CHAPTER 8

Habitat suitability modelling

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8.1 Context

Projecting the likely effect of environmental change on bird species' distributions is one of the approaches developed to better understand and counteract negative impacts of climate change. Generally, modelling projections of future distributions can build on two different types of models: either on dynamic simulation models that explicitly describe demographic processes (e.g. population viability analysis, PVA) or on statistical models that, by definition, describe correlative—but not necessarily causal—relationships. Although PVAs have been proven powerful in modelling spatio-temporal population responses to environmental change, they require extensive knowledge on demography and population processes. This knowledge is unavailable for the great majority of bird species and especially difficult to gain when studying multi-species' bird communities. Alternatives are less complex and less 'information hungry' statistical models called habitat suitability models (HSMs). These models aim at identifying both the most influential variables explaining presences, presence/absences, abundances, or even breeding success of birds and the optimal relationships between bird species' distributions and these explanatory variables. In HSMs, future projections of bird species' distributions do not depend on profound prior knowledge of population processes but on environmental and species' distribution data. Ultimately, the interpretation of the parameterized HSM can help to better understand the processes underlying the found correlative relationships.

In this chapter, we first describe the conceptual idea of HSMs (section 8.2) and give a rough overview of commonly used methods (section 8.3). Based on this introduction, we discuss problems and limits of HSMs and suggest possible validation tests (section 8.4). Finally, we outline the latest developments and future directions that we find especially promising (section 8.5).

8.2 Theory and concept

HSMs aim at defining, for any chosen species, the 'envelope' that best describes its spatial range limits by identifying those environmental variables that limit its distribution (Figure 8.1; Guisan and Thuiller, 2005; Soberon and Peterson, 2005). They are built by relating current species' distributions to current environments. Future species' biogeographical ranges are modelled by projecting these relationships to selected environmental change scenarios (Peterson, 2003b; Thuiller *et al.*, 2005).

Note that these environmental variables can be anything important for the species of interest. For bird species, commonly used variables are measures of climate (e.g. temperature), landscape structure (e.g. connectivity indices), landscape heterogeneity (e.g. ecotone cover), resources (e.g. insect availability), and biotic information (e.g. co-occurring competitors). Environmental variables can exert direct or indirect effects on species and are optimally chosen to reflect the three main types of influences on the species: (1) limiting factors, defined as factors controlling species' eco-physiology (e.g. minimum winter temperature) or appearance (e.g. competition

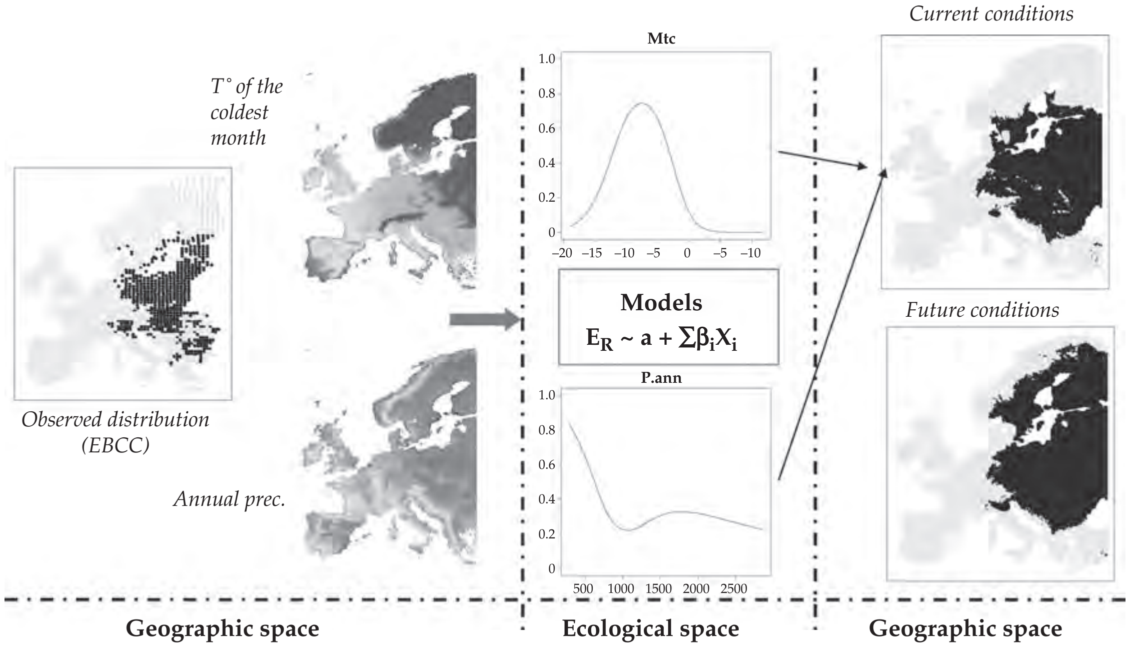

Figure 8.1 Diagram representing the concept of habitat suitability modelling. The observed distribution of a given species (e.g. from the European Bird Census Council atlas of European breeding birds, their distribution, and abundance) is related to relevant environmental data (e.g. climatic such as temperature (T°) of the coldest month and annual precipitation) using a statistical model (e.g. generalized additive model). Then, the niche of the species is projected back onto the geographic space to depict the potential current distribution (i.e. under current conditions) and the future potential suitable habitat (i.e. under future conditions). See Plate 7.

and facilitation), (2) disturbances, defined as all types of perturbations affecting environmental systems (e.g. fire frequency), and (3) resources, defined as all materials that can be assimilated by organisms (e.g. availability of seeds or insects). The environmental data related to these three main types of influence depict the environmental niche of the species (Hutchinson, 1957). In the majority of cases, the environmental niche is multi-dimensional and different dimensions may be important at different spatial scales. These scale-dependent relationships between niche characteristics and bird species' distributions often result in hierarchical structures in the patterns of habitat use (Thompson and McGarigal, 2002; Graf *et al.*, 2005). In extreme cases, the niche characteristics that relate positively to species' performance at local scales can even have negative effects at larger scales. For instance, Mueller *et al.* (2009) showed that common ravens *Corvus corax* in the primeval forest of Białowieża locally select coniferous dominated nesting habitats but at increasingly larger scales prefer deciduous dominated foraging habitats.

8.3 Different modelling approaches and algorithms to deal with imperfect data

For many years, researchers have compared different HSMs such as generalized linear models (GLMs), classification tree analysis, neural networks, genetic algorithms, and maximum entropy (MAXENT) without reaching a consensus on which of these models perform best under which conditions (e.g. Elith *et al.*, 2006; cf. Table 8.1).

From our point of view, the main problem of most of these comparative studies is that they validate model performance (measured as the fit between predicted and observed species' distributions) only against data sampled under current conditions, and that most of the models are more or less reliable in

Table 8.1 Published predictive habitat suitability modelling packages, reference paper, related modelling methods, and www link.

Tool	Reference	Methods implemented	URL
BIOCLIM	Busby (1991)	CE	www.arcscripts.esri.com
ANUCLIM	See BIOCLIM	CE	www.cres.anu.edu.au/outputs/anuclim.php
BIOMAPPER	Hirzel *et al.* (2002)	ENFA	www.unil.ch/biomapper
BIOMOD	Thuiller (2003); Thuiller *et al.* (2009)	ANN, BRT, CE, CTA, GAM, GLM, MARS, MDA, and RandomForest	www.r-forge.r-project.org/projects/biomod/
DIVA	Hijmans *et al.* (2001)	CE	www.diva-gis.org
DOMAIN	Carpenter *et al.* (1993)	CE	www.cifor.cgiar.org/docs/_ref/research_tools/domain/index.htm
GARP	Stockwell and Peters (1999)	GA	www.lifemapper.org/desktopgarp
GDM	Ferrier *et al.* (2007)	GDM	www.biomaps.net.au/gdm/
GRASP	Lehmann *et al.* (2003)	GAM	www.cran.r-project.org/web/packages/grasp/index.html
MAXENT	Phillips *et al.* (2006)	ME	www.cs.princeton.edu/~schapire/maxent/
OPEN MODELLER	Sutton *et al.* (2007)	ANN, GARP, SVM, and CE	www.openmodeller.sourceforge.net/
SPECIES	Pearson *et al.* (2002)	ANN	To the discretion of the author
WHY WHERE	David and Stockwell (2006)		www.landshape.org/enm/whywhere-20-server-2/

ANN, artificial neural networks; BA, Bayesian approach; BRT, boosted regression trees, CE, climatic envelop; CART, classification and regression trees; ENFA, ecological niche factor analysis; GA, genetic algorithm; GAM, generalized additive models; GDM, generalized dissimilarity modelling; GLM, generalized linear models; MARS, multivariate adaptive regression splines; MDA, mixture discriminant analysis, ME, maximum entropy; SVM, support vector machine.

Statistical software such as R, Splus, or SAS provides most of these techniques.

projecting distributions under current environmental conditions. However, seemingly small differences in predictions of current distributions may be caused by very different model structures that result in disturbingly dissimilar projections for new situations, e.g. for future climate change scenarios (e.g. Thuiller, 2004; Araújo *et al.*, 2005b; Pearson *et al.*, 2006; Figure 8.2). This well-known but not always thoroughly considered shortcoming of HSMs is discussed in more detail in the following section.

The different approaches to model habitat suitability differ in their underlying hypotheses and how they build the multi-dimensional environmental niche of the species. Some models assume linear relationships and/or parametric stochastic distributions of the errors they make (e.g. GLM) while others can fit more complex and non-parametric relationships (e.g. general additive models (GAM), MAXENT, boosted regression trees (BRT)). Most of the existing tools have different optimization procedures, which are used to firstly select the best set of environmental variables and secondly to estimate their influence such that overall model performance is maximized (e.g. 'step-wise selection' in GAM or GLM, 'out-of-bag' selection in random forest, and 'cross-validation' in neural networks). The underlying idea is to find a representation that fits the data well but avoids over fitting (a model is over fitted when it shows a very good fit with the training data that were used to parameterize the model but a bad fit with new independent test data). All models are susceptible to multi-collinearity, i.e. will most probably not find a meaningful subset of variables if the initial set of variables is highly inter-correlated. This is because it is impossible to decide which variables exert a direct causal effect and which variables show high correlation just because they are correlated to the true causal variable as well. In general, there is no universal best model and most of the models have advantages and disadvantages.

In comparative studies more flexible models like GAMs and BRTs frequently outperform other HSMs. If one prefers a single-model approach, these models may provide a good basis. However, if possible, we suggest applying more advanced multi-model approaches (cf. section 8.5).

Besides the choice of the right modelling approach, biases in data sets are common and well-acknowledged challenges of species distribution modelling. If the data are biased, the HSM and

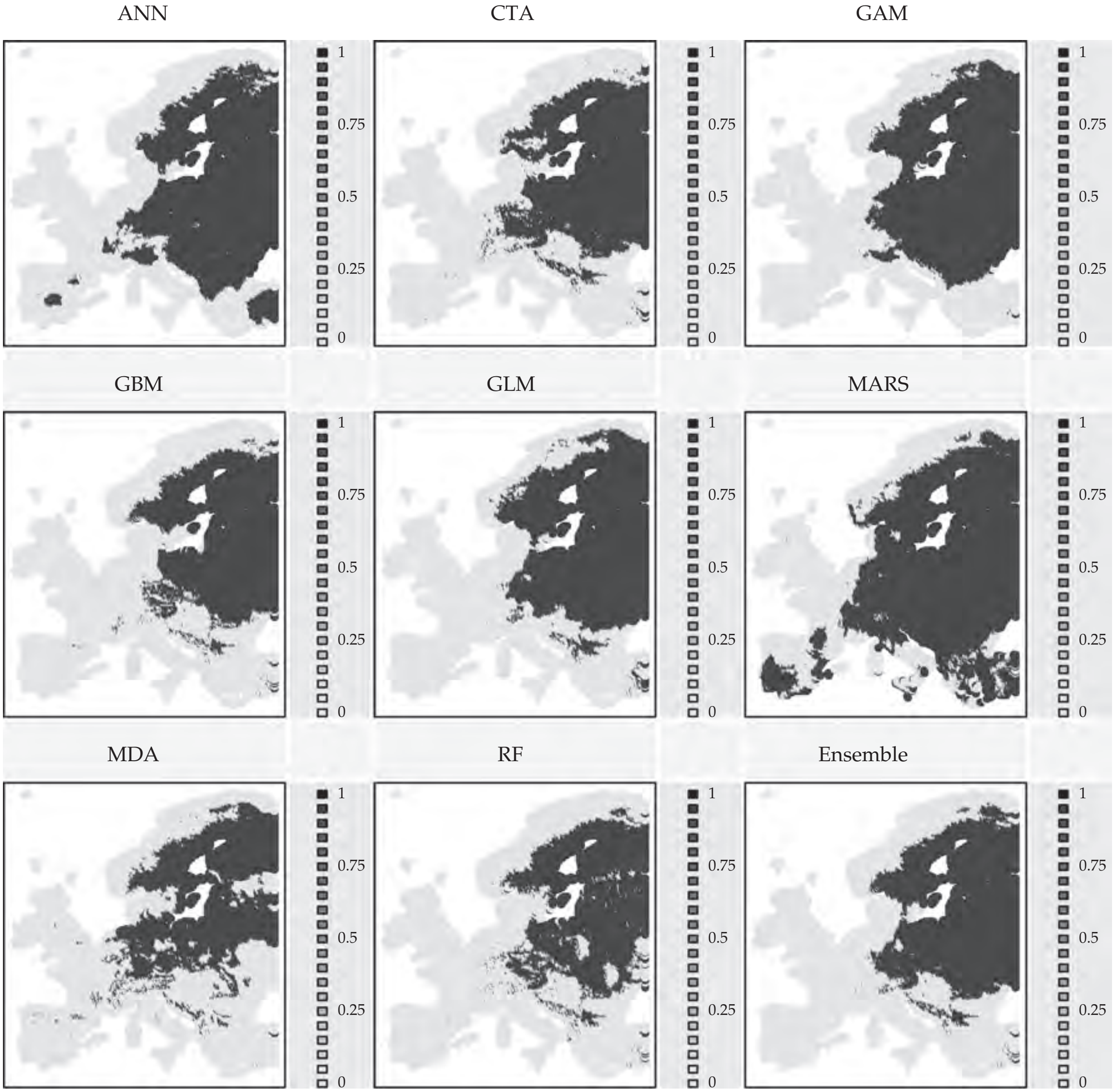

Figure 8.2 Future potential suitable habitat of *Sylvia nisoria* using a scale from least (0) to most suitable (1) under the scenario A1FI (climatic model HadCM3) by 2080 (2070–2099) and according to different statistical models (see Table 8.1 for abbreviations) implemented into the BIOMOD framework (Thuiller *et al*., 2009) using four explanatory variables (growing degree days, annual precipitation, minimum temperature of the coldest month and moisture index). This set of figures highlights the potential discrepancies between different models once they are applied under future conditions. The 'ensemble' projections correspond to the weighted average of the eight other techniques.

its outcome will be biased. There are plenty of reasons why data might be biased, and a comprehensive review goes beyond the scope of this chapter. One particular problem with the data used to calibrate HSMs for very mobile organisms like birds is in non-detectability. Whereas we can be rather confident about a recorded presence of a bird, its absence could stem from three different reasons: (1) the habitat is unsuitable, (2) the habitat is suitable but the species has not colonized it yet (limited dispersal), and (3) the species is present but is not detected. The last two cases are often named ‘false absences’ or ‘false negatives’. Models using presence data only, e.g. ENFA (Hirzel *et al.*, 2002), should not be very sensitive as soon as recorded presences are meaningful and span most of the niche of the species. HSMs using presence–absence data are more seriously influenced by false negatives. Makenzie and other proposed methods to deal with false negatives in the case of co-occurrence data, counts of individuals, or abundance data (Mackenzie *et al.*, 2004; Mackenzie, 2006; Royle *et al.*, 2005; Royle and Link, 2006). However, when dealing with atlas or museum data, sampling efforts, abundance, or individual counts are simply not available, and one needs to make inference on recorded presences and absences at a given spatial and temporal resolution. In cases where absence data are not trustable, different methods have been suggested. Among them are algorithms to correct for false negatives based on sampling efforts or counts of individuals (e.g. a weighting factor into the model to down-weight sites with low sampling efforts; Vallecillo *et al.*, 2009), multi-step selection procedures of absence data using a combination of expert knowledge and existing data (Le Maitre *et al.*, 2008) and use of background data that allow to account for sampling bias (Phillips *et al.*, 2009).

8.4 Robustness and validation

It is important to note that species’ distribution models are not made to predict the future distribution of a target species but to project spatially the geographic area that might be suitable to the species. The distinction between projections in time vs. space is subtle but becomes important once these models are used to infer conservation or management guidelines. HSMs are only correlative and based on current observations.

In most cases, HSMs do not explicitly account for biotic interactions but assume that their influence on realized species’ distributions is implicitly covered by the used predictor variables (cf. Mueller *et al.* (2009) for an exception where they used success of breeding neighbours as an explanatory variable for breeding success of common ravens). They often ignore dispersal abilities of species. If the suitable climatic conditions of a given bird are projected to shift for about 100 km, the species will first have to disperse into the shifted suitable habitat (100 km can be relatively far for some bird species) and then establish, given the existing (and newly forming) communities (e.g. potential competitors and different food resources) and the local availability of habitat. An additional difficulty is that identified influential climatic variables often relate only indirectly to species’ performance as they influence additional and directly important variables such as vegetation structure and food availability (Beale *et al.*, 2008; but see Araújo *et al.*, 2009). Using these indirect variables as predictors assumes constant relationships with directly influential variables over time. If these relationships change, models are prone to produce erroneous predictions. This may happen when utilizing models for spatial extrapolation but is especially dangerous when extrapolating in time. If available, the inclusion of the directly influential variables would most likely improve the robustness of models (e.g. Hughes *et al.*, 2008; Anderson *et al.*, 2009). However, if the directly influential variables are unknown or unavailable, it is good scientific practice to test the predictive power of the fitted model across space (cf. Beerling *et al.*, 1995; Peterson, 2003a; Randin *et al.*, 2006 for examples) and/or time (e.g. by extrapolating from a known distribution to another one at a different point in time (Pearman *et al.*, 2008) or by comparing predictions with observed population trends (Green *et al.*, 2008; Gregory *et al.*, 2009)).

For bird species, the utilization of retrospective data to calibrate models with data from the past and project them to current conditions has brought up interesting results. In a climate change context, Araújo *et al.* (2005a) published one of the first direct validation test for HSMs applying them at two different time slices. Using observed distribution shifts of 116 British breeding bird species over the past 20 years, they provided an independent validation of four HSMs under climate change. Results showed good-to-fair predictive performance on independent validation, although rules used to assess model performance were difficult to interpret in a decision-planning context. Artificial neural networks and generalized additive models provided generally more accurate predictions of species' range shifts than GLMs or classification tree analysis. In a land use change context, a complementary paper tested the ability of HSMs to predict the effects of land-cover changes on species' distribution shifts at large spatial and temporal scales. The study was performed for open-habitat birds in Mediterranean landscapes and early successional stages (Vallecillo *et al.*, 2009). Based on current presence–absence data, Vallecillo *et al.* (2009) applied six different HSMs for 10 bird species, using climate, topographic, and land-cover predictors, and back-projected them on land-cover conditions from 1980 (First Catalan Breeding Bird Atlas 1975–1983). Finally, in addition to changes in habitat suitability resulting from land-cover shifts, they analysed whether fire frequency and intensity contributed to explain species' demography (colonization and local extinction). The tested models were able to predict current and past patterns of species' distribution, but their ability to predict species' demography was rather low. Colonization dynamics were generally more strongly related to fire occurrences than to changes in overall habitat suitability derived from land-cover changes. This study demonstrated that processes behind species' demography (e.g. fire) should be explicitly included when they are known, as they may help to explain better species' dynamics (Vallecillo *et al.*, 2009). However, other studies show that simple HSMs are able to capture broad demographic dynamics quite well. Using data on long-term population trends of European birds, Gregory *et al.* (2009) found a significant relationship between inter-specific variation in population trend and the change in potential range extent between the late 20th and late 21st centuries, forecasted by HSMs.

In many case studies, the unavailability of independent test data hampers evaluating the predictive power of statistical models, especially when they are used for projections to the future. One possible route to overcome this limitation is to use virtual data generated by mechanistic models to investigate explicitly the effects of transient dynamics and ecological properties and processes on the prediction accuracy of HSMs (Hijmans and Graham, 2006; Zurell *et al.*, 2009). Direct evaluation of predictive accuracy is possible as the predictions of the HSMs can be compared with the 'virtual reality' of the mechanistic model.

8.5 Latest developments and perspectives in a global change context

A possible solution to make use of the advantages of the different modelling approaches for HSMs is to fit ensembles of different models. This approach includes simulating across more than one set of initial conditions, model classes, and model parameters (Araújo and New, 2007). Fitting ensembles of models allows the analysis of the resulting range of uncertainties with bounding box, consensus, and probabilistic methodologies (Coetzee *et al.*, 2009) and/or the use of model averaging to project species' distributions. The former depicts areas of high certainties (and uncertainties) and partition the uncertainty to reveal the most sensitive factors (Buisson *et al.*, 2010). The latter balances extreme predictions of some modelling approaches. Naturally, this approach can only identify uncertainties resulting from modelling choices that are varied across models. If, for example, uncertain predictions result from the use of presence-only data and these data are the input of different models, then uncertainty due to the use of presence-only data cannot be assessed.

However, there exist some principal limits for HSMs that are due to their concept. Compared to process-based simulation models HSMs are quite intuitive but also simplistic. They offer a very good approximation of what could happen to biodiversity in the short to medium term. However, to be useful for long-term conservation planning, re-introduction and biodiversity management these models need to be further improved. A strong limitation so far is that they do not incorporate population dynamics determining species' distribution, abundance, population structure, and local extinction risk that might lead to misleading extinction rates (Thuiller *et al.*, 2008). The recent years have seen a surge in several hybrid frameworks combining, for instance, HSMs with meta-population models (e.g. Anderson *et al.*, 2009), meta-population models with landscape models (e.g. Wintle *et al.*, 2005), or HSMs with individual-based movement models (Graf *et al.*, 2007). Anderson *et al.* (2009) modelled the dynamics of range margins of two lagomorphs of conservation interest under climate change scenarios. They first built an environmental suitability map based on habitat and climatic variables using HSMs from the years 2000 to 2100 (e.g. Figure 8.1). Then, they used this suitability map as an input for suitable patches for a spatially explicit pre-breeding stage-based matrix model that described population structure and dynamics over time. The model was female based and incorporated demographic and environmental stochasticity, dispersal, and density dependence. This hybrid of different model types improved the simple HSMs by regarding limits of the actual area that could be occupied by the metapopulation, caused by population dynamics and dispersal. There is a potential drawback of this 'simple' stage-wise approach to combining HSMs with dynamic models. If dynamic processes affect the distributional pattern of organisms, then an HSM that does not incorporate these processes will be biased. This bias is then carried over to a dynamic model that is built on top of the HSM. Instead of simple one-way interaction between models, a truly integrated approach is called for (Thuiller *et al.*, 2008). One possible approach would be to fit the parameters of all sub-models of the hybrid model at the same time to find the parameter values that are best, given the parameterized further sub-models. This could, for example, be based on a Bayesian hierarchical framework of parameter estimation.

It is a general rule that the choice of the modelling tool should be directed by the research question and a well-known limit that data availability is restricted. In this chapter, we have focused on HSMs as modelling approaches typically applied to presence/ absence data or abundances for predicting species' distributions in time and space. Most HSMs have proved to predict powerfully under constant environmental conditions. In changing environments, studies found that some modelling tools outperform others but that in general single-model approaches are prone to producing erroneous predictions. As a first relatively simple measure we suggest using ensembles of models to at least estimate the uncertainty of predictions. If possible, building hybrid models would be preferable. We believe that hybridization of models is a powerful and promising avenue towards further improvements in predicting species' range shifts and resulting biodiversity scenarios under environmental change. Use and utilization of hybrid models could be enhanced by conceptual guidelines that outline the possibilities and give rules of thumb to decide on the important processes and usable model types. Demographic studies are the basis for implementing the rule-based sub-models. Furthermore, to enhance the parameterization of efficient and reliable hybrid dynamic models we need to further develop and integrate trait, distribution, and GIS databases.

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