

Testing the efficacy of downscaling in species distribution modelling: a comparison between MaxEnt and favourability function models

J. Olivero, A. G. Toxopeus, A. K. Skidmore & R. Real

Olivero, J., Toxopeus, A. G., Skidmore, A. K. & Real, R., 2016. Testing the efficacy of downscaling in species distribution modelling: a comparison between MaxEnt and favourability function models. *Animal Biodiversity and Conservation*, 39.1: 99–114, <https://doi.org/10.32800/abc.2016.39.0099>

Abstract

Testing the efficacy of downscaling in species distribution modelling: a comparison between MaxEnt and favourability function models.— Statistical downscaling is used to improve the knowledge of spatial distributions from broad-scale to fine-scale maps with higher potential for conservation planning. We assessed the effectiveness of downscaling in two commonly used species distribution models: Maximum Entropy (MaxEnt) and the favourability function (FF). We used atlas data (10x10 km) of the fire salamander, *Salamandra salamandra*, distribution in southern Spain to derive models at a 1x1 km resolution. Downscaled models were assessed using an independent dataset of the species' distribution at 1x1 km. The FF model showed better downscaling performance than MaxEnt, and the models that were based on linear combinations of environmental variables performed better than models allowing higher flexibility. The FF model minimized model overfitting compared to the MaxEnt.

Key words: Atlas distribution data, Model transferability, Favourability function model, Maximum Entropy model, Overfitting, *Salamandra salamandra*

Resumen

Eficacia del aumento de resolución espacial en modelos de distribución de especies: comparación entre el modelo MaxEnt y el de la función de favorabilidad.— El aumento estadístico de la resolución espacial se utiliza para mejorar el conocimiento de las distribuciones espaciales, transformando mapas de resolución gruesa en mapas de resolución fina, que son más adecuados para planificar la conservación. Se ha evaluado la eficacia de este aumento de la resolución en dos modelos muy utilizados de distribución de especies: el de máxima entropía (MaxEnt) y la función de favorabilidad (FF). Se han obtenido modelos con resolución de 1x1 km a partir de datos de atlas (10x10 km) de la distribución de la salamandra común *Salamandra salamandra* en el sur de España. Para evaluar estos modelos con mayor resolución, se ha utilizado un conjunto de datos independientes sobre la distribución de la especie a 1x1 km. Se ha observado que el modelo de favorabilidad es más eficaz para aumentar la resolución espacial que el de MaxEnt y los modelos basados en combinaciones lineales de variables ambientales son más eficaces que los modelos que permiten una mayor flexibilidad. Comparado con MaxEnt, el modelo de favorabilidad minimizó el sobreajuste del modelo.

Palabras clave: Datos de atlas de distribución, Transferibilidad de modelos, Modelo de favorabilidad, Modelo de máxima entropía, Sobreajuste, *Salamandra salamandra*

Received: 10 IX 15; Conditional acceptance: 24 XI 15; Final acceptance: 22 II 16

Jesús Olivero & Raimundo Real, Grupo de Biogeografía, Diversidad y Conservación, Depto. de Biología Animal, Fac. de Ciencias, Univ. de Málaga, Campus de Teatinos s/n., 29071 Malaga, Spain.— Albertus G. Toxopeus & Andrew K. Skidmore, Dept. of Natural Resources, Geo-information Science and Earth Observation (ITC), Univ. of Twente, P. O. Box 217, Hengelosestraat 99, 7500 AE, Enschede, The Netherlands.

Introduction

Atlases are available for a large variety of taxa worldwide and represent species occurrence in the form of maps (Harrison, 1989). These maps often cover extensive geographic regions and their production usually involved large numbers of volunteers collecting data. Finer-scale maps of the distribution of species, required for conservation planning, can be derived from atlas maps by using statistical downscaling techniques (Kunin et al., 2000; Araújo et al., 2005; Barbosa et al., 2010). Such finer resolution maps have been valuable to understand how environmental variables and different spatial resolutions affect species distributions (Barbosa et al., 2010) and to determine the impact of climate change on species ranges (Araújo & Rahbek, 2006) and the links between human nutrition and biodiversity protection (Fa et al., 2014, 2015). Downscaling assumes that a property within larger units is the arithmetic average of the property within smaller units (Bierkens et al., 2000).

The ability of a model to produce fine-scale species distributions from a coarser resolution has been described as model generality or model transferability (Vanreusel et al., 2007; Gray et al., 2008). Comparisons of model transferability using different Species Distribution Models (SDMs) have been undertaken by several authors (Peterson et al., 2007; Gray et al., 2008). In this paper, we test for the first time the performance of the favourability function (FF) model and the Maximum Entropy (MaxEnt) model. The FF model was designed to derive species distribution maps by obtaining, from logistic regression, an environmental favourability function from a species occurrence whose results are not affected by an uneven proportion of presences and absences (Real et al., 2006; Acevedo & Real, 2012); this property permits direct comparison between models when different species are involved in the analysis, and allows for model combinations (e.g., Fa et al., 2014). MaxEnt is a presence-background profile method that has been successfully applied in a number of fields (Phillips et al., 2006). Considered consistently competitive with the highest performing methods (Elith et al., 2006, 2010), this is the most widely used SDM algorithm (Fourcade et al., 2014). MaxEnt uses input from a set of layers or environmental variables as well as a set of georeferenced occurrence locations, to produce a model of relative suitability across the study area.

Here, we evaluate the performance of MaxEnt and FF in downscaling (from a spatial resolution of 10 x 10 km squares to 1 x 1 km squares) by using the known distribution of a terrestrial species, the fire salamander, *Salamandra salamandra* (Linnaeus, 1758) (Urodela, Salamandridae) in Andalusia (southern Spain). We test how well each model performs by assessing whether it: (1) displays sufficient discrimination power at finer spatial resolutions; (2) accurately predicts observed distributions at finer resolutions; and (3) significantly resembles predictions obtained with models trained using independent data at a finer resolution.

Material and methods

Species and study area

The fire salamander, *Salamandra salamandra*, occurs throughout most of the western Palaearctic region. This species is not included in the worldwide IUCN Red List, but is considered vulnerable in Spain (Pleguezuelos et al., 2004). The Andalusian region (fig. 1A) harbours three of the nine subspecies present in the Iberian peninsula: the entire distribution of *S. s. longirostris* in the south, most of the range of *S. s. morenica* in the north, and some populations of *S. s. crespoides* in the west. The presence of *S. salamandra* is closely related to specific environments: wet and shaded zones with high rainfall located on medium to high mountainous areas; forests with ponds or streams; and wet grasslands surrounded by hedges or stone walls (García-París et al., 2004; Pleguezuelos et al., 2004). The specific habitat requirements of the selected species result in a clear environmentally-defined distribution that makes it suitable for model evaluation.

To test the downscaling performance of the various models we first used presence-absence atlas data (10 x 10 km UTM square grids) of *S. salamandra* in Andalusia (figs. 1A, 1B). Data from the species distribution map published in Pleguezuelos et al. (2004) were used. The species was present in 328 (37%) 10 x 10 km UTM squares. Additionally, we used an independent dataset of 1,090 presences of the species (1 x 1 km resolution) to evaluate the results of the downscaled models. These records were direct observations of the species throughout Andalusia, obtained from field surveys undertaken between 1980 and 2003 (Tejedo et al., 2003; fig. 1C).

Environmental variables

We considered a total of 34 environmental variables for our modelling procedures (table 1). These variables included climate, topography, land cover, and human activities. Climate may affect the distribution of species, mainly at global and meso-scales, whereas topography and land cover act at meso- and micro-scales (Mackey & Lindenmayer, 2001). A set of climatic variables was selected to provide information about average annual values, average seasonal values, and intra-annual variation. Topographical variables were selected because they represent a level of strong integration between multiple factors that are biogeographically important for species (Hof et al., 2012), for example, temperature, air pressure, humidity, precipitation, availability of area with certain environmental conditions, soil erosion, risk of extinction, and refuges for Pleistocene species. Vegetation cover could be a suitable descriptor for the distribution of *S. salamandra* since the most favourable areas for the species in southern Spain are ecosystems associated with forests but not with pastures and crops (Miñano et al., 2003; Romero et al., 2012); the Normalized Difference Vegetation Index (NDVI; Tucker, 1979) was used as a descriptor of vegetation because it

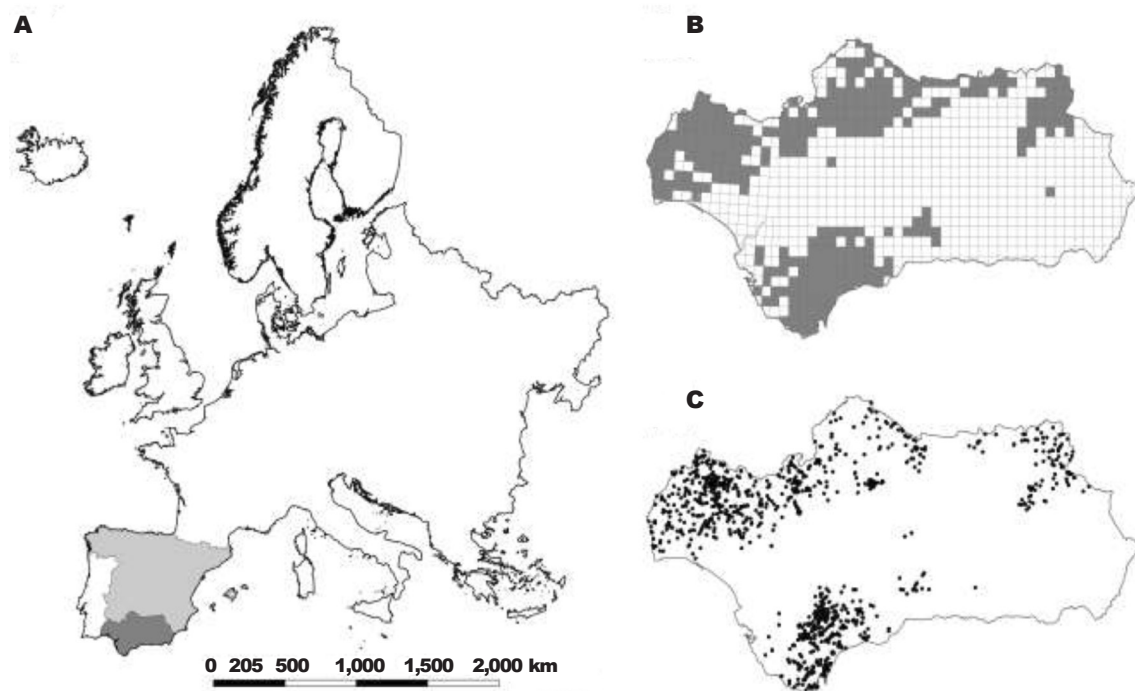


Fig. 1. Geographical context of the study area and distribution of the fire salamander, *Salamandra salamandra*, in Andalusia: A. Spain is coloured grey, with Andalusia (southern Spain) shaded dark grey; B. Distribution in 10x10 km UTM squares according to Pleguezuelos et al. (2004); C. Location of 1x1 km grids with presence according to Tejedo et al. (2003).

Fig. 1. Contexto geográfico del área de estudio y distribución de la salamandra común, *Salamandra salamandra*, en Andalucía: A. Se ha sombreado España en gris, con Andalucía (sur de España) en gris oscuro; B. Distribución en cuadrículas de UTM de 10x10 km según Pleguezuelos et al. (2004); C. Localización de las cuadrículas de 1x1 km con presencia según Tejedo et al. (2003).

is considered a good indicator of photosynthetically active biomass (Sellers, 1985; Khan et al., 2010). Distance to inland waters was selected because *S. salamandra* uses river courses and water bodies for reproduction (Miñano et al., 2003). Finally, anthropogenic factors (or human activities), such as roads or settlements, as well as land cover change due to agricultural activities, may have serious impacts on the habitats of *S. salamandra* in southern Spain (Pleguezuelos et al., 2004).

All variables were available at a 1x1 km resolution, or were resampled at this resolution from finer ones. We computed the means of all variables within each 10x10 km square. Before inclusion in the modelling procedure, all variables were tested for multi-collinearity. Variables with high multi-collinearity were removed until all remaining variables had a variance inflation factor (VIF) of < 10 (Marquardt, 1970; Montgomery & Peck, 1982). The remaining variables were included in the modelling routines, so that all models operated with the same variable set. Figure 2 shows a schematic description of the subsequent methodological procedure.

Modelling techniques

The FF model assesses variation in the probability of occurrence of a species, under certain conditions, with respect to the overall prevalence of the event (Real et al., 2006; Acevedo & Real, 2012). Favourability values are, thus, independent from the species prevalence. This property enables direct comparison between models when several species are involved in the analytical design, and allows for model combinations through fuzzy logic (Barbosa & Real, 2012). For this model, we used a forward-backward stepwise logistic regression to obtain a linear combination of variables (y). Favourability values were then computed using the following equation:

$$F = e^y / [(n_1/n_0) + e^y] \quad (\text{equation 1})$$

where e is the basis of the natural logarithm, and n_1 and n_0 are the number of presences (= 328) and of absences (= 638), respectively. Absences were considered to be those squares not included in the presences subset. The use of a large number of

Table 1. List of variables considered for the environmental models of *Salamandra salamandra* in Andalusia. The relative importance of each variable entered in the models was measured with the Wald parameter for the favourability function (FF), and with the percentage contribution for the two MaxEnt models: AMx. Auto-feature model; LMx. Linear-feature model; ^a WorldClim (Hijmans et al., 2005); ^b Mu et al. (2007); ^c Kumar et al. (1997); ^d Greif & Scharmer (2000); ^e GlobDEM50 (Farr & Kobrick, 2000); ^f Decadal NDVI images at 1x1 km spatial resolution collected by the VGT1 sensor onboard the System Probatoire d'Observation de la Terre 4 (SPOT4) platform (Oindo & Skidmore, 2002); ^g NIMA (1997); ^h IGN (1999); ⁱ Dobson et al. (2000).

Tabla 1. Lista de variables ambientales consideradas en los modelos de distribución de Salamandra salamandra en Andalucía. La importancia relativa de las variables introducidas en los modelos se ha estimado mediante el parámetro de Wald para la función de favorabilidad (FF) y mediante el porcentaje de contribución en el caso de dos modelos de MaxEnt: AMx. Modelo con ajuste automático entre presencias y variables; LMx. Modelo con ajuste lineal. (Para las otras abreviaturas, véase arriba.)

Predictor variables	Relative importance		
	FF	AMx	LMx
Climatic variables			
Average annual temperature (°C) ^a			
Average temperature in January (°C) ^a			
Average temperature in July (°C) ^a	31.6	5.4	3.3
Annual temperature range (°C) ^a		1.6	1.8
Annual rainfall (mm) ^a			
Average monthly spring rainfall (mm) ^a		1.3	1.0
Average monthly summer rainfall (mm) ^a			
Average monthly autumn rainfall (mm) ^a			
Average monthly winter rainfall (mm) ^a			
Annual rainfall coefficient of variation ^a	15.5	1.6	< 0.1
Average annual evapotranspiration (mm) ^b			
Average spring evapotranspiration (mm) ^b			
Average summer evapotranspiration (mm) ^b			
Average autumn evapotranspiration (mm) ^b			
Average winter evapotranspiration (mm) ^b			
Average annual solar radiation (Wh/m ²) ^{c,d}			
Average spring solar radiation (Wh/m ²) ^{c,d}			
Average summer solar radiation (Wh/m ²) ^{c,d}	53.9	7.3	6.7
Average autumn solar radiation (Wh/m ²) ^{c,d}			
Average winter solar radiation (Wh/m ²) ^{c,d}	24.6	0.9	3.8
Topographic variables			
Elevation (m) ^e			
Slope (°) ^e	5.5	2.2	4.1
Exposure to south (°) ^e		< 0.1	0.2
Exposure to west (°) ^e		0.1	< 0.1
Land-cover variables			
Average annual NDVI ^f			
Average spring NDVI ^f			
Average summer NDVI ^f	8.6	6.9	6.7
Average autumn NDVI ^f			

Table 1. (Cont.)

Predictor variables	Relative importance		
	FF	AMx	LMx
Average winter NDVI ^f	55.6	68.1	74.3
Annual NDVI coefficient of variance ^f		0.3	< 0.1
Distance from inland waters (km) ^g	8.2	0.8	0.9
Anthropogenic variables			
Distance to nearest large city (km) ^h		0.9	< 0.1
Distance to nearest highway (km) ^h		1.9	3.5
Population density in 2000 (pop/m ²) ⁱ		0.5	0.1

variables in the model building process could cause type-I error. To avoid this, we controlled the false discovery rate (FDR) due to multiple tests using the procedure proposed by Benjamini & Hochberg (1995). To estimate the weight of variables in the model, we used the estimated Wald test (Hosmer & Lemeshow, 2000, p. 16).

MaxEnt estimates the most uniform probability distribution (*i.e.*, maximum entropy) of each environmental variable within the study area with the constraint that the expected value of each variable under this estimated distribution matches the mean values for the set of occurrence data (Phillips et al., 2006). MaxEnt is based on distinguishing known occurrence sites for a species from the 'background', that is the sum of presences and absences. For the occurrence of a given species, MaxEnt defines a probability distribution $q_\lambda(x)$ according to this equation:

$$q_\lambda(x) = [\exp(\sum_{j=1}^n \lambda_j \cdot f_j(x))] / Z_\lambda \quad (\text{equation 2})$$

where $f_j(x)$ is the value of a set of features (f_1, \dots, f_n), which are derived from environmental variables, at each x site, $\lambda = (\lambda_1, \dots, \lambda_n)$ is a vector of feature weights, and Z_λ is a normalizing constant which ensures that $q_\lambda(x)$ sum to 1 over the study area. The results of the analyses were presented in a logistic output format (Q) so that large differences in output values better matched large differences in suitability:

$$Q = [e^H q_\lambda(x(z))] / [1 + e^H q_\lambda(x(z))] \quad (\text{equation 3})$$

where z is a vector of environmental variables, $q_\lambda(x(z))$ is the probability distribution in sites x with environmental conditions z , and H is the entropy of q_λ .

We ran 500 iterations using the Maximum Entropy Species Distribution Modelling v3.3.3 software. Two alternative procedures were considered for feature classes and they determined two degrees of flexibility for the model fit: (1) auto features —where linear, quadratic, product, threshold, and hinge features were combined— with the application's auto-option for datasets having more than 80 training samples

(Phillips & Dudík, 2008); and (2) linear features, where only linear features are permitted —as performed in the FF model. We used the regularization parameter settings (aimed at minimizing overfitting) proposed by Phillips & Dudík (2008) for more than 100 occurrence records, but we did not apply regularization multipliers (Radosavljevic & Anderson, 2014). Through the choice of these options in MaxEnt, we aimed to analyse the performance of downscaling at the edges of a whole range of degrees in model flexibility.

Maps resulting from SDMs were downscaled from a 10 x 10 km resolution to 1 x 1 km squares. The models were thus projected to a 1 x 1 km resolution grid across the study area by applying the model equations (*i.e.*, equation 1 for the FF model, and equation 3 for the MaxEnt models) to predictor variables at this resolution (see examples in Araújo et al., 2005; Barbosa et al., 2010). This method was chosen for simplicity. It is known as the direct downscaling approach (Bombi & d'Amen, 2012), and classified by Bierkens et al. (2000) as 'downscaling based on mechanistic models through a deterministic function (*i.e.*, either equation 1 or equation 3)'.

Comparison of model transferability

We assessed the capacity of the models to discriminate between presence and absence the receiving operating characteristic (ROC) plot. The area under the ROC curve (AUC) provides a single-number discrimination measure across all possible thresholds (Fielding & Bell, 1997). For the initial models, the ROC was assessed for the 10 x 10 km training data, and re-calculated after downscaling to the 1 x 1 km dataset. A higher AUC can indicate better performance on condition that models are compared for the same species in the same study area (Lobo et al., 2008), because AUC can be influenced by the species prevalence or relative occurrence area (Chefaoui et al., 2011; Khaoruba et al., 2013). Sensitivity and specificity were also calculated before and after downscaling, considering thresholds throughout the whole suitability range.

Suitability values predicted for the study species in presence grids were analysed for the FF and MaxEnt models. We used the Mann–Whitney U–test to evaluate changes in suitability resulting from downscaling to a finer spatial resolution.

We performed a threshold–dependent assessment to evaluate the model's capacity to describe and predict. A threshold defining 'highly suitable' areas is needed to classify the distribution of a species. Suitability values obtained with the FF model were divided into three classes: highly suitable, *i.e.* $= > 0.8$; intermediate, 0.2–0.8; and 'highly unsuitable', $= < 0.2$. This is equivalent to defining a prediction with odds higher than 4:1 for 'highly suitable' and 'highly unsuitable' sites (Muñoz & Real, 2006). For the MaxEnt models, we used the 'equalized predicted area' criterion for model comparison, which selects a threshold so that the compared models have the same predicted area (Phillips et al., 2006). Thus, for every MaxEnt model, thresholds were chosen in such a way that the sum of the grids in the results map—classified as 'highly suitable' and 'highly unsuitable'—equated those in the FF model. Thresholds calculated for the 10x10 km resolution outputs were also used in the 1x1 km outputs.

We determined the descriptive capacity of the models before downscaling (at 10x10 km) by computing the percentage of presence grids in the 'highly suitable' and 'highly unsuitable' areas. To assess the models' predictive capacity after downscaling, we used presences at a 1x1 km resolution from Tejedo et al. (2003) as independent data (see also Araújo et al., 2005; Barbosa et al., 2010). To calculate if the differences between percentage presences were significant we used the arcsine test of equality of percentages (Sokal & Rohlf, 1979, p. 663).

Finally, we also compared the downscaled models with alternative models trained using the 1x1 km dataset derived from Tejedo et al. (2003). Absences of *S. salamandra* were recorded if the species was not cited within the grid. The Pearson correlation coefficient was used for model comparison.

Results

Model description

Only 16 of the original 34 variables were retained after the multicollinearity analysis. The set of variables related to actual evapotranspiration was deleted, because these variables were strongly correlated with the NDVI (correlations were often higher than 0.8) and with temperature, radiation, and rainfall (correlations were sometimes higher than 0.7). All the average annual variables were also deleted because of their high VIF. If the values were reasonable, we preserved the variables that provided information on mean seasonal values and intra–annual variations of temperature, rainfall, and NDVI. Therefore, the annual temperature range and the average monthly spring rainfall were retained, despite the VIF being higher than 10 in the MaxEnt models (12.8 and 11.3, res-

pectively). The 16 remaining variables were included in the three modelling routines, although only eight of these variables were selected by the stepwise procedure for the FF model (table 1).

Both the 'linear–feature' and 'auto–feature' MaxEnt models showed great similarities in ranking the importance of the variables (table 1). The FF model also selected variables with high relevance in the MaxEnt models; average winter NDVI and average summer solar radiation were the most important variables in the three models. In general, suitability for *S. salamandra* was defined by mountain areas close to inland water, with high vegetation cover and climatically conditioned by variables describing energy and water availability throughout the year (see table 1), in agreement with the known habitat requirements for the species.

Model discrimination, sensitivity, and specificity

The FF and MaxEnt models produced visually similar geographical outputs and predictions (fig. 3A). Higher suitability values were obtained for areas where *S. salamandra* was present (compare with fig. 1). The discriminatory capacity of the three models at the lower resolution was > 0.9 for the AUC, *i.e.*, 'outstanding' (Hosmer & Lemeshow, 2000, p. 162), and around 3% higher when comparing the 'auto–feature' MaxEnt model with the models combining variables linearly (see table 2). After downscaling, the capacity of the three models to discriminate between 1x1 km squares with and without presences was between 0.8 and 0.9 *i.e.*, 'excellent'; the AUC was around 2.5% higher for the FF model.

For all three models, the minimised difference between sensitivity and specificity was close to the 0.4 suitability value for the higher spatial resolution (fig. 4A). The sensitivity of the FF model was significantly higher than for the MaxEnt models where suitability was > 0.4 . After downscaling (fig. 4B), the minimised difference between sensitivity and specificity was at the 0.8 suitability value for the FF model, but remained close to the 0.4 suitability value using MaxEnt. Sensitivity increased considerably after downscaling in the FF model, whereas it decreased minimally in MaxEnt; the specificity decreased in all three models, though more strongly in the FF.

Suitability values

Average suitability for presence grids increased significantly after downscaling in the FF and 'linear–feature' MaxEnt models (Mann–Whitney U–test, $p < 0.001$); the increase was steeper in the FF model (see table 3, fig. 5), but suitability values remained stable in the 'auto–feature' MaxEnt model ($p > 0.1$).

Threshold–dependent evaluation

After downscaling, the percentage of 'highly suitable' squares increased (almost doubling) and the percentage of 'highly unsuitable' grids decreased slightly when using the FF model. Both percentages remained almost stable when using MaxEnt (fig. 3B; table 2).

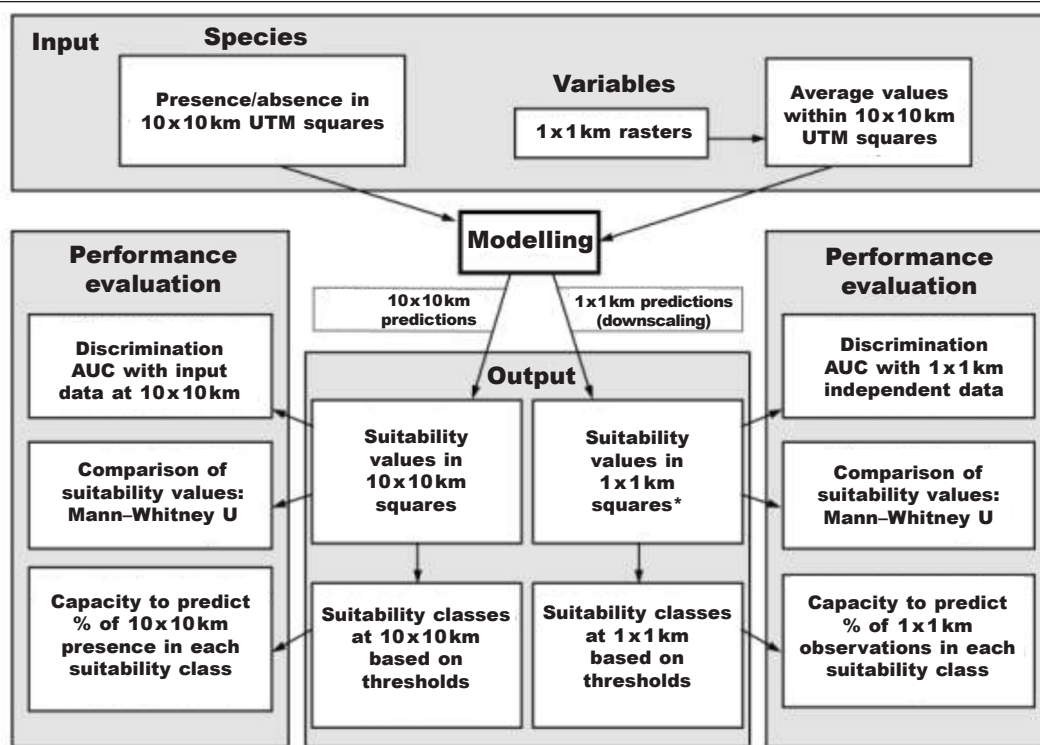


Fig. 2. Schematic description of the methodological procedure: * Downscaled suitability values in 1 x 1 km squares are also compared to suitability values predicted by models trained with 1 x 1 km data.

Fig. 2. Descripción esquemática del procedimiento metodológico: * Los valores de idoneidad al aumentar la resolución en cuadrículas de 1 x 1 km también se compararon con los valores de idoneidad predichos por los modelos calibrados con datos de 1 x 1 km.

Compared to the results of the MaxEnt models, the FF model showed significantly more presence grids in the 'highly suitable' area after downscaling (arcsine test of equality of percentages, $p < 0.01$) and significantly fewer presence grids in the 'highly unsuitable' area ($p < 0.01$). The results computed using the 'linear-feature' MaxEnt showed significantly more presence grids in the 'highly suitable' area than the results computed using 'auto-feature' MaxEnt ($p < 0.01$).

The percentage of recorded presence grids in 'highly suitable' areas significantly increased after downscaling when using the FF model and also when using 'linear-feature' MaxEnt (arcsine test of equality of percentages, $p < 0.01$; the increase was steeper in the former case, see table 2, fig. 5). Within the 'highly unsuitable' areas, this percentage of presence grids increased significantly using 'auto-feature' MaxEnt ($p < 0.01$), and decreased significantly using the FF model ($p < 0.01$).

Downscaled models vs. models trained with high resolution data

The AUC of the models trained with independent 1 x 1 km data (fig. 3C) were higher than 0.8 (table 2) which-

ever modelling technique was used; this was only slightly higher than the corresponding downscaled models. Correlation coefficients between models derived from downscaling and models trained with 1 x 1 km data performed using the same algorithm (main diagonal in table 4) were significant ($p < 0.01$), being higher than 0.7 using 'auto-feature' MaxEnt, higher than 0.8 using 'linear-feature' MaxEnt, and higher than 0.9 using the FF model. The three downscaled models had their highest correlation with the model trained with 1 x 1 km data using the FF model (left column in table 4), and correlations with the downscaled FF model (upper line in table 4) equalled the intra-technique correlation with the models trained at 1 x 1 km (main diagonal).

Discussion

Model downscaling: valuable for conservation planning?

Species distribution maps from biological atlases are often too coarse for real-world conservation planning (Kunin et al., 2000; Araújo et al., 2005; Barbosa et al., 2010; Bombi & D'Amen, 2012). National atlases, such as those for mammals in Spain, are at best at resolutions no

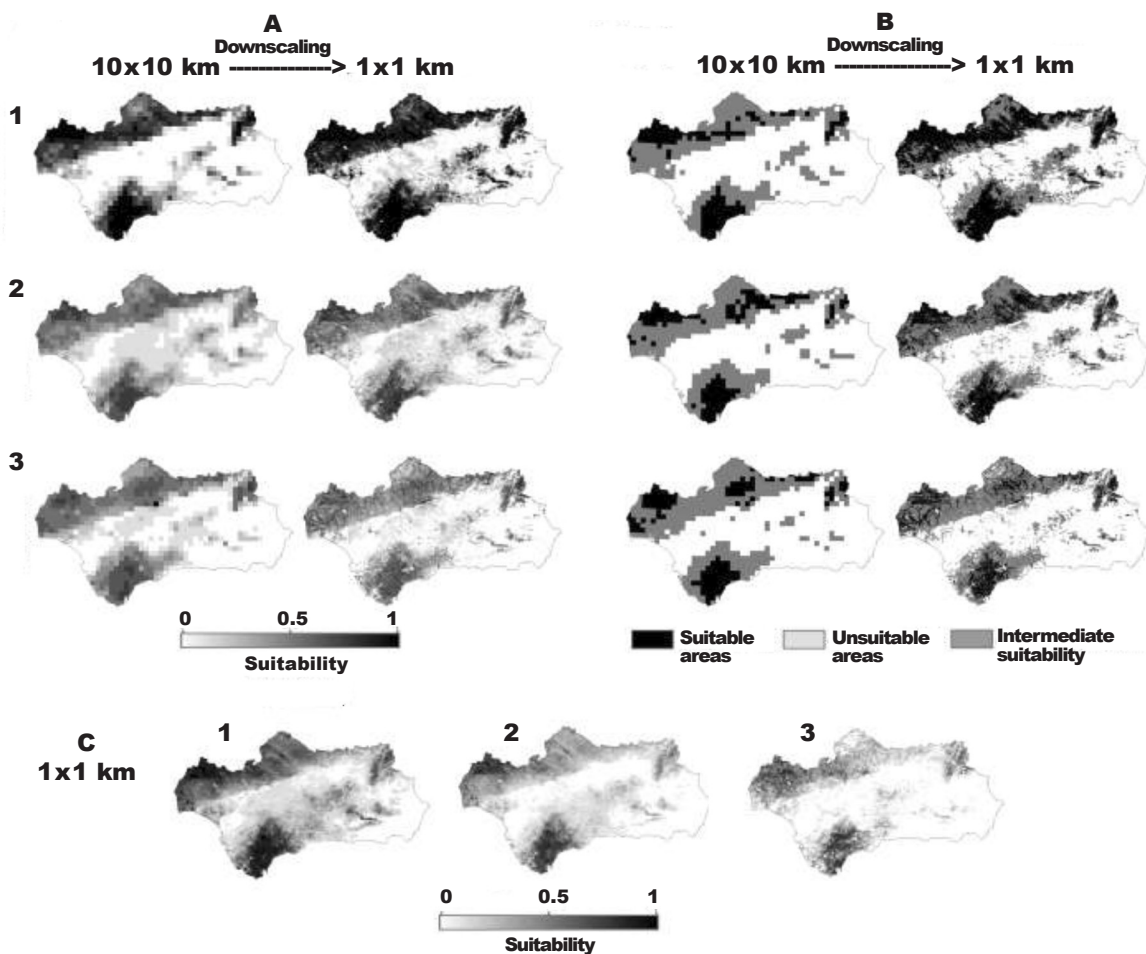


Fig. 3. Geographical representation of the three distribution models performed for the fire salamander, *Salamandra salamandra*, in Andalusia: A. Suitability based on the models performed with 10x10 km resolution data, before and after downscaling to a 1x1 km resolution; B. Subdivision of Andalusia in highly suitable, intermediate and highly unsuitable areas (the threshold criterion for the FF model was defining a prediction with odds higher than 4:1 for 'highly suitable' grids, and lower than 1:4 for 'highly unsuitable' grids; the equalized predicted area criterion was chosen with MaxEnt, *i.e.*, equating the 'highly suitable' and the 'highly unsuitable' surface areas to those in the FF); C. Suitability based on the models performed with 1x1 km resolution data; 1. Favourability; 2. Linear-feature MaxEnt; 3. Auto-feature MaxEnt.

Fig. 3. Representación geográfica de los tres modelos de distribución realizados para la salamandra común, *Salamandra salamandra*, en Andalucía: A. Idoneidad basada en los modelos realizados con datos con resolución de 10x10 km, antes y después del aumento de resolución a 1x1 km; B. Subdivisión de Andalucía en áreas altamente idóneas, de idoneidad intermedia y altamente inadecuadas (el criterio para establecer umbrales en la función de favorabilidad consistió en definir como "altamente idóneas" las cuadrículas con un pronóstico de presencia mayor que 4:1, y como "altamente inadecuadas" las cuadrículas con un pronóstico de presencia menor que 1:4; con MaxEnt se ha utilizado el criterio de área predicha igualada, que consiste en igualar la superficie de las áreas "altamente idóneas" y "altamente inadecuadas" a las observadas con la función de favorabilidad); C. Idoneidad basada en los modelos realizados con datos con resolución de 1x1 km; 1. Favorabilidad; 2. Ajuste lineal de MaxEnt; 3. Ajuste automático de MaxEnt.

less than 10x10 km (Palomo & Gisbert, 2008), but those for larger areas, such as those for continental European mammals, can be coarser (50x50 km) (Mitchell-Jones et al., 1999). For management purposes, downscaling to finer resolutions is useful. Although some authors argue

that it is not possible to achieve a higher level of detail beyond that contained in the initial coarser-resolution maps (Stockwell & Peterson, 2003), others suggest that the properties that define a species distribution are the same at whatever resolution (Kunin, 1998).

Table 2. Model assessment: FF. Favourability function; LMx. Maxent using only linear features; AMx. MaxEnt using the auto-feature option; ^a State variables were based on the distribution of *S. salamandra* according to Pleguezuelos et al. (2004) (10x10 km resolution) and to Tejedo et al. (2003) (1x1 km resolution); ^b Models performed with 10x10 km resolution data; ^c Models downscaled to a 1x1 km resolution; ^d Models performed with 1x1 km resolution data; ^e Asterisks indicate significant differences between percentages (arcsine test of equality of percentages; $p < 0.01$) compared to FF; ^f Asterisks indicate significant differences between percentages (arcsine test of equality of percentages; $p < 0.01$) compared to those before downscaling.

Tabla 2. Evaluación del modelo: FF. Función de favorabilidad; LMx. MaxEnt utilizando solo el ajuste lineal; AMx. MaxEnt utilizando el ajuste automático; ^a Las variables se basaron en la distribución de *S. salamandra* según Pleguezuelos et al. (2004) (resolución de 10x10 km) y Tejedo et al. (2003) (resolución de 1x1 km); ^b Modelos realizados con datos con resolución de 10x10 km; ^c Modelos con resolución aumentada a 1x1 km; ^d Modelos realizados con datos con resolución de 1x1 km; ^e Los asteriscos indican diferencias significativas entre porcentajes (transformación arcoseno de igualdad de porcentajes; $p < 0,01$) en comparación con FF; ^f Los asteriscos indican diferencias significativas entre porcentajes (transformación arcoseno de igualdad de porcentajes; $p < 0,01$) en comparación con los porcentajes antes del aumento de resolución.

Parameter		FF	LMx	AMx
Area under the ROC curve ^a				
AUC	10x10 km ^b	0.920	0.925	0.948
	10x10 → 1x1 km ^c	0.828	0.807	0.810
	1x1 km ^d	0.841	0.842	0.879
Percentage of grids ^e				
Highly suitable for <i>Salamandra salamandra</i>				
	10x10 km ^b	14.9	14.9	14.9
	10x10 → 1x1 km ^c	27.0	16.3*	11.2*
Highly unsuitable for <i>S. salamandra</i>				
	10x10 km ^b	51.9	51.9	51.9
	10x10 → 1x1 km ^c	43.2	51.5*	54.6*
Percentage of presence grids ^f				
In areas highly suitable for <i>S. salamandra</i>				
	10x10 km ^b	40.7	38.2	42.5
	10x10 → 1x1 km ^c	76.0*	52.8*	41.0
In areas highly unsuitable for <i>S. salamandra</i>				
	10x10 km ^b	8.3	7.3	4.6
	10x10 → 1x1 km ^c	3.1*	7.0	7.3*

In our study, we showed that downscaling from 10x10 km maps to a 1x1 km resolution caused only a slight loss of discriminatory capacity. Overall, both methods had outstanding discriminatory capacities at the coarser resolution, even though the species' prevalence in Andalusia (37%) was not remarkably low; these capacities remained excellent after downscaling. Some loss of discriminatory capacity after downscaling is not surprising. As spatial resolution becomes finer, local effects become more important (Hewitson & Crane, 1996). Thus, a reduction in accuracy is expected because the importance of climate in influencing species distributions decreases at more local scales, whereas the influence of micro-environmental factors such as topography increases (Pearson et al., 2002;

Trivedi et al., 2008). Araújo et al. (2005) suggested that interpolation is possible if governing processes affecting species' distributions at coarser resolutions are also important in driving distributions at finer resolutions. In our case study, a combination of environmental factors that could affect the distribution of *S. salamandra* at different spatial resolutions was used to prevent excessive loss in the biological meaning of the model.

According to Guisan et al. (2007) and Bombi & D'Amen (2012), a 10-fold shortening of the grain size—referring to pixel side length—as is our case, should not severely affect predictions of species distributions. However, this meant that the number of finer-scale observations and predictions was roughly 100 times higher, and that the proportion between observed pres-

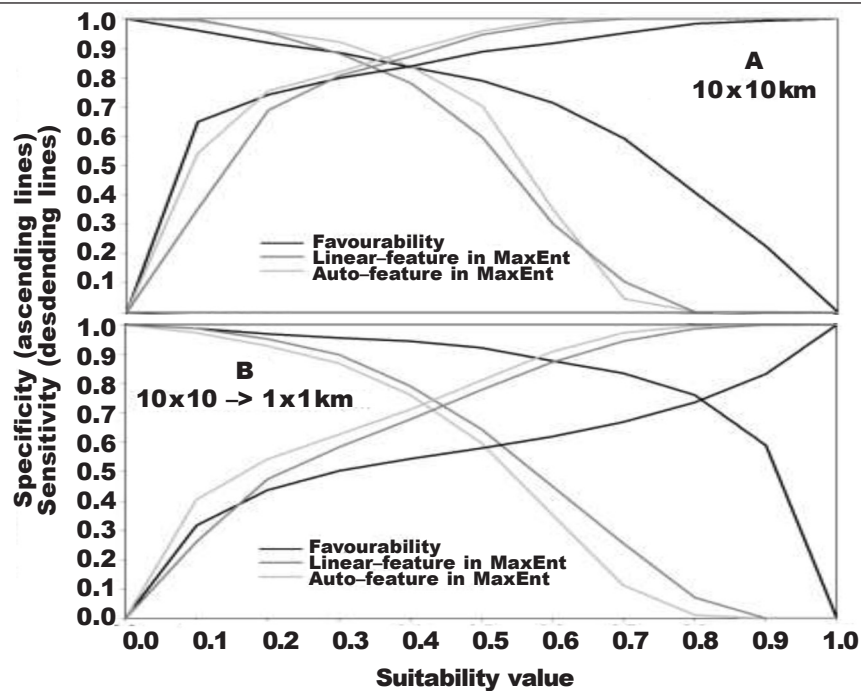


Fig. 4. Sensitivity and specificity of the three models before (A) and after (B) their interpolation to a finer resolution. The fire salamander, *Salamandra salamandra*, distribution data provided by Pleguezuelos et al. (2004) were used at a 10x10 km resolution, and by Tejedó et al. (2003) at a 1x1 km resolution (see fig. 1).

Fig. 4. Sensibilidad y especificidad de los tres modelos antes (A) y después (B) de su interpolación para aumentar la resolución espacial. Se han utilizado los datos sobre la distribución de la salamandra común, *Salamandra salamandra*, proporcionados por Pleguezuelos et al. (2004) con resolución de 10x10 km y por Tejedó et al. (2003) con resolución de 1x1 km (véase la fig. 1).

ence and absence was much lower than that at the coarser-scale. Consequently, in many suitable 1x1 km sites, the species was not observed, reducing the discriminative capacity of the model. In this situation, the downscaled model cannot—and should not—be very specific, and sensitivity should be considered as a better measurement of performance than specificity. This is why AUC, which weighs sensitivity and specificity equally, is expected to be lower after downscaling as a result of a much lower presence/absence ratio in the 1x1 km resolution dataset than in the training data. Bombi & D'Amen (2012) also observed that a more general effect of downscaling is a reduction of specificity.

Our finding that our downscaled models had excellent discriminatory capacity, with a high capacity to predict species occurrences, suggests that this approach can be valuable for decision-making in conservation. Nonetheless, model downscaling will be more successful for wide-ranging taxa than for taxa with smaller home ranges that often have especially aggregated distributions, and low dispersal (Kaliontzopoulou et al., 2008; Barbosa et al., 2010). This is because the former are more dependent on macro-environmental factors than spatially restricted species.

Threshold independent comparison

Using a visual inspection of the geographic output, Araújo et al. (2005) found that downscaled maps were not only able to recover original spatial patterns of richness observed at the coarser resolution, but were also able to identify finer gradients that were invisible in the original resolution. In our study, the 'auto-feature' MaxEnt model produced a more fragmented 1x1 km geographical pattern than the other models (fig. 3A); this could be related to the degree of flexibility of this model being higher than the other two. The 'hinge' feature class in the auto-features option makes MaxEnt resemble the procedure for generalized additive models (GAMs) that find a flexible geographical relationship between species and the environment (Elith et al., 2010). This leads to a high model fit to observed species distributions (see fig. 6), which in our case provided a clear match between predicted highly suitable areas for *S. salamandra* and mountain rivers (see fig. 3A). Barbosa et al. (2010) also observed that the courses of rivers emerged as suitable areas for *Lutra lutra* and for *Galemys pyrenaicus* in Spain after downscaling from a 10x10 km resolution model, despite the fact that river locations were not explicitly included as predictor variables in their models.

At a more quantitative level, AUC comparisons suggested that model flexibility may have enhanced the discrimination capacity of the original output, at the cost of hindering its capacity to discriminate after downscaling. This is demonstrated by the fact that the 'auto-feature' MaxEnt model was the best discriminator before downscaling, whereas the FF model was the best discriminator after downscaling (table 2). As observed in our results, previous MaxEnt-GLM comparisons showed AUC values that were on average 2%–3% higher in MaxEnt models than in logistic-regression models (e.g., Elith et al., 2006 [n = 10]; Gibson et al., 2007 [n = 1]; Marini et al., 2010 [n = 12]). Here, this only happened with the 'auto-feature' MaxEnt model, which permitted the highest flexibility, and also yielded the lowest AUC values when downscaled at the 1x1 km resolution.

Threshold-dependent comparison

The FF model was more sensitive to both 10x10 km and 1x1 km presence observations of *S. salamandra* than the MaxEnt models, especially when the suitability threshold was high (fig. 4). Once a threshold for 'highly suitable' areas was defined, the FF model produced the highest proportion of presence observations in 'highly suitable' areas at the 1x1 km resolution (table 2). However, below the threshold for very low unsuitability, the FF model had the lowest proportion of presences, that is, the lowest over-prediction rate at this threshold (Barbosa et al., 2013). In contrast, the lowest proportion of presence grids in 'highly suitable' areas was obtained in the 'auto-feature' MaxEnt model (table 2). A possible explanation for this is that the detailed definition of water courses in the downscaled 'auto-feature' MaxEnt model

Table 3. Mann-Whitney U-test to compare the rank of suitability values for *Salamandra salamandra* before and after downscaling: R10. Rank (10x10 km); R1. Rank (1x1 km) FF. Favourability function; LMx. MaxEnt using only linear features; AMx. MaxEnt using the auto-feature option; ^a Models performed with 10x10 km resolution data; ^b Models downscaled to a 1x1 km resolution.

Tabla 3. Prueba de U de Mann-Whitney para comparar el rango de valores de idoneidad para *Salamandra salamandra* antes y después del aumento de resolución espacial: R10. Rango (10x10 km); R1. Rango (1x1 km); FF. Función de favorabilidad; LMx. MaxEnt utilizando solo el ajuste lineal; AMx. MaxEnt utilizando el ajuste automático; ^a Modelos con datos con resolución de 10x10 km; ^b Modelos con resolución aumentada a 1x1 km.

	R10 ^a	R1 ^b	N	U	P
FF	455.19	783.40	1,412	95,218	< 0.001
LMx	620.12	732.53	1,412	149,151	< 0.001
AMx	729.50	699.57	1,412	184,917	0.245

(see fig. 3B and discussion of the threshold-independent comparison) may be an artefact; it excluded locations, often far from water courses, in which individuals of this species are generally found outside the breeding season.

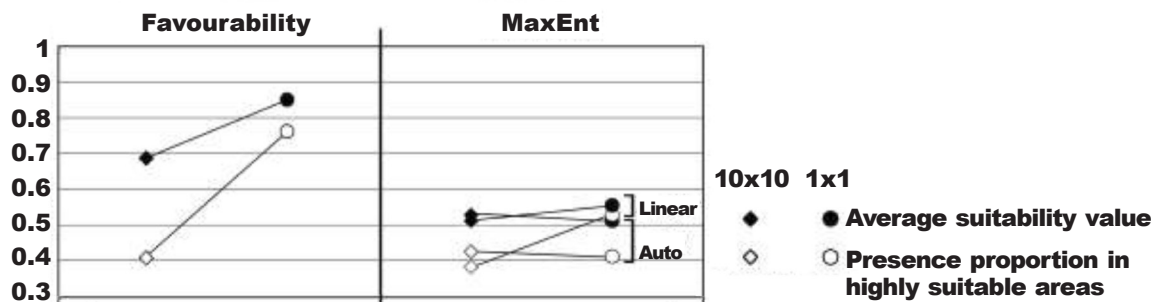


Fig. 5. Average of suitability: F for favourability function (equation 1), and Q for MaxEnt (equation 3) in fire salamander, *Salamandra salamandra*, presence grids, and the proportion of presence grids in areas considered environmentally highly suitable by the models, before and after downscaling. MaxEnt values are represented according to both the 'linear-feature' and the 'auto-feature' options for the relationship between presences and environmental variables.

Fig. 5. Promedio de la idoneidad: de F para la función de favorabilidad (ecuación 1), y de Q para MaxEnt (ecuación 3) en las cuadrículas con presencia de salamandra común (*Salamandra salamandra*), y proporción de cuadrículas con presencia en áreas consideradas muy idóneas desde el punto de vista ambiental según los modelos, antes y después del aumento de resolución espacial. Los valores de MaxEnt se han representado de acuerdo con ambas opciones de ajuste, "lineal" y "automático", entre presencias y variables ambientales.

Table 4. Pearson coefficients for pairwise correlations between model outputs. All correlations were significant ($p < 0.01$): 1x1 km. Models performed with 1x1 km resolution data; 10x10→1x1 km. Models downscaled to a 1x1 km resolution; FF. Favourability function; LMx. MaxEnt using only linear features; AMx. MaxEnt using the auto-feature option.

Tabla 4. Coeficientes de Pearson para las correlaciones entre modelos. Todas las correlaciones fueron significativas ($p < 0,01$): 1x1 km. Modelos realizados con datos con resolución de 1x1 km; 10x10→1x1 km. Modelos con resolución aumentada a 1x1 km; FF. Función de favorabilidad; LMx. MaxEnt utilizando solo el ajuste lineal; AMx. MaxEnt utilizando el ajuste automático.

	1x1 km		
	FF	LMx	AMx
10x10→1x1 km			
FF	0.912	0.872	0.776
LMx	0.886	0.876	0.761
AMx	0.833	0.817	0.770

Downscaled models vs. models trained with high resolution data

The comparison between the downscaled models and those trained with 1x1 km data, either based on prediction map visualization (figs. 3A, 3C), on correlation (table 4), or on discriminatory capacity (table 2), demonstrates that transferring the model from 10x10 km squares to 1x1 km squares worked well with all three methods. However, some noteworthy differences between models were found (table 4): the FF model not only had the highest correlation with the downscaled Favourability model, but also showed the highest correlations with any other downscaled model; at the opposite extreme was 'auto-feature' MaxEnt model, for which the lowest correlations with the downscaled models were obtained. Thus, the equivalence between downscaled models and models trained with fine-resolution data was higher with the FF model than with the MaxEnt models, though the 'linear-feature' model provided closer equivalences than when making the model as flexible as possible (as recommended by Phillip & Dudík, 2008).

The two 1x1 km resolution maps created by the 'auto-feature' MaxEnt model produced a similar pattern of strips classified as 'highly suitable' areas for *S. salamandra* (compare figs. 3A, 3C). However, whereas these land strips corresponded to river courses in the downscaled model, in the model trained with the 1x1 km data they corresponded to secondary roads denoting sampling bias (compare figs. 1, 3C). Even though regularization parameters were set in MaxEnt

models as proposed by Phillips & Dudík (2008), a certain degree of overfitting is the most probable cause for the spatial coincidence between occurrences and roads in the 1x1 km model prediction.

Conclusions

Three main conclusions can be drawn from our results: (1) both MaxEnt and the FF model performed correctly when transferring models to a finer spatial resolution; (2) the FF model transferred better to a finer resolution compared to MaxEnt (*i.e.*, the downscaled FF model got higher discrimination capacity and more accurate predictions); (3) the models that were based on linear combinations of environmental variables provided more accurate and less overfitted predictions after they were downscaled than the model that combined variables using a highly flexible function.

Model accuracy and generality are characteristics that may compete with each other (Araújo & Rahbek, 2006; Elith et al., 2010), *i.e.*, highly accurate models, in terms of the training data, might not be transferable. The main difference between a very flexible model and other models based on more restricted adjustments is exemplified in the response curves representing how each environmental variable affects the predictions of the three models in this study (fig. 6). The 'auto-feature' MaxEnt model seems to maximize the fit between the model and the training distribution data, whereas the other models adjusted the environmental response of *S. salamandra* to a logistic curve. The way MaxEnt models tried to fit the geographical relationship between species and the environment using auto-features resembles the procedure in generalized additive models (GAM, see Elith et al., 2010). The latter has been considered less robust regarding transferability than generalized linear models (GLM) because of overfitting (Randin et al., 2006). The use of regularization parameters for the control of overfitting has been recently revised (*e.g.*, Radosavljevic & Anderson, 2014), and conclusions point to the need to increase the regularization values proposed by Phillips & Dudík (2008). In our case study, the 'auto-feature' option in MaxEnt would clearly need regularization multipliers in order to avoid overfitting; however, our results did not suggest the existence of overfitting in the 'linear-feature' MaxEnt model. Alternatively, GLMs may produce models flexible enough to detect non-linear responses of the species to the environment but also constrained enough to avoid modelling stochastic variation in the species distributions. Our results contradict Gastón & García-Viñas (2011)' suggestion that the lower AUC values in GLMs, compared to MaxEnt models, are due to GLM overfitting.

Low transferability has been described for MaxEnt when models are extrapolated beyond the study area (Peterson et al., 2007), though such criticism has been countered by Phillips (2008) as based on confusion between transferability and the problem of sample selection bias. Because MaxEnt is based on distinguishing known occurrence sites for a species

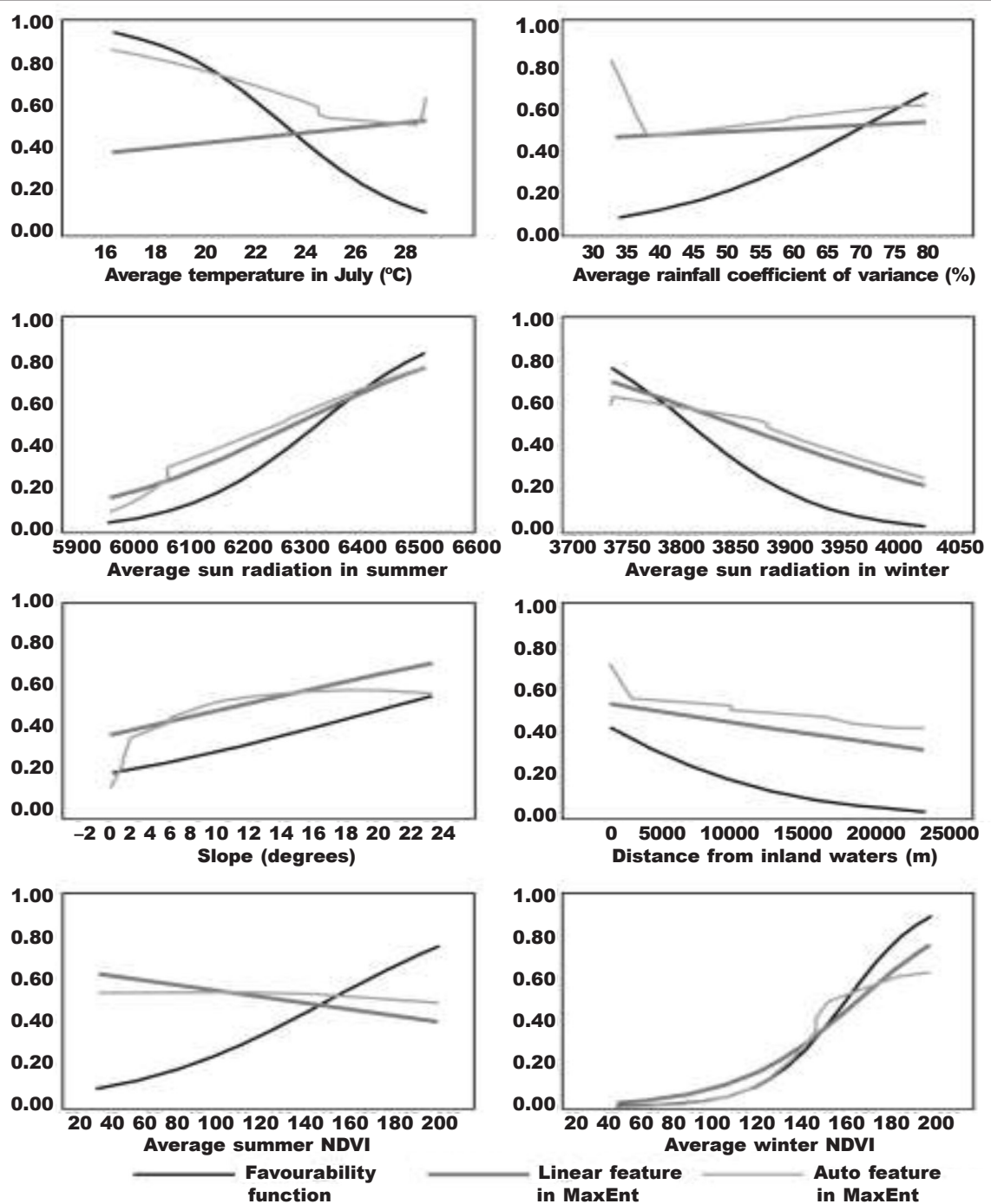


Fig. 6. Response curves showing how four environmental variables (x-axes) affected the model predictions (i.e., suitability for the fire salamander, *Salamandra salamandra*, in the y-axes, that is either the favourability function value F in equation 1 or the MaxEnt output Q in equation 3) while keeping all other variables constant in their average sample value: Black. Favourability function; Dark grey. Linear feature in MaxEnt; Light grey. Auto feature in MaxEnt.

Fig. 6. Representación gráfica de la influencia de cuatro variables ambientales (eje de las X) en las predicciones de los modelos (es decir, la idoneidad para la salamandra común, *Salamandra salamandra*, en los ejes de las Y, que en la función de favorabilidad representa el valor F de la ecuación 1 o en MaxEnt, el valor Q en la ecuación 3) cuando las demás variables se mantienen constantes en su valor medio observado: Negro. Función de favorabilidad; Gris oscuro. MaxEnt con ajuste lineal; Gris claro. MaxEnt con ajuste automático.

from the 'background', selecting 'wrong' backgrounds may cause erroneous outputs that could be incorrectly interpreted as failures of transferability. In this study, the two MaxEnt models used the same 'background' for comparisons, *i.e.*, the entire set of 10x10 km squares in the study area. When a very flexible combination of variables was accepted, our results suggested the same relationship between overfitting and transferability cost in MaxEnt as that described in Peterson et al. (2007). Constraining MaxEnt to linear combinations of variables largely solved the problem of overfitting, but the transferred Favourability model still showed a better fit to the finer-resolution data than the MaxEnt models.

Acknowledgements

This work was supported by the Spanish Ministry of Agriculture, Food and Environment, Spanish National Park Network, project 1098/2014, by the FORAGES Research Program at the ITC (Faculty of Geo-Information Science and Earth Observation, University of Twente), and by the Program 'José Castillejo' (Ref. JC2007-00260). We also thank C. A. J. M. de Bie and V. Venus for their help in deriving key variables for this paper, Dr. J. E. Fa for his useful comments and suggestions, and Mr. S. Coxon for his help in revising the language used in this article.

References

- Acevedo, P. & Real, R., 2012. Favourability: concept, distinctive characteristics and potential usefulness. *Naturwissenschaften*, 99: 515–522.
- Araújo, M. B. & Rahbek, C., 2006. How does climate change affect biodiversity? *Science*, 313: 1396–1397.
- Araújo, M. B., Thuiller, W., Williams, P. H. & Reglinster, I., 2005. Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography*, 14: 17–30.
- Barbosa, A. M. & Real, R., 2012. Applying fuzzy logic to comparative distribution modelling: A case study with two sympatric amphibians. *ScientificWorld-Journal* 10.1100/2012/428206.
- Barbosa, A. M., Real, R., Muñoz, A. R. & Brown, J. A., 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Diversity and Distributions*, 29: 1333–1338.
- Barbosa, A. M., Real, R. & Vargas, J. M., 2010. Use of coarse-resolution models of species' distributions to guide local conservation inferences. *Conservation Biology*, 24: 1378–1387.
- Benjamini, Y. & Hochberg, D., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B*, 57: 289–300.
- Bierkens, M. F. P., Finke, P. A. & de Willigen, P., 2000. *Upscaling and downscaling methods for environmental research*. Kluwer Academic Publishers, Dordrecht.
- Bombi, P. & d'Amen, M., 2012. Scaling down distribution maps from atlas data: a test of different approaches with virtual species. *Journal of Biogeography*, 39: 640–651.
- Chefaoui, R. M., Lobo, J. M. & Hortal, J., 2011. Effects of species' traits and data characteristics on distribution models of threatened invertebrates. *Animal Biodiversity and Conservation*, 34: 229–247.
- Dobson, J. E., Bright, E. A., Coleman, P. R., Durfee, R. C. & Worley, B. A., 2000. A Global Population database for estimating populations at risk. *Photogrammetry Engineering and Remote Sensing*, 66: 849–857.
- Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M. M., Peterson, A. T., Phillips, S. J., Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Soberón, J., Williams, S., Wisz, M. S. & Zimmermann, N. E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29: 129–151.
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E. & Yates, C. J., 2010. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17: 43–57.
- Fa, J. E., Olivero, J., Farfán, M. A., Márquez, A. L., Vargas, J. M., Real, R. & Nasi, R., 2014. Integrating sustainable hunting in biodiversity protection in central Africa: Hot spots, weak spots, and strong spots. *PLOS ONE*, 9: e112367.
- Fa, J. E., Olivero, J., Real, R., Farfán, M. A., Márquez, A. L., Vargas, J. M., Ziegler, S., Wegmann, M., Brown, D., Margetts, B. & Nasi, R., 2015. Disentangling the relative effects of bushmeat availability on human nutrition in central Africa. *Scientific Reports*, 5: 8168.
- Farr, T. G. & Kobrick, M., 2000. Shuttle Radar Topography Mission produces a wealth of data. *Eos Transactions American Geophysical Union*, 81: 583–585.
- Fielding, A. H. & Bell, J. F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24: 38–49.
- Fourcade, Y., Engler, J. O., Rödder, D. & Secondi, J., 2014. Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. *PLOS ONE*, 9: e97122.
- García-París, M., Montori, A. & Herrero, P., 2004. Amphibia, Lissamphibia. In: *Fauna Ibérica*, volumen 24: 43–275 (M. A. Ramos, J. Alba, X. Bellés, J. Gosálbez, A. Guerrero, E. Macpherson, J. Serrano, J. Templado, Eds.) Museo Nacional de Ciencias Naturales-CSIC, Madrid.
- Gastón, A. & García-Viñas, J. I., 2011. Modelling species distributions with penalised logistic regressions: A comparison with maximum entropy models.

- Ecological Modelling*, 222: 2037–2041.
- Gibson, L., Barrett, B. & Burbidge, A., 2007. Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. *Diversity and Distributions*, 13: 704–713.
- Gray, T. N. E., Borey, R., Hout, S. K., Chamnan, H., Collar, N. J. & Dolman, P. M., 2008. Generality of models that predict the distribution of species: Conservation activity and reduction of model transferability for a threatened bustard. *Conservation Biology*, 23: 433–439.
- Greif, J. & Scharmer, K., 2000. *ESRA: The European Solar Radiation Atlas*. École des Mines de Paris, Paris.
- Guisan, A., Graham, C. H., Elith, J., Huetmann, F. & the NCEAS Species Distribution Modelling Group, 2007. Sensitivity of predictive species distribution models to change in grain size. *Diversity and Distributions*, 13: 332–340.
- Harrison, J. A., 1989. Atlassing as a tool in conservation, with special reference to the Southern African Bird Atlas Project. In: *Biotic Diversity in Southern Africa: Concepts and Conservation*: 157–169 (B. J. Huntley, Ed.). Oxford University Press, Cape Town.
- Hewitson, B. C. & Crane, R. G., 1996. Climate downscaling: techniques and application. *Climate Research*, 7: 85–95.
- Hof, A. R., Jansson, R. & Nilsson, C., 2012. The usefulness of elevation as a predictor variable in species distribution modelling. *Ecological Modelling*, 246: 86–90.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25: 1965–1978.
- Hosmer, D. W. & Lemeshow, S., 2000. *Applied logistic regression*, 2nd ed. John Wiley & Sons, New York.
- IGN, 1999. *Mapa de Carreteras: Península Ibérica, Baleares y Canarias*. Instituto Geográfico Nacional, Ministerio de Fomento, Madrid.
- Kalioantzopoulou, A., Brito, J. C., Carretero, M. A., Larbes, S. & Harris, D. J., 2008. Modelling the partially unknown distribution of wall lizards (*Podarcis*) in North Africa: ecological affinities, potential areas of occurrence, and methodological constraints. *Canadian Journal of Zoology*, 86: 992–1001.
- Khan, M. R., de Bie, C. A. J. M., van Keulen, H., Smaling, E. M. A. & Real, R., 2010. Disaggregating and mapping crop statistics using hypertemporal remote sensing. *International Journal of Applied Earth Observation and Geoinformation*, 12: 36–46.
- Kharouba, H. M., McCune, J. L., Thuiller, W. & Huntley, B., 2013. Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? A global meta-analysis using species distribution models. *Ecography*, 36: 657–664.
- Kumar, L., Skidmore, A. K. & Knowles, E., 1997. Modelling topographic variation in solar radiation in a GIS environment. *International Journal of Geographic Information Sciences*, 11: 475–497.
- Kunin, W. E., 1998. Extrapolating species abundance across spatial scales. *Science*, 281: 1513–1515.
- Kunin, W. E., Hartley, S. & Lennon, J. J., 2000. Scaling down: on the challenge of estimating abundance from occurrence patterns. *American Naturalist*, 156: 560–566.
- Lobo, J. M., Jiménez-Valverde, A. & Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17: 145–151.
- Mackey, B. G. & Lindenmayer, D. B., 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography*, 28: 1147–1166.
- Marini, M., Barbet-Massin, M., Lopes, L. & Jiguet, F., 2010. Predicting the occurrence of rare Brazilian birds with species distribution models. *Journal of Ornithology*, 151: 857–866.
- Marquardt, D. W., 1970. Generalized inverses, ridge regression, biased linear estimation and non-linear estimation. *Technometrics*, 1: 591–612.
- Miñano, P. A., Egea, A., Oliva-Paterna, F. J. & Torralba, M., 2003. Hábitat reproductor de *Salamandra salamandra* (Linnaeus, 1758) en el Noroeste de la Región de Murcia (S.E. Península Ibérica): distribución actualizada. *Anales de Biología*, 25: 203–205.
- Mitchell-Jones, A. J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P. J. H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralik, V. & Zima, J., 1999. *Atlas of European Mammals*. T & AD Poyser Ltd, London.
- Montgomery, D. C. & Peck, E. A., 1982. *Introduction to linear regression analysis*. John Wiley and Sons, New York.
- Mu, Q., Heinsch, F. A., Zhao, M. & Running, S. W., 2007. Development of a global evapotranspiration algorithm based on MODIS and global meteorology data. *Remote Sensing of Environment*, 111: 519–536.
- Muñoz, A. R. & Real, R., 2006. Assessing the potential range expansion of the exotic monk parakeet in Spain. *Diversity and Distributions*, 12: 656–665.
- NIMA, 1997. *Digital Chart of the World*. National Imaginery and Mapping Agency (NIMA), Fairfax.
- Oindo, B. O. & Skidmore, A. K., 2002. Interannual variability of NDVI and species richness in Kenya. *International Journal of Remote Sensing*, 23: 285–298.
- Palomo, L. J. & Gisbert, J., 2008. *Atlas de los mamíferos terrestres de España*. Dirección General de la Conservación de la Naturaleza–SECEM–SECEMU, Madrid.
- Pearson, R. G., Dawson, T. P., Berry, P. M. & Harrison, P. A., 2002. SPECIES: A spatial evaluation of climate impact on the envelope of species. *Ecological Modelling*, 154: 289–300.
- Peterson, A. T., Papes, M. & Eaton, M., 2007. Transferability and model evaluation in ecological niche modelling: a comparison of GARP and Maxent. *Ecography*, 30: 550–560.
- Phillips, S. J., 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). *Ecography*, 31: 272–278.
- Phillips, S. J., Anderson, R. P. & Schapire, R. E.,

2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190: 231–259.
- Phillips, S. J. & Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31: 161–175.
- Pleguezuelos, J. M., Márquez, R. & Lizana, M., 2004. *Atlas y libro rojo de los anfibios y reptiles de España*. Dirección General de la Conservación de la Naturaleza–Asociación Herpetológica Española, Madrid.
- Radosavljevic, A. & Anderson, R. P., 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography*, 41: 629–643.
- Randin, C. F., Dirnböck, T., Dullinger, S., Zimmermann, N. E., Zappa, M. & Guisan, A., 2006. Are niche-based species distribution models transferable in space? *Journal of Biogeography*, 33: 1689–1703.
- Real, R., Barbosa, A. M. & Vargas, J. M., 2006. Obtaining environmental favourability functions from logistic regression. *Environmental and Ecological Statistics*, 13: 237–245.
- Romero, D., Olivero, J. & Real, R., 2012. Comparative assessment of different methods for using land–cover variables for distribution modelling of *Salamandra salamandra longirotris*. *Environmental Conservation*, 40: 48–59.
- Sellers, P. J., 1985. Canopy reflectance, photosynthesis, and transpiration. *International Journal of Remote Sensing* 6: 1335–1372.
- Sokal, R. R. & Rohlf, F. J., 1979. *Biometría. Principios y Métodos Estadísticos en la Investigación Biológica*. H. Blume, Madrid.
- Stockwell, D. & Peterson, A. T., 2003. Comparison of resolution of methods used in mapping biodiversity patterns from point–occurrence data. *Ecological Indicators*, 3: 213–221.
- Tejedo, M., Reques, R., Gasent, J. M., González, J. P., Morales, J., García, L., González, E., Donaire, D., Sánchez, M. J. & Marangoni, F., 2003. *Distribución de los anfibios endémicos de Andalucía: Estudio genético y ecológico de las poblaciones*. Consejería de Medio Ambiente (Junta de Andalucía)–CSIC, Seville.
- Trivedi, M. R., Berry, P. M., Morecroft, M. D. & Dawson, T. P., 2008. Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology*, 14: 1089–1103.
- Tucker, C. J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, 8: 127–150.
- Vanreusel, W., Maes, D. & Van Dyck, H., 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation Biology*, 21: 201–212.
-