Forum

Ecography 31: 417–422, 2008
doi: 10.1111/j.2008.0906-7590.05221.x

Subject Editor: Jane Elith. Accepted 13 February 2008

Favourability functions versus probability of presence: advantages and misuses

Cécile H. Albert and Wilfried Thuiller

C. H. Albert (cecile.albert@m4x.org) and Wilfried Thuiller, Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Univ. Joseph Fourier, BP 53, FR-38041 Grenoble Cedex 9, France.

Logistic regression has been used to predict species distribution since the early age of predictive biogeography (Austin et al. 1984, Guisan and Thuiller 2005, Austin 2007). This is a parametric generalisation of usual linear regression that deals with a non-normally distributed response, and it has been utilized successfully to explain and model the distribution of various organisms over local to large spatial scales (Guisan et al. 1998, Teixeira et al. 2001, Fleishman et al. 2003, Thuiller et al. 2006a, b). The probability outputs of these models are commonly used under two forms: either they are summarised into binary results by choosing a threshold (Liu et al. 2005) or they are used un-summarised as raw probabilities or indexes (Real et al. 2006) where high values are taken as characterising highly suitable sites for the modelled species. The raw probability outputs are calibrated so they depend on the prevalence (ratio between the number of presences and the total number of records in the dataset) of the training dataset: the mean fitted value across all sites is equal to the prevalence in the training dataset. Because of this, rare species tend to have many low predicted values at sites across a region compared with more common species, so comparing suitability of sites across species in a conservation planning context can be a complex task. That is, the common species can effectively swamp the rare species in inter-species comparisons. In a recent paper, Real et al. (2006) proposed a method to circumvent this potential drawback by introducing a favourability function. They introduced the idea that a biased dataset is one where sampling prevalence (as deduced from samples) differs from 50%. Rescaling the probability outputs of logistic regression with reference to a so called ideal sample prevalence of 50%, the favourability function is expected to improve predictions in terms of description of the favourable areas for the species and to facilitate the comparison between species (and so that 0.5 would become the threshold for all species). Real et al. (2006) also claim that this function makes the model probability outputs independent of the sampling prevalence of the training dataset. The proposed formula for favourability F is the following:

$$F = \frac{\frac{P}{1 - P}}{\frac{n_1}{n_0} + \frac{P}{1 - P}},$$

with P the probability output of the logistic regression and n_1 and n_0 the respective number of presences and absences in the dataset.

To test this favourability function, Real et al. (2006) used virtual species that respond to a single environmental factor, providing "true" species distributions that can be sampled in different ways, and used to evaluate model outcomes (Hirzel et al. 2001, Reineking and Schroder 2006, Austin et al. 2006, Jimenez-Valverde and Lobo 2007, Meynard and Quinn 2007). The species all used the same environmental variable, and the same logistic relationship, but had varying population prevalence. A first test was realized with a single virtual species constructed with a 50% population prevalence to test the effect of sampling prevalence on the probability and the favourability outputs. Three sub-samples were extracted with respective sampling prevalences of 20% (presences are under represented compared to the true distribution), 50% (full distribution) and 80% (presences are over represented compared to the true distribution). Each sample was used to fit a logistic regression and results were compared: probability outputs were very different (maps) and favourability outputs were said to be qualitatively similar. Then on this specific case the favourability function was able to improve outputs resulting from unbalanced training datasets. The favourability function was then applied to two other virtual species with respective population prevalences of 20 and 80% to show that the favourability function makes it easier to compare species with different population prevalences. Both fully sampled (sampling prevalence equal to population prevalence), the two virtual species obviously presented very different logistic regression outputs. However, rescaling these probability outputs, the favourability function allowed direct comparison of the two species in the overall landscape.

We found this method appealing for its modelling approach and innovative in its use of virtual species. In particular, Real et al. (2006) have clearly indicated why they require model probability outputs to be independent of the sampling prevalence and therefore comparable across prevalences. The method (Real et al. 2006) has merit in dealing with this problem but relies on a problematic definition of bias (sampling prevalence other than 50%) not ecologically justified. We propose that bias be defined as a sampled prevalence different from the "true" prevalence (the real probability of finding the species in the landscape), because it seems meaningful to consider as unbiased a sample which represents the ecological reality. Predictions from a logistic regression model will be calibrated in such a way that they accurately reflect the prevalence of a species throughout a region. We have to deal carefully with the word "bias" because it is commonly used but has several meanings; outputs of logistic regressions are not biased in the sense that they reflect the input data, but if built on biased samples they can be difficult to interpret.

Let us then move on without focussing on the word "bias", and consider what the favourability function (Real et al. 2006) does. We propose to test the favourability function ("Favourability 50") and compare it with a modified function ("Modified favourability") defined as follows:

$$F = \frac{\dfrac{P}{1-P}}{\dfrac{\Pr_{\text{Sample}}}{\Pr_{\text{True}}} + \dfrac{P}{1-P}},$$

where $\Pr_{\text{Sample}}$ and $\Pr_{\text{True}}$ are respectively the prevalence of the sampled dataset and the true prevalence of the virtual species using simulations with a range of both sample prevalence and population prevalence.

We first built a virtual landscape of 32 per 20 pixels (each pixel representing a 10 × 10 km area) based on a mean temperature parameter. This mean temperature parameter was distributed along a realistically varying gradient (0–15°C) and slightly modified with the addition of a random normal value. This led to a landscape with a temperature parameter ranging from −5 to 20°C and a mean of 7.6°C (Fig. 1a). We then established a logistic response to this single environmental factor. The response was higher for higher mean temperatures. This response to the environment was then used to create three virtual species distributions with respective population prevalence of 20% (VS20), 50% (VS50) and 80% (VS80) (Fig. 1b, c, d).

For each species, samples of 80 pixels with prevalence of 20, 50 and 80% were randomly extracted. They represented random partial samplings in the field, with perfect detection. This sampling strategy was chosen to cross-test the effect of the true and the sampling prevalence on the logistic regression, the Favourability 50 and Modified favourability outputs. For VS20, three more samples of 200 pixels were also selected with prevalences of 5, 10 and 15%, which are

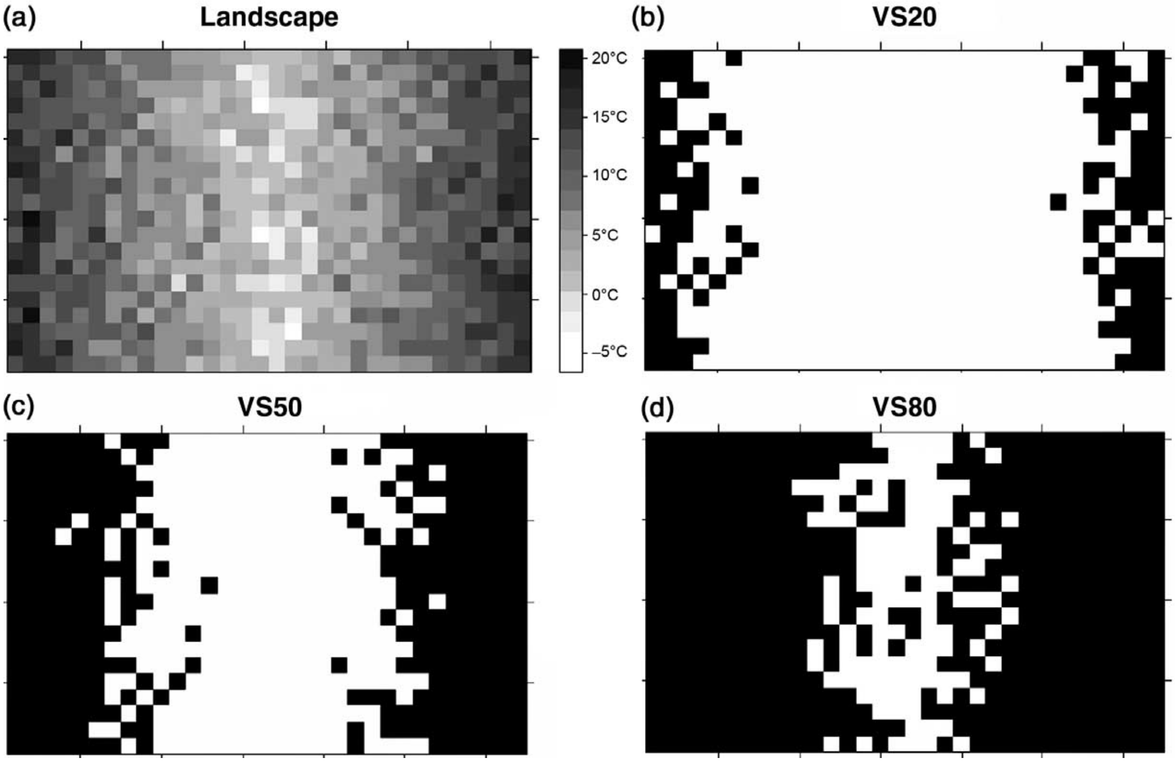

Figure 1. Map of the virtual landscape: mean annual temperature (from −5 to 20°C) (a), VS20 species in presence (black) vs absence (white) (b), VS50 species in presence vs absence (c), VS80 species in presence vs absence (d).

sample prevalences close to those observed in datasets obtained in natura.

Logistic regressions were performed on the sampled datasets and on the true distributions (full distribution) of the three species. The probability outputs obtained with the sampled dataset were then transformed with the Favourability 50 and the Modified favourability functions. For each model, the raw predictions as well as the Favourability 50 and Modified favourability predictions were evaluated using the area under the receiver operating characteristic curve (AUC) (Swets 1988) for the whole landscape.

We then compared each output dataset (probability or favourability) to the model fitted with the full dataset to explore the performance of each model and formula outputs for the different sampling and population prevalence. To determine if predictions for a single species were consistent and independent from the sample prevalence, we also compared the outputs obtained from samples with a prevalence of 20% (and 10% for VS20) and those with a prevalence of 80%.

To quantify this we used a weighed Kappa coefficient (Cohen 1960) with multiple modalities. We used 5 classes: 0–0.2 (very low suitable environment), 0.2–0.4 (low suitable), 0.4–0.6 (medium suitable), 0.6–0.8 (quite suitable) and 0.8–1 (suitable) to discriminate the outputs values. N being size of the datasets, the n_{ij} were defined as the counts in the resulting confusion table and a weight matrix W (5, 5) was chosen to classify errors by their seriousness: $Wij = 1 - \frac{|i-j|}{5-1}$. Then the Kappa coefficient was calculated as follows:

$$\text{with } Po = \sum_{i=1}^{5}\sum_{j=1}^{5} W_{ij} \times \frac{n_{ij}}{N} \text{ and}$$

$$Pe = \sum_{i=1}^{5}\sum_{j=1}^{5} W_{ij} \times \frac{n_{i.}}{N} \times \frac{n_{.j}}{N}, \; K = \frac{Po - Pe}{1 - Pe}.$$

We finally used a rough guideline to classify the kappa values: above 0.8, the two models were considered as equivalent, between 0.6 and 0.8, the two models were considered as nearly different and under 0.6 the two models were considered as very different.

Obviously, the raw regression and the Favourability 50 were identical for a sampling prevalence of 50% and the raw regression and the Modified favourability were identical for a sampling prevalence equal to the population one, leading to the same values of the Kappa coefficient (K) (Fig. 2).

For the three species the best predictions (higher Kappa values, Kappa >0.88) with the raw model were obtained when sampling and population prevalences coincide (for instance with a sampling prevalence of 20 for the species VS20). However, as soon as the sampling prevalence was different from the population one, raw predictions were very different from the model performed on the exhaustive distribution of the species (Fig. 2). The Favourability 50 led to better predictions than the raw model (for example Kappa =0.9 instead of 0.47) when the sampling prevalence was very different from the population one. Nevertheless predictions became worse than the raw ones when the sampling prevalence was close to the population one (for example Kappa = 0.25 instead of 0.74). As for the Modified

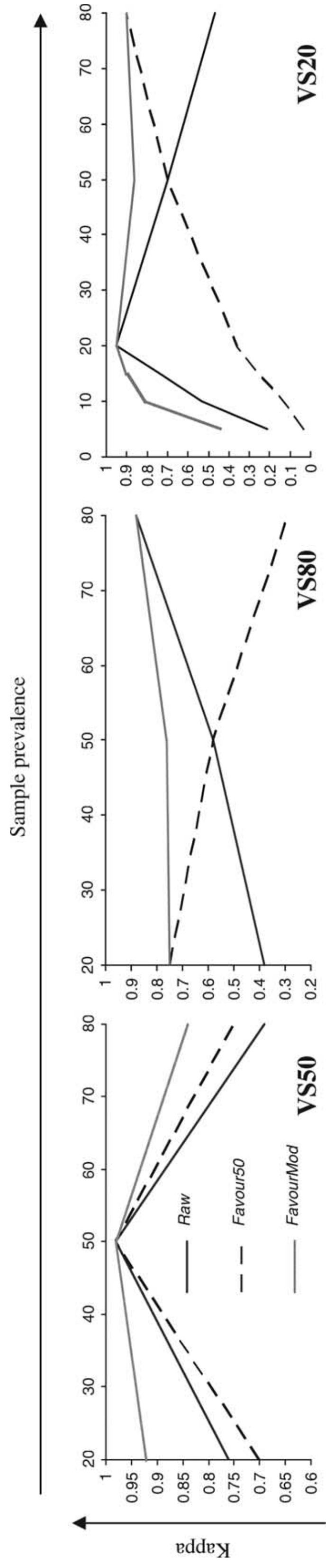

Figure 2. Cohen's Kappa values between each model/formula outputs and the ones of the model performed on the true distributions, for each sample prevalence and for each species. For Kappa values under 0.8 both predictions sets can be considered as different.

Table 1. Cohen's weighted Kappa coefficients for each species and each model/formula between two outputs resulting from samples with prevalences of 20 and 80% for the three species and 10 and 80% for VS20.

	Species	Raw	Favourability 50	Modified favourability
VS20	Sample prevalence 20 vs 80	0.43	0.38	0.88
VS20	Sample prevalence 10 vs 80	0.20	0.16	0.72
VS50	Sample prevalence 20 vs 80	0.49	0.45	0.87
VS80	Sample prevalence 20 vs 80	0.33	0.39	0.72

favourability, it gave predictions ($0.81 < \text{Kappa} < 0.98$ except for the sampling prevalence of 5%) as good as or better than the raw ones in all cases (Fig. 2).

The Kappa coefficients calculated between two models outputs resulting from two samples of the same species differing by their sampling prevalence are presented in the Table 1. As expected the raw regression led to higher probability outputs when the sampling prevalence was high (80%) compared to when it was low (20%) (Table 1, Fig. 3). This results in relatively low Kappas for the three species (0.33–0.49, Table 1). The Favourability 50 function reversed these tendencies (Fig. 3) and still led to low Kappas (0.38–0.45, Table 1). Modified favourability properly adjusted the outputs (Fig. 3), leading to higher values of kappa (0.72–0.88, Table 1).

All AUC values (predictions tested against observations, Table 2) were very high (over 0.98), showing that all the performed models discriminate a presence from an absence almost perfectly. As the Favourability 50 and Modified favourability are rescaling formulas they are changing only calibration and not discrimination, so their use leads necessarily to the same AUC values and to rescaled thresholds, (Jimenez-Valverde and Lobo 2007).

This research sought to improve the favourability formula proposed by Real et al. (2006) with a formula relying on the ratio between the sampling and the true prevalence of a virtual species. The improved formula has proven to be efficient in reducing sampling-induced error in the logistic regression outputs, even for consequent bias of the training sample (sampling prevalence of 80% instead of 20% or the contrary) and for datasets close to those obtained in natura (sample prevalence of 5 or 10% for VS20). It also yielded similar predictions for a given species, even for samples with different prevalences. We believe that this formula is more realistic than the one proposed by Real et al. (2006) because it does not suppose that a particular prevalence of 50% is the reference one. However, this formula will be difficult to apply to real species for which true prevalences are poorly known. In these cases, one should investigate the origin of the low prevalence problem and the possible solutions for getting around it.

The possible origins of a low prevalence in a sample are multiple. First, such a sample might properly represent the true distribution of a rare species because most environments are unsuitable for it (Guisan and Thuiller 2005, Jimenez-Valverde and Lobo 2007, Meynard and Quinn 2007). Secondly, it can result from a sampling-induced bias due to either low detectability or poor sampling strategy (Mackenzie et al. 2004, Wintle et al. 2005). Thirdly, it can result from the fact that the considered area is at the edge of the species environmental niche or does not include its whole niche (Hernandez et al. 2006, Randin et al. 2006, Vanreusel et al. 2007). Fourth, the sample area may be too large in relation to the whole niche of the species as it is often the case for restricted and rare species (Martin et al. 2005). These four cases differ both in the origin of the low prevalence of the sample they induce and in the relevant solutions. The first case is not an error as such, because the modelled probabilities truly reflect the species prevalence. In fact, given relevant predictors, a suitable site, if it exists, can be modelled with a high probability – one would simply not expect many of them overall. If, alternatively, there are no predictors that identify highly suitable sites, many probabilities may be low, and sensible strategies for dealing with this in the light of higher predictions for more common species will be required. The second case is a substantial problem, highly mobile or small vagile species are often difficult to detect and good sampling strategies are always difficult to design in such a way as to be both statistically and ecologically sound. Quantifying the detection probability for a given species could be a solution to obtain a more statistically conclusive statement about possible reasons for not detecting a given species as opposed to a simple "none were found" conclusion (Wintle et al. 2004, Royle et al. 2005, Mackenzie 2006). The third and the fourth cases are modelling problems. The choice of the scale and of the resolution in statistical habitat modelling is one of the greatest challenges in this field (Guisan and Thuiller 2005). To obtain reliable probability outputs, input data should include the whole niche (the core, the edge and the outside of the niche) of the species (Austin and

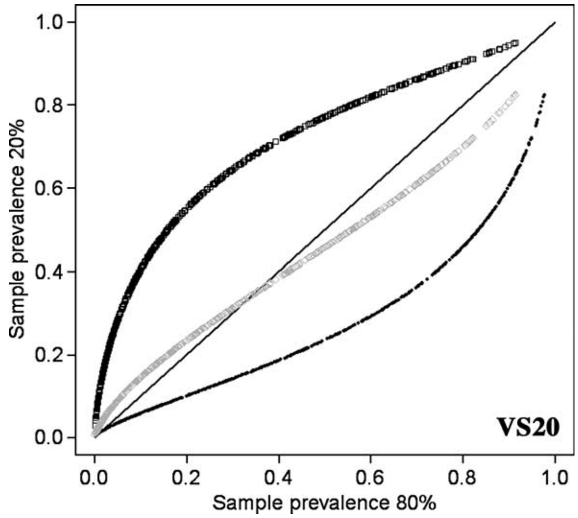

Figure 3. VS20 species. Comparison between outputs resulting from a training data with a sample prevalence of 20% against one of 80%. Black dots are representing raw regression outputs, black squares the Favourability 50 outputs and grey squares the Modified favourability. This comparison shows the sample prevalence dependence of the models.

Table 2. Values of the area under the curve of the receiver operating characteristic curve for the different species and the different sampling prevalences. The three model/formula lead in each case to the same AUC value.

Species	Prevalence	AUC
VS20	5	1
VS20	10	1
VS20	15	1
VS20	20	1
VS20	50	1
VS20	80	1
VS50	20	1
VS50	50	1
VS50	80	1
VS80	20	0.98
VS80	50	0.98
VS80	80	0.98

Meyers 1996, Thuiller et al. 2004, Strauss and Biedermann 2007, Tsoar et al. 2007). However, the study area must not be too large compared to the extent of occurrence of the species to avoid the inclusion of a large number of inappropriate absences and lower the probability outputs.

It therefore seems that a single formula aiming at getting around this sampling prevalence problem cannot be universal and that the situation has to be considered case by case with an accurate ecological knowledge of the species to make the right modelling choices (Pearce et al. 2001, McPherson and Jetz 2007).

Our analysis also shows that innovative mathematical formula have to be developed and tested carefully before being used by decision makers. Models and in particular habitat models, as simplifications of reality and predictive tools are more and more used to guide conservation and restoration planning, management and support the formulation of policy decisions (Bayliss et al. 2005, Thompson et al. 2006, Titeux et al. 2007, Vanreusel et al. 2007). For this reason, predictions and models have to be as reliable and consistent as possible (Mech 2006, Nicholson and Possingham 2007) and need to be used carefully. Sampling strategies have to be statistically and ecologically sound (Guisan and Thuiller 2005) and supported by a strong ecological knowledge of the studied species (Pearce et al. 2001, McPherson and Jetz 2007). Habitat models should also satisfy the underlying assumptions: the studied species should be in quasi-equilibrium with its environment and not, for example, colonising a new area, the studied area should include the whole niche of the species without being too large (Guisan and Thuiller 2005) and environmental explanatory variables should be as proximal as possible (Austin 2002). Users of habitat suitability models have to bear in mind that the models are correlative and static in nature and usually focus on abiotic conditions (but see Leathwick and Austin 2001). Habitat suitability models should not thus be applied to species whose distributions are constrained for example by the occurrence of a specific prey or a competitor if these are not accounted for. Moreover, the outputs of habitat suitability models have to be interpreted with the clarification from expert opinion.

In species distribution modelling two kinds of results are commonly used: the first one is the binary transformation of logistic regression outputs (Liu et al. 2005, Jimenez-Valverde and Lobo 2007); this is based on the choice of a threshold which aims to separate occupied from unoccupied sites. The selection of this threshold and the possible ways to calculate it have been extensively discussed during the last ten years (Fielding and Bell 1997, Pearce and Ferrier 2000, Vayssières et al. 2000, Manel et al. 2001, Fielding 2002, Liu et al. 2005, Allouche et al. 2006, Jimenez-Valverde and Lobo 2007). The resulting binary outputs and their predictive performance can be influenced by the training sample prevalence and also by the validation sample prevalence per se (Manel et al. 2001, Liu et al. 2005), but are not depending on a rescaling formula like the Favourability 50 (rescaling results only lead to a rescaling in the threshold) (Jimenez-Valverde and Lobo 2007). The threshold must then be chosen carefully and according to the final goal of the modelling study (Liu et al. 2005).

The second kind of results is raw probability outputs. Those results can be interpreted in two different ways; they can be seen as an absolute measure of probability of occurrence but must be validated by calibration plots (Pearce and Ferrier 2000) or as a relative measure of the likelihood of species occurrence (Pearce and Ferrier 2000). If there is bias in the training sample, it is more robust to use them as an ordinal suitability index.

Finally, when binary results are not sufficient, it is possible to avoid the drawback of unbalanced species by considering the results as relative values and using them for example as a percentage of the maximum of the raw probability outputs. It is also possible to weight the logistic regression (Teixeira et al. 2001) in a way to balance the sample without losing information and to avoid a biased rescaling afterward, but this again relies either on the knowledge of the true prevalence of the species or on the assumption of an ideal 0.5 prevalence. Another way to use those models outputs would be to confront them systematically with expert opinion and eventually rescale them by including this field knowledge. For example the maximum, minimum and medium values of the probability outputs could be compared with in situ measures of abundance, fitness or other ecological performances.

Acknowledgements – This work was funded by the "Agence National pour la Recherche" through the QDiv project (Quantifying the Effects of Global Environmental Change on Terrestrial Plant Diversity). WT received support from European Commission's FP6 MACIS (Minimisation of and Adaptation to Climate change Impacts on biodiverSity No. 044399) and ECOCHANGE (Challenges in assessing and forecasting biodiversity and ecosystem changes in Europe) projects. We thank three anonymous reviewers for their very helpful comments and critics on the manuscript and Jane Elith for all her comments and her major help.

References

Allouche, O. et al. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). – J. Appl. Ecol. 43: 1223–1232.

Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. – Ecol. Model. 200: 1–19.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. – Ecol. Model. 157: 101–118.

Austin, M. P. and Meyers, J. A. 1996. Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. – For. Ecol. Manage. 85: 95–106.

Austin, M. P. et al. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. – Vegetatio 55: 11–27.

Austin, M. P. et al. 2006. Evaluation of statistical models used for predicting plant species distributions: role of artificial data and theory. – Ecol. Model. 199: 197–216.

Bayliss, J. L. et al. 2005. The use of probabilistic habitat suitability models for biodiversity action planning. – Agricult. Ecosyst. Environ. 108: 228–250.

Cohen, J. 1960. A coefficient of agreement for nominal scales. – Educ. Psychol. Meas. 20: 37–46.

Fielding, A. H. 2002. What are the appropriate characteristics of an accuracy measure. – In: Scott, J. M. et al. (eds), Predicting species occurrences – issues of accuracy and scale. Island Press, pp. 303–313.

Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. – Environ. Conserv. 24: 38–49.

Fleishman, E. et al. 2003. Validation tests of predictive models of butterfly occurrence based on environmental variables. – Conserv. Biol. 17: 806–817.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. – Ecol. Lett. 8: 993–1009.

Guisan, A. et al. 1998. Predicting the potential distribution of plant species in an alpine environment. – J. Veg. Sci. 9: 65–74.

Hernandez, P. A. et al. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. – Ecography 29: 773–785.

Hirzel, A. H. et al. 2001. Assessing habitat-suitability models with a virtual species. – Ecol. Model. 145: 111–121.

Jimenez-Valverde, A. and Lobo, J. M. 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. – Acta. Oecol. 31: 361–369.

Leathwick, J. R. and Austin, M. P. 2001. Competitive interactions between tree species in New Zealand's old-growth indigenous forests. – Ecology 82: 2560–2573.

Liu, C. et al. 2005. Selecting thresholds of occurrence in the prediction of species distributions. – Ecography 28: 385–393.

Mackenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. – J. Wildl. Manage. 70: 368–374.

Mackenzie, D. I. et al. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. – J. Anim. Ecol. 73: 546–555.

Manel, S. et al. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. – J. Appl. Ecol. 38: 921–931.

Martin, T. G. et al. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. – Ecol. Lett. 8: 1235–1246.

McPherson, J. M. and Jetz, W. 2007. Effects of species' ecology on the accuracy of distribution models. – Ecography 30: 135–151.

Mech, D. L. 2006. Prediction failure of a wolf landscape model. – Wildl. Soc. Bull. 34: 874–877.

Meynard, C. N. and Quinn, J. F. 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. – J. Biogeogr. 34: 1455–1469.

Nicholson, E. and Possingham, H. P. 2007. Making conservation decisions under uncertainty for the persistence of multiple species. – Ecol. Appl. 17: 251–265.

Pearce, J. and Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. – Ecol. Model. 133: 225–245.

Pearce, J. L. et al. 2001. Incorporating expert opinion and fine-scale vegetation mapping into statistical models of faunal distribution. – J. Appl. Ecol. 38: 412–424.

Randin, C. F. et al. 2006. Are niche-based species distribution models transferable in space? – J. Biogeogr. 33: 1689–1703.

Real, R. et al. 2006. Obtaining environmental favourability functions from logistic regression. – Environ. Ecol. Stat. 13: 237–245.

Reineking, B. and Schroder, B. 2006. Constrain to perform: regularization of habitat models. – Ecol. Model. 193: 675–690.

Royle, A. et al. 2005. Modelling occurence and abundance of species when detection is imperfect. – Oikos 110: 353–359.

Strauss, B. and Biedermann, R. 2007. Evaluating temporal and spatial generality: how valid are species–habitat relationship models? – Ecol. Model. 204: 104–114.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. – Science 240: 1285–1293.

Teixeira, J. et al. 2001. Biogeography of the golden-striped salamander *Chioglossa lusitanica*: a field survey and spatial modelling approach. – Ecography 24: 618–624.

Thompson, L. M. et al. 2006. A spatial modeling approach to identify potential butternut restoration sites in Mammoth Cave National Park. – Restor. Ecol. 14: 289–296.

Thuiller, W. et al. 2004. Effects of restricting environmental range of data to project current and future species distributions. – Ecography 27: 165–172.

Thuiller, W. et al. 2006a. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. – Global Change Biol. 12: 424–440.

Thuiller, W. et al. 2006b. Endemic species and ecosystem vulnerability to climate change in Namibia. – Global Change Biol. 12: 759–776.

Titeux, N. et al. 2007. Fitness-related parameters improve presence-only distribution modelling for conservation practice: the case of the red-backed shrike. – Biol. Conserv. 138: 207–223.

Tsoar, A. et al. 2007. A comparative evaluation of presenceonly methods for modelling species distribution. – Divers. Distrib. 13: 397–405.

Vanreusel, W. et al. 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. – Conserv. Biol. 1: 201–212.

Vayssières, M. P. et al. 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. – J. Veg. Sci. 11: 679–694.

Wintle, B. A. et al. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. – J. Wildl. Manage. 69: 905–917.

Wintle, B. A. et al. 2004. Precision and bias of methods for estimating point survey detection probabilities. – Ecol. Appl. 14: 703–712.