 model runs is shown in fig. 5 (AUC = 0.943 ± 0.001). First what can be seen is the increasing gap separating the “northern” cluster of the species from other such clusters and an accompanying trend leading towards the increased fragmentation of the home range in other places, exemplified, for instance, by the splitting of the “Dnipro” cluster and turning the species in the Southern Buh (*Bu*) into an isolated pocket. Furthermore, the modeling predicts a reduction of total area of suitable habitat by 2050 from around 15 % of the country to 11.6 %. In some way this trend has already been captured by N. Stel'mashchuk and A. Stadnychenko (Stel'mashchuk, Stadnychenko, 2011), which argue that the northern border of the “southern” clusters of the species since the 1970s has shifted down south from the line Zalishchyky–Oleksandria–Vinnytsia–Talne–Dnipropetrovs'k to its nowadays position (see above).

Conclusions

Knowledge of the necessary physical environmental attributes aids greatly in understanding issues regarding regional distribution, offer important new insights into the autecology of species. This study makes available the first predicted potential distribution map for the freshwater snail *F. esperi* in Ukraine for both contemporary climatic conditions and conditions projected for 2050. The present study utilized the species occurrence information to generate the distribution map of the target species and accomplish its validation. The average training AUCs for the replicate runs of 0.965 and 0.943 indicated acceptable success rates.

Of the 19 predictor variables used to build our model, the strong negative contribution of temperature variables featuring the thermal dimension of the niche of *F. esperi* raise concern on the future of the species under a scenario of a warming climate. The species seems particularly susceptible to variations of parameters expressing the homogeneity of temperatures throughout the year, pointing it out to be a thermal specialist.

In this study, it is shown by predictions of snail habitat suitability and conclusions from field study reports that there is a distinct north-south gradient of suitability, dividing the home range of *F. esperi* across Ukraine into separate clusters. Predicted changes of spatial distribution in the future climate are apparent with a trend towards more locations with unsuitable habitats and further fragmentation of the home range.

Research and development of conservation strategies for such range-restricted and stenobiotic aquatic species as *F. esperi* is urgently needed to avoid the high probability of future extinctions and aquatic ecosystem change. For this purpose the results of species distribution modeling should provide a useful guidance.

References

- Anistratenko, V. V., Anistratenko, O. Y. 2001. *Fauna of Ukraine. Mollusca*. Veles, Kyiv, **29** (1), 240 [In Russian].
- Baldwin, R. A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy*, **11** (4), 854–866.
- Blank, L., Blaustein, L. 2012. Using ecological niche modeling to predict the distributions of two endangered amphibian species in aquatic breeding sites. *Hydrobiologia*, **685** (1), 121–134.
- Burnham, K. P., Anderson, D. R. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, 353.
- Carpenter, S. R., Kraft, C. E., Wright, R. et al. 1992. Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. *American Naturalist*, **140** (5), 781–798.
- Dudgeon, D., Arthington, A. H., Gessner M. O. et al. 2006. Freshwater biodiversity: importance, threats, status

- and conservation challenges. *Biological Reviews*, **81** (2), 163–182.
- Eichwald, E. 1830. *Naturhistorische Skizze von Lithauen, Vollhynien und Podolien in geognostisch–mineralogischer, botanischer und zoologischer Hinsicht*. Zawadzki, Wilna, 256.
- Elith, J., Graham, C. H., Anderson, R. P. et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29** (2), 129–151.
- Elith, J., Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 677–697.
- Elith, J., Phillips, S. J., Hastie, T. et al. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17** (1), 43–57.
- Ghalambor, C. K., Huey, R. B., Martin, P. R. et al. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, **46** (1), 5–17.
- Guisan, A., Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8** (9), 993–1009.
- Hammer, Q., Harper, D. A. T., Ryan, P., D. 2001. Past: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, **4** (1), 4–9.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22** (2), 415–427.
- Janzen, D. H. 1967. Why mountain passes are higher in tropics. *American Naturalist*, **101** (919), 233–239.
- Kriticos, D. J., Webber, B. I., Leriche, A. et al. 2012. CliMond: global high resolution historical and future scenario climate surfaces for bioclimatic modeling. *Methods in Ecology and Evolution*, **3** (1), 53–64.
- Kumar, S., Spaulding, S. A., Stohlgren, T. J. et al. 2009. Potential habitat distribution for the freshwater diatom *Didymosphenia geminata* in the continental US. *Frontiers in Ecology and the Environment*, **7** (8), 415–420.
- Milanovich, J. R., Peterman, W. E., Nibbelink, N. P., Maerz, J. C. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. *Plos One*, **5** (8), 12–189.
- Phillips, S. J., Anderson, R. P., Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling*, **190** (3–4), 231–259.
- Poff, N. L., Brinson, M. M., Day, J. W. 2002. *Aquatic ecosystems and global climate change: Potential impacts on inland freshwater and coastal wetland ecosystems in the United States*. Dew Center on Global Climate Change, Washington, D. C., 44.
- Research Fronts 2014. *100 Top Ranked Specialties in the Sciences and Social Sciences*. Compiled by Thompson Reuters in cooperation with the National Science Laboratory, Chinese Academy of Sciences (NSCL), Annual report, 62.
- Stadnichenko, A. P., Skok, T. L., Stelmashchuk, N. M. 2011. Saving and restoring species of mollusks in Ukraine for environmentally sustainable development of freshwater fauna — an important task of modern zoology. *Visnyk of the Volynian University. Ser. Biology*, **19**, 76–81 [In Ukrainian].
- Starobogatov, Y. I. 1970. *The Molluscan Fauna and Zoogeographical Zoning of the Continental Water Bodies of the World*. Nauka, Leningrad, 372 [In Russian].
- Stelmashchuk, N., Stadnichenko, A. 2011. What do we know now about *melanopsids* (Mollusca: Pectinibranchia: Melanopsidae) of Ukraine. *Visnyk of the Lviv University. Ser. Biology*, **57**, 12–23 [In Ukrainian].
- Stefan, H. G., Preud'homme, E. B. 1993. Stream temperature estimation from air temperature. *Journal of the American Water Resources Association*, **29** (1), 27–45.
- Swets, K. 1988. Measuring the accuracy of diagnostic systems. *Science*, **240** (4857), 1285–1293.
- Wenger, S. J., Isaak, D. J., Luce, C. H. et al. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proc Natl Acad Sci USA*, **108** (34), 14175–14180.
- Wenz, W. 1938. Gastropoda, Teil 1. In: *Handbuch der Paläozoologie*. Berlin, 1639.
- Wiens, J. J., Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36** (1), 519–539.

Received 27 May 2015

Accepted 4 August 2015