# MULTI-SCALE ASSESSMENT OF THE POTENTIAL DISTRIBUTION OF TWO HERPETOFAUNAL SPECIES

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# Multi-Scale Assessment of the Potential Distribution of Two Herpetofaunal Species

By

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# Abstract

The geographic distribution of reptiles and amphibians has been estimated over the years using several different modeling techniques which employ a set of environmental predictor variables and sets of occurrence records. This study aims at estimating and comparing two herpetofaunal species potential distribution maps generated using: 1- different spatial scales, 2- different sets of environmental predictor variables at each scale and 3- three different modeling techniques (BIOCLIM, GARP, MAXENT). Receiver operating characteristic (ROC) curves and the Kappa statistic were utilized to measure the classification accuracy of the models. The McNemar test was applied to evaluate if there were significant differences between the models. Finally, a Jackknife procedure implemented in MAXENT allowed for a qualitative analysis of variables importance regarding their influence in the description of the species distributions.

Overall, the MAXENT technique achieved better predictions than the other modeling techniques, except at the local scale where GARP performed better. Through the use of only climatic variables, all models predicted better than a prediction by chance ($p < 0.0001$) at the continental scale. For *Bombina variegata* at the regional scale, MAXENT was the only algorithm capable to integrate other type of data different from climate and predict correctly its distribution ($p < 0.0001$). All models predicted correctly the distribution of *V. ursinii* at the regional scale. At the regional scale not only climatic variables but soils and slope are important predictor defining the distribution of *Bombina variegata* while for *Vipera ursinii* climatic variables were still the most important ones. At the local scale both algorithms predicted correctly ($P < 0.0001$) except in the case of *Bombina variegata* where only GARP was able to predict correctly. Distance to streams appeared to have a significant influence on *B. variegata* and climatic plus land cover to *V. ursinii*. The use of different scales to model the spatial distribution of the target species gave a better understanding of their habitat relationships and their variation in space.

# Acknowledgements

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I remember one lecture given by Dr. Jan de Leeuw; he was talking about the Neanderthals and how through the language and communication skills humans managed to survive and evolved in those times. My dear friend Dan, we were a couple of Neanderthals when we started our projects but we managed to survive and to accomplish this task. I truly appreciate our conversations and discussions that made me understand and gave me brilliant ideas about my topic.

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Sigo avanzando en mi vida personal y profesional y siempre tengo a mi lado el apoyo de toda mi familia. Una dedicación especial a mi mama, a los berraquitos de mis hermanos y a mis abuelos mami Inés y papi Ricardo.

Definitely, one do things better when there is a motivation. Thanks for being next to me all this time, thanks for listening to me, thanks for your love. You are my motivation; you are my life Olga Sacharow.

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# 1. Introduction

Habitat loss, land cover change, over exploitation, alien species, infectious diseases and even global change, are all recognized causes of herpetofaunal diversity decline (Alford et al., 2001; Collins and Storfer, 2003; Cushman, 2006; Goode et al., 2005; Goode et al., 2004). Even though these processes are continuously taking place all over the world, Hounahan et al. (2000) stated that amphibians decline stabilized after the 1960s in Western Europe. Thus, a key step in any conservation plan involving herpetofauna is to estimate its potential geographic distribution and the environmental factors that determine it.

Different attempts have been made to describe herpetofaunal spatial distribution. In some cases the authors have divided the group into amphibians and reptiles (Bock et al., 1981; Rodriguez et al., 2005; Segurado and Araujo, 2004), or into lizards, snakes and amphibians (Lee, 1980) or even into salamanders, frogs, toads, turtles, lizards, and snakes (Owen, 1989) all of them assuming that the chosen taxonomic treatment is considered to be evolutionarily and ecologically relevant. General relationships between distributional patterns and environmental factors have been described and ecological hypotheses have been tested by means of these investigations. Nevertheless, general patterns that apply for the herpetofauna as a group may not apply for some specific species. For example, the suggestion that reptiles benefit from forest cover in the landscape may not apply to particular reptile species that depend on nonforested habitats. There is very limited knowledge of specific amphibian and reptiles species-environment relationships and their distribution (Hazell, 2003).

Reliable understanding of species distribution and interactions with their environment requires careful attention to both characterization of the environment and scale (Cushman, 2006). The environmental characteristics that define the species distribution at one scale may not be the same that influence it and define it at different scales (Grand and Cushman, 2003; Levin, 1992). Consequently, it is a difficult task to estimate which is the right scale to study species-habitat relationships (distributional ranges). Investigations have been carried out concerning the multi-scale approach but most of them applied to birds (Fuhlendorf et al., 2002; Thompson and McGarigal, 2002). But when it comes to herpetofaunal spatial distribution studies, very few investigations considering the multi-scale approach can be found (Fischer et al., 2004).

To address the issue of the multi-scale approach in species distribution studies, Geographical Information Systems (GIS) and remote sensing technology have played an important role (Guisan and Zimmermann, 2000). The availability of different types of images (e.g. multispectral images, digital elevation models) on a broad range of spatial resolutions provides a mean to generate sets of environmental variables at different scales that can potentially influence the distribution of species in space.

There is also a great variety of statistical tools and techniques to model the species geographic distribution (Guisan and Zimmermann, 2000). These tools and techniques have diverse approaches to handle the species occurrence data that are being used as input to the models (Elith, 2002; Guisan and Zimmermann, 2000; Segurado and Araujo, 2004). After an extensive analysis of different modeling performances, Segurado & Araujo (2004) concluded that it is doubtful a unique and optimal distribution for accurately modeling will ever be identified and they recommend the modeller either (1) to use expert system models or models seen to be generally robust or; (2) choose a method that adjusts to the type of data and objectives pursued.

## 1.1. Research Problem

Guisan and Zimmermann (2000) pointed out that choosing a statistical technique to model the species distribution would be facilitated if comparatives studies are carried out. Since there are a great variety of models it is then a challenging task to choose the appropriate modeling technique and only multi-model comparisons can deal with this issue. This approach was employed here to evaluate the performance of three different modeling techniques.

There are few investigations both, where the spatial distribution of single herpetofaunal species is being model at different scales (Real et al., 2005) and where the important predictor variables at varying spatial scales for the same species are studied (Fischer et al., 2004). It is the purpose of this research to gain insight as to which predictor variables define better single species distribution at different scales.

## 1.2. Research Objectives

This study aims at estimating and comparing the potential spatial distribution of two herpetofaunal species *(Bombina variegata* and *Vipera ursinii)* by using: 1- different spatial scales, 2- different sets of environmental predictor variables at each scale and 3- three different modeling techniques, BIOCLIM, GARP (Genetic Algorithm for Rule-set Production) and MAXENT (Maximum Entropy). To accomplish this, the following specific objectives are proposed:

1. To generate different sets of predictor variables at each scale by means of spatially explicit data.

2. To investigate the accuracy of the species potential spatial distribution maps.

3. To determine if there is a significant difference between the accuracy of the different species potential spatial distribution maps.

4. To evaluate, *a posteriori*, the predictor variables that are more significant at each scale to model the potential spatial distribution of the target species.

## 1.3. Research Question

Following the sequence of the research objectives, the research questions that can be derived were formulated as follows:

1. Based on the chosen set of predictor variables and the species occurrence observation points at each scale, how accurate are the species potential spatial distribution maps?

2. Is there any significant difference between the accuracy of the maps generated from different modeling techniques? Does any model perform significantly better than the others?

3. Which predictor variables are more significant, at each scale, to model the potential spatial distribution of the target species?

## 1.4. Research Hypothesis

Given a set of predictor variables and a set of species occurrence observations at each scale, the three modeling techniques can generate accurate potential spatial distribution maps of the target herpetological species.

*Hypothesis 1:*

- $H_o$: Based on the chosen predictor variables, the estimated potential spatial distribution of the species does not predict better than a prediction by chance.
- $H_a$: Based on the chosen predictor variables, the estimated potential spatial distribution of the species do predict better than a prediction by chance.

*Hypothesis 2:*

- $H_o$: There is no a significant difference between the accuracy of the maps generated using different modeling techniques.
- $H_a$: There is a significant difference between the accuracy of the maps generated using different modeling techniques.

## 1.5. Research Approach

Three main stages can be identified in the research approach: (1) Data Management, (2) Modeling, and (3) Validation and Comparison (figure 1). A detail description of every stage and the activities carried out is shown in the methods section.

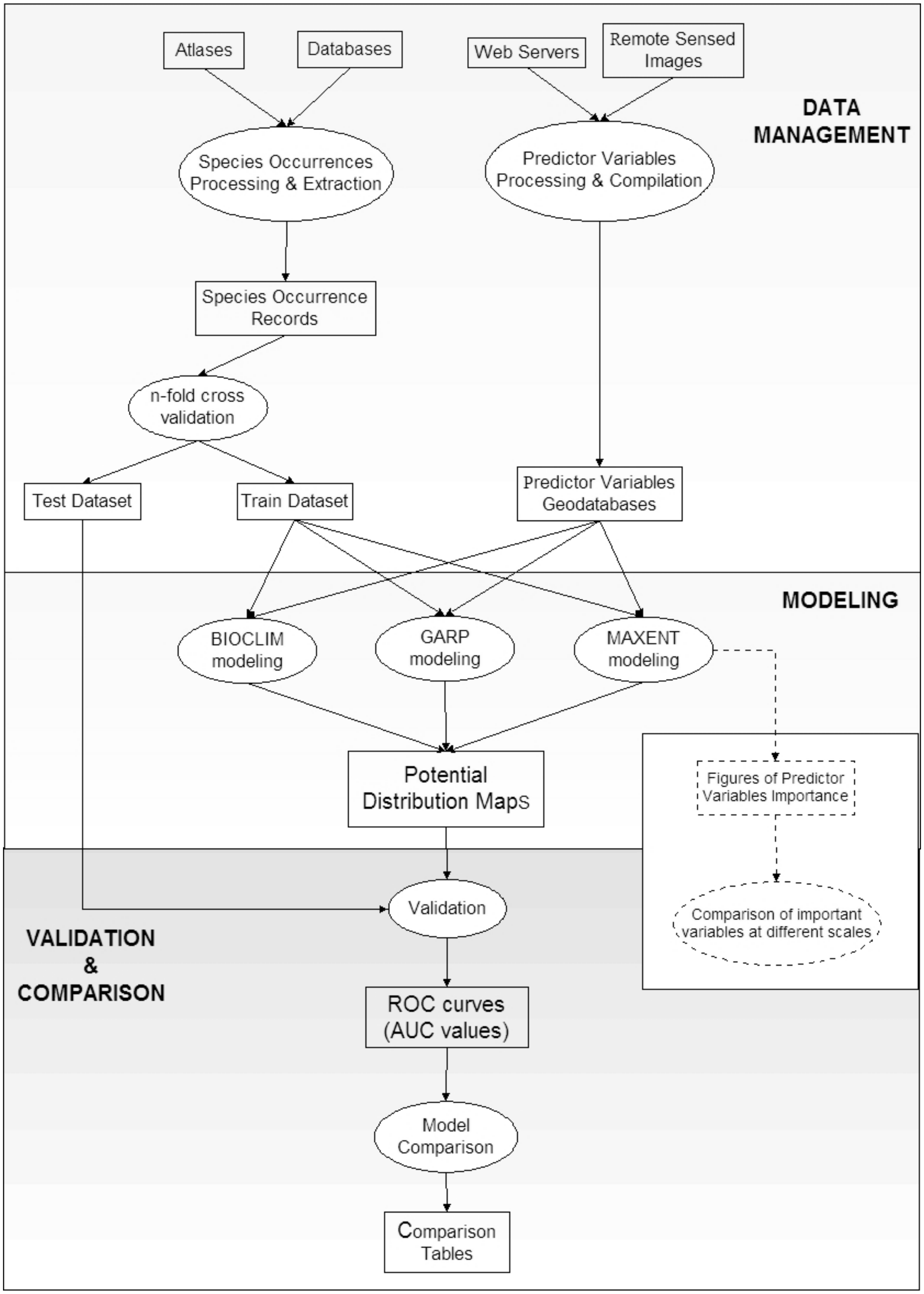


*Figure 1. Diagram showing the research approach and the different stages of the study*

# 2. Methods

## 2.1. Study Areas

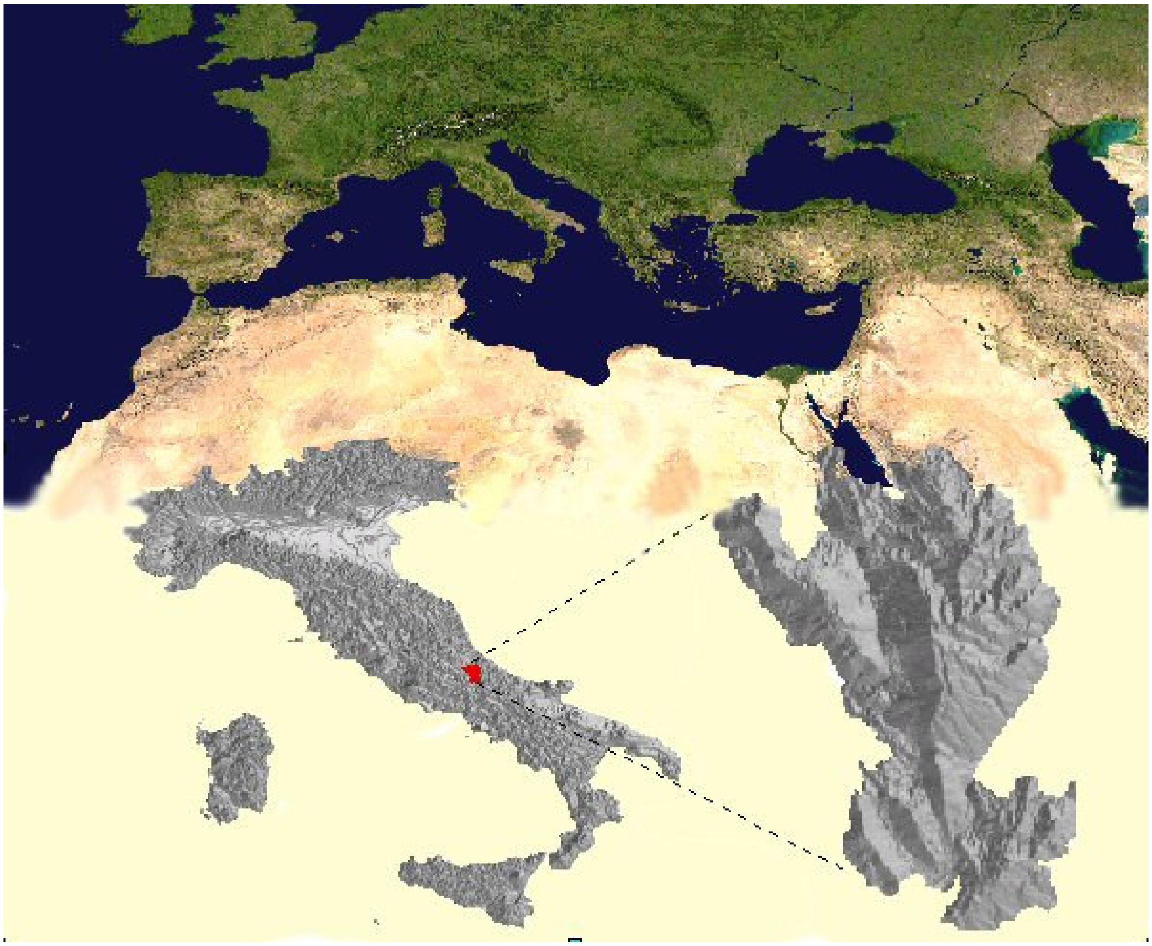


*Figure 2. Figure showing the three study areas selected to map the species' potential distribution: (1) Continental area (20 x 20 Km), (2) Italy (1 x 1 Km), (3) Majella National Park (15 x 15 m).*

Three study areas with different extents and managed at different scales (pixel resolution) were considered in this study to examine the species' potential distributions. Continental scale (54.21°N – 23.76°N, 18.14°W – 53.88°E). The area includes the Mediterranean Basin, north of Europe and part of west Asia. At this scale the data was handled at 20 km by 20 km pixel resolution.

At the regional scale Italy was chosen. It covers 294,020 km² and consists of the boot-shaped Italian peninsula, the Po River valley, and two large islands in the Mediterranean Sea, Sicily and Sardinia. The Apennine Mountains form the backbone of this peninsula, leading north-west to where they join the Alps, the mountain range that then forms an arc enclosing Italy from the north. Here is also found a large alluvial plain, the Po-Venetian plain, drained by the Po River and its many tributaries flowing down from the Alps (Wikipedia_Contributors, 2006). The information at this scale was treated at 1 km by 1 km pixel resolution.

The third study area is the Majella National Park, located in the Abruzzi region, Italy (figure 2); it covers a total area of 74095 hectares (Majella-National-Park-Authority, 2004). The Park is made up of four main elements: the *Majella*, a wide and compact calcareous massif, the *Morrone*, the *Porrara* and the *Monti Pizzi,* with the valleys and the karst planes interposing between them. Beech wood is predominant in the forests and alpine pines at high altitudes. The spatial information at this particular scale had a pixel resolution of 15 meters by 15 meters.

## 2.2. Herpetological Species

### *2.2.1.* ***Bombina variegata*** Linnaeus, 1758

This species is distributed over much of central and southern Europe. It is generally present from central France through southern Germany and northern Switzerland, much of Italy, the Balkan region and the Carpathian Mountains. Isolated populations are present in western France, north-western Italy, Sicily (Italy) and Hungary. It is probably extinct in Belgium, and has been introduced to the UK (IUCN-Conservation-International-and-NatureServe, 2004).

The isolated populations from the Apennine peninsula have an allopatric distribution and have been considered as a subspecies, *B. v. pachypus* Bonaparte, 1938. The subspecies however was afforded the species status by Lanza and Vanni (1991) on the basis of electrophoretic results. Nevertheless the two species are treated in this study as only one (i.e. *Bombina variegata*).

*Figure 3.* Bombina variegata*: (a) dorsal view, (b) ventral view. The pictures were taken from club100 (2006)*

The species can be found in coniferous, deciduous and mixed forests, bush lands and meadows, floodplains and grasslands. At low elevations this species lives in deciduous forests, at higher altitudes it is more often found in coniferous forests and highland glades. The species uses many types of wetland, including lakes, ponds, swamps, rivers, stream pools, springs (including mineral and thermal springs), puddles, reservoirs, gravel pits, ditches and even water filled wheel ruts. The breeding habitats are typically unshaded temporary pools within or close to woodlands (IUCN-Conservation-International-and-NatureServe, 2004).

The species occurs mainly in hills and medium altitude mountains but does not go above tree line. The species has an altitudinal range of 100 to 2100 meters above sea level. Population decrease is due to climatic factor such as low precipitation or temperature. The disappearance of small water bodies is their main threat (Gasc et al., 1997).

### *2.2.2.* ***Vipera ursinii*** Bonaparte, 1833

The ursinii taxon has most fragmented distribution due to its two extreme habitat priorities: lowland warm dry meadow-steppe habitats and alpine/subalpine dry meadow-steppe habitats. The lowland distribution has been reduced to about four remaining populations in Hungary. The situation is the same for the Moldavian, Ukrainian and Russian lowland populations which has been reduced to small pocket, often along the river valleys and in topographic landscapes difficult to bring under cultivation. The alpine/subalpine populations are distributed in a belt from France in the West to China in the East. In France the distribution is restricted to the southeast corner. In central Italy it is known from the three central Apennine massifs (Gasc et al., 1997).

*Figure 4.* Vipera ursinii *Bonaparte, 1933. Taken from Mazzei et al. (2006)*

In lowlands, the species is distributes from sea level to about 800 meters above sea level and in alpine/subalpine, between 1200 and 3000 meters above sea level (Gasc et al., 1997; Joger et al., 2005). Lowland populations are in a critical situation; the habitats are destroyed by monocultural agriculture, draining, repeated fires, road constructions, and overgrazing by cattle, sheep and geese. Reconstruction of building of ski-runs, radar stations and roads are important reasons for the habitat destruction in the Alpine environment (Gasc et al., 1997).

The taxon is composed of several subspecies and at least the populations located in Russia and Ukraine have been considered to be a separate species, *V. u. renardi* Christoph, 1861 (Nilson and Andrén, 2001). All the subspecies and *V. renardi* were considered in this study as only and the same one species; *Vipera ursinii*.

## 2.3. Data Management

The first task of the research was to search and to process both the information available concerning data-points representing species occurrence and the environmental predictor variables, which were derived from remote sensing images. The set of predictor variables used at each scale was chosen using a deductive approach; the selection relied on expert knowledge and on secondary information regarding the particular species.

### 2.3.1. Species records extraction

***Continental Scale***

The species presence records were extracted from the Atlas of Amphibians and Reptiles in Europe (Gasc et al., 1997). In this Atlas, the regular presence of the species is displayed according to the European network of meshes (50 km x 50 km) using the UTM system (ERTS89/UTM35N). However, in the final maps, only points (not the grid itself) are displayed.

In order to extract the species presence points from the maps, the same 50 km x 50 km polygon vector grid was created according to the set of rules mentioned in the book as follows: when the base of the polygon was between 16 and 33 Km wide, two twin polygons were merged into one. When the base was less than 16 Km wide the two twin polygons were added to the regular polygon immediately to the left from one of them or to the right from the other (Gasc et al., 1997).

Finally, the polygon vector grid was reprojected to geographical coordinates (GCS_WGS84) and clipped to the continental area to avoid having areas over the ocean. Therefore, the final polygon vector grid consisted of polygons with different shapes and sizes. Given this, and because the predictor variables are 20 km by 20 km resolution, random points were generated for the polygons where the species were present. The number of random points selected was proportional to the size of the polygon. The rest of the polygons were considered as absences.

***Regional Scale (Italy)***

The occurrence points for Italy were obtained from two sources. For each source a different method was applied. The first source of information was an Excel database with a list of different herpetological species in the Lazio province in Italy. From this database the information with reference to the specific location (latitude and longitude coordinates) of the species of interest was extracted.

The second source of information (only for *B. variegata*) consisted of a set of jpg images of the distribution of the species in some of the provinces in Italy. These images were georeferenced and projected to geographic coordinates (GCS_WGS84). However, the distribution maps were originally generated using a grid size of 10 km x 10 km. Thus, an Italy polygon grid of 1 km x 1 km grid size was created. This Italy polygon grid was overlaid over the georeferenced maps and the occurrence points were extracted marking all the cells of the Italy polygon grid where the species were present. Finally 5 random single polygons of 1 km by 1 km were chosen from the Italy polygon grid within the extent of each 10km by 10 km occurrence locations. The rest of the polygons were considered as absences.

***Local Scale (Majella National Park)***

The datasets containing the occurrence points for the species were obtained from previous fieldwork campaigns done by researchers at the University of Rome "La Sapienza". These datasets include the geographic coordinates where the species were collected. The information was projected to UTM coordinates (WGS84/UTM33N). A polygon grid of 15 mt by 15 mt was created to the extent of the Park and the single polygons where the species were present were marked as presence and the rest as absence.

### 2.3.2. Predictor variables compilation

The species' potential distributions were examined at three different extents and scales (e.g. pixel resolution). All variables at the continental scale were recorded at a pixel size of 0.166° by 0.166° (aprox. 20 $Km^2$), at the regional scale (Italy) at a pixel size of 0.0083° by 0.00083° (aprox. 1 $Km^2$), and at a local scale (Majella National Park) at a pixel size of 15m by 15 m (Table 1).

The climatic data were extracted from the WORLDCLIM database. These data are described in Hijmans et al. (2005). The data were generated through interpolation of average monthly climatic data from weather stations around the world. The data were downloaded from the internet (Hijmans et al., 2006) in ESRI grid format (20 by 20 Km and 1 by 1 Km pixel resolution) and processed in ArcGIS® 9.0. To generate the climatic variables at 15 m by 15 m resolution, points were generated for each pixel of the 1 km by 1 km grids; then, based on this grid of points, interpolations were performed using the ordinary Kriging method.

All topographical predictors used in this study were derived from digital elevation models (DEM) at a resolution of 1 km x 1 km for Italy and 15 m x 15 m for Majella National Park. The DEM used at the local scale was generated using Aster Stereo Image data. Slope angle and aspect were derived from elevation in ArcGIS® 9.0 (in-built functions). These variables were left as continuous. The potential direct solar radiation was calculated also from the digital elevation model (DEM) following the method developed by Kumar et al. (1997) which incorporates topographic shading effects. The values were calculated every 30 minutes and summed up for a complete year. The soil layer used in the models at regional scale (Italy) was taken from the digital soil map of the world (FAO-UNESCO, 1997).

An ASTER image, dated June 9, 2001 was used to generate the land cover map of Majella National Park. A neural network backpropagation algorithm was implemented to classify the image (Skidmore et al., 1997) . A three layer network was employed. The algorithm assigns random weights to the input nodes hence every time the process is run different outputs are obtained. The classification was performed 20 times (learning rate 0.2, momentum 0.3) and the critical system parameters (number of epochs, total system error,) were written to a file. These files were compared and the output with the highest percentage of test data correctly predicted was chosen. All the procedures were developed in

ENVI 4.1. (RSI, 2004). The final land cover map consisted of six land cover classes: (1) pines; (2) forest; (3) natural grass; (4) bare soil; (5) cultivated grass; and (6) urban areas.

During the modeling process not only the outputs must be validated by an accuracy assessment analysis but also the data used as input to the models have to be validated (Corsi, 2004). To validate the six classes land cover map through a valid error matrix, 706 samples should be taken according to the number of samples required based on a multinomial distribution (95% confidence interval, 5% precision) (Congalton and Green, 1999). Due to time and accessibility limitations, a mix of cluster and random sampling techniques (Lo and Watson, 1998; Plourde and Congalton, 2003) was carried out. A 200 meters buffer to the roads was established and within that buffer random points were selected. Only accessible points were sampled. The accuracy of the land cover map was estimated using overall accuracy and the *Khat* statistic (Cohen, 1960; Congalton, 1991). The accuracy analysis was performed in the ArcView extension Cohen's Kappa and Classification Table Metrics 2.0. (Jennes and Wynne, 2005).

*Table 1. List of the predictor variables used in the models. They represent aspects of topography, climate, habitat and human disturbance*

| | ***Bombina variegata*** | | | ***Vipera ursinii*** | | |
|---|---|---|---|---|---|---|
| **Predictor Variables** | CONTINENTAL | ITALY | MAJELLA | CONTINENTAL | ITALY | MAJELLA |
| Annual Mean Temperature | X | X | X | | | |
| Mean Temperature Driest Quarter | | | | X | X | X |
| Mean Temperature Warmest Quarter | X | X | X | X | X | X |
| Annual Precipitation | X | X | X | X | X | X |
| Precipitation of the Wettest Quarter | X | X | X | | | |
| Precipitation of the Driest Quarter | | | | X | X | X |
| Precipitation of the Warmest Quarter | | | | X | X | X |
| Altitude | | X | X | | X | X |
| Aspect | | X | X | | X | X |
| Slope | | X | X | | X | X |
| Radiation | | | X | | | X |
| Land Cover | | X | X | | X | X |
| Soil | | X | | | X | |
| Distance to Roads | | | X | | | X |
| Distance to Streams | | | X | | | X |
| Distance to Towns | | | X | | | X |

The classified land cover map produced an overall accuracy of 82% and a *Khat* statistic of 0.72. It has been reported previously that the backpropagation neural network algorithm can perform well and better than other conventional classifiers when modeling general land cover classes as is the case here (Fitzgerald and Lees, 1992; Skidmore et al., 1997).

The distance to streams variable was produced based on the streams derived from the DEM using the Hydrology geo-tool in ArcGIS® 9.0 (in-built functions). The distance to roads variable was generated after digitalizing all the roads from the Majella National Park tourist map

(Parco_Nazionale_della_Majella, 2002). The variable distance to towns was created extracting the towns land cover from the land cover map and estimating the distance.

Although it is common use to apply some correlation analysis to evaluate which variables correlate to each other and extract the significant ones to use as inputs in the models (Barbosa et al., 2003), in this research it was decided on a more deductive approach, in which the set of predictor variables were chosen as they are believed to be causal, driving forces for the distribution of the target species at the different scales (Dettki et al., 2003; Guisan and Zimmermann, 2000). Thus, based on secondary information (e.g. literature) and personal conversation with experts, different sets of predictor variables were chosen for the target species.

## 2.4. Modeling Techniques

There is an extensive list of modeling techniques and algorithms available to investigate the relation between the predictor variables and species presence datasets in order to map their spatial distribution (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). Three of these techniques were used here: BIOCLIM (Busby, 1991; Nix, 1986), Genetic Algorithm for Rule-set Production (GARP) (Stockwell and Noble, 1992; Stockwell and Peters, 1999) and Maximum Entropy (MAXENT) (Phillips et al., in press; Phillips et al., 2004).

### 2.4.1. BIOCLIM (Environmental Envelope)

Skidmore (2002) explains briefly how BIOCLIM operates: "The BIOCLIM algorithm determines the distribution of plants and animals based on climatic surfaces. It models the species response to interpolated climatic variables by means of an environmental envelope. Firstly, the BIOCLIM process involves ordering each variable. Secondly, if the climate value for a grid cell falls within a user-defined range (for example, the 5th and 95th percentile) for each of the climatic variables being considered, the cell is considered to have a suitable climate for the species. Using a similar argument, if the cell values for one (or more) climatic variables fall outside the 95th percentile range but within the (minimum) 0-5th percentile and (maximum) 95-100th percentile, the cell is considered marginal for a species. Cells with values falling outside the range of the sample data (for any of the climatic variables) are considered unsuitable for the species."

The BIOCLIM model was implemented in the software *DIVA*-GIS (*DIVA*-GIS, 2005). Duplicates and points falling within the same grid were removed from the analysis. A percentile value of 0.01 was set to find out and exclude from the analysis the extreme observations in terms of climate. The outputs of the model are given in values between 0 and 500 representing the percentile values of areas suitable or not suitable for the target species. Those values were divided by 500 to obtained new values between 0 and 1.

The software *DIVA*_GIS brings *in-built* climatic layers, taken from the WORLDCLIM database. However, there are not available layers at the 15 meters by 15 meters pixel resolution, consequently, the BIOCLIM model was not used to estimate the potential spatial distribution of the species at the local scale.

### 2.4.2. GARP (Genetic Algorithm for Rule-set Production)

The algorithm seeks a collection of rules that together produce binary prediction. A genetic algorithm is used to search heuristically for a good rule-set (Stockwell and Noble, 1992). Since there is a large random variability in GARP prediction, the best-subset selection procedure was implemented as follows: 50 binary models were generated with default values for its parameters (0.01 covergence limit, 1000 maximum iterations and allowing the use of only logit rules). Then a hard omission threshold of 10% was established and all models greater than this threshold were eliminated. Finally, only ten models under the threshold value were selected and combined to make a composite GARP prediction, in which the value of a pixel was equal to the number of best-subset models in which the pixel was predicted present (0-10). Similar procedures have been implemented by Anderson et al. (2003) and Raxworthy et al. (2004). The final values were divided by ten to get values between 0 and 1.

### 2.4.3. Maxent (Maximum Entropy)

Maxent is a species distribution modeling technique that uses presence-only datasets. As Phillips, et al. (in press) mentioned: “The idea of MAXENT is to estimate a target probability distribution by finding the probability distribution of maximum entropy, subject to a set of constraints that represent our incomplete information about the target distribution. The information available about the target distribution often presents itself as a set of real-valued variables, called “features”, and the constraints are that the expected value of each feature should match its empirical average (average value for a set of sample points taken from the target distribution”.

The user-specified parameters were set as default (regularization multiplier = 1, maximum iterations = 500, convergence threshold = $10^{-5}$, maximum number of background points = 10000, and use of linear, quadratic, product, threshold and hinge features).

To analyze the variables importance used in the modeling process a Jackknife procedure was applied. This technique is an in-built functionality of MAXENT. Each variable is excluded and a model is created with the remaining ones. Then a model is created using each variable in isolation (Phillips, 2006). The explanations of the results of this technique were made in a qualitative manner.

## 2.5. Validation & Comparison

In order to prevent low precision estimates or to overestimate the error rates of the accuracy resulting from sacrificing sample cases for validation purposes, an n-fold cross validation technique was adopted and carried out. Verbyla & Litvaitis (1989) made a description of this statistical technique in which the original dataset is randomly partitioned into n-nearly equal-sized subsamples. Then one of the subsamples must be excluded (test sample) and the model must be developed with the remaining ones (training sample). The accuracy of the model is estimated with the subsample previously excluded (test sample). Then the excluded subsample must be returned, a second subsample must be excluded and the procedure should be repeated. The final estimate of model accuracy is the mean of the previous estimates (Verbyla and Litvaitis, 1989).

The same training and test samples created at each different scale were used as the input occurrence points and testing sets respectively for all modeling techniques. In this manner proper comparisons could take place between the final accuracy estimates of the different distribution maps.

The five-fold cross validation was carried out for the continental occurrence datasets and also for *B. variegata* Italy dataset. For *V. ursinii* Italy dataset a three-fold validation was implemented. In the case of Majella National Park datasets a different method was applied due to the small sample of occurrence records. In this case the re-substitution method was performed (Verbyla and Litvaitis, 1989) in which the model's predictive ability was tested using the same samples used to train or to generate the model.

As mentioned in section 2.4 the original output values of the models was transformed to values between 0 and 1. However a value of 0.5 in all models does not have the same significance. This is due to the fact that the algorithms differ in the way they produce the output. Thus, an optimum threshold value ($P_{crit}$) was calculated to determine the value above or below which one declares a species to be present or absent. The threshold value at which sensitivity (conditional probability that case x is correctly classified) and specificity (conditional probability that x is miss-classified) are the same was chosen (Bonn and Schröder, 2001b; Schröder and Richter, 1999/2000). This threshold was used as the cut-off level to calculate the Kappa and the McNemar test.

### 2.5.1. Absence Data

One of the advantages of the models used in this research is that they do not need absence data like other models do (e.g. Generalized Linear Models). Unfortunately, the accuracy measures techniques available to estimate the accuracy of the model' outputs (i.e. Kappa, ROC curves), require absence records. Thus, random points to represent absence locations were taken from the polygon grids created previously to represent the presence locations of the species at the different scales. The absence points were chosen only within the geographic extent of the presence locations.

### 2.5.2. Kappa Statistic

The accuracy of the output of the different modeling techniques was calculated using the Kappa statistic (Cohen, 1960; Congalton, 1991). The kappa statistic assesses the extend to which models predict occurrence at a rate higher than expected by chance (Monserud and Leemans, 1992). The results vary between 1.0 for perfect agreement down to 0.0 for agreement only due to chance.

Because the prediction results from the models are given in continuous number ranging from 0 to 1 a cut-off point was established above or below which one declares a species to be present or absent (see section 2.5). Thus, the performance of the models were summarized in an error matrix that crosstabulates the observed and predicted presence/absence pattern (Fielding and Bell, 1997) and based on the values of this matrix the Kappa was calculated (Figure 5). Since Kappa is asymptotically normally distributed, a basic *z*-score can be used for significance testing, based on the associated *p* value (Congalton and Green, 1999). The calculations were made in the Cohen's Kappa and Classification Table Metrics 2.0 extension of ArcView® (Jenness and Wynne, 2005).

(a)

Actual

|  |  | + | - |
|---|---|---|---|
| Predicted | + | a | b |
|  | - | c | d |

(b)

$$K = \frac{(a+d) - \frac{(a+c)(a+b)+(b+d)(c+d)}{N}}{N - \frac{(a+c)(a+b)+(b+d)(c+d)}{N}}$$

*Figure 5. (a) confusion matrix for presence/absence patterns and (b) formula to calculate the Kappa statistic based on confusion matrix.*

### 2.5.3. Receiver Operating Characteristic (ROC) curves

The ROC is a threshold-independent technique. A ROC plot is obtained by plotting the fraction of correct classified cases on the *y* axis (sensitivity) against the fraction of wrong classified cases (1-specificity) for all possible thresholds on the *x* axis (Fielding and Bell, 1997). The area under the ROC function curve (AUC) is taken as a measure of overall accuracy that is not dependent upon a particular threshold (Deleo, 1993). It measures the probability, that in a pair randomly chosen out of the presence and absence data, the model will assign a higher probability of occurrence to the case with the observed presence (Bonn and Schröder, 2001a). The values of the AUC vary from 0.5 (no apparent accuracy) to 1.0 (perfect accuracy).

The ROC Plotting and AUC Calculation Transferability Test 1.3. software developed by Boris Schröder for the Institute for Geoecology, Potsdam University (Schröder, 2004), was used to calculate the AUC. ASCII tables were prepared having one column with the presence-absence values (e.g. 1 and 0) and a second column representing the prediction values generated by the modeling techniques. The tables where imported into the software and the calculation were run.

To estimate if the AUC values were significant different as compared to a prediction by chance (e.g. AUC = 0.5) a standard bootstrap method was implemented. This technique is a re-sampling method with replacement (Manly, 1997). The execution of the bootstrap was made in The ROC Plotting and AUC Calculation Transferability Test 1.3. A 95% confidence interval was chosen and 2000 bootstrap samples were used. The standard error, the *z* statistic, the *p* probability and the significance difference from the critical AUC (i.e. 0.5) were estimated.

### 2.5.4. Testing Differences in Model Performances – McNemar Test

As mentioned before the same training and test samples were used as the input and testing sets respectively for all modeling techniques. In that sense, the data in the error matrices generated with each model correspond to dependent samples. The McNemar test can cope with dependent test samples and its use has been recommended when comparing the performance of alternative modeling techniques (de Leeuw et al., 2006).

The McNemar test (McNemar, 1947) can be applied for dichotomous data represented in a 2 x 2 table (Table 2). The test calculates a measure, $(b - c)^2 / (b + c)$ that has an approximate $\chi^2$ value with 1 degree of freedom if b + c is larger than 10; if not, a binomial test must be applied (Zar, 1999).

Table 2. *Cross tabulation of number of correct and wrongly classified pixels for two modeling techniques. Based on two separate error matrices for method 1 and 2 respectively.*

|  | Model 2 |  |
|---|---|---|
| Model 1 | Correct | Incorrect |
| Correct | *a* | *b* |
| Incorrect | *c* | *d* |

# 3. Results

## 3.1. *Bombina variegata*

### 3.1.1. Potential distribution maps

Visually, BIOCLIM and GARP algorithms produced broadly similar predictions for the potential spatial distribution of *B. variegata* at the continental scale. For this species only BIOCLIM and GARP algorithms indicated suitable conditions throughout Belarus, West Russia and West Ukraine. GARP indicates also areas throughout Poland and East Germany while the MAXENT algorithm predicted absent for these areas (Figure 6).

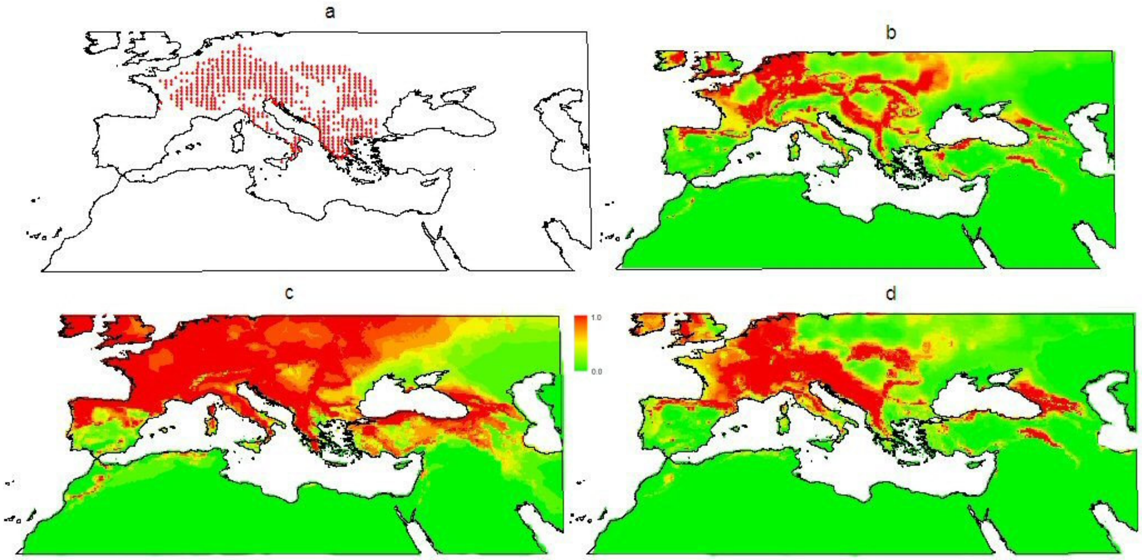


*Figure 6. Predicted potential distribution of Bombina variegata at the continental scale using all occurrence records. The location of the occurrence points are shown in (a). Results are given for BIOCLIM (b), GARP (c) and MAXENT (d). For comparison purposes the optimum threshold value ($P_{crit}$) was calculated: BIOCLIM = 0.07, GARP = 0.90, MAXENT = 0.19.*

From a visual interpretation of the prediction maps at the regional scale, it can be seen that the output prediction of BIOCLIM (which uses only climatic variables) is quiet different from the predictions obtained with GARP and MAXENT at the regional scale (Figure 7). First of all, the BIOCLIM prediction map shows a more homogeneous pattern while GARP and MAXENT showed a more patchy pattern. Secondly, BIOCLIM predicted a more extensive distribution for the species; it indicated suitable conditions for the species in the Po-Venetian plain at low altitudes whereas GARP and MAXENT did not (Figure 7).

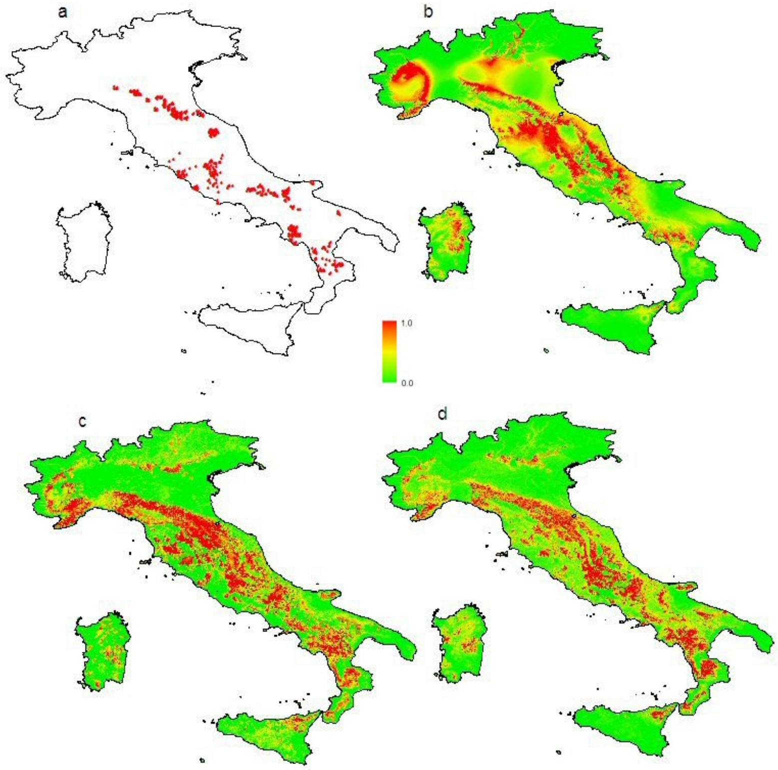


*Figure 7. Predicted potential distribution of Bombina variegata at the regional scale (Italy) using all occurrence points. The location of the occurrence points are shown in (a). Results are given for BIOCLIM (b), GARP (c) and MAXENT (d). For comparison purposes the optimum threshold value ($P_{crit}$) was calculated: BIOCLIM = 0.16, GARP = 0.30, MAXENT = 0.26.*

Considering the threshold values identified for both models, the two algorithms predicted quite different the location where the species could potentially be present (Figures 8). GARP indicated a more restricted distribution of the species (Figure 8c) while MAXENT predicted a more extensive distribution, especially along the streams (Figure 8d).

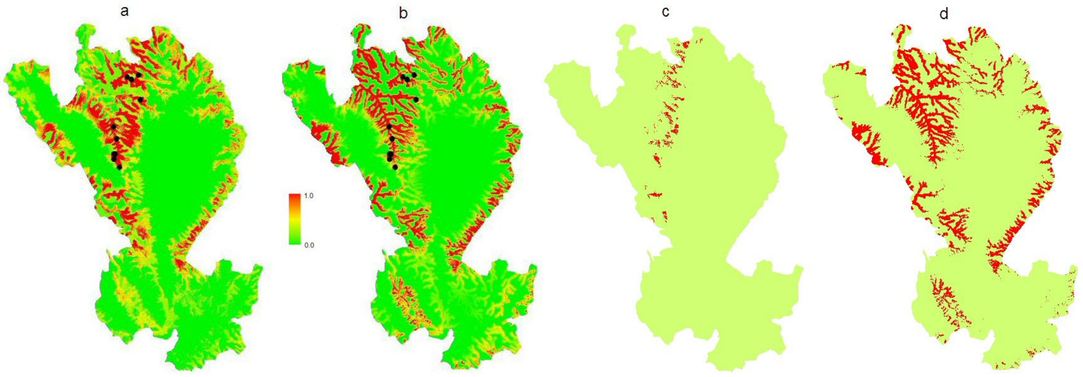
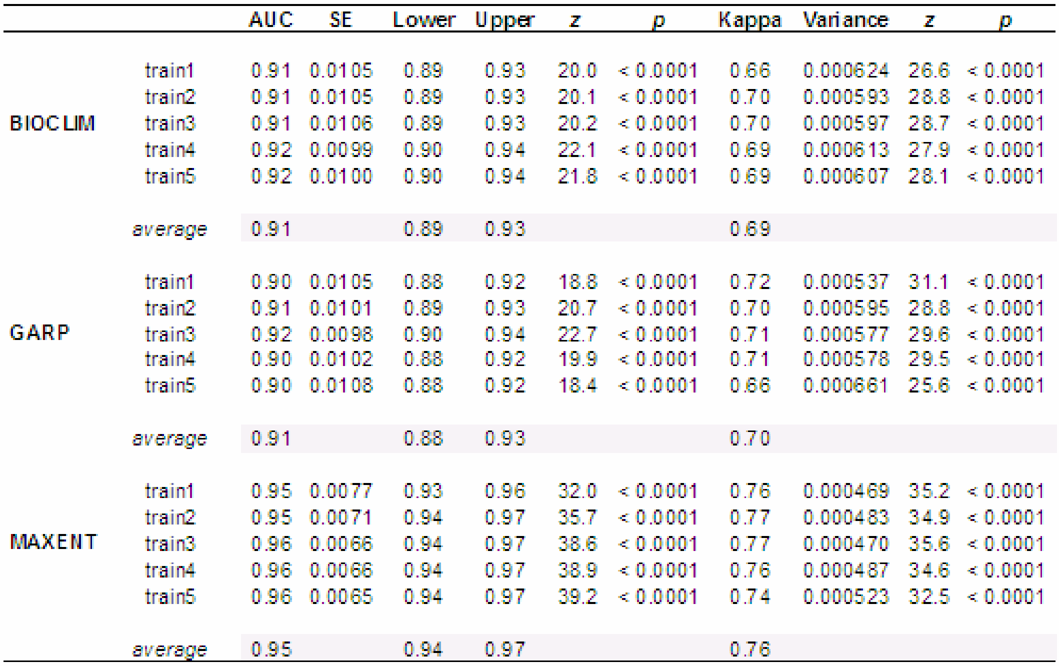


*Figure 8. Predicted potential distribution of* Bombina variegata *at the local scale (Majella). The black dots represent the occurrence points. Results are given for GARP (a) and MAXENT (b). For comparison purposes the optimum threshold value ($P_{crit}$) was calculated and displayed here as: GARP = 0.95(c), MAXENT = 0.43(d).*

### 3.1.2. Accuracy Assessment and Model Comparison test

For all training samples of the occurrence data, the AUC and Kappa values were highly statistically significant for all algorithms ($p < 0.0001$) indicating better than random predictions (Table 3). Figure 9a shows the ROC curves for the three algorithms at the continental scale using the third partition of the training samples. The performance of MAXENT was better across the entire spectrum: for any given proportion of test localities predicted correctly, MAXENT achieved that proportion with a lower false positive rate. The MAXENT prediction was significantly higher than that of GARP and BIOCLIM ($p < 0.001$; McNemar test). Furthermore, no significant difference was found between GARP and DIVA ($p > 0.05$; McNemar test). Results for other training samples were similar.

*Table 3. Results of receiver operating characteristic (ROC) and Kappa statistic analyses for* Bombina variegata *at the continental scale produced with the three modeling techniques. For each training sample, the area under the curve (AUC) and the Kappa statistic is given for BIOCLIM, GARP and MAXENT.*

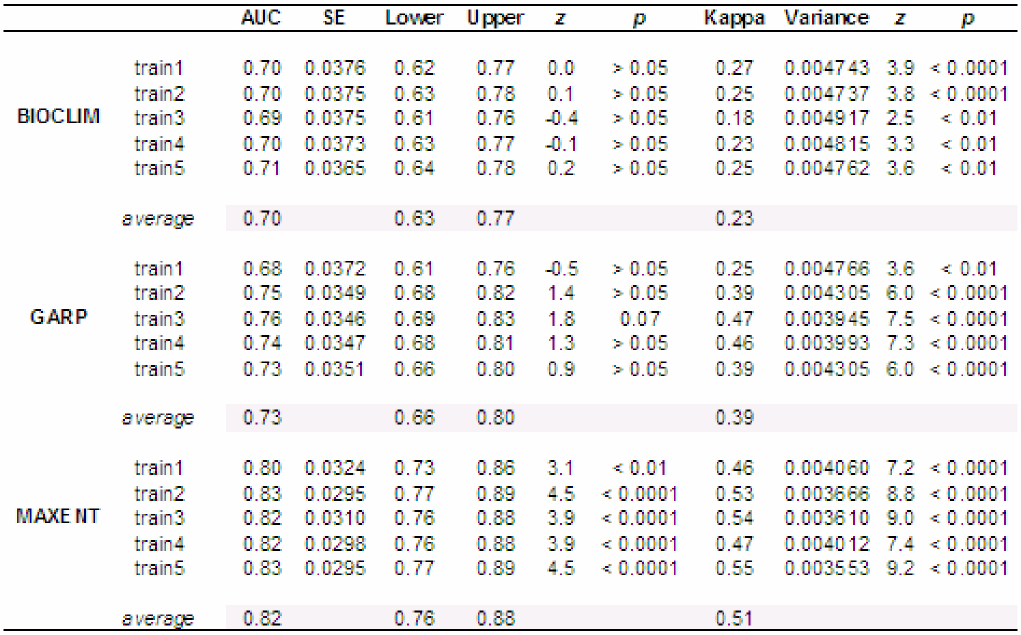


| | | AUC | SE | Lower | Upper | z | p | Kappa | Variance | z | p |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BIOCLIM | train1 | 0.91 | 0.0105 | 0.89 | 0.93 | 20.0 | < 0.0001 | 0.66 | 0.000624 | 26.6 | < 0.0001 |
| | train2 | 0.91 | 0.0105 | 0.89 | 0.93 | 20.1 | < 0.0001 | 0.70 | 0.000593 | 28.8 | < 0.0001 |
| | train3 | 0.91 | 0.0106 | 0.89 | 0.93 | 20.2 | < 0.0001 | 0.70 | 0.000597 | 28.7 | < 0.0001 |
| | train4 | 0.92 | 0.0099 | 0.90 | 0.94 | 22.1 | < 0.0001 | 0.69 | 0.000613 | 27.9 | < 0.0001 |
| | train5 | 0.92 | 0.0100 | 0.90 | 0.94 | 21.8 | < 0.0001 | 0.69 | 0.000607 | 28.1 | < 0.0001 |
| | *average* | 0.91 | | 0.89 | 0.93 | | | 0.69 | | | |
| GARP | train1 | 0.90 | 0.0105 | 0.88 | 0.92 | 18.8 | < 0.0001 | 0.72 | 0.000537 | 31.1 | < 0.0001 |
| | train2 | 0.91 | 0.0101 | 0.89 | 0.93 | 20.7 | < 0.0001 | 0.70 | 0.000595 | 28.8 | < 0.0001 |
| | train3 | 0.92 | 0.0098 | 0.90 | 0.94 | 22.7 | < 0.0001 | 0.71 | 0.000577 | 29.6 | < 0.0001 |
| | train4 | 0.90 | 0.0102 | 0.88 | 0.92 | 19.9 | < 0.0001 | 0.71 | 0.000578 | 29.5 | < 0.0001 |
| | train5 | 0.90 | 0.0108 | 0.88 | 0.92 | 18.4 | < 0.0001 | 0.66 | 0.000661 | 25.6 | < 0.0001 |
| | *average* | 0.91 | | 0.88 | 0.93 | | | 0.70 | | | |
| MAXENT | train1 | 0.95 | 0.0077 | 0.93 | 0.96 | 32.0 | < 0.0001 | 0.76 | 0.000469 | 35.2 | < 0.0001 |
| | train2 | 0.95 | 0.0071 | 0.94 | 0.97 | 35.7 | < 0.0001 | 0.77 | 0.000483 | 34.9 | < 0.0001 |
| | train3 | 0.96 | 0.0066 | 0.94 | 0.97 | 38.6 | < 0.0001 | 0.77 | 0.000470 | 35.6 | < 0.0001 |
| | train4 | 0.96 | 0.0066 | 0.94 | 0.97 | 38.9 | < 0.0001 | 0.76 | 0.000487 | 34.6 | < 0.0001 |
| | train5 | 0.96 | 0.0065 | 0.94 | 0.97 | 39.2 | < 0.0001 | 0.74 | 0.000523 | 32.5 | < 0.0001 |
| | *average* | 0.95 | | 0.94 | 0.97 | | | 0.76 | | | |

At the regional scale (Italy) BIOCLIM was not able to predict better than chance ($p > 0.05$) considering the AUC values (Table 4). Regarding the Kappa values, they show a poor agreement but still better than a random prediction ($p < 0.01$) (Table 4). Addition of potential variables different from climate should increase the AUC and Kappa, since there is more information available to the classifiers. However, GARP was not able to predict better than a prediction by chance considering the AUC ($p > 0.05$); also moderate kappa values were estimated from GARP results although better than a prediction by chance ($p < 0.01$) . At this scale only the MAXENT algorithm was able to predict correctly indicating a better than random prediction for both AUC and Kappa ($p < 0.0001$) (Table 4).

The ROC curves for the three algorithms at the regional scale showed the superiority of MAXENT over GARP and DIVA (Figure 9b). However, at low sensitivity and false positive rates the three algorithms performed similar. For all partitions of the training sample MAXENT was significantly better than that of GARP ($p < 0.05$; McNemar test) and highly significantly better than that of BIOCLIM ($p < 0.001$; McNemar test). No significant difference was found between GARP and DIVA ($p > 0.05$; McNemar test).

*Table 4. Results of receiver operating characteristic (ROC) and Kappa statistic analyses for* Bombina variegata *at the regional scale produced with the three modeling techniques. For each training sample, the area under the curve (AUC) and the Kappa statistic is given for BIOCLIM, GARP and MAXENT.*



| | | AUC | SE | Lower | Upper | z | p | Kappa | Variance | z | p |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BIOCLIM | train1 | 0.70 | 0.0376 | 0.62 | 0.77 | 0.0 | > 0.05 | 0.27 | 0.004743 | 3.9 | < 0.0001 |
| | train2 | 0.70 | 0.0375 | 0.63 | 0.78 | 0.1 | > 0.05 | 0.25 | 0.004737 | 3.8 | < 0.0001 |
| | train3 | 0.69 | 0.0375 | 0.61 | 0.76 | -0.4 | > 0.05 | 0.18 | 0.004917 | 2.5 | < 0.01 |
| | train4 | 0.70 | 0.0373 | 0.63 | 0.77 | -0.1 | > 0.05 | 0.23 | 0.004815 | 3.3 | < 0.01 |
| | train5 | 0.71 | 0.0365 | 0.64 | 0.78 | 0.2 | > 0.05 | 0.25 | 0.004762 | 3.6 | < 0.01 |
| | average | 0.70 | | 0.63 | 0.77 | | | 0.23 | | | |
| GARP | train1 | 0.68 | 0.0372 | 0.61 | 0.76 | -0.5 | > 0.05 | 0.25 | 0.004766 | 3.6 | < 0.01 |
| | train2 | 0.75 | 0.0349 | 0.68 | 0.82 | 1.4 | > 0.05 | 0.39 | 0.004305 | 6.0 | < 0.0001 |
| | train3 | 0.76 | 0.0346 | 0.69 | 0.83 | 1.8 | 0.07 | 0.47 | 0.003945 | 7.5 | < 0.0001 |
| | train4 | 0.74 | 0.0347 | 0.68 | 0.81 | 1.3 | > 0.05 | 0.46 | 0.003993 | 7.3 | < 0.0001 |
| | train5 | 0.73 | 0.0351 | 0.66 | 0.80 | 0.9 | > 0.05 | 0.39 | 0.004305 | 6.0 | < 0.0001 |
| | average | 0.73 | | 0.66 | 0.80 | | | 0.39 | | | |
| MAXENT | train1 | 0.80 | 0.0324 | 0.73 | 0.86 | 3.1 | < 0.01 | 0.46 | 0.004060 | 7.2 | < 0.0001 |
| | train2 | 0.83 | 0.0295 | 0.77 | 0.89 | 4.5 | < 0.0001 | 0.53 | 0.003666 | 8.8 | < 0.0001 |
| | train3 | 0.82 | 0.0310 | 0.76 | 0.88 | 3.9 | < 0.0001 | 0.54 | 0.003610 | 9.0 | < 0.0001 |
| | train4 | 0.82 | 0.0298 | 0.76 | 0.88 | 3.9 | < 0.0001 | 0.47 | 0.004012 | 7.4 | < 0.0001 |
| | train5 | 0.83 | 0.0295 | 0.77 | 0.89 | 4.5 | < 0.0001 | 0.55 | 0.003553 | 9.2 | < 0.0001 |
| | average | 0.82 | | 0.76 | 0.88 | | | 0.51 | | | |

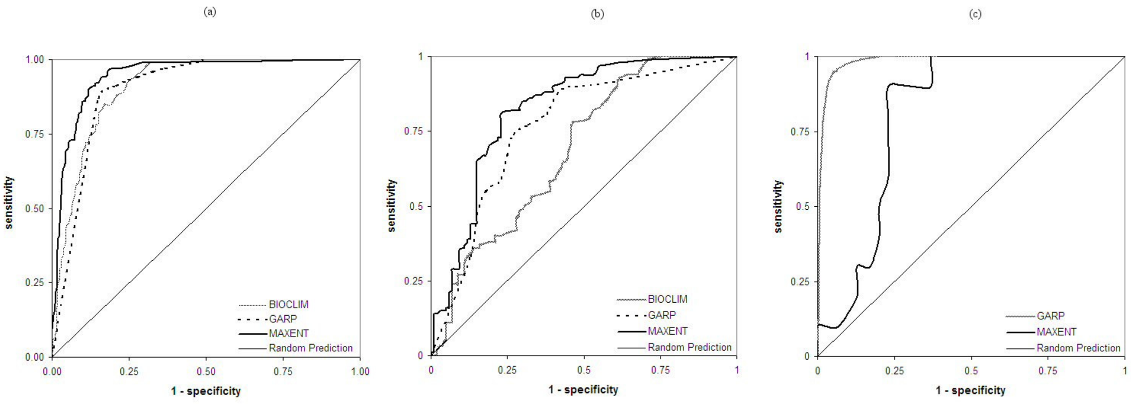
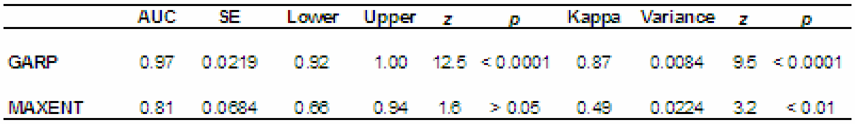


*Figure 9. Receiver operating characteristic (ROC) curves for the three algorithms on the third training sample of occurrence records. The results are given for* Bombina variegata *at the continental scale (a), at the regional scale (b) and at the local scale (c). Sensitivity equals the proportion of test localities correctly predicted present. The quantity (1 – specificity) equals the proportion of all map pixels predicted to have suitable condition for the species.*

At the local scale the AUC values and Kappa statistic for the GARP algorithm were highly significant ($p < 0.0001$) indicating better-than-random prediction. For the MAXENT algorithm the AUC was not significant ($p > 0.05$) but it was significant better than a prediction by random regarding the Kappa which showed a moderate agreement (Table 5). The ROC curves show how GARP performed better and always higher than MAXENT (Figure 9c). GARP performed significantly greater than MAXENT ($p < 0.05$; McNemar test).

*Table 5. Results of receiver operating characteristic (ROC) and Kappa statistic analyses for* Bombina variegata *at the local scale produced with two modeling techniques. For each training sample, the area under the curve (AUC) and the Kappa statistic is given for GARP and MAXENT.*



| | AUC | SE | Lower | Upper | z | p | Kappa | Variance | z | p |
|---|---|---|---|---|---|---|---|---|---|---|
| GARP | 0.97 | 0.0219 | 0.92 | 1.00 | 12.5 | < 0.0001 | 0.87 | 0.0084 | 9.5 | < 0.0001 |
| MAXENT | 0.81 | 0.0684 | 0.66 | 0.94 | 1.6 | > 0.05 | 0.49 | 0.0224 | 3.2 | < 0.01 |

### 3.1.3. Predictor Variables Importance

From an evaluation of the jackknife procedure at the continental scale it is concluded that precipitation related variables have the highest gains when used in isolation compared with temperature related ones (Figure 10). The same pattern was found for all partitions of the occurrence data (Appendix A). However, excluding the precipitation of the wettest quarter from the analysis did not decrease the total gain as the annual precipitation did, being the latest the most important variable at this scale. Table 6 shows the range of values for the two more important variables at which the species response is higher. The response curves for all predictor variables can be seen in appendix B.

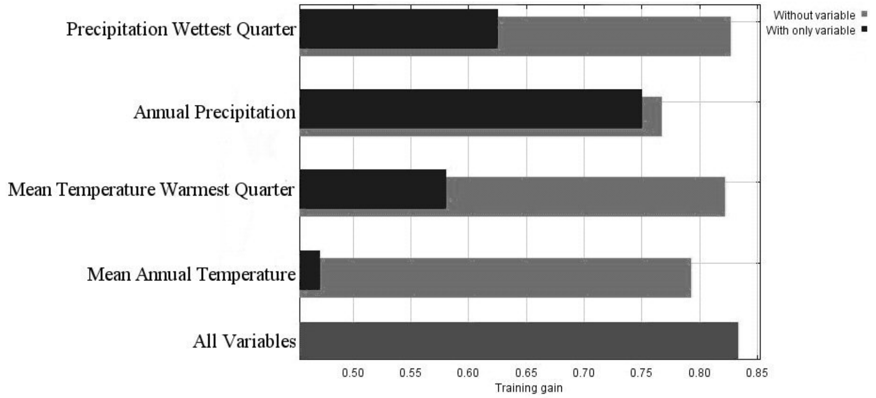


*Figure 10. Jackknife of training gain for* B. variegata *at continental scale on the second random partition of occurrence records (train 2). The climatic variable with highest gain when used in isolation is annual precipitation, which therefore appears to have the most useful information by itself. The climatic variable that decreases the gain the most when it is omitted is again annual precipitation, which therefore appears to have the most information that isn't present in the other variables.*

At the regional scale (Italy) soils appeared having the strongest influence in predicting the spatial distribution of *B. variegata* on all random partitions of the occurrence records (Figure 11, Appendix C). In addition, climatic related variables (mean annual temperature, mean temperature of warmest quarter and annual precipitation) have also a substantial influence on the distribution of the species, as well as the altitude and slope. Table 6 shows the range of values for these variables. Appendix D shows the response curves of these variables.

*Table 6. Suitable range of values of the predictor variables that contribute the most to the general MAXENT distribution gain. Values are for the species* Bombina variegata *at the different scales.*

| *Predictor variables* | *units* | CONTINENTAL | ITALY | MAJELLA |
|---|---|---|---|---|
| Altitude | *m.a.s.l.* | | 500 - 1600 | |
| Annual Precipitation | *mm* | 600 - 2000 | 550 - 1000 | |
| Precipitation Wettest Quarter | *mm* | 600 - 700 | | |
| Mean Annual Temperature | °C | | 9.0 - 16 | |
| Mean Temperature Warmest Quarter | °C | | 22 - 24 | 15 - 23 |
| Slope | *degrees* | | < 30 | |
| Soils | | | Vertisols | |
| Distance to Streams | *m* | | | < 100 |
| Distance to Roads | *m* | | | < 1000 |
| Distance to Towns | *m* | | | < 800 |

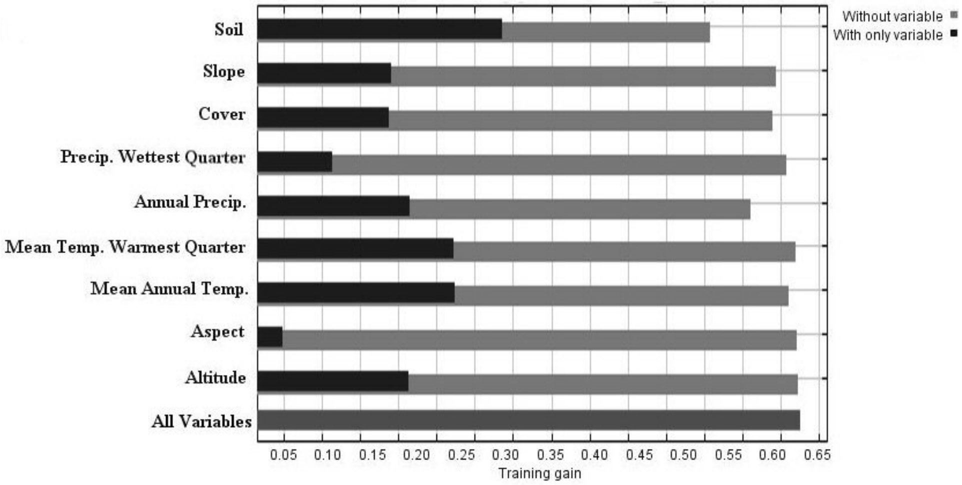


*Figure 11. Jackknife of training gain for* B. variegata *at regional scale (Italy) on the second random partition of occurrence records (train 2). The environmental variable with highest gain when used in isolation is soil which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is again soil which therefore appears to have the most information that isn't present in the other variables.*

From the Jackknife analysis at the local scale it can be seen that human induced variables (distance to streams, distance to roads and distance to towns) gain more importance in predicting the spatial distribution of *B. variegata*, together with the altitude (figure 12). Regarding the climatic variables at this particular scale, only the mean temperature of the warmest quarter appeared to have important information to predict the species potential distribution. Table 6 shows the range of values for these variables at which the species response is higher. The response curves of the predictor variables can be observed in appendix E.

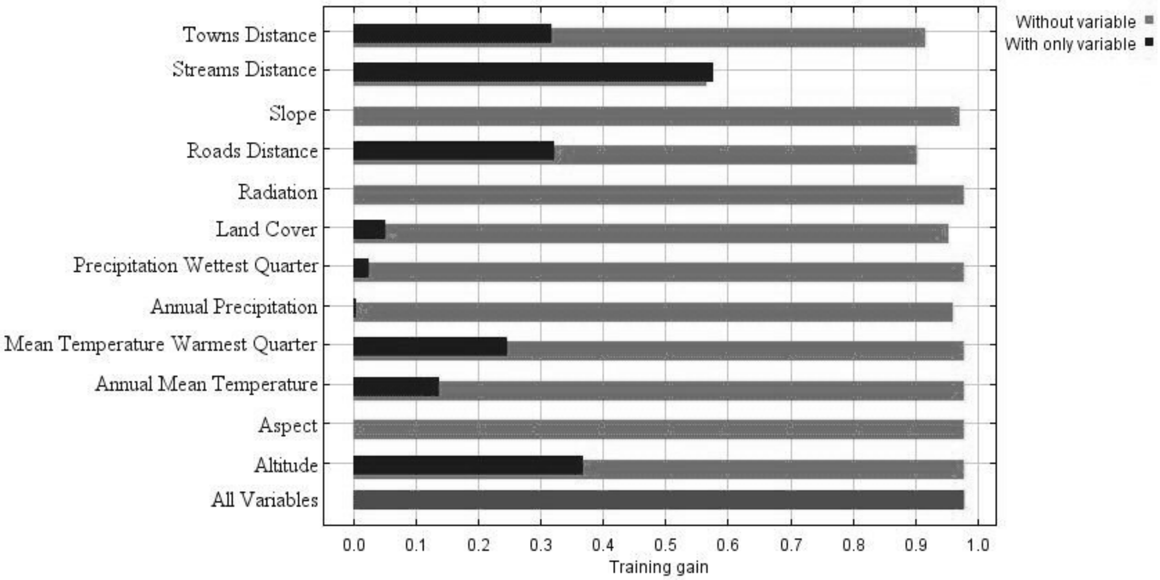


*Figure 12. Jackknife of training gain for* B. variegata *at local scale (Majella). The environmental variable with highest gain when used in isolation is distance to streams which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is again distance to streams, which therefore appears to have the most information that isn't present in the other variables.*

## 3.2. *Vipera ursinii*

### 3.2.1. Potential distribution maps

When using all occurrence locations for the species the three algorithms produced quiet different predictions for *Vipera ursinii* potential distribution at the continental scale (figure 13). BIOCLIM and GARP indicated suitable conditions throughout Russia, Belarus, Poland, and Hungary. In addition, BIOCLIM also indicated suitable areas in Germany, The Netherlands, North and Middle France and North of Spain. MAXENT on the contrary predicted more correctly within the species' known range.

The three algorithms indicated similar suitable areas for *V. ursinii* at the regional scale in Middle Italy, in the Abruzzo region (figure 14). However, the GARP algorithm indicated also suitable areas in the North of Italy, over the Alps (figure 14c).

At the local scale (Majella National Park), the two algorithms (GARP and MAXENT) produced similar predictions for the potential distribution of *V. ursinii* considering the thresholds established for each algorithm (figure 15c and 15d).

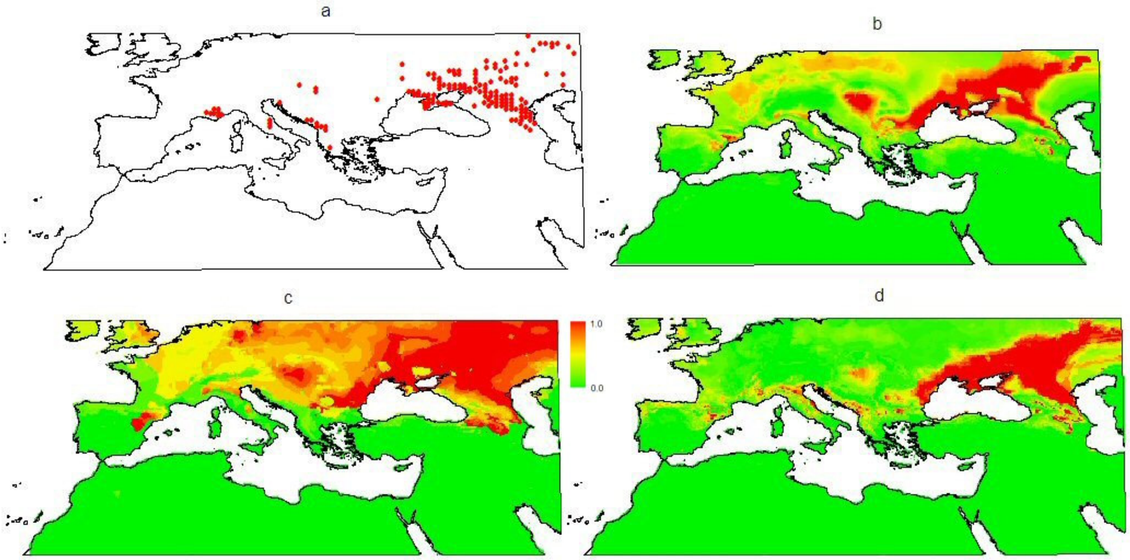


*Figure 13. Predicted potential distribution of* Vipera ursinii *at the continental scale () using all occurrence records. The location of the occurrence points are shown in (a). Results are given for BIOCLIM (b), GARP (c) and MAXENT (d). For comparison purposes the optimum threshold value ($P_{crit}$) was calculated: BIOCLIM = 0.09, GARP = 0.65, MAXENT = 0.21.*

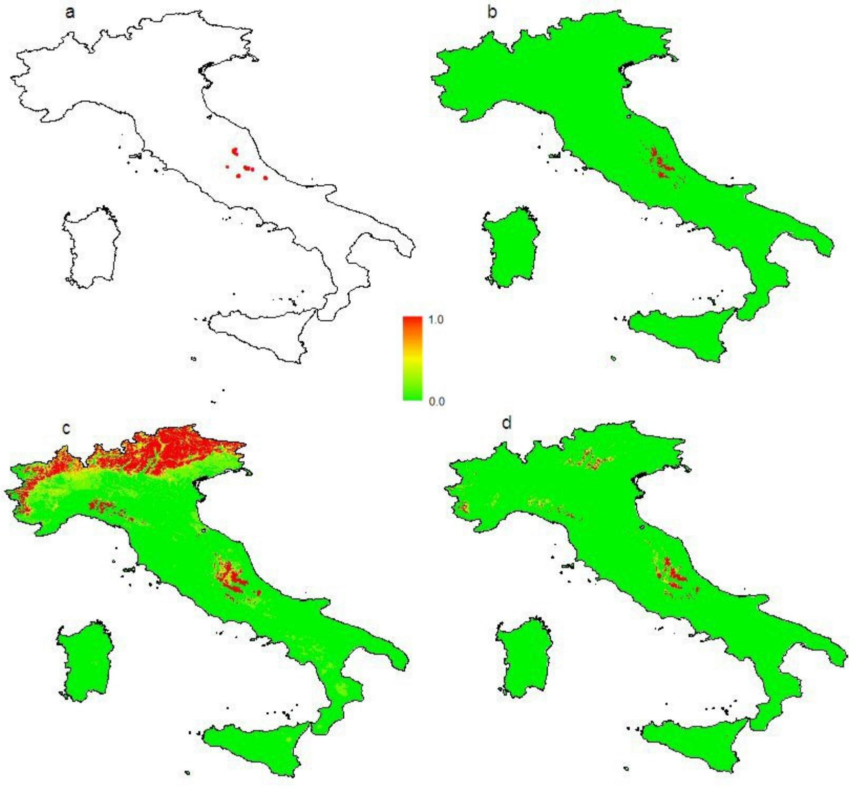


*Figure 14. Predicted potential distribution of* Vipera ursinii *at the regional scale (Italy). The location of the occurrence points are shown in (a). Results are given for BIOCLIM (b), GARP (c) and MAXENT (d). For comparison purposes the optimum threshold value ($P_{crit}$) was calculated: BIOCLIM = 0.03, GARP = 0.91, MAXENT = 0.18.*

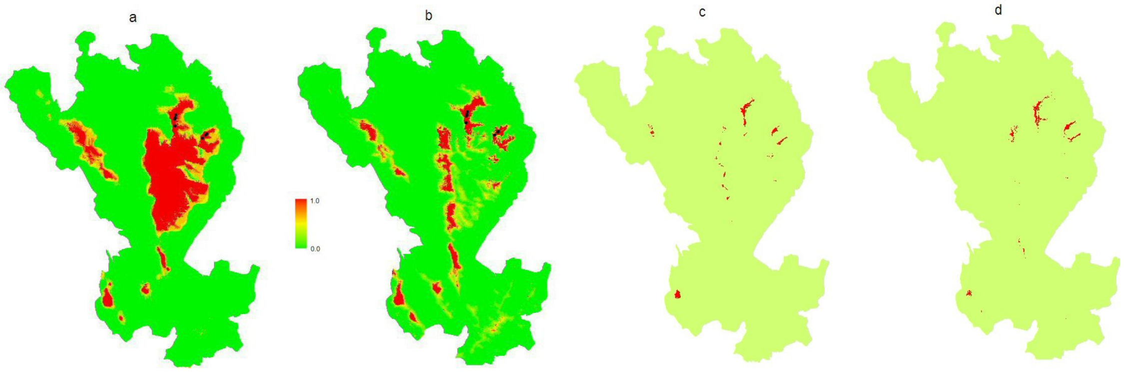


*Figure 15. Predicted potential distribution of* Vipera ursinii *at the local scale (Majella). The black dots represent the occurrence points. Results are given for GARP (a) and MAXENT (b). For comparison purposes the optimum threshold value ($P_{crit}$) was calculated: GARP = 0.95(c), MAXENT = 0.42(d).*

### 3.2.2. Accuracy analysis and Comparison test

For all training sets of the occurrence data at the continental scale, the AUC and Kappa values were highly statistically significant for all algorithms ($p < 0.0001$), indicating better than chance predictions (Table 7). The AUC values indicated strong predictions (AUC > 0.88) while the Kappa values indicated moderate to strong agreement between the prediction and the test samples (Kappa > 0.5) (Table 7). The ROC curve showed that the performance of MAXENT was better than BIOCLIM and GARP across the entire spectrum (Figure 16a). The MAXENT prediction was significantly greater than that of GARP and BIOCLIM ($p < 0.01$; McNemar test). A non-significant difference was found between BIOCLIM and GARP predicitons ($p > 0.05$; McNemar test). Results for other training samples were similar.

*Table 7. Results of receiver operating characteristic (ROC) and Kappa statistic analyses for* Vipera ursinii *at the continental scale produced with the three modeling techniques. For each training sample, the area under the curve (AUC) and the Kappa statistic is given for BIOCLIM, GARP and MAXENT.*

| | | AUC | SE | Lower | Upper | z | *p* | Kappa | variance | z | *p* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| BIOCLIM | train1 | 0.91 | 0.0165 | 0.87 | 0.94 | 12.5 | < 0.0001 | 0.62 | 0.00237 | 12.7 | < 0.0001 |
| | train2 | 0.90 | 0.0182 | 0.86 | 0.93 | 10.8 | < 0.0001 | 0.62 | 0.00231 | 13.2 | < 0.0001 |
| | train3 | 0.90 | 0.0185 | 0.86 | 0.93 | 10.6 | < 0.0001 | 0.62 | 0.00234 | 12.9 | < 0.0001 |
| | train4 | 0.92 | 0.0156 | 0.89 | 0.95 | 14.1 | < 0.0001 | 0.65 | 0.00223 | 13.7 | < 0.0001 |
| | train5 | 0.90 | 0.0183 | 0.86 | 0.93 | 10.9 | < 0.0001 | 0.61 | 0.00236 | 12.7 | < 0.0001 |
| | *Average* | 0.90 | | 0.87 | 0.94 | | | 0.62 | | | |
| GARP | train1 | 0.92 | 0.0162 | 0.88 | 0.95 | 13.4 | < 0.0001 | 0.61 | 0.00239 | 12.5 | < 0.0001 |
| | train2 | 0.88 | 0.0207 | 0.84 | 0.92 | 8.8 | < 0.0001 | 0.55 | 0.00267 | 10.6 | < 0.0001 |
| | train3 | 0.89 | 0.0194 | 0.85 | 0.93 | 9.8 | < 0.0001 | 0.56 | 0.00260 | 11.1 | < 0.0001 |
| | train4 | 0.89 | 0.0186 | 0.86 | 0.93 | 10.5 | < 0.0001 | 0.53 | 0.00273 | 10.2 | < 0.0001 |
| | train5 | 0.89 | 0.0202 | 0.84 | 0.92 | 9.2 | < 0.0001 | 0.55 | 0.00264 | 10.7 | < 0.0001 |
| | *Average* | 0.89 | | 0.85 | 0.93 | | | 0.56 | | | |
| MAXENT | train1 | 0.94 | 0.0136 | 0.92 | 0.97 | 17.9 | < 0.0001 | 0.73 | 0.00177 | 17.4 | < 0.0001 |
| | train2 | 0.95 | 0.0115 | 0.93 | 0.98 | 22.1 | < 0.0001 | 0.77 | 0.00155 | 19.6 | < 0.0001 |
| | train3 | 0.96 | 0.0105 | 0.94 | 0.98 | 24.9 | < 0.0001 | 0.81 | 0.00132 | 22.3 | < 0.0001 |
| | train4 | 0.97 | 0.0085 | 0.95 | 0.98 | 31.6 | < 0.0001 | 0.79 | 0.00141 | 21.1 | < 0.0001 |
| | train5 | 0.95 | 0.0128 | 0.92 | 0.97 | 19.5 | < 0.0001 | 0.76 | 0.00158 | 19.2 | < 0.0001 |
| | *Average* | 0.96 | | 0.93 | 0.98 | | | 0.77 | | | |

For all training samples of the occurrence data at the regional scale, the AUC values were highly statistically significant for all algorithms ($p < 0.0001$) indicating better than random predictions except for the first training sample of the BIOCLIM algorithm (Table 8). The Kappa values also indicated a statistically significant difference than a prediction by chance ($p < 0.0001$) with moderate Kappa values. Note how for the first training sample in BIOCLIM has the lowest AUC value but the highest Kappa value. There were no significant differences between the performances of the three algorithms ($p > 0.05$; McNemar Test) (figure 16b).

*Table 8. Results of receiver operating characteristic (ROC) and Kappa statistic analyses for* Vipera ursinii *at the regional scale produced with the three modeling techniques. For each training sample, the area under the curve (AUC) and the Kappa statistic is given for BIOCLIM, GARP and MAXENT.*

| | | AUC | SE | Lower | Upper | z | p | Kappa | variance | z | p |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **BIOCLIM** | train1 | 0.82 | 0.0739 | 0.65 | 0.95 | 1.6 | 0.11 | 0.64 | 0.015358 | 5.2 | < 0.0001 |
| | train2 | 0.92 | 0.0550 | 0.79 | 1.00 | 4.0 | < 0.0001 | 0.61 | 0.013797 | 5.2 | < 0.0001 |
| | train3 | 0.92 | 0.0553 | 0.79 | 1.00 | 4.0 | < 0.0001 | 0.61 | 0.013797 | 5.2 | < 0.0001 |
| | *average* | 0.88 | | 0.74 | 0.98 | | | 0.62 | | | |
| **GARP** | train1 | 0.92 | 0.0376 | 0.84 | 0.98 | 5.8 | < 0.0001 | 0.68 | 0.012402 | 6.1 | < 0.0001 |
| | train2 | 0.89 | 0.0304 | 0.83 | 0.95 | 6.2 | < 0.0001 | 0.60 | 0.013147 | 5.2 | < 0.0001 |
| | train3 | 0.93 | 0.0256 | 0.88 | 0.98 | 9.1 | < 0.0001 | 0.73 | 0.010274 | 7.2 | < 0.0001 |
| | *average* | 0.91 | | 0.85 | 0.97 | | | 0.67 | | | |
| **MAXENT** | train1 | 0.97 | 0.0235 | 0.91 | 1.00 | 11.5 | < 0.0001 | 0.68 | 0.012402 | 6.1 | < 0.0001 |
| | train2 | 0.98 | 0.0175 | 0.93 | 1.00 | 15.9 | < 0.0001 | 0.76 | 0.010404 | 7.4 | < 0.0001 |
| | train3 | 0.98 | 0.0174 | 0.93 | 1.00 | 16.0 | < 0.0001 | 0.76 | 0.010404 | 7.4 | < 0.0001 |
| | *average* | 0.98 | | 0.93 | 1.00 | | | 0.73 | | | |

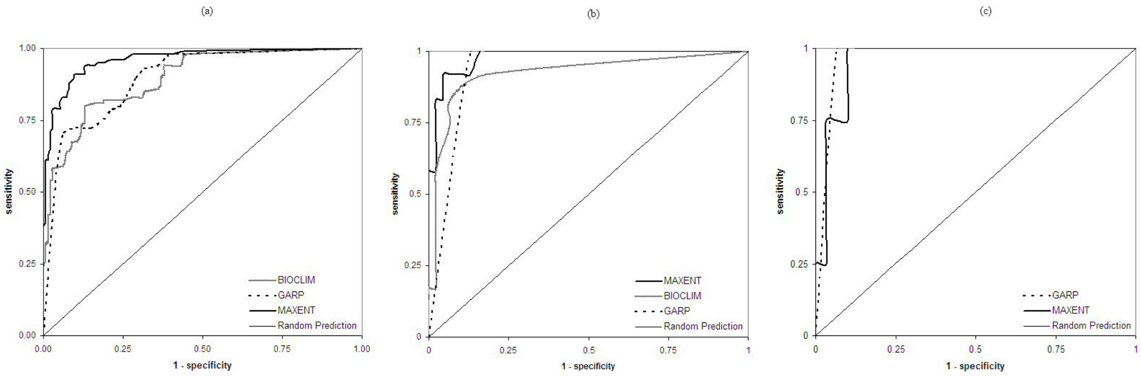


*Figure 16. Receiver operating characteristic (ROC) curves on the third partition of the training samples for the three algorithms for* Vipera ursinii *at each different scale: Continental (a), Italy (b) and Majella (c). Sensitivity equals the proportion of test localities correctly predicted present. The quantity (1 – specificity) equals the proportion of all map pixels predicted to have suitable condition for the species.*

The AUC and Kappa values calculated for the two algorithms at the local scale were highly statistically significant ($p < 0.0001$) indicating a better than random predictions (Table 9). There was not a significant difference between the prediction performance of the two models ($p > 0.05$; McNemar test) (figure 14C).

*Table 9. Results of receiver operating characteristic (ROC) and Kappa statistic analyses for* Vipera ursinii *at the local scale produced with two modeling techniques. For each training sample, the area under the curve (AUC) and the Kappa statistic is given for GARP and MAXENT.*

| | AUC | SE | Lower | Upper | *z* | *p* | Kappa | variance | *z* | *p* |
|---|---|---|---|---|---|---|---|---|---|---|
| GARP | 0.97 | 0.02425 | 0.91 | 1 | 11.0 | < 0.0001 | 0.86 | 0.009801 | 8.64 | < 0.0001 |
| MAXENT | 0.96 | 0.03203 | 0.88 | 1 | 8.1 | < 0.0001 | 0.71 | 0.018248 | 5.26 | < 0.0001 |

### 3.2.3. Predictor Variables Importance

Figure 17 shows that precipitation and mean temperature of the warmest quarter are the most important variables in predicting the potential distribution of *Vipera ursinii* at the continental scale. The Jackknife analysis resulted in the same variables behaviour for all partitions of the occurrence records for the species. Table 10 shows the range of values for this variable at which the species response is higher. Appendix F shows the response curves for these variables.

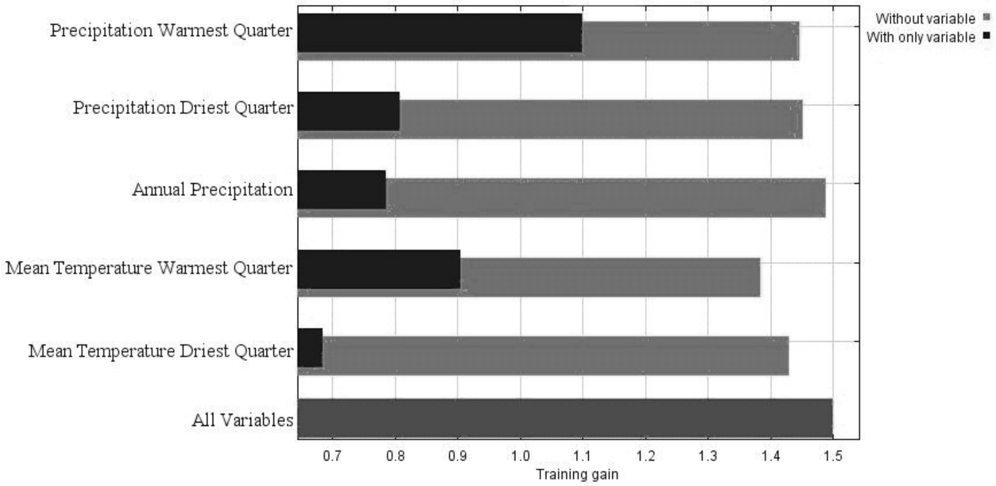


*Figure 17. Jackknife of training gain for* V. ursinii *at continental scale on the second random partition of occurrence records. The climatic variable with highest gain when used in isolation is precipitation of the warmest quarter, which therefore appears to have the most useful information by itself. The mean temperature of the warmest quarter is the variable that decreases the gain the most when it is omitted, which therefore appears to have the most information that isn't present in the other variables.*

The Jackknife analysis for all partitions of the occurrence data showed the same variables response, being temperature related variables together with the altitude the most important in predicting the potential distribution of *V. ursinii* at the regional scale (Figure 18). However, the precipitation of the warmest quarter appeared to have a strong influence since removing it from the analysis decreases considerably the total gain (Figure 18). Table 10 shows the range of values for this variable at which the species response is higher. Appendix G shows the response curves for these variables.

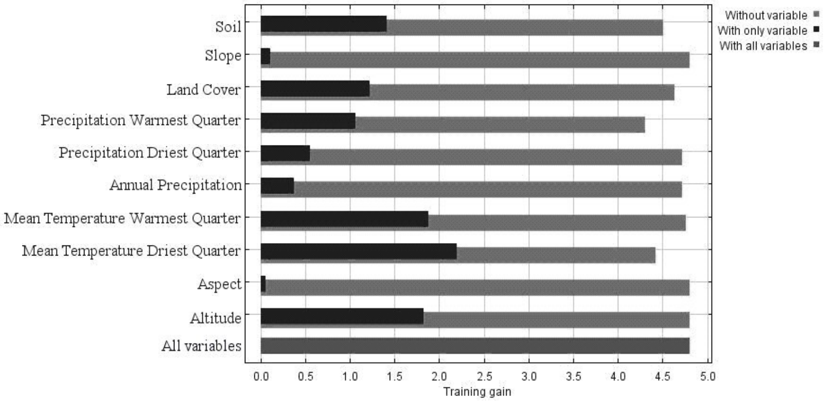


*Figure 18. Jackknife of training gain for* V. ursinii *at regional scale on the second random partition of occurrence records. The environmental variable with highest gain when used in isolation is the temperature of the driest quarter, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is the precipitation of the warmest quarters, which therefore appears to have the most information that isn't present in the other variables.*

*Table 10. Suitable range of values of the predictor variables that contribute the most to the general MAXENT distribution gain. Values are for the species* Vipera ursinii *at the different scales.*

| *Predictor variables* | *units* | CONTINENTAL | ITALY | MAJELLA |
|---|---|---|---|---|
| Altitude | *m.a.s.l.* | | 1500 - 3500 | 1000 - 2700 |
| Annual Precipitation | *mm* | 90 - 600 | | |
| Precipitation Warmest Quarter | *mm* | | 0 - 50 | |
| Mean Temperature Warmest Quarter | °C | 22 - 24 | 0 - 2.5 | |
| Mean Temperature Driest Quarter | °C | | -10 - 10 | -8 - -6 |
| Land Cover | | | | Pines - Grasslands |

At the local scale, the variables that contribute the most to the total gain are the mean temperature of the driest quarter, elevation, and land cover (figure 19). Appendix H shows the response curves for these variables.

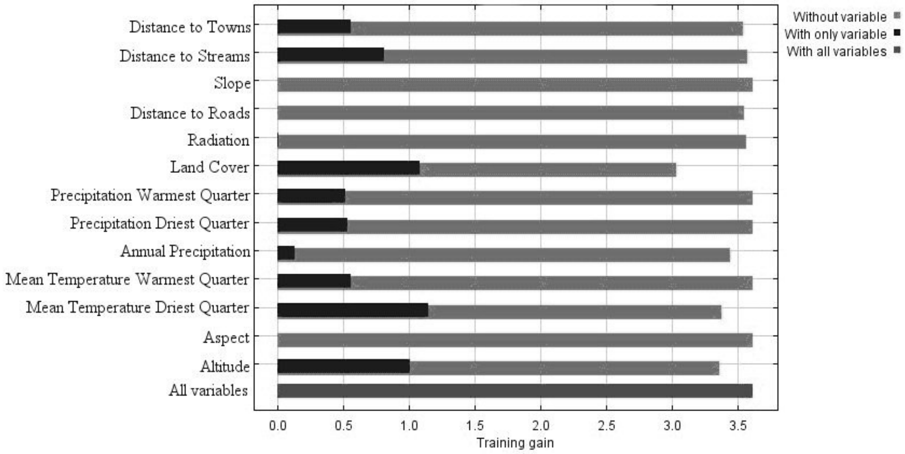


*Figure 19. Jackknife of training gain for* V. ursinii *at local scale. The environmental variable with highest gain when used in isolation is the mean temperature of the driest quarter, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is the Land Cover, which therefore appears to have the most information that isn't present in the other variables.*

# 4. Discussion

## 4.1. What is really being modeled?

The spatial distribution of a species is determined by different factors operating at different scales and with different intensities (Pearson and Dawson, 2003). Soberon and Peterson (2005) describe four classes of factors that determine the areas in which a species is found: (1) abiotic conditions (e.g. climate, physical environment) that impose physiological limits on species' ability to persist, (2) biotic factors (e.g. interactions with other species), (3) regions that are accessible to dispersal by the species from some original area, and (4) the evolutionary capacity of populations of the species to adapt to new conditions.

When using factors 1 to estimate the spatial distribution of species, the fundamental niche (FN) is being estimated (Hutchinson, 1957), which includes the total range of environmental conditions that are suitable for the existence of the species without the influence of inter-specific competition or predation from other species. The realized niche (RN) describes that part of the fundamental niche actually occupied by the species and is represented through the integration of factors 1 and 2 (Hutchinson, 1957). Finally, Soberon and Peterson (2005) stated that stable populations of a species will be found only in regions where factors 1, 2 and 3 intersect.

Given these conditions, the question is how the results of the modeling process in this research can be interpreted? Basically, the layers provided as input to the models were abiotic (Table 1). No biotic information was included in the analysis. The occurrence records databases created for the species, excluded all observations where the species was known to be introduced, therefore, areas accessible to dispersal by the species were excluded from the analysis. In that sense, the three modeling techniques used here were presented with abiotic information (factor 1) and with occurrence points coming from source populations and the output maps must be interpreted as the fundamental niches of the species.

As an example, the distribution maps of *B. variegata* at the continental scale can be used (Figure 6). The three algorithms are predicting suitable conditions in the north of Spain. Note that factors such as biotic or geographic barriers that can prevent the species to disperse are not taking into account (i.e. not used as predictor variables). However, looking at the map showing the occurrence observation records, no observations have been made for this species in Spain. It is then concluded that the potential distribution has been mapped but not the actual distribution of the species.

Contrary to this view, Guisan and Thuiller (2005) stated that the observed distributions (i.e. occurrence records) are already constrained by biotic interactions and limiting resources and in that sense, species distribution models are quantifying Hutchinson's realized niche of species. The discussion is still open.

## 4.2. Model Performance

At the continental scale, threshold-independent ROC analysis and Kappa index showed that the three algorithms performed significantly better than random. The MAXENT algorithm however, performed significantly better than the other algorithms on all data partitions for both species. It is also MAXENT the one generating a better prediction within the species' known range for both species at this particular scale, while extensive areas of potential distribution indicated by GARP and BIOCLIM appeared to overestimate the extent of suitable environmental conditions for the species. Phillips et al. (in press) found the same models behaviour when comparing prediction maps generated by MAXENT and GARP.

Another issue concerning the ability of species distribution models to predict the organisms' spatial distribution, is the type of predictor variables that can be included in the analysis and how models can handle such variables. Specifically, this refers to continuous vs. categorical data. When statistically comparing the performance of the models at the regional scale (Italy) for *B. variegata*, only MAXENT was able to predict significantly better than a prediction by chance regarding the AUC values and with moderate agreement considering the kappa value; soil (i.e. categorical variable) was the most relevant predictor variable (Figure 11). Knowing that, it was expected to obtain significantly better results from GARP algorithm, since categorical data can be included into the model. However, it appeared that GARP algorithm is not able to integrate properly this type of data. These findings support the results of Phillips et al. (in press) who concluded that through the inclusion of the potential vegetation, GARP did not improve the prediction accuracy of a model treated at first with only climatic and elevation variables (i.e. continuous variables).

The AUC and Kappa values for MAXENT and GARP algorithms for both species at the local scale (i.e. Majella) were relatively high (AUC > 0.8 and Kappa > 0.49 respectively). However, the AUC value of MAXENT for *B. variegata* (AUC = 0.82) was not significantly different than a prediction by chance ($p > 0.05$) considering the confidence intervals which support the AUC value stability (Table 5). This high values in general could be explained based on the method applied at this scale to test the performance of the models. Verbyla and Litvaitis (1989) describe the re-substitution method as testing the model's predictive ability by using sample cases that were used to develop the model. This method produces an optimistically biased estimate of the model's true classification accuracy, especially if many predictor variables are used in relation to sample cases (Verbyla, 1986) which is the case in this study when examining the distribution of the species at the local scale.

There are, however, some factors that can be considered as having an effect on overall model performance. It could be that some of the variables used to model the spatial distribution of the species were not the appropriate ones at the specific scale. Data quality can also have a strong influence in model performance (Segurado and Araujo, 2004): imprecise location of species occurrences for example. This can apply for *B. variegata* at the regional scale (i.e. Italy 1 km x 1 km), given that most of the occurrence points were generated randomly from the occurrence record grids available in atlases with resolution of 10 km by 10 km.

The AUC comparison is somewhat biased in MAXENT's favor, as a continuous prediction will typically have a higher AUC than a discrete prediction as is the case here when compared to GARP (Phillips et al., 2004). However, the Kappa values throughout the sets of analysis showed the same pattern, being always higher in favor of MAXENT, except at the local scale cases.

One of the main advantages of the algorithms used in this study is that they do not require absence data localities like the generalized linear models (GLM) (McCullagh and Nelder, 1989) or the generalized additive models (GAM) (Hastie and Tibshirani, 1990) do. However, the problem arises when the accuracy of the models wants to be measure; in order to use the ROC curves and the Kappa statistic as an estimate of the models' performance, negative examples must be interpreted from all grid cells with no occurrence localities, even if they support good environmental conditions for the species (Phillips et al., 2004). In this research, random points, representing species absences, were selected from the polygon grids representing the extent of the known distribution of the species and where the species has not been reported (see section 2.5.1). This is a common approach to generate populations of points representing "pseudoabsences" (Stockwell and Peterson, 2002).

Soberón and Peterson (2005) mentioned that pseudoabsences should be delineated carefully based on *a priori* hypotheses about the region and species to be modeled. For example Graf et al. (2005) assumed habitat suitability based on the habitat range of the species to be the factor used to select areas of species absence. Based on those hypotheses, Soberón and Peterson (2005) explain an argument of why the different distribution modeling techniques are mapping the fundamental niche (FN) of the species rather than the realized niche (RN).

## 4.3. Habitat-Species Relationships

The species *Bombina variegata* had a broad distribution pattern. At the different scales the species was associated with precipitation (annual precipitation) and temperature related variables. The optimal range found for these variables (Table 2) are consistent with published information (Bernini et al., 2006; Gasc et al., 1997; IUCN-Conservation-International-and-NatureServe, 2004). Owen (1989) found that the mean annual precipitation was the most important predictor for frogs at large scale (50 by 50 Km grid resolution) in a landscape in Texas. The findings of an association of moderate slopes and Vertisol soils with the presence of the species at regional scale may be related to water bodies' formation. Gasc et al. (1997) noted that the species uses many types of wetlands. Vertisol soils are characterized by a horizon with 30% or more of clay which makes it susceptible to water bodies' formation, like small ponds and reservoirs, places that *B. variegata* will use as breeding habitats. This is also the reason why the species is more likely to be found near streams which is supported by the findings at local scale (Table 6). The apparent preferences of *B. variegata* at the local scale for areas nearby roads and towns (Table 6) could be a biased estimated towards sampling schemes carried out in accessible areas. Reddy and Dávalos (2003) found also a high correlation between occurrence localities and nearby presence of roads. On the other hand, other works have shown a negative relationship between frogs and urban developments (Delis et al., 1996) and roads (Fahrig et al., 1995).

The habitat relations found for *Vipera ursinii* are consistent with the known habitat requirements described in different field guides (Gasc et al., 1997; Gruber, 1989; Joger et al., 2005). The findings at the continental scale match with the requirements of the species distributed in lowland warm dry meadow-steppe habitats where the climatic conditions are characterized by low precipitation values and high temperature values (Table 10). On the other hand, the values found for Italy and Majella are in conformity with the species distributed in alpine/subalpine dry meadow-steppe habitats. Here, the species is located at higher altitudes, with low precipitation and temperature values (Table 10). At the local scale the species is associated also with pine and grassland covers. The species has been observed in pine forest gaps (grassland cover) in the Majella National Park (Bologna, M. *pers. commun.*). The park has been subject to abandonment processes since its establishment and natural regeneration processes have been taking place. The gaps within the Pine stands are reducing in size, factor that could have a negative influence on the habitats of the snake and conservation efforts must take this into account.

## 4.4. Effects of *Scale* (grain size) and *Extent*

The scale in this study was expressed as the grain size (pixel size) and the extent expressed by the study areas. One common problem in modeling species distribution is the mismatch between the resolutions at which species occurrences are presented (e.g. grid size in atlas surveys) and the one at which environmental predictor are available (Guisan and Thuiller, 2005). A common approach to deal with this issue is to aggregate the predictor variables to a coarser resolution to match the resolution of the occurrence records resolution (e.g. Owen, 1989; Thuiller et al., 2004). The opposite approach was taken in this research. From the occurrence record grids (e.g. 50 km by 50 km at continental scale) random points were generated within each grid to properly represent the variability of the environmental predictor represented at lower resolutions (e.g. 20 km by 20 km at continental scale) (see section 2.3.1).

However, some of these points could have fallen over areas with extreme values outside the known range of the species ecological requirements. In BIOCLIM it is possible to exclude the extreme values from the analysis by identifying the outliers. The outliers were recognized by defining a range of optimum values for each of the climatic variables considered (see section 2.4.1). However the other algorithms do not have this capability and all the occurrence observation points were included in the analysis. As a result, different predictions were estimated from every algorithm. For example, BIOCLIM is predicting the species *B. variegata* absent at higher altitudes in the Alps (> 1.600 m.a.s.l.) while MAXENT and GARP predicted positively the species in these areas (Figure 6).

Comparing these results with the actual altitude known range of the species, being this range from a few metres at sea level to about 1800 m a.s.l. (Bernini et al., 2006), it can be concluded that BIOCLIM is giving a better estimate than GARP and MAXENT of the actual known distributional range of *Bombina variegata* at the continental scale.

The importance of the *extent* on the interpretation of the processes driving the observed distribution patterns of the species could be recognized from the findings for *Vipera ursinii*. Patterns observed at one extent were not apparent on another extent. The optimal ecological requirements were quite different for the species when analyzed at different extents (e.g. continental vs. regional) (Tables 6 and 10). If the spatial distribution of *V. ursinii* is to be model only at the regional scale (e.g. in this research using a political boundary: Italy), then the resulting response would be expressing a biased estimate of the real response of the species to climatic variables. Van Horn (2002) demonstrated how an incorrect interpretation could be made when only part of an important gradient is sampled when using political instead of natural boundaries and Patthey (2003) reveal how some environmental variables best characterize the overall species range when analyzed on a large scale, whereas other features best characterize the habitat of the same species at the population or home range level.

## 4.5. Predictor Variables and Scale

Usually, researchers calculate correlation coefficients (e.g. Pearson coefficient or PCA) to avoid using correlated variables and to reduce the effects of multi-colinearity (e.g. Mas et al., 2004). However, from this type of analysis ecologically relevant variables could be excluded. Bumhan and Anderson (1998) have made clear that applying correlation analysis in order to find the significant set of variables will most probably expose false correlations. In this study no correlation analysis was carried out.

Different classification schemes exist to categorize the environmental predictors employ to predict species distribution. Austin (2002) for example divide these predictor into three categories: (1) indirect predictors, having no physiological effect on species (e.g. altitude), (2) direct predictors, having a direct physiological influence on species (e.g. temperature) and (3) resource predictors, those variables that are consumed by the organism (e.g. water).

With the modeling approach presented here, different combination sets of direct and indirect predictor variables were chosen and were believed to have a potential influence on the species distributions. Those variables, however, should affect the species' distribution at the relevant scale, determined by the geographic extent and scale (grain) of the modeling task (Pearson et al., 2004). In words of Mackey and Lindenmayer (2001), climatic variables such as temperature and precipitation are appropriate at global and meso-scales; topographic variables (e.g. aspect, slope) likely affect species distribution at meso- and topo-scales; and land cover variables influence species distributions at the micro-scale. Other authors have mentioned that topography no longer has any predictive power at coarse resolution (e.g. Neilson, 1995). In the present study some variables actually had a strong influence in determining the species distribution at larger scales, while others were stronger at small scales (Tables 6 and 10). In a study where a multi-scale approach was undertaken (Fischer et al., 2004) similar scale dependencies were found.

Following these ideas, different sets of predictor variables were chosen to model the species' distributions at different scales and extents (Table 1). At the continental level, only climatic related variables (direct predictors) were used and statistically speaking, all models for both species predicted better than a prediction by chance (AUC > 0.90). In a different research (Thuiller et al., 2004), the authors included land cover to a bioclimatic model to estimate the spatial distribution of species in

Europe (50 km by 50 km grid resolution); the findings demonstrated that the addition of land cover does not improve the model's predictive accuracy. In addition, Guisan and Hofer (2003) concluded that climatic predictors more closely match the actual reptile distributions when compared with distributions based on topography at meso-scale.

In the case of *B. variegata* at the regional scale, soils together with climatic variables were the most important predictor variables defining the species distribution (Figure 11). That could explain why at the regional scale BIOCLIM (which uses only climatic variables) was not able to predict correctly the spatial distribution of this species (Table 4). In contrast, for *V. ursinii* climatic variables were more important at the regional and local scales (Figures 18 and 19) and in this case all algorithms were able to predict correctly. This demonstrates that the integration of direct and indirect predictors at regional scales generates better prediction than using only direct predictors (climate) when the species is in fact influenced strongly by indirect predictors as well (e.g. soils for *B. variegata*). But if the species is influenced strongly by climatic variables, the inclusion of other type of predictors does not have a strong influence in the spatial prediction.

# 5. Conclusions

Species occurrences records and sets of environmental variables at three different scales and extent as well as three different modeling techniques were utilised to estimate the potential spatial distribution of two herpetological species, *Bombina variegata* and *Vipera ursinii*.

A proper interpretation of the distribution maps obtained by way of the modeling techniques relies on the concept of the species ecological niche. Thus, given the set of abiotic predictor variables and the set of occurrence records, the fundamental niche of the species were mapped in this study.

The MAXENT technique achieved better predictions than the other modeling techniques, except at the local scale where GARP performed better. When MAXENT proved to be better, it did it both with higher AUC and Kappa values, and generating a better prediction within the species' known range. MAXENT is a robust algorithm than can deal with different types of data (categorical and continuous) at different resolutions.

The main assumption of the BIOCLIM technique is that the distribution of the species is influenced primarily by climate. In fact, when the distribution of any species is driven by climatic variables at different scales, as was the case here for *Vipera ursinii*, BIOCLIM performed better than a prediction by chance. On the contrary, *Bombina variegata* showed a strong dependency for variables different from climate at the regional scale and in this case BIOCLIM was not able to predict correctly the distribution of the species. Thus a thoroughly study of the ecology of the species and models capabilities and assumption is required when modeling the species' geographic distribution.

At the continental scale, only climatic variables were chosen to model the potential spatial distribution of the species, and all models predicted correctly ($p < 0.0001$) (prediction better than a prediction by chance) taking into account the area under the curve (AUC) and Kappa as measures of their accuracy. Although no other types of predictor variables were used at this scale for comparison purposes, the results support the idea that climatic variables alone are adequate to model species' distributions at larger scales.

The multi-scale approach developed in the present study provided significant insights in the habitat-relationships of the target species. The use of different scales to model the spatial distribution of the species gives a better understanding of the diverse responses of the species to different environmental variables at different geographic extents.

# 6. Recommendations

A recommended approach that might improve the actual geographic distribution of the species is to use a deductive approach in which the *a priori* known ecological requirement of the species is used to extrapolate suitable areas from the environmental layers available (Corsi, 2004). One of these environmental layers could be the output map showing the fundamental niche generated by means of the models that use an inductive approach like the ones used in this study.

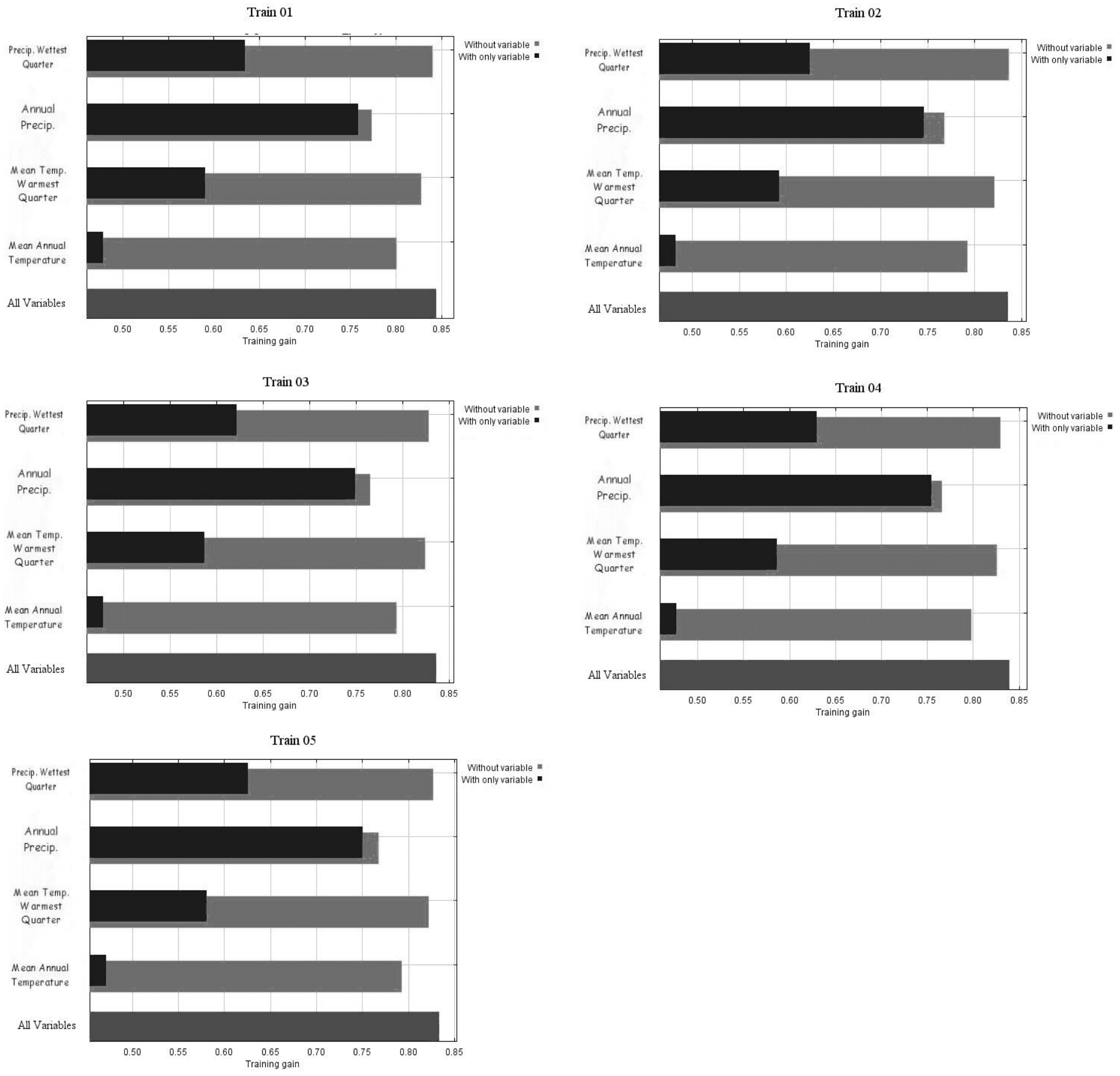
The general performance of the models could be influenced by errors in the environmental variables used as input. Although an accuracy assessment was carried out to the land cover map at the local scale, a step forward should include the validation of all layers used as input to the models and an evaluation of error propagation during the generation of the models' predictions (Corsi et al., 2000).

The analysis performed in this study regarding the predictor variables importance was made in a qualitative way.  Recent advances in the software package that carries out the MAXENT algorithm allows for a proper quantitative analysis of this aspect.

Although the models used in this research have the advantage of working with only presence data, the validation techniques available to estimate the accuracy of the output predictions still have the limitation of working with absence data.  New validation statistical procedures must be created to deal with this issue.

# 7. Appendices

## 7.1. **Appendix A.** Jackknife of training gain for *B. variegata* at continental scale on all random partitions of occurrence records. The environmental variable with highest gain when used in isolation is Annual Precipitation, which therefore appears to have the most useful information by itself. It is also the Annual Precipitation that decreases the gain the most when it is omitted; therefore it appears to have the most information that isn't present in the other variables.



Train 01

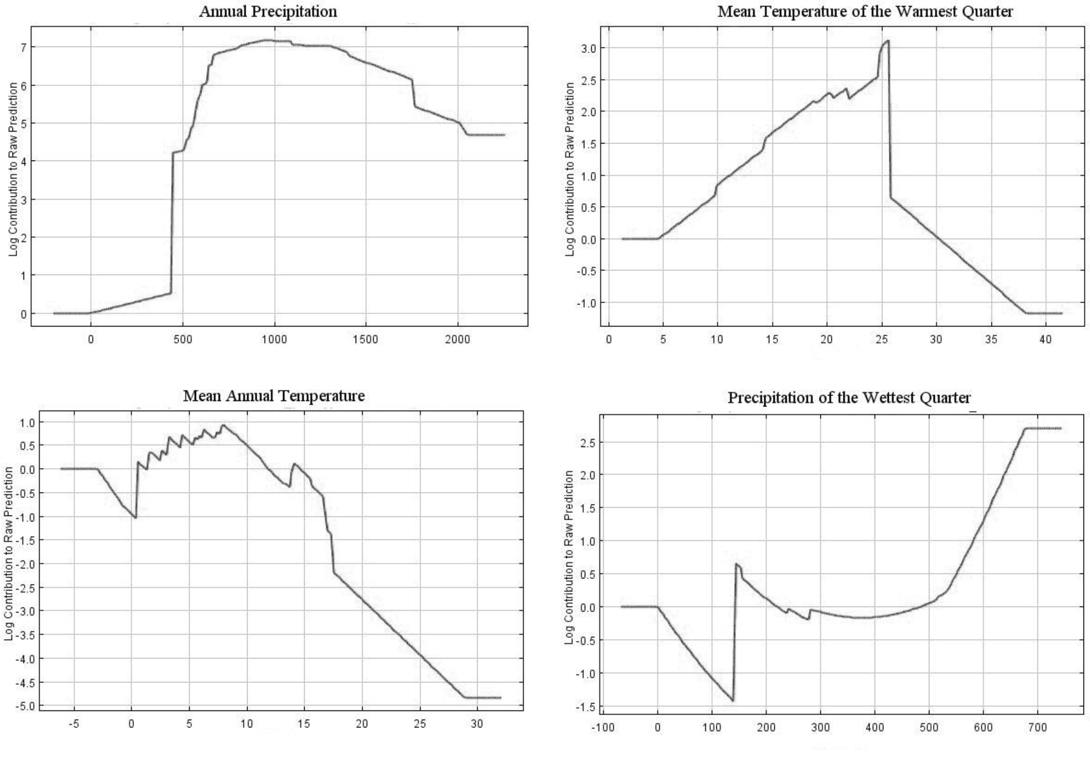
Train 02

Train 03

Train 04

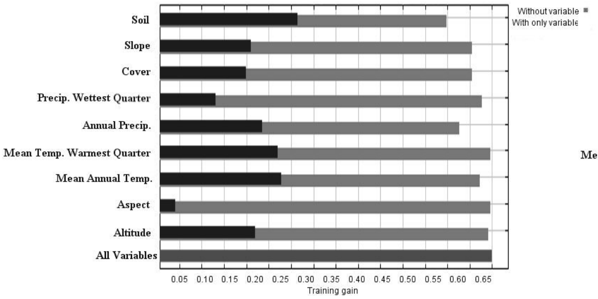
Train 05

7.2. **Appendix B**. Response curves of the environmental variables predicting the potential distribution of *Bombina variegata* at the continental scale on the second random partition of the occurrence records. The MAXENT model has the form exp(…)/constant, and the curves show how the exponent changes as each environmental variable is varied, keeping all others at their average sample value.

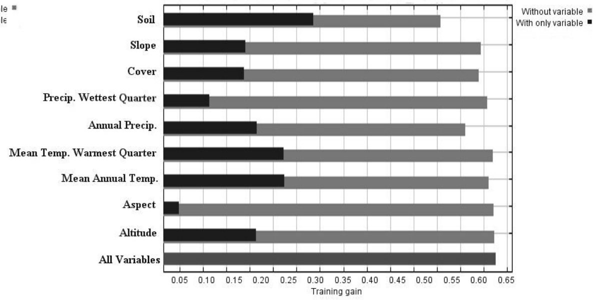


**7.3.** **Appendix C**. Jackknife of training gain for *B. variegata* at regional scale on all random partitions of occurrence records. The environmental variable with highest gain when used in isolation is the is soil, which therefore appears to have the most useful information by itself. It is also the soil variable that decreases the gain the most when it is omitted; therefore it appears to have the most information that isn't present in the other variables.

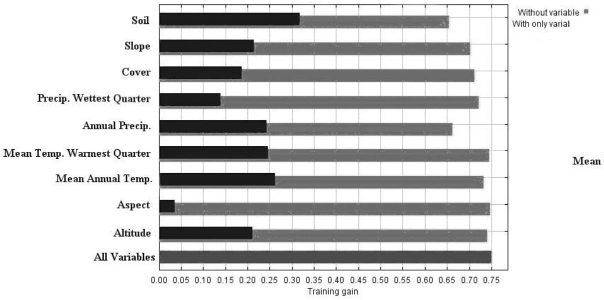
Train 01



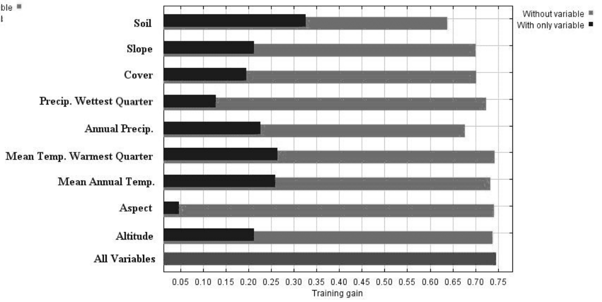
Train 02



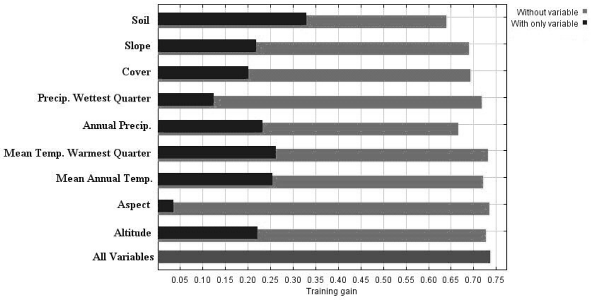
Train 03



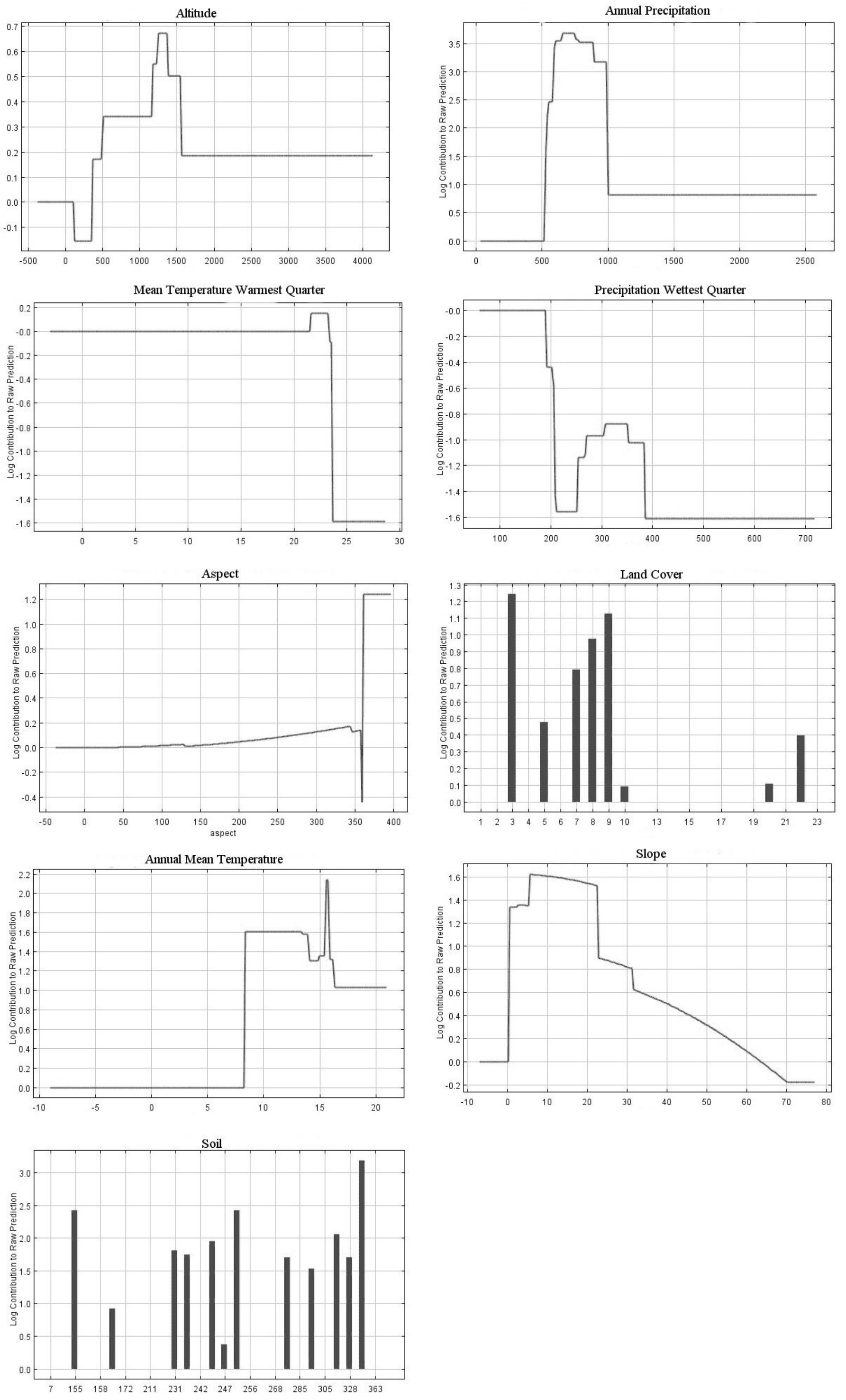
Train 04



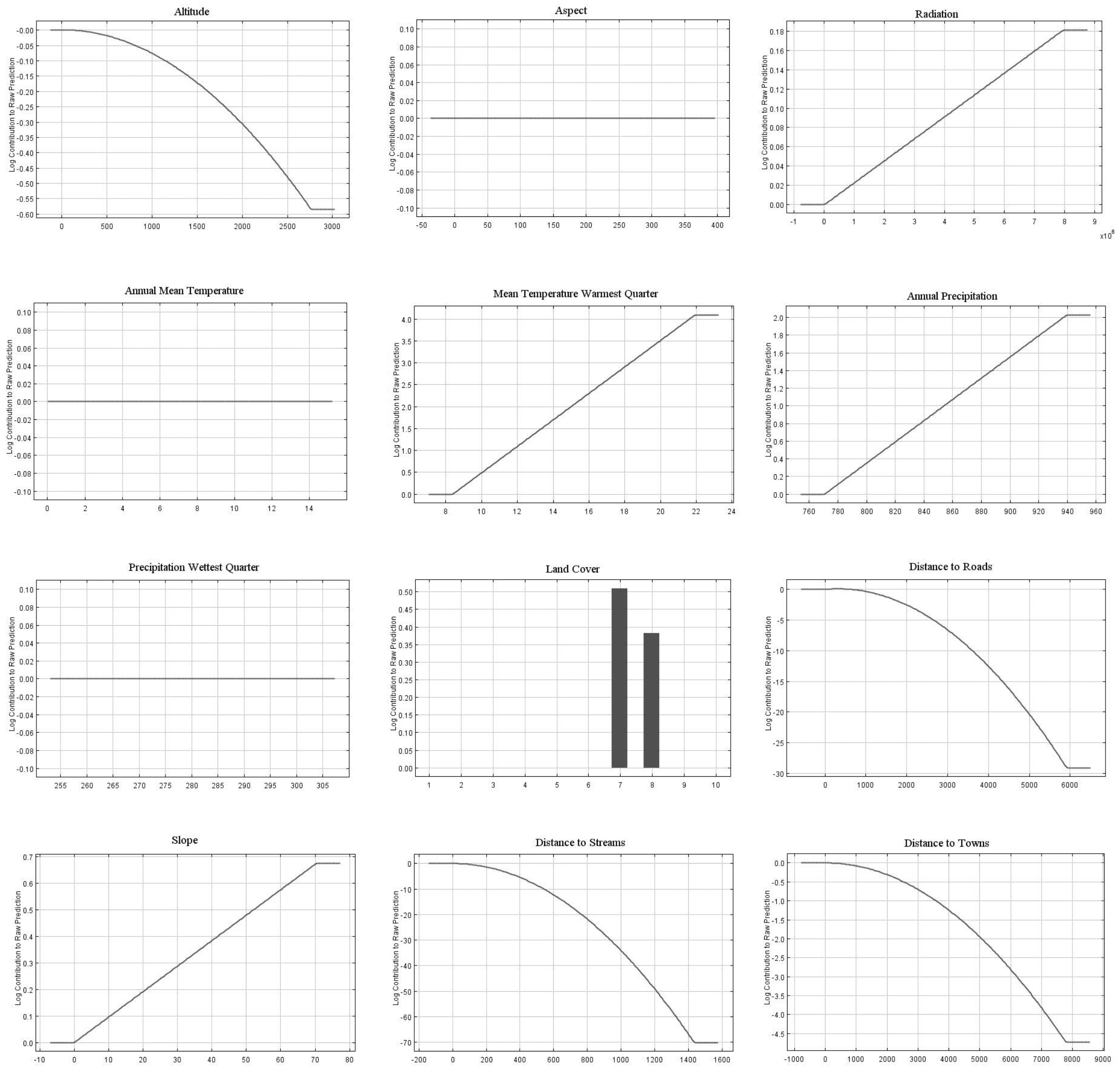
Train 05



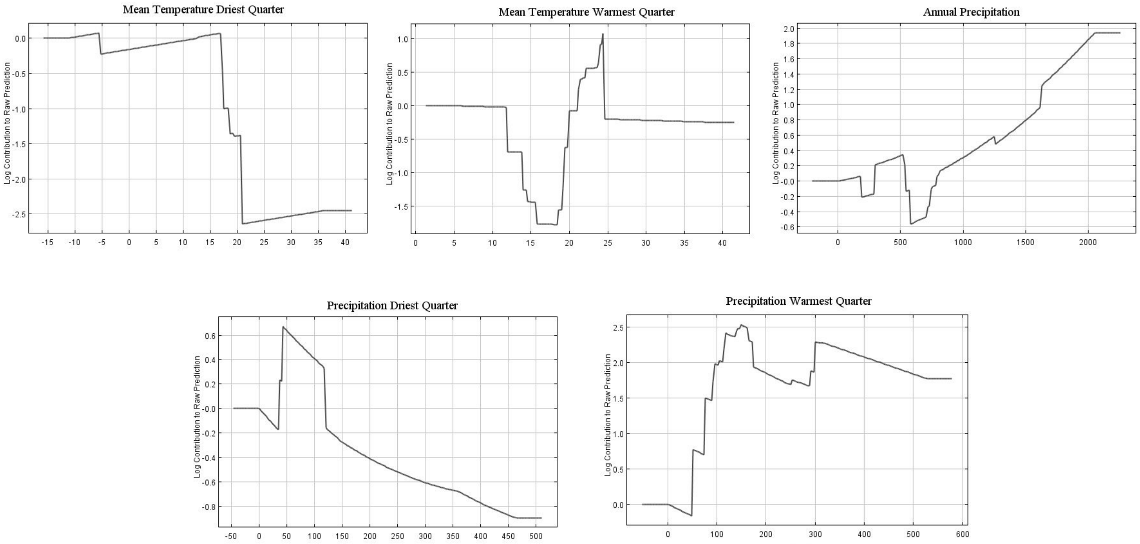
### 7.4. **Appendix D**. Response curves of the environmental variables predicting the potential distribution of *Bombina variegata* at the regional scale (Italy) on the second random partition of the occurrence records. The MAXENT model has the form exp(…)/constant, and the curves show how the exponent changes as each environmental variable is varied, keeping all others at their average sample value.



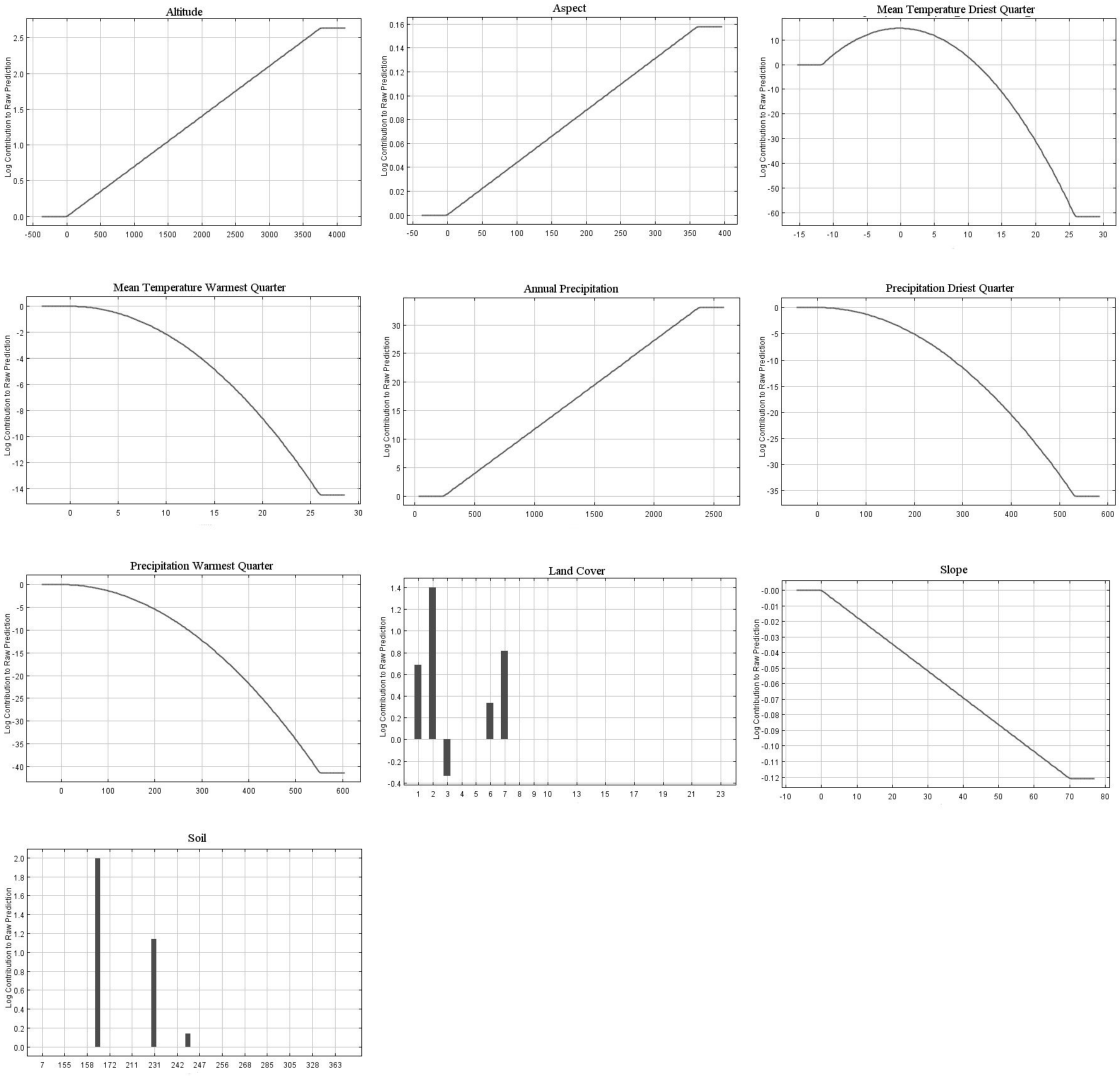
## 7.5. **Appendix E**. Response curves of the environmental variables predicting the potential distribution of *Bombina variegata* at the local scale (Majella) The MAXENT model has the form exp(…)/constant, and the curves show how the exponent changes as each environmental variable is varied, keeping all others at their average sample value.



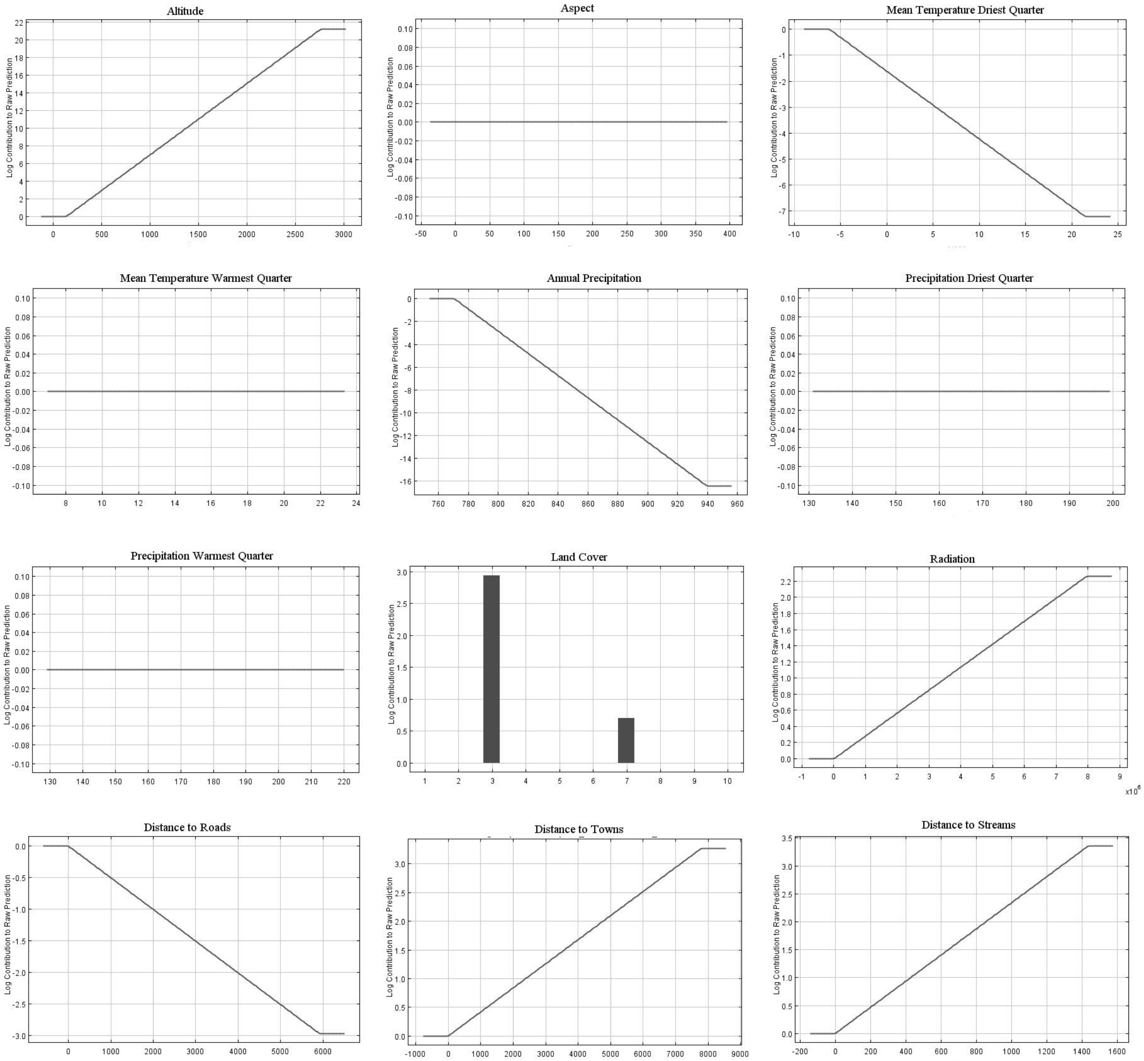
### 7.6. **Appendix F**. Response curves of the environmental variables predicting the potential distribution of *Vipera ursinii* at the continental scale. The MAXENT model has the form exp(…)/constant, and the curves show how the exponent changes as each environmental variable is varied, keeping all others at their average sample value.



## 7.7. **Appendix G**. Response curves of the environmental variables predicting the potential distribution of *Vipera ursinii* at the regional scale (Italy) The MAXENT model has the form exp(…)/constant, and the curves show how the exponent changes as each environmental variable is varied, keeping all others at their average sample value.



## 7.8. **Appendix H**. Response curves of the environmental variables predicting the potential distribution of *Vipera ursinii* at the local scale (Majella) The MAXENT model has the form exp(…)/constant, and the curves show how the exponent changes as each environmental variable is varied, keeping all others at their average sample value.



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