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MACRO-SCALE ENVIRONMENTAL PREFERENCES OF *BOMBINA BOMBINA*: A MODELING APPROACH

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Environmental factors governing the distribution of *Bombina bombina* throughout its home range have been explored using an approach based upon maximum entropy distribution modeling. Components strongly associated with “minimum temperatures of coldest week”, “mean temperatures of coldest quarter” and “radiation during the wettest quarter” are most likely responsible for shaping macro-scale environmental (or narrowly, bioclimatic) preferences of the species. In terms of climate change, modeling results show that warming winters could considerably favor *B. bombina*.

Key words: *Bombina bombina*, species distribution modeling, Maxent, Bioclim, CliMond, jackknife test.

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INTRODUCTION

Factors that influence species distributions and habitat selection across home ranges are of great importance to researchers and wildlife conservationists (Baldwin 2009), particularly in the face of global climate change (Peterson et al. 2002). Climate change is expected to cause shifts in species distributions, threatening their viability and altering their representation in protected areas (Araujo et al. 2004, 2011, Thuiller et al. 2006).

In this paper, we explore the factors governing the distribution of *Bombina bombina* (Linnaeus, 1761) (Fig.1.) using an approach based upon maximum entropy distribution modeling (DM), which importantly can aim at explaining ecological relationships in nature (Halvorsen 2012).

MATERIAL AND METHODS

We used *Maxent* (version 3.3.3k), a general-purpose algorithm that generates predictions or inferences from an incomplete set of information, which has been introduced for the modelling of species distributions (Phillips et al. 2006). The maxent approach is based upon a probabilistic framework. The main assumption is that the incomplete empirical probability distribution (consisting of the species occurrences) can be approximated by a probability distribution of maximum entropy subject to certain environmental constraints, and that this distribution approximates a species' potential geographic distribution.

Like most maximum-likelihood estimation approaches, the maxent algorithm a priori assumes a uniform distribution and performs a number of iterations in which the weights associated with the environmental variables, or functions thereof, are adjusted to maximize the average probability of the point localities (also known as the average sample likelihood), expressed as the training gain (Phillips 2006). These weights are then used to compute the maxent distribution over the entire geographic space. Consequently, this distribution expresses the suitability of each grid cell as a function of the environmental variables for that grid cell. A high value of the function (in units of cumulative probability) for a particular grid cell indicates that this grid cell is predicted to have suitable conditions for the species in question (Phillips 2006).

There are several aspects of the *Maxent* software that support the interpretation of the model results. For example, maxent has a built-in jackknife (Fig.4.) option through which the importance of separate environmental data layers can be estimated. It also provides response curves showing how the prediction depends on a particular environmental variable (Phillips 2006). For all model runs in this study, we used the default settings for regularization and in selecting the feature classes.

We ran models with 50 bootstrap replicates, and assessed model performance using the average AUC (area under the receiver operating curve, ROC) score to compare model performance. AUC values >0.9 are considered to have

Fig. 1. Foto *Bombina bombina* (yellow ventral side) from Kanev.

'very good', >0.8 'good' and >0.7 'useful' discrimination abilities (Swets 1988). The logistic output format was used, because it is easily interpretable with logistic suitability values ranging from 0 (lowest suitability) to 1 (highest suitability).

Occurrences consisted of 148 *B. bombina* genetic samples from Hofman et al. (2007), forming a presence-only dataset (the training set). The modeling calculations used the environmental data from a buffered polygon bounding the study area. The first five principal components (*PC1-5*) of the 35 *Bioclim* variables in the *CliMond 1975H* dataset (Kriticos et al. 2014) were employed. These capture more than 90% of the variance in the full dataset.

RESULTS AND DISCUSSION

The average AUC score for our *Maxent* model was 0.856±0.002, which is considered to be a good fit and indicates a good discriminatory capacity of the model (i.e., *Maxent* model was significantly better than random in binomial test of omission and predicted area curve, Fig.2.).

The absolute and relative importance of individual environmental variables as predictors of the distribution of the toad can be estimated through the training gains when the variable of

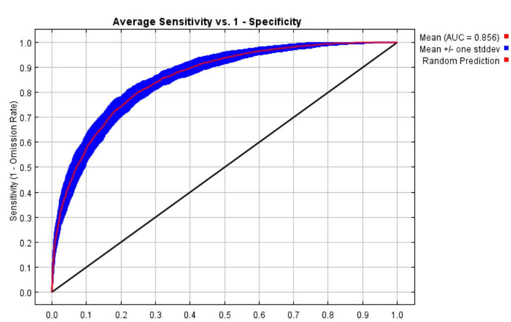

Fig. 2. The receiver operating characteristic (ROC) curve generated in *Maxent*, showing an average of 50 repetitions of the model; the dark blue range shows the mean of the standard deviations.

interest is used in isolation and excluded from the whole set of variables in the *Maxent* runs.

This test indicated that the layer with the most useful information by itself is the *PC1* (primarily a temperature dominated variable with strong contributions from the “minimum temperature of coldest week” and “mean temperature of coldest quarter”). The environmental variable that decreases the gain the most when it is omitted is *PC4* (mostly “radiation during the wettest quarter”, i.e. in the summer), which therefore appears to have the most information that isn’t present in the other variables.

The responses of the most important environmental variables in the predictions for the toad in this study generally agree well with the corresponding variable contributions (percentage and permutation importance, see Table) and response curves (Fig.4., exemplified by the response to *PC1* and supported by the linear component of the correlation between

Table 1. Analysis of variable contributions for *Bombina bombina*

Variable	Percent contribution	Permutation importance
PC1	38	37.9
PC2	17.2	14.1
PC3	16.4	18.4
PC4	14.4	14.5
PC5	14	15.1

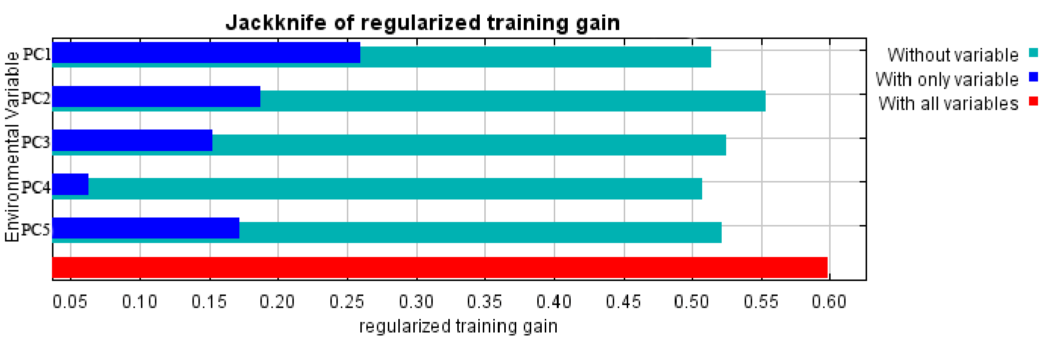

Fig. 3. Results of jackknife test of variable importance, using training gain. The jackknife test in blue bars shows individual environmental variable importance relative to the red bar which shows all environmental variables. Light blue bar shows whether a variable has any information that isn’t present in the other variables, and a dark blue bar shows whether a variable has any useful information by itself. Values shown are averages over replicate runs.

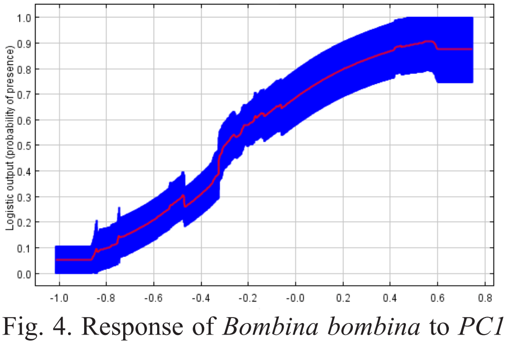

Fig. 4. Response of *Bombina bombina* to *PC1*: *x*-axis – PC scores; *y*-axis – logistic output (probability of presence).

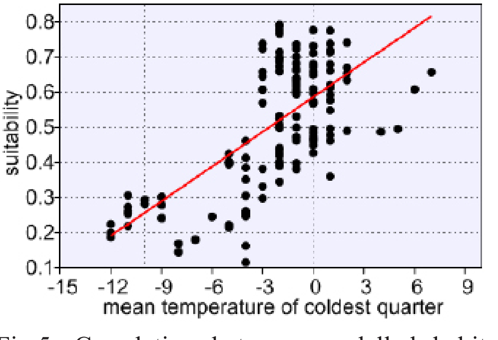

Fig.5. Correlation between modelled habitat suitability and “mean temperature of coldest quarter”.

the modelled habitat suitability and "mean temperature of coldest quarter"(r=0.665, p<0.01, Fig.5.).

The following table gives estimates of relative contributions of the environmental variables to the *Maxent* model. To determine the first estimate, in each iteration of the training algorithm the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages.

CONCLUSIONS

DMs can enhance our knowledge on the ecology of species, help to quantify their requirements. In turn, these may be used to predict responses to climate change. Modeling results, for instance, show that warming winters should considerably favor *B. bombina*, particularly in terms of survival. However, even if *B. bombina* could theoretically benefit from changing climatic conditions in the future, this does not necessarily imply a raise in population sizes, as dispersal and habitat suitability may be compromised by other factors, particularly anthropogenic (Dolgener et al. 2013). In addition, global warming has the potential to cause adverse changes in breeding phenology (Blaustein et al. 2001), disease-mortality dynamics (Daszak et al. 2003; Pounds et al. 2006) and food supply (Donnelly, Crump 1998). Nevertheless, given the complexity of the task, we consider a deeper use of DMs will add to improve our understanding of the environmental conditions important for habitat selection of *B. bombina* and support the development of suitable proactive conservation strategies designed to maintain population viability both from a demographic and evolutionary point of view.

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