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Article *in* Herpetological Conservation and Biology · May 2018

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MODELING POTENTIAL DISTRIBUTIONS OF THREE EUROPEAN AMPHIBIAN SPECIES COMPARING ENFA AND MAXENT

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Abstract.—Understanding the distribution and habitat preferences of amphibians is crucial to protecting their declining populations. It remains a challenge because most species are difficult to detect, enough data on their occurrence are needed, and the contribution of climatic and habitat factors is not well known. Various modeling approaches exist both to infer habitat preferences based on known locations, and to extrapolate species geographic distributions. We used presence-only data of three anuran species from original naturalist databases covering 34,750 km² in the western part of France, including 660 occurrences for the Common Midwife Toad (*Alytes obstetricans*), 1,910 for the Spined Toad (*Bufo spinosus*), and 975 for the Common Brown Frog (*Rana temporaria*). We compared two current modeling approaches, the Ecological Niche Factor Analysis (ENFA) and Maximum Entropy (MaxEnt) to model their potential distributions by including high resolution climate variables, and habitat and landscape variables. For each species, both analyses allowed a refined understanding of the relationships between habitat factors and the species distribution. We showed that climate and natural grasslands are key factors in explaining the species distributions and that the surrounding environment of aquatic habitats is an important driver of amphibian presence. The two models gave different predictions of distributions, which may lead to different planning of conservation areas. Our study confirms the importance of using and comparing several models, and evidenced the importance of collecting field data at a regional scale.

Key Words.—anurans; climate; ecological niche models; land-use

Résumé.—Comprendre la répartition et les préférences d'habitat des amphibiens est crucial pour protéger leurs populations en déclin. Cela reste un défi car la plupart des espèces sont difficiles à détecter, les données d'occurrence doivent être suffisantes et l'importance des facteurs climatiques et de l'habitat n'est pas bien connue. Différentes approches de modélisation existent à la fois pour inférer les préférences de l'habitat en fonction des emplacements connus et pour extrapoler les distributions géographiques des espèces. Nous avons utilisé des données de présence pour trois anoures, provenant de bases naturalistes couvrant 34,750 km² dans la partie ouest de la France. Nous avons utilisé 660 points géoréférencés pour l'alyte accoucheur (*Alytes obstetricans*), 1910 pour le crapaud épineux (*Bufo spinosus*) et 975 pour la grenouille rousse (*Rana temporaria*). Nous avons comparé deux approches de modélisation actuelles, l'analyse des facteurs de niche écologique (ENFA) et l'entropie maximale (MaxEnt) pour modéliser leurs distributions potentielles en incluant des variables climatiques à haute résolution spatiale, des variables de l'habitat et du paysage. Pour chaque espèce, les deux analyses ont permis une compréhension affinée des relations entre les facteurs de l'habitat et leur répartition. Nous avons montré que le climat et la proximité aux prairies naturelles sont des facteurs clés pour expliquer les répartitions des espèces et que les milieux environnant les habitats aquatiques sont une variable importante de la présence d'amphibiens. Les deux modèles ont donné des prédictions différentes des distributions qui peuvent conduire à une planification très différente des zones de conservation. Notre étude confirme l'importance d'utiliser et de comparer plusieurs modèles et a mis en évidence l'importance de collecter des données de terrain à l'échelle régionale.

Mots-clés.—anoures; climat; modèles de niche écologiques; occupation du sol

INTRODUCTION

Several modeling approaches and tools mainly known as species distribution models (SDMs), ecological niche models (ENMs), and species niche models have been developed to estimate the actual and potential distribution of a species. All these approaches are used to investigate issues in biogeography, to analyze biodiversity patterns over space and time, and to understand relationships between species and abiotic and biotic environment factors. Moreover, all have applications in conservation biology (Thorn et al. 2009; Syfert et al. 2014), such as in predicting impacts associated with invasive species (Lobos et al. 2013; Fernández and Hamilton 2015). The term ENM refers to mechanistic and correlative models. Correlative models are presence/absence approaches, as well as presence/pseudo-absence and presence-only approaches, that result in different representations of realized niches of the species (Sillero 2011). An ENM relies on the species niche concept in environmental and geographical space (Hirzel and Le Lay 2008). Hutchinson (1957) defined the concept of fundamental niche as a multidimensional hypervolume determined by the set of environmental factors that allows a species to live and persist and the realized niche as the occupied part of the fundamental niche when niche exclusion by competition occurs.

Presence/absence correlative models forecast the probability of finding the species in a particular place. A presence-only correlative model predicts the suitability of habitats across the landscape. Many ENM methods exist and it is beyond the scope of this article to cite all the modeling methods that have been developed or applied to amphibian and reptile studies. Nevertheless, one can refer to the synthesis by Guisan and Thuiller (2005) who cited the most currently used software and related algorithms, including generalized linear models (GLM), generalized additive models (GAM), genetic algorithms (GARP), artificial neural networks (ANN), ecological niche factor analysis (ENFA), and maximum entropy (MaxEnt). Among these, ENFA (Hirzel et al. 2002) and MaxEnt (Phillips et al. 2006) have been successfully applied in situations where absence data were not available (Elith et al. 2006).

Due to the continuing worldwide amphibian decline (Beebee and Griffiths 2005; Hof et al. 2011), there is an urgent need to better understand the habitat relationships of amphibians and to develop methods to predict habitat suitability for amphibians in the landscape (Torres et al. 2016). European amphibians are a challenging group for ENM because of the bi-phasic life cycle of most species. To understand their distributions we must take into account environmental and climate variables that are linked both to aquatic and terrestrial habitats (Blaustein and Kiesecker 2002). Among climate variables, temperature and precipitation are two fundamental drivers of amphibian distribution (Otto et al. 2007). The type of habitat plays an important role by acting on the microclimate; for instance, dense vegetation and forests provide enough air moisture for many species (Nöllert and Nöllert 2003). Precipitation has also great importance because it regulates the availability of water bodies within the landscape, therefore contributing to breeding success and to the development of larvae. Patterns of species diversity and distribution are linked to the number and spatial distribution of permanent and temporary ponds and streams (Barnaud et al. 1996; Wood et al. 2003) but also to the availability and suitability of terrestrial habitats in past and present climates (Araújo et al. 2006). However, besides these general relationships with environmental variables, habitat preferences are species-specific and need further understanding.

In this study, we aimed to model the potential distributions of three species by comparing ENFA and MaxEnt, and to identify the environmental factors related to their occurrence. We used georeferenced field observations of the Common Midwife Toad (*Alytes obstetricians*), the Spined Toad (*Bufo spinosus*), and the Common Brown Frog (*Rana temporaria*) in six administrative departments of the western part of France and analyzed several ecological, landscape, and topographical variables. These species are protected by law in France (Bern convention, European habitat directives, regional protections).

MATERIALS AND METHODS

Study site.—We worked with a set of presence-only data covering six administrative departments in western and central western France for a total area of 34,989 km². From north to south the departments were: Indre-et-Loire (I&L), Indre (I), Creuse (Cr), Haute-Vienne (HV), Corrèze (Co), and Ariège (A). The distance between the northern part of Indre-et-Loire and the southern part of Ariège is about 650 km, with an altitude ranging from 80 m to 3,147 m (above sea level). This area combines different landscapes of hills, mountains, agricultural lands, valleys, plains, and urban and semi-urban zones. There is a main climatic north-south gradient and west-east gradient due to the influence of the Atlantic Ocean. The mean annual temperature and precipitation for each department is 11.8° C/696 mm (I&L), 11° C/728 mm (I), 10.7° C/1,050 mm (Cr), 11.4° C/1,023 mm (HV), 10.5° C/901 mm (Co), 12° C/992 mm (A; data from the National Center of Meteorology, MeteoFrance).

Species data.—We used occurrence data for three anuran species: *Alytes obstetricans*, *Bufo spinosus*, and *Rana temporaria*. We collaborated with five

naturalist associations that gathered data from over 15 y of field investigations conducted by trained people: The Naturalist Association of Study and Protection of Ecosystems CAUDALIS (9, rue du Nouveau Calvaire, 37100 Tours, France), the Society of Study, Protection and Planning of Nature in Touraine (7, rue Charles Garnier, 37200 Tours, France), Indre-Nature (44, avenue François Mitterrand, Parc Balsan, 36000 Châteauroux, France), the Mammalogical and Herpetological Group of the Limousin (Pôle Nature Limousin, ZA du Moulin Cheyroux, 87700 Aixe-sur-Vienne, France), and the Association of Naturalists of Ariège (Vidalac, 09240 Alzen, France). We also participated to the inventory for Indre-et-Loire and Ariège beginning in 2013. To minimize sampling bias, which is known to influence model accuracy, we only used data from 2000 to 2015 because the majority of the data acquired before 2000 came from opportunistic observations. Observers investigated systematically subdivisions (grid cells) of the departments. As a result of this first down-sampling, we used 660, 1,910, and 975 verified georeferenced occurrence points for *A. obstetricans*, *B. spinosus* and *R. temporaria*, respectively (1, subsampled dataset). There were many points represented in all the provinces for all species, except there were relatively few points for *R. temporaria* in the northern two provinces. We used two approaches to reduce spatial autocorrelation between occurrence points. First, we performed spatial filtering: the process of removing spatially autocorrelated points to improve calibration and evaluation of the model (Boria et al. 2014). We used the SDMtoolbox (Brown 2014) with multiple rarefying distance (from 1 to 10 km) and a heterogeneity raster for topography (10 km being the default value) based on high spatial heterogeneity measured for moderately mountainous to mountainous regions (see Boria et al. 2014 and references therein; our study region includes high mountains in the south, and low mountains, hills, and valleys in the center). This resulted in 329, 444, and 490 filtered occurrence points for *A. obstetricans*, *B. spinosus*, and *R. temporaria*, respectively (2, spatially filtered dataset). Second, we constructed bias grid files for each species to reduce potential locally dense sampling (3, bias file). The bias grid consisted of Gaussian kernel density maps of the species occurrences (Elith et al. 2010).

Ecological and landscape variables.—We initially selected 23 ecological and landscape variables, all being potentially related to species preferences and requirements within the study area. We applied pairwise Pearson's correlation test on these variables using ENMtools (Warren et al. 2010) to avoid high collinearity between the variables (Elith et al. 2011). When $|r| \geq 0.7$, the variable within the pair having less relevance to the ecology of the focal species (based on

expert knowledge) was removed. We kept 20 variables of the 23 for modeling (Appendix 1). We divided the study area into cells of 500 × 500 m, each representing a resource unit (RU) potentially exploitable by the studied species. We calculated the distance between the centroid of each RU and the nearest environmental variable using GIS tools in ArcGIS 10.3 (Esri, Redlands, California, USA). Consequently, each RU was defined by a value of distance to each habitat and habitat fragmentation variable.

Concerning climate variables, we used a set of raw climatic data provided by the national agency for meteorology and climate (MeteoFrance, Paris, France) and the European Climate Assessment & Dataset (ECA&D; Available from http://www.ecad.eu/ [Accessed 2 February 2009]). We did not use Bioclim datasets (WorldClim) in this study mainly because the time period (1960–1990) for which the bioclimatic variables were calculated did not fit our field observations, multicollinearity exist between the derived bioclimatic variables, and we worked with a better spatial resolution dataset. We used annual means of monthly maximum and minimum temperatures, mean annual temperatures, and mean precipitation over the 2002–2014 period. We inferred such climate variables at a spatial resolution of 1 km² by downscaling two climate data sets having complementary spatio-temporal characteristics (Tabor and Williams 2010). First, we computed the climate anomalies between coarse European climate grids (Haylock et al. 2008) for 2002–2014 and 1961–1990 as absolute and relative differences for temperature and precipitation, respectively. Second, we re-sampled the anomaly grids through bilinear interpolation to achieve 1 km² grids covering the French territory. Third, we added these 1 km² climate anomaly grids to a second set of 1 km² French climate grids of temperature and precipitation averaged over 1961–1990 to achieve an accurate estimation of the climate conditions for 2002–2014 (i.e., the time period corresponding to the years for which amphibian occurrence records were available). The second set of 1 km² French climate grids used for this step is part of a spatio-temporal climate data set computed through a modeling approach predicting temperatures ($r^2 = 0.93$ and Root-Mean-Square Deviation [RMSD] = 0.56 for 13,620 independent temperature observations) and precipitation ($r^2 = 0.83$ and RMSD = 132 for 17,865 independent precipitation observations) from solar radiation, geographical, physiographical, and habitat variables (Bertrand et al. 2011; Bertrand 2012).

Species distribution modeling with ENFA and MaxEnt.—We performed ENFA using R 3.3.2 software (R Core Team 2015) through the adehabitatHS 0.3.12 package (https://cran.r-project.org/web/packages/adehabitatHS/index.html). This modeling approach

evaluates the species ecological niche based on the magnitude of the difference between the unbounded distance from the average environmental conditions where the species is found and the entire range of environmental conditions observed in the study area. The ENFA summarizes all environmental variables related to the species occurrence into independent factors called marginality and specialization (see Hirzel et al. 2002 for details). We can identify the contribution of each environmental variable to the axis of marginality by calculating the correlation coefficient for each variable on it. A positive correlation indicates preference for the environmental variable whereas a negative correlation means the contrary. A high absolute value of this coefficient indicates that environmental conditions used by the species differ strongly from those encountered in the study area. We used an absolute value of 0.25 to determine if the species is considered as marginal for each variable. Specialization measures the narrowness of the niche. It is the difference in the magnitude of the standard deviation of a variable within the available ecological space to the standard deviation of the same variable within the realized ecological niche of the species. A species is specialist if it occupies strict environmental conditions compared to the extent of a variable in the study area. We used an absolute value of 0.25 to determine if the species is considered as specialist for each variable. For each species, we performed the ENFA first on the subsampled dataset of occurrence points and second on the spatially filtered dataset of occurrence point. We used Monte-Carlo test to assess the significance of the difference between the values obtained for the marginality and specialization axes using a Monte-Carlo procedure of 999 permutations. This test compares the distribution of simulated RU with actual scores of RU used (from the 999 random draws) on the axes of marginality and specialization (Fonderflick et al. 2015).

The MaxEnt software (Phillips et al. 2004) uses the method of maximum entropy and is extensively used for analyzing presence-only data. MaxEnt estimates the potential distribution of a species in a geographical area which is closest to uniform but concurrently constrained by some environmental conditions (Phillips et al. 2006). This permits identification of species requirements and environmental preferences. The software allows us to study the importance of each variable in predicting the distribution of the species using two coefficients: the percentage contribution assigned to each variable in the model and the importance of permutation based on the random permutation of the values of each variable among the training points, which may be more relevant if the variables are correlated. For each species, we ran 10 replicates with 30% of test data (subsample, random seed), and we set the other parameters by default (Phillips et al. 2006). We used an average of the 10 replicates to have a single prediction of presence probabilities for each the species. We ran the models with only (1) subsampled dataset, or (2) spatially filtered dataset, with subsampled dataset and bias file (1)(3), and with spatially filtered dataset and bias file (2)(3).

Graphical outputs of the models.—We used the Mahalanobis distance (Package adehabitatHS. https://cran.r-project.org/web/packages/adehabitatHS/adehabitatHS.pdf) for ENFA to predict habitat suitability across the six departments. This produced a spatial representation of the relative habitat suitability values from 0 to 1 calculated for every cell. MaxEnt also produces suitability maps based on the prediction of the probability distribution of the species.

Model evaluation and comparisons.—For both ENFA and MaxEnt, we assessed model performance with Receiver Operating Characteristic (ROC) curves, calculated for each model (Hanley and McNeil 1982; Lobo et al. 2010; Robin et al. 2011). We used the area under the ROC curve (Area Under the Curve, AUC), calculated from 30% of the occurrence points, as an estimate of the performance of each model. We calculated AUC with the pROC-package in R for the ENFA model and in MaxEnt for the MaxEnt model (Phillips et al. 2004; Robin et al. 2011). A random prediction gets an AUC value of 0.5 whereas an AUC value close to 1 indicates higher performance of the model (Dolgener et al. 2013). The predictions are described as excellent for AUC between 0.9 and 1, good between 0.8 and 0.9, fair between 0.7 and 0.8, and poor below 0.7. For better evaluation of model accuracy and precision (Lobo et al. 2008) we also used the maximum True Skill Statistics (TSS = sensitivity + specificity – 1; Allouche et al. 2006). The TSS ranges from -1 to 1, where -1 to 0.4 = poor, 0.4 to 0.5 = fair, 0.5 to 0.7 = good, 0.7 to 0.85 = very good, 0.85 to 0.9 = excellent, 0.9 to 1 = almost perfect to perfect.

RESULTS

Model evaluation and comparisons.—We used test AUC and maximum TSS to evaluate the performance of the models run either with subsampled dataset (1), after the spatial filtering (2), or with the bias file (3; Appendix 2). The best model according to AUC and TSS were: for *A. obstetricans*, ENFA (2) and MaxEnt (1); for *B. spinosus*, ENFA (2) and MaxEnt (2; best TSS and second best AUC); and for *R. temporaria*, ENFA (1) and MaxEnt (2). AUC showed fair predictive performance for *A. obstetricans* and *R. temporaria* for MaxEnt models, fair predictive performance for *A. obstetricans* ENFA model, and good for *R. temporaria* ENFA model.
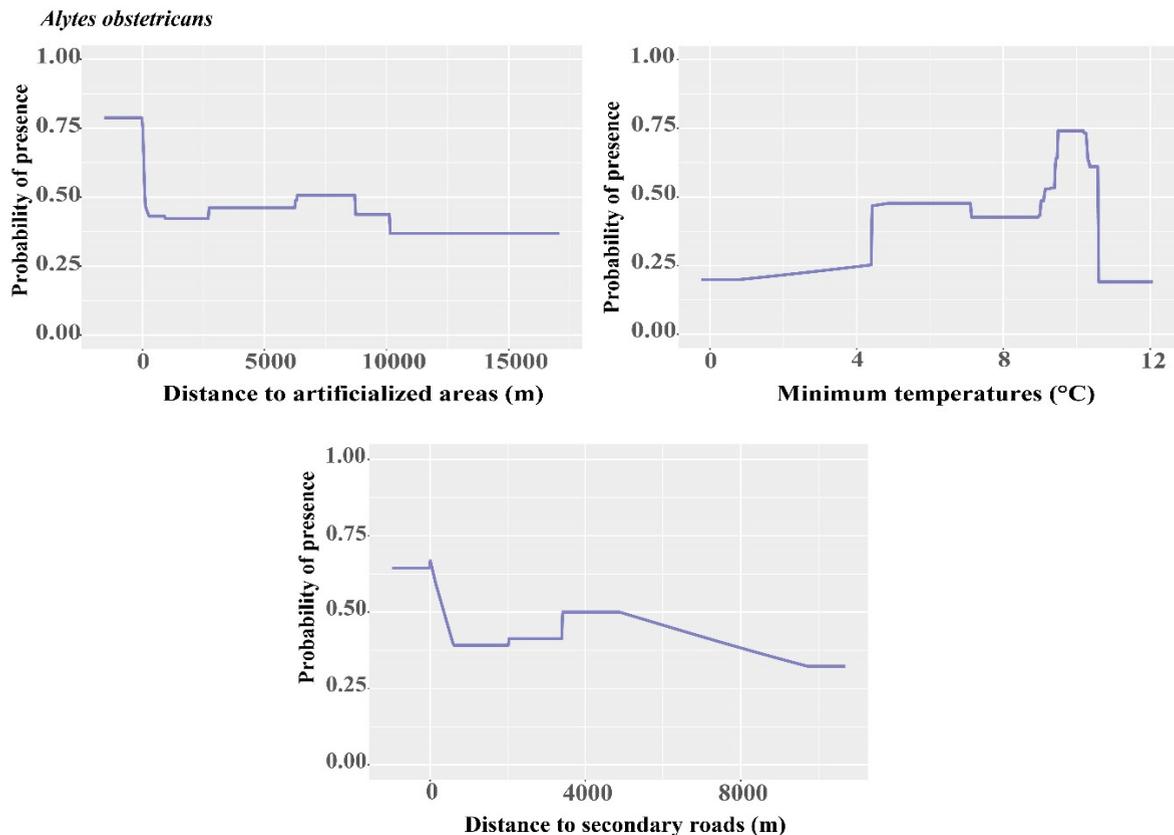
Alytes obstetricans

Figure 1. MaxEnt response curves of the most contributive variables for the Common Midwife Toad (*Alytes obstetricans*).

AUC also showed poor predictive performance for *B. spinosus* MaxEnt and ENFA models. TSS showed poor performances of prediction for all ENFA models and MaxEnt models for *A. obstetricans* and *B. spinosus*. TSS evaluated *R. temporaria* MaxEnt model as fair.

ENFA and MaxEnt analysis.—Monte-Carlo tests showed significant differences ($P < 0.001$) for both marginality and specialization, which indicates that the three species are not randomly distributed across the study area. According to the results of the best selected ENFA models of each species (Appendix 3), *A. obstetricans* and *B. spinosus* showed preferences for short distance to natural grasslands and long distance to wetlands. *Rana temporaria* showed preferences for short distance to natural grasslands as well, but also appeared to avoid orchards. For each best selected MaxEnt model, we ranked predictor variables according to their percent contribution to model gain. Starting with the variable that contributed the most, we proceeded down this ranked list, and identified the subset of variables required to achieve a summed contribution of at least 50%. For *A. obstetricans*, distance to urban areas, minimum temperature, and distance to secondary roads contributed the most to the distribution model (Appendix 3). For *B. spinosus*, the most contributive variables

were distance to water bodies, minimum temperature, and distances to natural grasslands and secondary roads. For *R. temporaria*, the most contributive variables were precipitation, minimum temperature, distance to natural grasslands, and the maximum temperature. The response curves showed that *A. obstetricans* (Fig. 1) seemed to be favored by short distances to urban areas and secondary roads. The probability of presence for the species was higher between 9.5° C and 10.5° C for minimum temperature. The probability of presence of *B. spinosus* (Fig. 2) was higher at short distances to natural grasslands. For water bodies and secondary roads, the probability of presence was higher at short distances to those elements, but increased again at greater distances. The probability of presence dropped between 4° C and 10° C for minimum temperatures. The probability of presence of *R. temporaria* (Fig. 3) was also higher at short distances to natural grasslands. The probability of presence was the highest with high precipitation, around 3° C for minimum temperature, and around 6° C for maximum temperature.

Patterns of habitat suitability.—Comparing the ENFA and MaxEnt methods, all maps show dissimilar distribution patterns of habitat suitability. With the ENFA (Fig. 4), moderate to high values of suitability
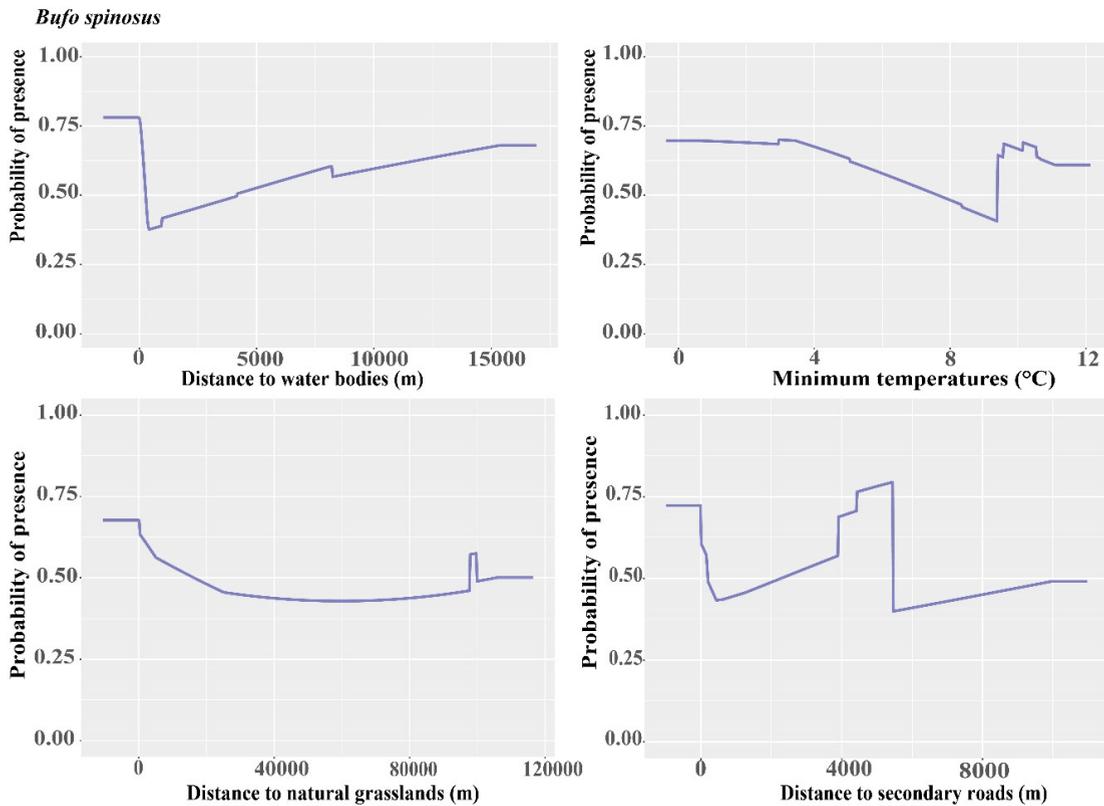
Bufo spinosus

FIGURE 2. MaxEnt response curves of the most contributive variables for the Spined Toad (*Bufo spinosus*).
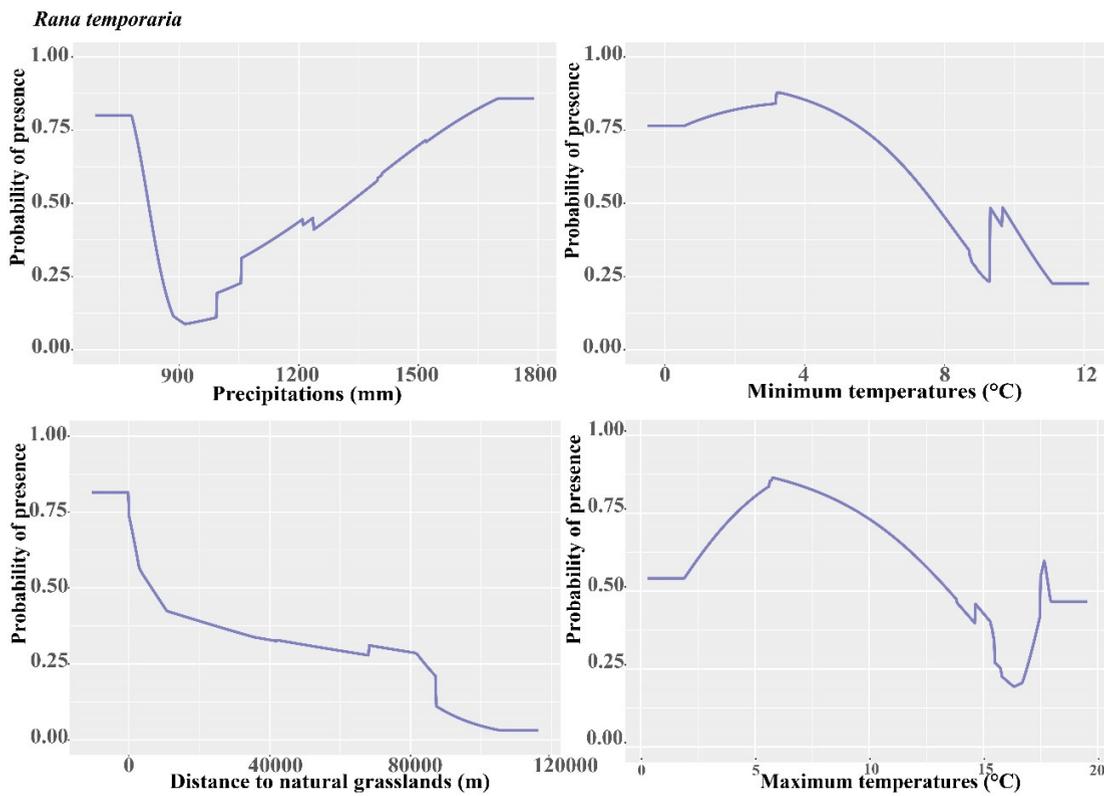
Rana temporaria

FIGURE 3. MaxEnt response curves of the most contributive variables for the Common Brown Frog (*Rana temporaria*).
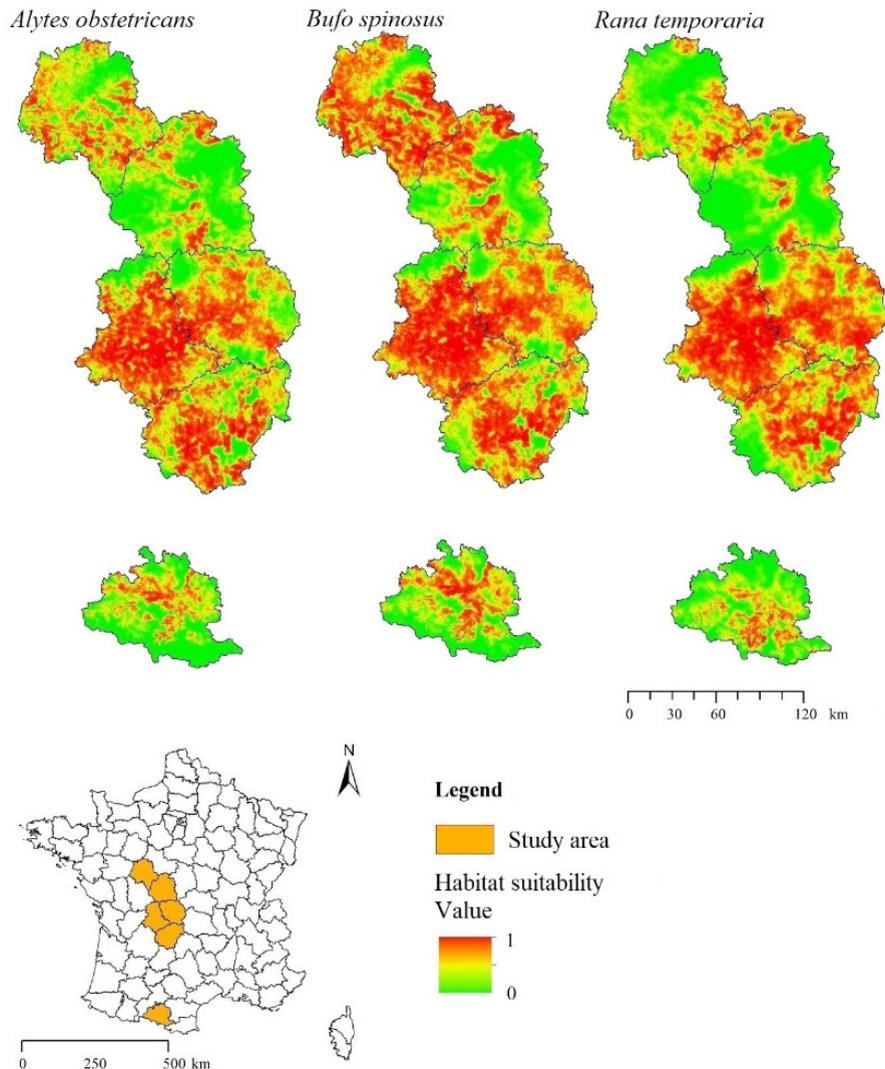
FIGURE 4. Maps of relative habitat suitability predicted by the ENFA for the Common Midwife Toad (*Alytes obstetricans*), the Spined Toad (*Bufo spinosus*), and the Common Brown Frog (*Rana temporaria*) across the six French administrative departments. The relative habitat suitability is represented by a gradient, from very low suitability (0, in green) to very high suitability (1, in red).

(yellow to red) occupy very large areas whereas maps with MaxEnt (Fig. 5) are dominated by areas with low values of habitat suitability (yellow to green).

DISCUSSION

Model performance and comparison.—Common problems to produce accurate ENMs are (1) the limited number of occurrence data, (2) the sampling bias related to field observations, and (3) the model-based uncertainty in predictions. In this study, we were able to use a large database of 3,545 amphibian presence points over a large area (34,989 km²) with various types of habitats and differences in climate. The spatial rarefying process improved the performance of four of

six of our models, whereas the use of the bias file did not improve the models. For more discrimination between models it has been recommended to use complementary statistics for evaluation of model performance (Allouche et al. 2006; Lobo et al. 2008); therefore, we used both the AUC and TSS. However, we obtained different predictive performances depending both on the model, the evaluation method, and the species, but overall the differences were small. Other studies on different taxa found better performance of MaxEnt over ENFA (Fonderflick et al. 2015; González-Irusta et al. 2015), which was not obvious in our results.

Our AUC scores were not very high: AUC scores > 0.8 are common in many ENM studies. However, it was demonstrated that running ENM without correcting or
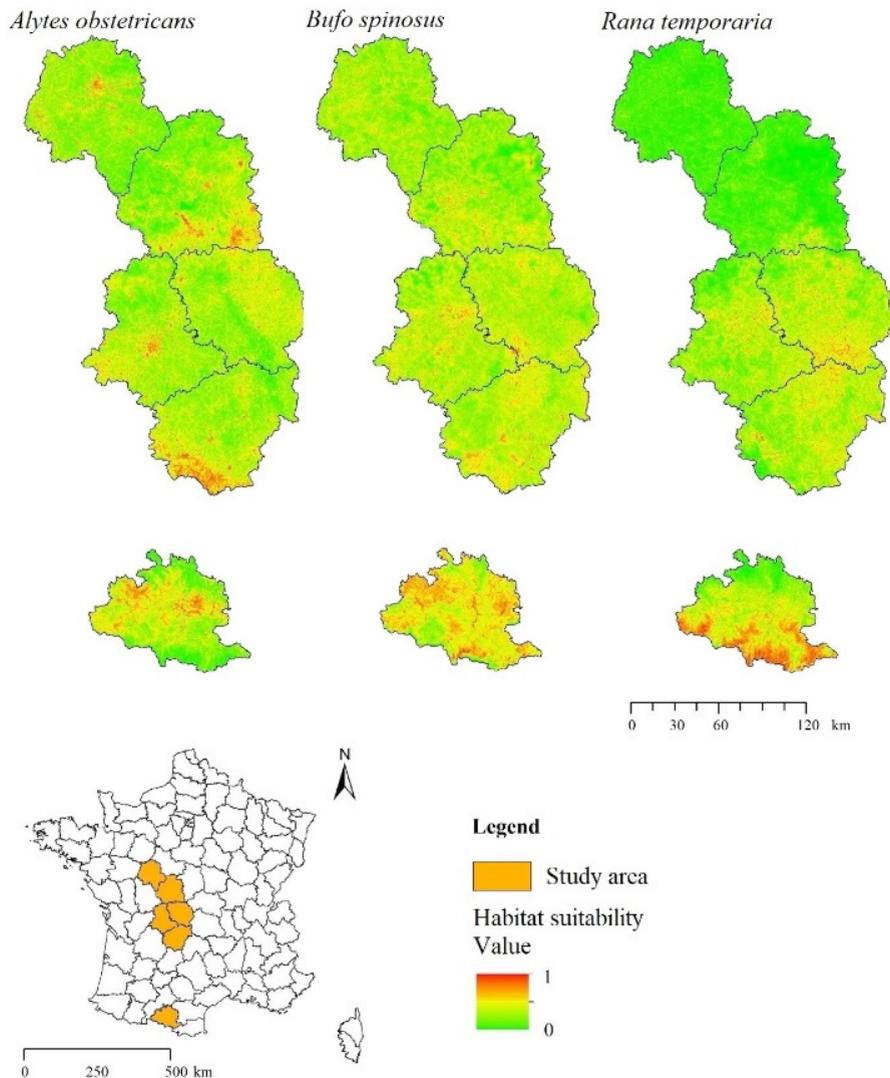
FIGURE 5. Maps of relative habitat suitability predicted by MaxEnt for the Common Midwife Toad (*Alytes obstetricans*), the Spined Toad (*Bufo spinosus*), and the Common Brown Frog (*Rana temporaria*) across the six French administrative departments. The relative habitat suitability is represented by a gradient, from very low suitability (0, in green) to very high suitability (1, in red).

checking for sampling bias and/or spatial autocorrelation leads to inflated measures of performance statistics (see for instance Boria et al. 2014). The downsampling and spatial filtering contributed to limit this kind of inflation. The AUC scores should be interpreted with caution and should not be directly compared between the species. In our results, the models for *B. spinosus* had the lowest AUC, but in fact, in the situation where background data are used instead of true absence (in case of presence-only data), AUC values indicate whether a species is widespread or restricted in range within the study area. Species with a low number of occurrence data are more specialist species, which leads to a better adjustment of the fit and as a consequence to a better disentanglement of presence/absence (Lobo et al. 2008). Thus, the low

AUC value for the *B. spinosus* model is consistent with the ecology of this species, which tends to be a generalist species. *Bufo spinosus* is more of a generalist than the other two species in the study, it is able to exploit various environments, it is distributed widely, and it occurs commonly in our study area (Brotons et al. 2004; Hernandez et al. 2006). For each model, TSS values were lower than AUC, which is often the case because this statistic is more rigorous and is supposed to be a less biased evaluation statistic than the AUC (Allouche et al. 2006). TSS is more sensitive and will decrease as sensitivity and specificity of the model decreases, along with the increase of omission errors and commission errors. The differences between the AUC values for each model were less than the differences between the TSS,

which makes this statistic more discriminant. Although the use of AUC has been criticized (see Allouche et al. 2006 and Lobo et al. 2008), it is still extensively used for ENM evaluation. Besides statistical considerations, we must take into account coherence with the biology and ecology of the species.

Habitat and species distribution.—The use of ENM often helps to better understand the biology and ecology of the species. Such tools may be particularly useful for amphibians such as our studied species because they live in both aquatic and terrestrial habitats and may respond to landscape changes at several scales. We also found contradictory results compared to what is usually known about the ecology of our species. ENFA results showed a negative relationship between presence of *A. obstetricans* and *B. spinosus* and wetlands (this variable included inland marshes and peatlands larger than 25 ha), whereas MaxEnt results showed that water bodies contributed to the presence of *B. spinosus*. These results seem to contradict the biology of these two species (Lescure and De Massary 2012), especially because the species require water bodies for breeding. However, *A. obstetricans* is known to shelter near urban areas, far from wetlands and natural water bodies (Nöllert and Nöllert 2003). During migration *B. spinosus* can travel several kilometers around its reproduction site (Nöllert and Nöllert 2003) and can be observed in habitats near or far away from the aquatic site. Very often these three species breed in small water bodies, like permanent and temporary ponds in forests, quarries, or grasslands, but these wetland types were not included in the categories water bodies and wetland in the present study. In many regions, small wetland features play a crucial role in amphibian conservation, but they are rarely included in geographic databases because expensive technologies (e.g., Light Detection and Ranging [LiDAR]) are required to remotely detect this habitat (Tiner et al. 2015). We expect that adding geographic information about small wetland features in our models would have changed the contribution between the variables and would also have changed some distribution patterns. Otherwise, our results argue that the environment near aquatic habitats could be an important driver determining the ability of individuals to reach aquatic sites.

We also expected the presence of the species to be correlated with short distances to forests because forests can provide shelter during winter (Le Garff 1991; Lescure and De Massary 2012). A species like *R. temporaria* may be difficult to model accurately over large areas because of its varyiable ecology. In France, the species is ubiquitous in the north; whereas in the rest of the country, it prefers either forests or grasslands on plains, or grasslands, and meadows above treeline (Duguet and Melki 2003). At the scale of our study

area, the two models for *R. temporaria* stressed the importance of natural grasslands variable.

Based on the negative effects of intense agriculture on amphibian populations, including related habitat fragmentation and intensive use of pesticides (Beja and Alcazar 2003; Beebee and Griffiths 2005; Duguet and Melki 2003; Smalling et al. 2015), we expected negative relationships between agricultural features and the presence of most of the species. For *A. obstetricans* and *B. spinosus*, the results of the models showed very poor contributions and absence of relationships with orchards, crops, and pastures variables, but showed a negative association with orchards variable for *R. temporaria*. Many of the variables included here as habitat fragmentation variables have negative impacts on the survival and persistence of amphibian populations.

Despite numerous studies showing the impact of roads on amphibian mortality (Fahrig et al. 1995; Hels and Buchwald 2001; Kobylarz 2001) and urbanization on population persistence (Hamer and McDonnell 2008), the presence of *A. obstetricans* seemed to be favored near areas with non-natural elements. This agrees with the ecology of species as a pioneer species that prefers habitats that are open, disturbed, and even close to urban and industrial areas, and can breed in ponds found in quarries (Brown and Crespo 2000). With MaxEnt, contribution of secondary roads variable was found to explain the distribution of *A. obstetricans* and *B. spinosus*, whereas primary roads variable had very low contribution. In addition, these two species can use ditches, ruts, and retention ponds that are located close to roads for their reproduction (Scher 2005). *Bufo spinosus* is frequently found near roads during migration (Nöllert and Nöllert 2003). These results support the idea that large roads, such as four lane roads and related infrastructure, can have much more detrimental effects than smaller roads. Species with greater dispersal abilities are expected to be more sensitive to the impact of roads (Carr and Fahrig 2001). However, a study in northern Spain showed that *A. obstetricans* and the urodele *Lissotriton helveticus* are affected differently by secondary roads, whereas both species have low dispersal capacities (Garcia-Gonzalez et al. 2012).

The ENFA analysis did not show relationships between climate variables and the presence of amphibians, whereas MaxEnt showed the importance of minimum temperature for all three species and the importance of maximum temperature and precipitation for *R. temporaria*. Regarding minimum temperature *A. obstetricans* seemed to prefer temperatures around 10° C. *Rana temporaria* seemed to prefer low temperatures and high precipitation. This is consistent with studies showing that the species can live in cold environments (Nöllert and Nöllert 2003; Grosselet et al. 2011). The importance of climate variables in the distribution of the

three species argues that the species could show limited tolerance to changing temperatures, especially to long-lasting extreme events of warm and dry days, which are predicted to increase in frequency during winter with climate change (Meehl et al. 2000). It would be interesting to model habitat suitability maps for these species under changing climatic conditions. In fact, applying scenarios corresponding to global warming forecasts would allow us to predict the distribution shifts of these species in France and identify priority areas for future conservation. To build more accurate predictions with the type of models we have used, however, will require more occurrence points in a larger area.

Conclusions.—Our results have allowed us to map potential habitat suitability for three anuran species at fine spatial scale with high resolution climate variables using two different modeling methods, ENFA and MaxEnt. Using the same landscape and climate variables with presence-only data, different estimates of habitat suitability and relationships with the environmental variables resulted from the two methods. The results provided by the MaxEnt modeling were more consistent with the ecology of the three species than those provided by the ENFA, which did not highlight many habitat relationships that were expected. This reinforces the good performance and accuracy of MaxEnt (Elith et al. 2006) that should be preferred over the ENFA. Such differences could be problematic for local scale conservation or management decisions because there is risk they could lead to arbitrary conclusions (Elith et al. 2006; Olivier and Wotherspoon 2006; Navarro-Cerrillo et al. 2011; Fonderflick et al. 2015). However, we recommend the use two or more modeling methods together. Even if one model appears to outperform the other, the advantage of running two or more models with the same datasets represents a cautious approach. Because all models have flaws, and are only estimations of reality, management decisions should be made based on as much information as possible. The issue of sampling bias also needs to be taken into account as much as possible during the field sampling and with statistical methods.

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APPENDIX 1. The ecological, landscape, and climate variables used in the models with data sources in parentheses: (1) CorineLandCover, www.statistiques.developpement-durable.gouv.fr; (2) Sandre database, www.sandre.eaufrance.fr; (3) IGN, www.ign.fr; (4) see Materials and Methods).

Variable		Description
Habitat variables	Coniferous forests	Distance to the closest coniferous forest (1)
	Mixed forests	Distance to the closest mixed forest (1)
	Deciduous forests	Distance to the closest deciduous forest (1)
	Orchards	Distance to the closest fruit trees or berry plantation (1)
	Crops	Distance to the closest crop (1)
	Pastures	Distance to the closest pasture (1)
	Natural grasslands	Distance to the closest natural grassland (1)
	Moors and heathlands	Distance to the closest moor or heathland (1)
	Water bodies	Distance to the closest water body (e.g., pond, lake) (2)
	Water courses	Distance to the closest water system (2)
	Wetlands	Distance to the closest wetland (1)
Habitat fragmentation variables	Extraction sites	Distance to the closest extraction site (1)
	Urban areas	Distance to the closest urban area (1)
	Primary roads	Distance to the closest highway, national or departmental road (3)
	Secondary roads	Distance to the closest communal or unpaved road (3)
	Railways	Distance to the closest railway (3)
Climate variables	Max. temperature	Averages of mean maximum temperatures between 2002 and 2014 (4)
	Min. temperature	Averages of mean minimum temperatures between 2002 and 2014 (4)
	Mean temperature	Averages of mean temperatures between 2002 and 2014 (4)
	Precipitation	Averages of yearly precipitations between 2002 and 2014 (4)

Appendix 2. Values of Area under the ROC curve (AUC_{test}) and True Skill Statistic (TSS) of the different models performed with ENFA and MaxEnt. Highest values are in bold. The combinations of data and settings used for the different models are indicated in parentheses: (1) the initial subsampled occurrence dataset, (2) after spatial filtering, and (3) model run with a bias file.

	Alytes obstetricans				*Bufo spinosus*				*Rana temporaria*			
	Mean AUC	SD	Mean TSS	SD	Mean AUC	SD	Mean TSS	SD	Mean AUC	SD	Mean TSS	SD
MaxEnt (1)	**0.731**	0.010	**0.364**	0.031	**0.684**	0.008	0.202	0.026	0.785	0.008	0.333	0.019
MaxEnt (2)	0.710	0.026	0.277	0.073	0.669	0.019	**0.263**	0.047	**0.793**	0.009	**0.443**	0.040
MaxEnt (1)(3)	0.686	0.026	0.248	0.076	0.638	0.011	0.025	0.007	0.779	0.013	0.265	0.029
MaxEnt (2)(3)	0.710	0.022	0.288	0.049	0.659	0.021	0.069	0.029	0.790	0.012	0.425	0.012
ENFA (1)	0.682	0.026	0.183	0.066	0.607	0.032	0.035	0.058	**0.804**	0.049	**0.384**	0.175
ENFA (2)	**0.790**	0.024	**0.374**	0.108	**0.679**	0.037	**0.210**	0.056	0.709	0.020	0.234	0.135

Appendix 3. Results of percentage contribution of MaxEnt best models and marginality of ENFA best models for the 20 variables. Bold values in Contribution column are variables with highest percentage contribution that contribute at least 50% of the gain of a model. Bold values in Marginality column indicate significant correlations of species preferences to corresponding variables. The data used for the different models are indicated in parentheses: (1) the initial subsampled occurrence dataset, (2) after spatial filtering.

		Alytes obstetricans		*Bufo spinosus*		*Rana temporaria*	
		MaxEnt (1)	ENFA (2)	MaxEnt (2)	ENFA (2)	MaxEnt (2)	ENFA (1)
Ecological, landscape, and climate variables		Contribution	Marginality	Contribution	Marginality	Contribution	Marginality
Habitat variables	Coniferous forests	1.7	0.03	3.1	0.05	2.1	0.09
	Mixed forests	2.8	0.03	1	0.05	1.2	0.05
	Deciduous forests	0.9	0.01	4.5	0.02	2	-0.01
	Orchards	2.4	0.05	3.7	-0.14	2.6	**-0.58**
	Crops	2.6	0.00	1.5	-0.02	2.2	-0.05
	Pastures	1.8	0.01	1.1	-0.02	2.6	-0.04
	Natural grasslands	4	**0.83**	**11.4**	**0.84**	**9.9**	**0.70**
	Moors and heathlands	6.4	-0.13	2	0.21	1	0.24
	Water bodies	6.2	-0.09	**21**	-0.03	3.9	0.02
	Water courses	2	-0.00	3.8	0.00	3.9	0.01
	Wetland	2.9	**-0.53**	1.2	**-0.46**	0.6	0.23
Habitat fragmentation variables	Extraction sites	4.6	0.04	3.9	0.00	0.5	-0.16
	Urban areas	**25**	0.01	6.1	-0.02	3.8	-0.06
	Primary roads	1.7	0.01	3.2	-0.03	0.9	-0.06
	Secondary roads	**11.4**	0.01	**10.4**	-0.01	7.4	-0.05
	Railways	2.6	-0.03	1.8	-0.08	1.1	-0.11
Climate variables	Max. temperature	0.7	-0.00	3.4	0.00	**9.1**	0.00
	Min. temperature	**15.1**	-0.00	**11.8**	0.00	**12.2**	0.00
	Mean temperature	0.5	-0.00	0.8	0.00	8.1	-0.00
	Precipitation	4.8	-0.00	4.5	-0.00	**24.8**	-0.01