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Research Article

How well can models predict changes in species distributions? A 13-year-old otter model revisited

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Abstract

Species distribution and ecological niche models are increasingly used in biodiversity management and conservation. However, one thing that is important but rarely done is to follow up on the predictive performance of these models over time, to check if their predictions are fulfilled and maintain accuracy, or if they apply only to the set in which they were produced. In 2003, a distribution model of the Eurasian otter (*Lutra lutra*) in Spain was published, based on the results of a country-wide otter survey published in 1998. This model was built with logistic regression of otter presence-absence in UTM 10 km^2 cells on a diverse set of environmental, human and spatial variables, selected according to statistical criteria. Here we evaluate this model against the results of the most recent otter survey, carried out a decade later and after a significant expansion of the otter distribution area in this country. Despite the time elapsed and the evident changes in this species' distribution, the model maintained a good predictive capacity, considering both discrimination and calibration measures. Otter distribution did not expand randomly or simply towards vicinity areas, but specifically towards the areas predicted as most favourable by the model based on data from 10 years before. This corroborates the utility of predictive distribution models, at least in the medium term and when they are made with robust methods and relevant predictor variables.

Introduction

The Eurasian otter (*Lutra lutra*) is a semi-aquatic carnivore whose worldwide distribution declined sharply between 1950 and 1970, largely due to direct persecution and habitat destruction. This trend was reversed by local conservation efforts towards the end of that century (Ruiz-Olmo and Delibes, 1998; Trindade et al., 1998). The species is still recovering nowadays, especially in Western Europe, but is considered Near Threatened globally, based mainly on sensitivity to changes and on ongoing declines in parts of its distribution range (IUCN, 2015).

Being able to predict the evolution of the geographical range of a species may be crucial when there is a need to design conservation or management plans that stay effective (e.g., Carone et al., 2014). Although it is difficult to collect variables that include all the ecological restrictions and species interactions that shape the geographical range of a species, it is often possible to develop accurate models (Liu et al., 2011). When creating a species distribution model (SDM), besides relevant information on environmental variables related to the occurrence of the target species, we need a representative set of presence (and preferably also absence) records to use as "training data" for the model (Fielding and Bell, 1997). After building the model, we need to evaluate its predictive ability. It is generally recommended that this evaluation is based on "testing data" not used in the development of the model (Fielding and Bell, 1997).

One way of assessing whether a model has correctly captured the species-environment relationships, and is thus actually capable of predicting species distributions, can be to confront the model with data from the "future" — i.e., data that did not exist at the time the model was built, and that ideally reflect actual changes in the target species' distribution. If the model still performs well after such unforeseen changes, then we can reasonably assume that it has captured the relevant drivers of species occurrence, and is thus reliable for use in management and conservation planning.

The Eurasian otter (*Lutra lutra*) provides an excellent case study for such an analysis, for several reasons. First, it is a well-known species, whose ecological behaviour and habitat preferences have been widely studied, and which has been the subject of thorough nation-wide distribution surveys (e.g., Delibes, 1990; Ruiz-Olmo and Delibes, 1998). Second, its distribution in Spain has been modelled previously, and the results were then published and extrapolated to a finer resolution (Barbosa et al., 2003). Third, a more recent otter survey in this country (López-Martín and Jiménez, 2008) reflected a substantial expansion regarding the occurrence area that was used for training the previously published model. This provides an excellent opportunity to assess if this expansion is happening towards the most favourable places predicted by the model based on data from ten years earlier, and if this SDM can thus keep a good performance on tracking the otter distribution.

In this paper we test an otter distribution model against data from the model's "future", i.e., from ten years after the survey whose data were used for model training. We quantify the changes in otter distribution and assess if those changes were in agreement with the model predictions, rather than happening simply around the vicinity of the previous presence areas. We thus assess the utility of SDMs for informing management and conservation plans.

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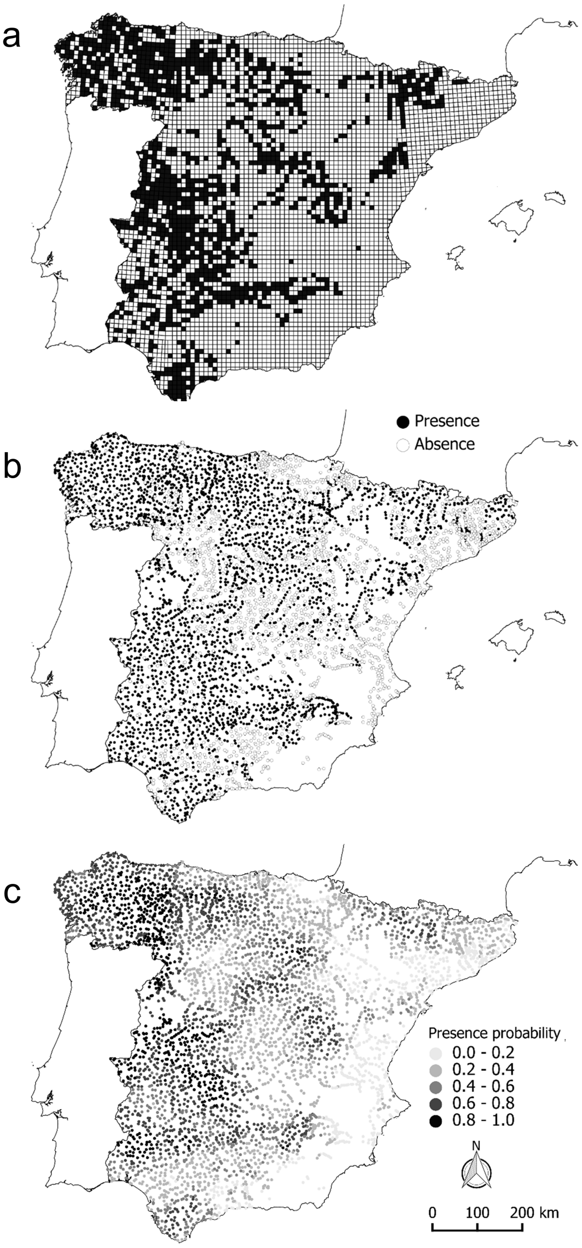

Figure 1 – (a) Presence/absence of otter records on UTM 10×10 km cells, after the penultimate Spanish otter survey (Ruiz-Olmo and Delibes, 1998); (b) presence/absence points georeferenced from the last otter survey (López-Martín and Jiménez, 2008); (c) presence probability predicted for these points by the model of Barbosa et al. (2003), built on the data in a).

Methods

Data gathering

Model predictions were those obtained by Barbosa et al. (2003). The model consisted of a logistic regression (generalized linear model with binomial error distribution and logit link) of the presence/absence of otter records on UTM 10×10 km cells of mainland Spain (Fig. 1a). These records resulted from a previous nation-wide otter survey (Ruiz-Olmo and Delibes, 1998). The predictors were a set of environmental, human and spatial variables (Tab. 1), which were included in the model with a forward conditional stepwise selection procedure (Barbosa et al., 2003).

In order to assess the predictive power of the model, we used the results of the most recent otter survey in Spain (López-Martín and Jiménez, 2008) as test data. We gathered all maps with the results from each mainland Spanish province, including both presence and absence points, digitized and georeferenced them in a single points layer. We used an open-source geographical information system, QGIS 2.4 (QGIS Development Team,QGIS, 2014), and its *Georeferencer* plugin.

Table 1 – Predictor variables used for building the otter distribution model evaluated here, and the signs of those that were finally included in the model. For more details see Barbosa et al. (2003).

Type	Variable	Sign
Environmental	Morning air humidity in January	
	Morning air humidity in July	+
	Annual air humidity range	
	Potential evapotranspiration	
	Actual evapotranspiration	+
	Annual insolation	
	Annual solar radiation	+
	Mean January temperature	–
	Mean July temperature	+
	Annual mean temperature	–
	Annual temperature range	
	Annual number of frost days	
	Annual number of rain days	
	Annual mean precipitation	+
	Maximum precipitation in 24 hours	
	Relative maximum precipitation	
	Pluviometric irregularity	
	Annual run-off	
	Soil permeability	–
	Mean altitude	–
Human	Distance to a motorway	+
	Distance to a town >100000 inhabitants	+
	Distance to a town >500000 inhabitants	+
Spatial	Mean latitude	+
	Mean longitude	–

We overlaid this map of recently surveyed presence and absence points to the UTM 10×10 km grid that was used for model training (Barbosa et al., 2003), to extract the sampled presences and absences at the same spatial resolution at which the model was built. We also extracted the predicted probability value for each sampling point, using the model predictions downscaled to 1 km^2 pixels (Fig. 7 of Barbosa et al., 2003), using the *Point Sampling Tool* plugin of QGIS.

Statistical analyses

To perform the statistical analyses, we used the open-source software R 3.1 (R Core Team, 2014). We first assessed the changes in otter distribution from the previous Spanish otter survey (Ruiz-Olmo and Delibes, 1998), used as model training data, to the latest survey (López-Martín and Jiménez, 2008), used here as model testing data. We quantified the gained, maintained and lost presences between both surveys on UTM 10×10 km grid cells.

We then confronted the model predictions with the test data derived from the latest survey. We used a suite of model evaluation measures implemented in the `modEvA` R package (Barbosa et al., 2013), which assess two different components of model performance: discrimination (i.e., the ability of the model to distinguish presence from absence localities); and calibration or reliability (i.e., the deviations of continuous model predictions from actual observations). Although the latter component is usually neglected, it is just as important in the evaluation of species distribution models (Pearce and Ferrier, 2000; Wintle et al., 2005; Jiménez-Valverde et al., 2013).

To investigate whether the changes in otter distribution occurred simply around the vicinity of previously occupied areas rather than specifically according to the combination of predictor variables in the model, we also did a spatial interpolation model based on simple inverse distance to presence (Takahashi et al., 2014), using the `distPres` function of the `fuzzySim` R package (Barbosa, 2015a). We then applied the set of model evaluation measures to this spatial interpolation model as well.

To evaluate the predictions of the model when extrapolated to 1 km^2 cells, we compared mean predicted probability among presence and absence points. For this we used box plot notches (Chambers et al., 1983) and the non-parametric signed rank test of Mann-Whitney-Wilcoxon (Wilcoxon, 1945).

Results

Observed changes in otter distribution

We georeferenced 4966 points surveyed in mainland Spain in the latest nation-wide otter survey (López-Martín and Jiménez, 2008). Among these, 3255 points (65.5%) were classified as presences and 1711 points (34.5%) were classified as absences (Fig. 1b).

When gridded to the 10×10 km UTM cells that were originally used for building the model (Barbosa et al., 2003), these recently surveyed points yielded 2625 presence cells and 2542 absence cells (i.e. cells with no presence records). When compared to the data from the previous otter survey (Ruiz-Olmo and Delibes, 1998), on which the model was built, there were 1384 new presences, representing a 90.6% increase; 1241 (81.3%) maintained presences; and 286 (18.7%) lost presences, i.e., UTM cells with presence records in the 1998 survey and no presence records in the latest survey.

Evaluation of the model on 10 km^2 grid cells

When applied to the test data from the latest otter survey, the model trained on the previous survey achieved generally similar performance measures. There was a visible decrease in sensitivity (i.e., the ability to detect presences) from the training to the test data (Fig. 2), indicating that the model did not predict such a substantial increase in the otter occurrence area. However, test presences did have higher predicted probabilities than test absences, as the area under the curve (AUC) of the receiver operating characteristic (ROC) of the model applied to the test

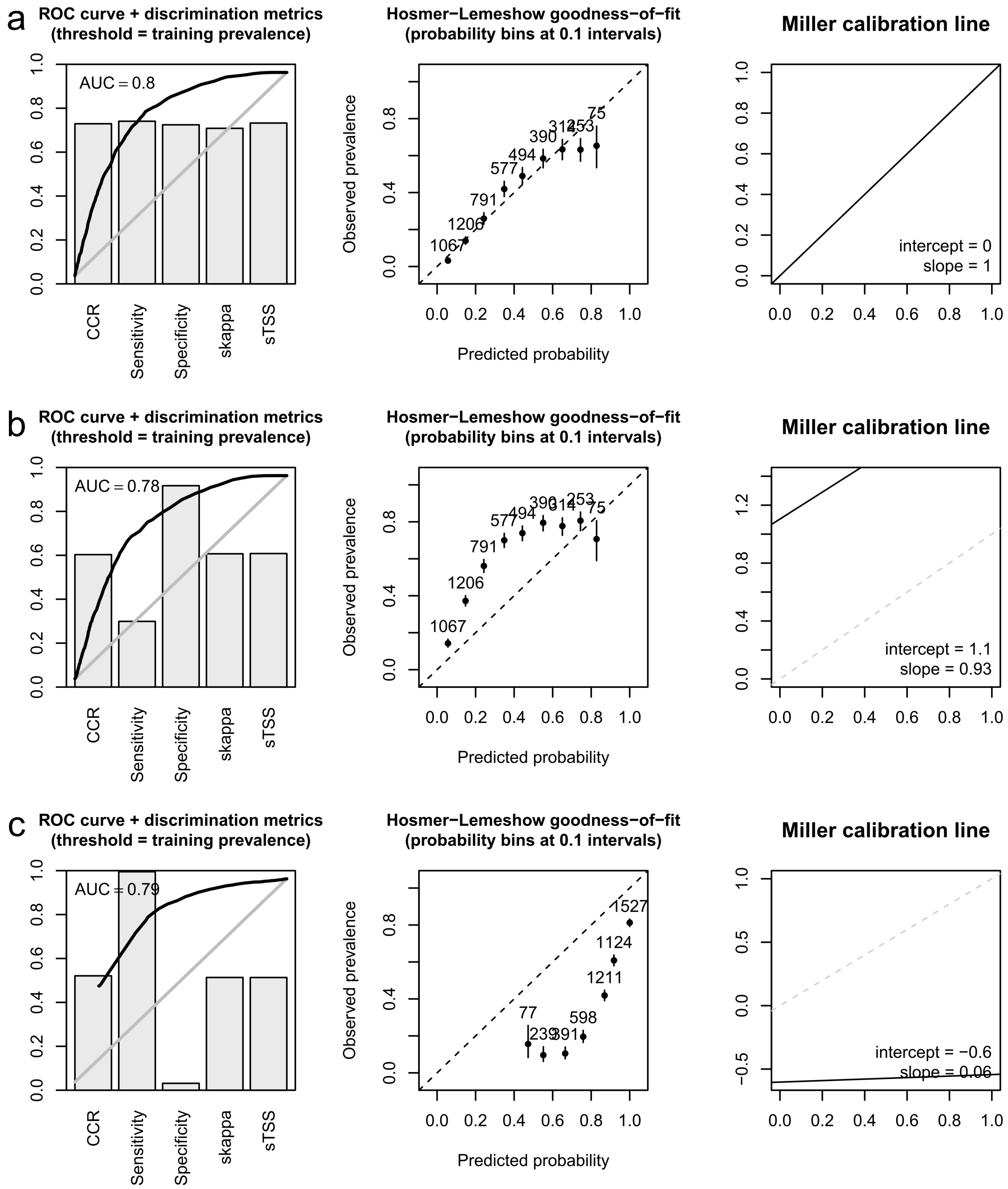

Figure 2 – Model evaluation measures obtained for the otter distribution model of Barbosa et al. (2003) when confronted with the training data (a) and with more recent test data (b), and the same measures for a distance interpolation of the training data compared to the test data (c). CCR: overall correct classification rate; TSS: true skill statistic. TSS and kappa were standardized (s) to vary between 0 and 1 and thus be directly comparable to the other measures (Barbosa, 2015b).

Table 2 – Proportion of explained deviance (D^2) and different pseudo-R^2 measures obtained for the otter distribution model of Barbosa et al. (2003) when compared to the training data (Ruiz-Olmo and Delibes, 1998) and to more recent test data (López-Martín and Jiménez, 2008); and the same measures for a distance interpolation model applied to the test data.

Evaluation	Model vs. training data	Model vs. test data	Distance vs. test data
D^2	0.19	0.18	0.13
R^2 Cox-Snell	0.21	0.22	0.16
R^2 Nagelkerke	0.30	0.29	0.21
R^2 McFadden	0.19	0.18	0.13
R^2 Tjur	0.22	0.19	0.13
R^2 Pearson	0.19	0.21	0.24

data was not significantly different from the AUC of the model on the training data (Fig. 2; DeLong's test for two ROC curves, calculated with the pROC package (Robin et al., 2011), p>0.05). The distance interpolation of training data had a slightly higher AUC than the model when classifying the test data, but the results of other discrimination measures (including e.g. the widely used True Skill Statistic and Cohen's kappa, which controls for chance effects in the agreement between predictions and observations) were generally worse than those obtained by the Barbosa et al. (2003) model on the test data (Fig. 2).

The proportion of variation accounted for by the model also did not vary visibly among training and test data, with explained deviance and most pseudo-R^2 measures remaining essentially the same in both datasets. Conversely, the distance interpolation yielded visibly smaller values for nearly all these metrics (Tab. 2). Regarding calibration, the model underestimated occurrence frequencies in the test data (again, not predicting such an extensive increase in the otter distribution area), according to both the Hosmer-Lemeshow goodness-of-fit and the Miller calibration plots (Fig. 2). However, the Miller calibration line was practically parallel to the diagonal, with a slope of nearly 1 — i.e., predictions were consistently below observations (bias), but varied proportionally to them (no spread). Conversely, the distance interpolation overestimated otter occurrence in the test data and not in a consistent or directly proportional way, as both Miller intercept and slope were far from the ideal values of 0 and 1, respectively (Fig. 2).

Evaluation of the model when downscaled to 1 km² pixels

The values of predicted probability provided by the model downscaled to 1 km² resolution (Barbosa et al., 2003) were visibly higher for test presence than for test absence points (Fig. 3). The notches ("waists") of their box plots did not overlap, thus providing strong evidence that the two medians differ (Chambers et al., 1983, p. 62). The Wilcoxon rank-sum test also showed a significant difference between the mean probability values predicted for presence and absence points (W=1315001, $p<2.2\times10^{-16}$).

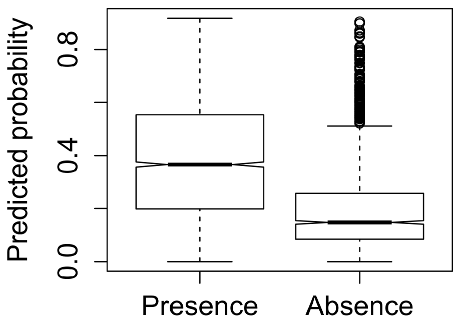

Figure 3 – Box plot of the otter presence probability values predicted by the model of Barbosa et al. (2003) for the test presence and absence points obtained from the latest otter survey (López-Martín and Jiménez, 2008).

Discussion

Species distribution models are now routinely used in ecology and biogeography (see e.g. Jiménez-Valverde and Lobo, 2007 for a brief review). A trustworthy evaluation of their predictive capacity is crucial, especially if models are to be taken into account when designing conservation and management plans. Such evaluation should be made not only on data contemporaneous to the model, but also on data that the modellers had no way of accessing when the model was built. Here we evaluated an otter distribution model using test data from several years after the model was published, and which included visible changes in the distribution of the modelled species.

As is usual with widespread species, measures of model discrimination (i.e., the ability to distinguish presence sites from absence sites) were already not very high for the original model when evaluated on the training data (Fig. 2a), and they remained essentially similar in the evaluation on the test data. Sensitivity was the clear exception, with a significant amount of new presences falling in areas predicted as having relatively low presence probability (Fig. 2b). However, this mismatch was only quantitative rather than qualitative: these areas still had generally higher probability than those where the otter remained absent, as was evidenced by an AUC not significantly lower than that obtained for the model on the training data (Fig. 2a). This means that not many places outside the training occurrence areas had high probability of being occupied, although they were; but, within those areas, the otter expanded to the ones with still relatively high probability.

The recently occupied areas were necessarily in the vicinity of the previously occupied ones, so the model based on simple distance interpolation also obtained a relatively high AUC. However, although the distance interpolation model did capture nearly all the new presences, it had very low specificity, i.e. was largely unsuccessful at predicting otter absences, unlike the distribution model of Barbosa et al. (2003), which did achieve a high prediction success on absences. Accuracy measures that take into account overall classification success correcting for chance effects, such as Cohen's kappa, also detected a visibly better performance of model predictions against the distance interpolation (Fig. 2b,c).

Measures of model calibration and explained deviance provided even stronger support for the superior reliability of the generalised linear model over simple distance interpolation. While the model did underestimate otter occurrence, its nearly parallel calibration line showed that it captured the species-environment relationships almost perfectly, unlike the distance interpolation (Fig. 2b,c). Hence, the otter expansion documented in López-Martín and Jiménez (2008) occurred not randomly, nor simply towards the neighbourhood of the occurrences detected in the previous otter survey, but rather precisely towards the areas predicted with higher probabilities by the model published several years before (Barbosa et al., 2003).

Resolution scale is important too, as coarse-scale data can sometimes disguise fine-scale discontinuities (e.g., Sales-Luís et al., 2012). The analysed model was previously extrapolated to predict otter distribution at a 100-times finer resolution scale (Barbosa et al., 2003), and it was evaluated at this scale using point data from the previous otter survey (Barbosa et al., 2010). Here we evaluated the model also on point data from the latest survey. The comparison between point records and downscaled model predictions kept in line with the previous results, with presence points located in pixels predicted with clearly higher probability values than absence points. There were, however, several outliers, with a set of absence points in areas predicted as having high probabilities of occurrence (Fig. 3), and a maximum predicted value for absences (0.958) very close to the maximum obtained for presences (0.964). There are thus few but visible areas of disagreement, where the model predicts highly favourable conditions for the otter to be present, but where no presence signs were detected. Fielding and Bell (1997) suggest that such cases indicate ecological interferences that the model could not predict — for example, dispersal barriers or biotic interactions such as competition or lack of prey. Another important justification might be the alteration or destruction of otter habitat, possibly associated to changes in the human variables over the last decade (e.g., Pedroso et al., 2014). Further research should focus on understanding what kinds of obstacles are inhibiting the otter from completely occupying its potential range.

Conversely, there were generally low predicted values in the north-east (Fig. 1c), where the otter is known to be currently expanding. The analysed model was based on data from the beginning of the otter recovery in Spain (Ruiz-Olmo and Delibes, 1998), when this species was still mostly distributed in the western half of this country (Fig. 1a). The otter had previously gone virtually extinct in eastern Spain (Delibes, 1990) and has since recovered increasingly in this region (López-Martín and Jiménez, 2008), as has happened in other parts of Europe (Romanowski et al., 2013). This probably had some weight in the results: the model was built for the complete country at an initial stage of the eastern recovery, so it gathered more occurrence information from the most typical or common otter habitats in western Spain. Typical habitats of the eastern Spanish otters, which can be different from those in the west, were thus less analysed by the model.

In addition, the model included two spatial variables, latitude and longitude (Tab. 1), reflecting spatial trends that are not explained by the available environmental and human variables (Barbosa et al., 2003). These variables can account for spatially contagious biotic processes such as reproduction, migration, and mortality (Legendre, 1993), and they may have limited the probability predictions in eastern Spain, where the recent otter expansion was aided, at least in part, by a reintroduction programme (Fernández-Morán et al., 2002).The existence of both favourable and unfavourable areas within the current otter range could also suggest a metapopulation structure or the occurrence of source-sink dynamics, with expanding populations occupying suboptimal habitats when optimal ones have reached their carrying capacity (Pulliam, 1988; Muñoz et al., 2005; John et al., 2010). Otters could also be increasing their habitat tolerances in formerly inadequate areas, as has already been observed in eastern Europe (Romanowski et al., 2013).

All in all, although the analysed model was developed with otter distribution data from the last century, it showed considerable accuracy in predicting the results of a subsequent otter survey carried out ten years later, and in distinguishing the otter expansion areas from those where the species still does not naturally occur. This provides support for the utility of SDMs in conservation and management planning, at least when these models are built with robust and extrapolable methods, as generalised linear models have widely proven to be (Ennis et al., 1998; Elith, 2000; Wintle et al., 2005; Farfán et al., 2008; Barbosa et al., 2009); with a diverse enough set of variables to capture the relevant correlates of the species' distribution (Tab. 1); and with strong statistical methods to select among such variables (see Barbosa et al., 2003). Evaluating models against data from their future is a reliable and necessary way to assess their actual predictive power.

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