

REVIEWS AND
SYNTHESESPredicting species distribution: offering more than
simple habitat models

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Abstract

In the last two decades, interest in species distribution models (SDMs) of plants and animals has grown dramatically. Recent advances in SDMs allow us to potentially forecast anthropogenic effects on patterns of biodiversity at different spatial scales. However, some limitations still preclude the use of SDMs in many theoretical and practical applications. Here, we provide an overview of recent advances in this field, discuss the ecological principles and assumptions underpinning SDMs, and highlight critical limitations and decisions inherent in the construction and evaluation of SDMs. Particular emphasis is given to the use of SDMs for the assessment of climate change impacts and conservation management issues. We suggest new avenues for incorporating species migration, population dynamics, biotic interactions and community ecology into SDMs at multiple spatial scales. Addressing all these issues requires a better integration of SDMs with ecological theory.

Keywords

Dispersal, ecological niche theory, future projections, habitat suitability maps, population dynamics, prediction errors, predictive biogeography, spatial scales, species distribution models.

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INTRODUCTION

The fascinating question of how plants and animals are distributed on Earth in space and time has a long history which has inspired many biogeographers and ecologists to seek explanations. Most modelling approaches developed for predicting plant or animal species distributions have their roots in quantifying species–environment relationships. Three phases seem to have marked the history of species distribution models (SDMs) (S. Ferrier, personal communication): (i) non-spatial statistical quantification of species–environment relationship based on empirical data, (ii) expert-based (non-statistical, non-empirical) spatial modelling of species distribution, and (iii) spatially explicit statistical and empirical modelling of species distribution.

Earliest found examples of modelling strategies using correlations between distributions of species and climate seems to be those of Johnston (1924), predicting the

invasive spread of a cactus species in Australia, and Hittinka (1963) assessing the climatic determinants of the distribution of several European species (quoted in Pearson & Dawson 2003). Earliest developments in computer-based predictive modelling of species distribution seem to originate in the mid-1970s, stimulated by the numerous quantification of species–environment available at that time (Austin 1971). The earliest species distribution modelling attempt found so far in the literature seems to be the niche-based spatial predictions of crop species by Henry Nix and collaborators in Australia (Nix *et al.* 1977).

These were succeeded, in the early 1980s, by the pioneering simulations of species distribution by Ferrier (1984). At about the same time, the publication of two seminal books (Verner *et al.* 1986; Margules & Austin 1991, resulting from a workshop in 1988) also contributed largely to promote this new approach, resulting in a growing number of species distributions models proposed in the literature. These advances were largely supported by the

Table 1 Some possible uses of SDMs in ecology and conservation biology

Type of use	References
Quantifying the environmental niche of species	Austin <i>et al.</i> (1990), Vetaas (2002)
Testing biogeographical, ecological and evolutionary hypotheses	Leathwick (1998), Anderson <i>et al.</i> (2002), Graham <i>et al.</i> (2004b)
Assessing species invasion and proliferation	Beerling <i>et al.</i> (1995), Peterson (2003)
Assessing the impact of climate, land use and other environmental changes on species distributions	Thomas <i>et al.</i> (2004), Thuiller (2004)
Suggesting unsurveyed sites of high potential of occurrence for rare species	Elith & Burgman (2002), Raxworthy <i>et al.</i> (2003), Engler <i>et al.</i> (2004)
Supporting appropriate management plans for species recovery and mapping suitable sites for species reintroduction	Pearce & Lindenmayer (1998)
Supporting conservation planning and reserve selection	Ferrier (2002), Araújo <i>et al.</i> (2004)
Modelling species assemblages (biodiversity, composition) from individual species predictions	Leathwick <i>et al.</i> (1996), Guisan & Theurillat (2000), Ferrier <i>et al.</i> (2002)
Building bio- or ecogeographic regions	No published example found
Improving the calculation of ecological distance between patches in landscape meta-population dynamic and gene flow models	No published example found

parallel developments in computer and statistical sciences, and by strong theoretical support to predictive ecology as 'more rigorously scientific, more informative and more useful ecology' (Peters 1991).

As a result, the number of related publications increased very significantly since the early 1990s, and the first partial reviews, such as those published by Franklin (1995) and Austin (1998), appeared shortly before the turn of the century. A large symposium on modelling species occurrence, organized in Snowbird, Utah, in September 1999, additionally provided a large review of the twentieth century state-of-the-art in this field (Scott *et al.* 2002). A synthesis review of this pre-2000 period can be found in Guisan & Zimmermann (2000).

In recent years, predictive modelling of species distribution has become an increasingly important tool to address various issues in ecology, biogeography, evolution and, more recently, in conservation biology and climate change research (see Table 1).

In this paper, we review the recent achievements in developing species distribution models (SDMs) and address some of their limitations. We devote particular attention to the challenge of projecting the impacts of climate change on the distribution of biodiversity, which currently yields some of the most spectacular progress in SDM research. To set the scene, we first define SDMs and provide an overview of basic ecological theory and working assumptions underpinning them. We then discuss some methodological issues, decisions to be made during the process of model building and evaluation, and the implications for conservation and management. We then summarize important challenges that must be addressed to overcome the limitations of SDMs.

WHAT ARE SDMS AND HOW DO THEY WORK?

Species distribution models are empirical models relating field observations to environmental predictor variables, based on statistically or theoretically derived response surfaces (Guisan & Zimmermann 2000). Species data can be simple presence, presence-absence or abundance observations based on random or stratified field sampling, or observations obtained opportunistically, such as those in natural history collections (Graham *et al.* 2004a). Environmental predictors can exert direct or indirect effects on species, arranged along a gradient from proximal to distal predictors (Austin 2002), and are optimally chosen to reflect the three main types of influences on the species (modified from Guisan & Zimmermann 2000; Huston 2002; Fig. 1): (i) *limiting factors* (or *regulators*), defined as factors controlling species eco-physiology (e.g. temperature, water, soil composition); (ii) *disturbances*, defined as all types of perturbations affecting environmental systems (natural or human-induced) and (iii) *resources*, defined as all compounds that can be assimilated by organisms (e.g. energy and water). These relationships between species and their overall environment can cause different spatial patterns to be observed at different scales (Fig. 1), often in a hierarchical manner (Pearson *et al.* 2004). For instance, a gradual distribution observed over a large extent and at coarse resolution is likely to be controlled by climatic regulators, whereas patchy distribution observed over a smaller area and at fine resolution is more likely to result from a patchy distribution of resources, driven by micro-topographic variation or habitat fragmentation (Fig. 1; see examples in Scott *et al.* 2002). The environmental data related to these three main

Table 2 Important features to consider when building a SDM, criteria for detecting potential problems, and some proposed solutions

Feature to consider	Possible problem	Detection criterion	Examples of proposed solution
<i>Conceptualization</i>			
Type of organism	Mobile species in unsuitable habitats Sessile species (e.g. plants) in unsuitable habitats Species not observed in suitable habitats Low detectability species Sibling species or ecotypes of a same species Invasive species Direct or indirect predictors? Selecting sampling strategy	Radio-tracking continuous time field observations Lack of fitness (e.g. no sexual reproduction) Knowledge of species life strategy (e.g. dispersal) Field knowledge, literature Genetic analyses Mostly commission errors Ecophysiological knowledge Simulation tests with virtual species in a real landscape Partial plots, smoothing curves	Neighbourhood focal functions; choice of grain size Use fitness criteria to select species observations to be used in model fitting Interpret the various types of errors Correct test for detectability Test niche-differentiation along environmental gradients Fit models in the area of origin Avoid indirect predictors Random-stratified sampling
Incorporating ecological theory	Linear or unimodal response of species to the predictors? Skew unimodal response curves Bimodal response curves	Partial plots, smoothing curves Skewness test Smoothing curves, partial plots	GAM or quadratic terms in GLM HOF, beta functions in GLM, GAM, fuzzy envelope models GAMs, \geq third order polynomials or beta-functions in GLMs
<i>Data preparation (data model)</i>			
Species data	Bias in natural history collections (NHC) Heterogeneous location accuracy in NHC	Cartographic and statistical exploration Only detectable if recorded in the database	Various ways of controlling bias Selecting only observations of known accuracy below threshold Generating pseudo-absences Aggregating all GIS layers at the limiting grain Enlarging the extent of study area to cover full gradients
Scale (grain/extent)	No absences Different grain sizes for the various predictors Truncated gradients within the considered extent	Type of data base and source (metadata) GIS exploration Preliminary exploration of species response curves	
<i>Model fitting</i>			
Type of data Multicollinearity	No absence Correlations between the predictor variables	Type of data base and source (metadata) Variance Inflation Factor (VIF)	Using profile methods Removing correlated predictors; orthogonalization
Spatial auto-correlation (SAC)	Non-independence of the observations	SAC indices	Sampling strategies to avoid SAC; correcting inference tests and possibly incorporating SAC in models
Type of statistical model	Overdispersion	Residual degrees of freedom > residual deviance	Quasi-distribution in GLMs and GAMs; scaled deviance
Model selection	Which approaches and criteria?	–	AIC-based model averaging; cross-validation; shrinkage

<i>Model evaluation</i>				
Type of data	No absence; usual measures not applicable	Type of database and source (metadata)	New method appearing for evaluating predictions of presence-only models (MPA, area-adjusted frequency index)	
Evaluation framework	No independent set of observations	-	Resampling procedures	
Association metrics	Choice of a threshold for binary data	-	Threshold independent measures (AUC)	
	Errors costs	-	Error weighting (e.g. weighted-Kappa)	
Model uncertainty	Lack of confidence	Uncertainty map, residual map	Bayesian framework; spatial weighting	
Model selection uncertainty	Lack of confidence	Comparing selection algorithms and competing models	Model averaging	
<i>Spatial predictions</i>				
Projection into the future and in new areas	Range of new predictors falls outside the calibration domain	Statistical summaries	Restrict area of projection; Control shape of response curves	
<i>Model applicability</i>				
Scope and applicability	Model not applicable to a distinct area	Unrealistic response curves	Avoid overfitting	
Problem of future projections	SDMs not transposable to distinct environments	Strongly dependent of the considered scale	Spatially explicit models incorporating population dynamics, dispersal and habitat	
Use in management	Difficult to implement in a management context	Software not available to practitioners	Free software	
	Not interpretable	Black box algorithms?	Choice of easy-to-read and easy-to-interpret methods (GLMs, GAM, CART)	

theoretical limitations often remain. These limitations come about when ecological theory is not fully integrated into the modelling process (Austin 2002; Huston 2002; Wiens 2002).

While SDMs are useful tools for resolving practical questions in applied ecology and conservation biology, they are also extremely relevant to fundamental sciences (e.g. biogeography and phylogeography), because of the ecological and evolutionary theories and assumptions underpinning them. Surprisingly, the ecological theory related to SDM has been sorely neglected in the literature, resulting in a weakening of the overall approach. Insights from ecological theory should be used more systematically to underpin decisions made at all stages of the model building process (Austin 2002), for instance: for selecting the most causal environmental predictors (Pearson *et al.* 2004; Thuiller *et al.* 2004a); for choosing ecologically realistic response curves for each predictor (e.g. Austin & Gaywood 1994); for determining a restricted set of competing models in multi-model inference (e.g. Rushton *et al.* 2004); for discussing the likely causes and cost of prediction errors (see Fitting and evaluating SDMs); or for assessing the validity of the underlying model assumptions when projections on future climate are to be made (Araújo *et al.* 2005a).

ASSUMPTIONS BEHIND MODELS AND THE NICHE CONCEPT

Equilibrium postulate

As both species and environmental data are usually sampled during a limited period of time or/and space, models fitted using these can only reflect a snapshot view of the expected relationship. A convenient working postulate is to assume that the modelled species is in pseudo-equilibrium with its environment (Guisan & Theurillat 2000). Although this is a required assumption for projecting the model in space or time, surprisingly few critical considerations have been raised in the recent literature on how close a given modelled system really is to an equilibrium (but see Araújo & Pearson 2005), and how long it would take to reach a new equilibrium, e.g. after an environmental change (but see Davis *et al.* 1998). For instance, Svenning & Skov (2004) measured low range filling (RF) – calculated as the realized/potential range size ratio – for many European tree species (RF < 50% for 36/55 species), suggesting that many of these species still appear strongly controlled by dispersal constraints on post-glacial expansion, and thus might not be in equilibrium with their environment throughout their whole range. Hence, using models that fit the observed distribution too closely might lead to underestimating the true potential range of the species. However, as Svenning & Skov (2004) only used very

simple bioclimatic models based on only three climatic variables (degree-days, minimum temperature and water balance), and ignored competition and dispersal, further testing of their hypotheses is still formally required. The same non-equilibrium consideration also applies to the issue of modelling the spread of invasive species. Many invasive species are not in equilibrium with environment in the invaded range, and thus should preferably be modelled using their distribution in the native range (Peterson 2003; but see Robertson *et al.* 2004).

Niche concept

A striking characteristic of SDMs is their reliance on the niche concept (Guisan & Zimmermann 2000). Leibold (1995) opposes two concepts of the niche as either driven (i) by the environmental *requirements* of species as defined by Grinnell or Hutchinson, or (ii) by the *impact* that the species can have on its environment as defined by Elton, MacArthur or Levins. Hence, the former is more embedded within an autecological and physiological approach to the niche (*environmental niche*, see e.g. Austin 1992), whereas the latter is related more to trophic levels and food web theory (*trophic niche* as termed by Elton; see Austin *et al.* 1990; Silvertown 2004). As they seem to apply to different spatial scales – respectively from global to local (see Fig. 1) – only the requirement concept and environmental niche are usually considered in SDMs. Within these, Pulliam (2000) further distinguishes between Grinnell's view of species occupying all of their suitable habitats – the *fundamental niche* – and Hutchinson's view of species being excluded from a part of their fundamental niche by biotic interactions, resulting in the *realized niche* that is actually observed in nature (Silvertown 2004).

The most frequent simplification found in the SDM literature is to state that, because of the observed distributions being already constrained by biotic interactions and limiting resources, SDMs are *de facto* quantifying Hutchinson's realized niche of species. It is also said that only mechanistic models, based on measured physiological or behavioural parameters (e.g. Kearney & Porter 2004), or SDMs based on *ex situ* data (e.g. a plant grown in botanical gardens outside its natural range; Vetaas 2002), can approach the fundamental niche. However, the realized niche in SDMs is usually assumed without having sound ecological evidence that this is truly the case for the modelled species.

Another simplification is to substitute one of the classical concepts of the niche by an additional one, the *potential niche*. The potential niche was originally defined as that part of the fundamental niche available to species, as constrained by the *realized environment* (Ackerly 2003). It considers that not all possible combinations of some given environmental variables exist in the study area, or possibly even on Earth (e.g.

Austin *et al.* 1990), and thus differ from Hutchinson's realized niche.

A useful framework for clarification was recently proposed by Pulliam (2000), who proposed four theoretical views of the relationship between niche and distribution: (a) the *Grinnellian niche*, where a species occurs wherever the environmental conditions are suitable (i.e. fundamental niche, with a population growth rate ≥ 1); (b) the *realized niche* of Hutchinson, where a species is excluded from part of its fundamental niche by a competitor or a predator, (c) the *source-sink dynamics*, where a species commonly occurs in a sink habitat where its population growth rate is < 1 , and thus where it would disappear without constant immigration from source habitats, and (d) the *dispersal limitation situation*, where a species is frequently absent from suitable habitats because of recurring extinction events and limited dispersal ability preventing full recolonization (e.g. Svenning & Skov 2004). Traditionally, plant ecologists have relied on niche concepts (a) and (b), whereas zoologists have been keener to additionally consider scenarios (c) and (d).

Any theoretical situation should be considered *a priori* for each species, unless experimental/field evidence clearly supports one over the other. Furthermore, each of these can only be considered within the realized environment, and thus it must be accepted that, for some species, their entire fundamental niche might never be captured from empirical data.

It is important to recall here that the niche should be defined from empirical observations of individuals that reproduce successfully, and thus support a positive growth rate for the entire population. In the case of SDMs, most are based on simple presence-absence observations, or sometimes on abundance values. We are well aware from early biogeographical studies on plants that, beyond certain species-specific climatic thresholds, most observed individuals no longer exhibit sexual reproduction. It is therefore preferable that observations of these individuals should not be used to fit SDMs, but in practice it can be difficult to measure sexual reproduction parameters from a single field visit.

These recent reconsiderations of the niche concept in relation to species distribution have inspired contemporary modellers to include other important parameters, such as dispersal (Carey 1996; Iverson *et al.* 1999; Dullinger *et al.* 2004) and population dynamics (Peng 2000), to explain and predict observed biogeographical patterns (Fig. 1). Unless these parameters are taken into account, SDMs are explicitly based either on the assumption of the fundamental Grinnellian niche or of the realized Hutchinsonian niche. As recently suggested by Vetaas (2002), based on data on *Rhododendron* species within their range and in *ex-situ* situations (botanical gardens worldwide), competitively dominant species might be expected to

suffer few biotic constraints – and thus rely more on the Grinnellian niche assumption – whereas subordinate species might be expected to undergo strong competition limitations – and thus rely more on the Hutchinsonian niche assumption.

COMPETITION AND OTHER BIOTIC INTERACTIONS

Competition is an important theoretical mechanism that is absent from most examples of SDM research. One classical theory originally derived from Darwin, and later by MacArthur, predicts that, along a key environmental gradient, species appear to find one direction to be physically stressful and the other to be biologically stressful (Brown *et al.* 1996). The idea of fundamental response curves being constrained by competition is not new (Austin *et al.* 1990), but the unilaterality of biotic vs. abiotic pressures along an environmental gradient remains to be tested, and has been only rarely discussed in the literature (e.g. Guisan *et al.* 1998). This theory has recently been upheld with the comparison of the realized and fundamental niches of four *Rhododendron* species (Vetaas 2002; see previous discussion) and deserves further investigation.

Recent analyses showed that the inclusion of additional predictor variables representing the presence–absence of known competitors can significantly increase the predictive power of models (Leathwick & Austin 2001; Anderson *et al.* 2002). Such findings suggest that even at relatively coarse resolution and regional extent, the presence or absence of a given competitor might influence the distribution of another species, but they do not provide a formal proof that the observed competition effect really occurs in nature. Including other species as predictors might simply provide information about physical conditions that are not accounted for by those environmental descriptors included in the model. Results from competition experiments might help here, but such attempts have only too rarely been performed outside a laboratory (Silvertown 2004). Simulations might provide additional support. Other biotic interactions should also be considered, such as facilitation, pollination, herbivory, predation, parasitism or symbiosis.

WHAT IS THE APPROPRIATE SPATIAL SCALE?

A central and recurrent problem in SDM building is identifying the appropriate scale for modelling (Wiens 2002). Scale is usually best expressed independently as *resolution* (grain size) and *extent* of the study area, because modelling a large area does not necessarily imply considering a coarse resolution. No question in spatial ecology can be answered without referring explicitly to these components at which data are measured or analysed (Wiens 2002).

A first possible mismatch can occur between the ‘resolution’ at which species data were sampled (e.g. plot size in field surveys, grid size in atlas surveys) and the one at which environmental predictors are available. Optimally, both should be the same, but such coherence is not always possible. For instance, the minimum resolution for GIS data might be too large to realistically allow an exhaustive field sampling of biological features to be conducted in the field, and thus smaller sampling units may need to be defined within larger modelling units or at the intersection of grids. Furthermore, many environmental data are indeed provided in a grid lattice format – i.e. regular point data – rather than a true raster format, which complicates the story, somewhat. This is for instance the case of many digital elevation models (DEM) and derived data (e.g. topographic and interpolated climatic maps). Indeed, designing field sampling in order to match raster units will work well in the case of true rasters (e.g. satellite images and derived products, such as CORINE landcover), whereas placing sampling plots at intersections of a grid may prove more appropriate in the case of lattice grids. The problem then is to combine these different types of data in a single model. Aggregating these to a coarser resolution can sometimes provide a simple yet efficient solution, as for instance allowing passing from locally valid point data (e.g. forest/non-forest information at a series of points) to some estimate of frequency in a cell (e.g. quantitative estimate of forest cover within a cell).

Similar problems arise when SDMs are used to make projections of species future distribution. Until recently, General Circulation Models (GCM) were the only source of data to make such projections. However, GCM typically involve much coarser scales (generally several orders of magnitude coarser) than those of the species and environmental data used to calibrate the SDM. Statistically downscaled GCM data can in part address this issue however, these products are still typically too coarse for local assessment or where spatial heterogeneity is high, for example in mountainous areas. The development of Regional Climate Models and fine scale GCM will also help in addressing this issue. These future climate surfaces are also limited by the resolution of the surfaces representing current climate as these current surfaces are perturbed with anomalies calculated from the GCM data (Hewitson 2003). Despite the availability of relatively fine-scaled climate data sets [e.g. worldclim at 0.5 min (see <http://biogeo.berkeley.edu/worldclim/worldclim.htm>)] these products are limited by the frequency of climate station data and the interpolation techniques used to create continuous climate surfaces.

Understanding the theory and processes driving the observed distribution patterns is also essential to avoid a mismatch between the scale used for modelling and the one

at which key processes occur. Patterns observed on one scale may not be apparent on another scale. Van Horn (2002) illustrates how an overly constrained *extent* can lead to an incorrect interpretation if only part of an important environmental gradient is sampled, e.g. when using political instead of natural boundaries (e.g. including a whole species range). For instance, the resulting response curves of a species might appear truncated – possibly expressing a negative (e.g. on the colder part of the temperature gradient), a positive (e.g. on the warmer part of the temperature gradient) or nearly no relationship (e.g. on the intermediate part of the temperature gradient) – when the full response should be unimodal. In such case, the use of different geographical extents might thus provide contradictory answers to the same ecological question (see also Thuiller *et al.* 2003).

A similar reasoning holds for *resolution*. For instance, interspecific competition can only be detected at a resolution where organisms interact and compete for the same resources (Huston 2002; see Fig. 1). The same environmental parameter sampled at different resolutions can thus have very different meanings for a species. This is in part because of the various aggregation properties and the possible problem of ‘released matching’ between various attributes within a cell at coarser resolution, when no more spatial matching is ensured between the predictors and the species occurrence. For some species, like sessile organisms, it will not be sufficient that a combination of suitable conditions occur within the same cell (as e.g. obtained by aggregating data), but these must additionally overlay at least at one specific location within the cell. In turn, for other species, like mobile animals, spatial matching of resources within the cell may not be necessary.

Hence, the selection of resolution and extent is a critical step in SDM building, and an inappropriate selection can yield misleading results. This issue is directly related to the transmutation problem, or ‘how to use ecogeographic predictors measured on one scale on another scale?’ (Wiens 2002). Their integration into a multiscale hierarchical modelling framework (e.g. Pearson *et al.* 2004) may provide the solution required to solve this spatial scaling paradigm (Wiens 2002), for instance, by associating scale domains to those environmental predictors identified as having dominant control over species distributions (Mackey & Lindenmayer 2001; see Fig. 1).

Pearson *et al.* (2002, 2004) developed an interesting approach to evaluate the impact of climate change on plant species in UK. As the modelled species were not endemic to UK, they first developed SDMs over Europe at a rather coarse resolution (50 km grid) to ensure capturing the full climatic range of the selected species. They then projected the species distributions in UK on a 1 km grid using previously fitted models and additionally incorporating land

cover data information. They showed that the incorporation of land cover at the finer resolution improved the predictive accuracy of models, compared with what had been shown at the coarser European resolution (Thuiller *et al.* 2004a). Such hierarchical approach could benefit from a Bayesian implementation, as carried out, for example, by Gelfand *et al.* (2005). Although these latter authors mainly used it for combining SDMs with prior information on sampling intensity, the same approach could be extended to combine environmental information from different spatial scales. The additional advantage here would be the possibility to integrate current modelling approaches (as GLM or GAM) and uncertainty analyses into a more general, hierarchical framework (Gelfand *et al.* 2005).

The choice of scale is also closely related to the type of species considered (e.g. its detectability and prevalence in the landscape). Here, we distinguish two main situations.

Models for highly mobile organisms

Here, various types of habitats might need to be included in each cell, to fulfil the different requirements of the species (e.g. for foraging, reproducing or nesting; Mackey & Lindenmayer 2001). This might either require the use of (i) larger modelling cells accounting for larger portions of the landscape (to ensure that all habitat types can be included; e.g. Jaberg & Guisan 2001); (ii) focal predictors that summarize information on the neighbouring landscape within the focal cell; or (iii) fitting a separate model for each type of habitat use or for various types of individuals (young vs. adult, male vs. female). Due to this neighbourhood influence, release matching is thus not expected to be an important issue here, but valid absences are hard to obtain for these species (Boyce *et al.* 2002). The latter is a serious concern, requiring in most cases specific presence-only models to be fitted, or generating pseudo-absences (see e.g. Brotons *et al.* 2004; Graham *et al.* 2004a).

Models for sessile or very locally mobile organisms

Finer resolution usually provides better predictions for fixed or very locally mobile organisms. Local predictors are thus more meaningful and focal predictors are likely to have lower predictive power unless an ecological rationale can be provided (exceptions are slope, topographical position or flow accumulation for plant that are all derived from focal analyses). Hence, precise spatial matching is important here. Contrary to mobile organisms, valid absences can be more realistically obtained here, at least for non-cryptic species without large interannual fluctuations in their occurrence, thus allowing presence-absence models to be fitted (Brotons *et al.* 2004).

Table 3 Published predictive SDM packages, reference paper, related modelling methods, and www link (when available)

Tool	Reference	Methods implemented	URL
BIOCLIM	Busby (1991)	CE	http://www.arcscrippts.esri.com
ANUCLIM	See BIOCLIM	CE	http://www.cres.anu.edu.au/outputs/anuclim.php
BAYES	Aspinall (1992)	BA	ArcView extension available at the discretion of the author
BIOMAPPER	Hirzel <i>et al.</i> (2002)	ENFA	http://www.unil.ch/biomapper
BIOMOD	Thuiller (2003)	GLM, GAM, CART, ANN	At the discretion of the author
DIVA	Hijmans <i>et al.</i> (2001)	CE	http://www.diva-gis.org
DOMAIN	Carpenter <i>et al.</i> (1993)	CE	http://www.cifor.cgiar.org/docs/_ref/research_tools/domain/index.htm
ECOSPAT	Unpublished data	GLM, GAM	http://www.ecospat.unil.ch ; at the discretion of the author
GARP	Stockwell & Peters (1999)	GA (incl. CE, GLM, ANN)	http://www.lifemapper.org/desktopgarp
GDM	Ferrier <i>et al.</i> (2002)	GDM	At the discretion of the author
GRASP	Lehmann <i>et al.</i> (2002)	GLM, GAM	http://www.cscf.ch/grasp
MAXENT	Phillips <i>et al.</i> (2005)	ME	At the discretion of the author
SPECIES	Pearson <i>et al.</i> (2002)	ANN	At the discretion of the author
Coupled with cellular automata			
Disperse	Carey (1996)	CE	At the discretion of the author
Shift	Iverson <i>et al.</i> (1999)	CART	At the discretion of the author

ANN, artificial neural networks; BA, Bayesian approach; 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; ME, maximum entropy.

FITTING AND EVALUATING SDMS

The last 5 years have seen an explosion of papers on methodological aspects of SDMs, allowing some considerable progress to be made, but also concealing some of their recurrent weaknesses within the mass of new information.

An impressive diversity of modelling tools has become available for modelling species distribution (Table 3), depending on the type of response variables and predictors at hand. The choice of the right statistical method in a specific modelling context is now supported by many published comparisons (e.g. Elith 2000; Moisen & Frescino 2002; Segurado & Araújo 2004). In the following paragraphs, we detail only a few issues that currently seem most important; nevertheless, a careful examination of all aspects is necessary when fitting a new model (Table 2).

Model selection and predictor interactions

Model selection is the process of selecting the most influential predictors in the model (Johnson & Omland 2004). For instance, serious shortcomings have been identified in the popular stepwise selection procedures in regressions (see Guisan *et al.* 2002) and new approaches have recently been proposed, such as multi-model inference, boosting and model averaging (Wintle *et al.* 2003), shrinkage methods (i.e. forcing nonsignificant coefficients to take value close or equal to zero)

or hierarchical partitioning (i.e. averaging the influence of a predictor over the subset of models in which it was selected) coupled with a randomization procedure (Mac Nally 2002). Other modelling approaches such as regression and classification trees (CART), artificial neural networks (ANN), genetic algorithms (GA) or Bayesian analyses (BA) have their own background selection criteria, based on the explained deviance of a multinomial model for CART, or based on multiple simulations to optimize selection for ANN, GA and BA. Harmful multicollinearity can also affect model selection and thus needs careful consideration. It can be fixed by either combining predictors into a few orthogonal axes under debatable linear correlation assumption (Rushton *et al.* 2004) or removing one predictor when two of them are too highly correlated.

In addition, interactions between predictor variables have too often been omitted from SDMs (Austin 2002), although frequently improving the fit when included (Guisan *et al.* 1999; Thuiller *et al.* 2003). Apart from the fact that interactions among predictor variables are difficult to interpret, a practical reason why they are seldom included is that they greatly increase the number of parameters in the model, because each interaction term requires its own parameter. From a validation and estimation perspective, the number of potential parameters to be estimated for interactive effects increases exponentially with the number of predictor variables in the model (Rushton *et al.* 2004). Nevertheless, combina-

tions of different modelling approaches can be used to identify significant interactions, as implemented in generalized boosting models (Friedman *et al.* 2000).

Dealing with spatial dependence

Independence of observations is a fundamental prerequisite for applying most statistical methods. Yet, spatial dependence of true biological origin (dispersal, demography or behaviour) is certainly observed in ecological data. Solutions to this problem include: (i) correcting the number of degrees of freedom used in model inference tests; (ii) adding a spatial autocorrelation (SAC) term to the linear predictor until no more spatial structure can be detected in the residuals (Lichstein *et al.* 2002); or (iii) (re)sampling plots at sufficient spatial distance to avoid autocorrelation (Guisan & Theurillat 2000). Adding a SAC term is certainly the most appealing solution to many ecologists, as being likely to incorporate useful additional ecological information in the model. However, spatial patterns observed in the residuals could as well result from failure to include an important autocorrelated predictor in the model (Lichstein *et al.* 2002) just as much as from a real biological process. As a result, models that incorporate a SAC term reflecting environmental rather than biological spatial structure will hardly be applicable to other situations in space and/or time, because the spatial arrangement of environmental gradients might differ between ranges (e.g. current and future).

Probably even more appealing to ecologists is thus the alternative to combine dispersal and population dynamic models (Huston 2002) with SDMs (Carey 1996; Iversen *et al.* 1999). Indeed, promoting both autoregressive (geostatistics) and spatially explicit population/dispersal models within the same approach is redundant. The former already provides an empirical solution to the latter, although putting less emphasis on process to the benefit of more easily performed broad-scale predictions. The final decision on which approach to use depends strongly upon the study objectives and the time and spatial frames for predictions. From the standpoint of variance partitioning of species distributions into environmental and pure spatial effects (see Lichstein *et al.* 2002 and references therein), there might still be advantages to using descriptive spatial statistics, particularly in the absence of knowledge about which processes lead to species aggregation.

Robust predictions and evaluation

SDMs are useful if they are robust. Addressing ecological questions with a model that is statistically significant but only explains a low proportion of variance might lead to weak, possibly erroneous, conclusions (Mac Nally 2002). Similar problems may well arise in the opposite case, when a

model is overfitted. Indeed, there is no absolute measure of robustness and the latter should always be discussed in relation to the primary, intended use of the model (Fielding 2002; Araújo *et al.* 2005a). For instance, a model based on climatic predictors may hypothetically have a low goodness-of-fit (e.g. $R^2 = 0.2$), yet could potentially explain all the climate-related variance for the target species. Such a model may be sufficient to assess overall impact of climate change on the worldwide distribution of the species, but be insufficient to answer specific conservation management questions at a local scale. Other predictors, such as the distribution of resources, or other factors not related to climate may prove essential to illustrate the distribution correctly.

Techniques for statistically evaluating models and their predictions have improved in many ways (Fielding 2002; Pearce *et al.* 2002). A wide range of metrics are increasingly used to compare predictions with observations, whether based on a totally independent test data set, or on resampled observations within the training set, as in the case of cross-validation or bootstrapping. Some metrics might not be appropriate for all situations. For example, in evaluating presence-absence model classification accuracy, threshold dependent statistics are known to be sensitive to the level of prevalence (proportion of presences) in the training and test data set (e.g. Manel *et al.* 2001). Moreover, multiple assessments based on several measures should be preferred over reporting of a single measure (Fielding 2002). Small sample size has also been shown to be a significant source of instability and errors in models. Collecting new data is costly and needs to be optimized (Hirzel & Guisan 2002). Some work has attempted to identify the minimum sample requirements for deriving robust predictions at minimal costs, and have shown that different modelling methods might require different minimum sampling size (Stockwell & Peterson 2002; Kadmon *et al.* 2003). Prediction errors may also not be evenly distributed across the landscape, eventually requiring improved models through spatial weighting solutions (Fielding 2002).

In presence-absence models, two kinds of prediction errors are possible. Commission errors arise from predicting a species where it does not occur, while omission errors stem from failing to predict a species where it does occur. Whereas one part of the overall error (omission and commission) rate results from environmental errors (a failure to include relevant environmental predictors in the model) and algorithmic errors, another corresponds to biological errors (e.g. equilibrium theory, inefficient sampling). Accuracy measures used to assess the quality and predictive ability of a model typically consider environmental and algorithmic errors only. Two major questions arise when considering biological errors (Pulliam 2000; Huston 2002): (i) why and how often are species observed in unsuitable

habitats?, and (ii) why and how often are species absent from suitable habitats? Reasons are numerous and should be considered in a species-specific context. Part of what is considered a mistake by standard evaluation procedures might actually be adequately explained by ecological theory and historical events, had the temporal and stochastic dimensions of population dynamics been taken into account. In cases where conservation issues are concerned – say the design of a reserve for preserving an endangered species – distinguishing what are truly suitable from unsuitable habitats will be of prime importance (Pulliam 2000). Sink habitats, where the species does occur but would not persist without at least one close source population, should not be included in a reserve design unless the source populations are also included. Pulliam (2000) provides evidence of plants occurring in sink habitats where net reproduction is negative and populations are only maintained through positive net gain from source habitats. The case of metapopulation dynamics, involving stochastic extinction and recolonization, potentially poses a greater problem for modelling species distributions because habitats are often assumed to be of similar quality and occupancy dynamics are stochastic not deterministic. Thus, unless historical events can be traced down through time to explain certain stochastic extinctions, these situations may constitute important sources of commission errors.

Accuracy assessments should thus have a close connection to the intended use of the model and the species biology (Fielding 2002). Different costs may be related to prediction errors in terms of their impact on the evaluation measure used for further interpretation. For instance, in the case of invasive species with expanding distributions (Peterson 2003), only omission errors are considered serious flaws, as commission errors inherently arise from the species not yet having colonized all suitable locations. For some species, dispersal-limitations may also lead to commission errors. In contrast, omission errors can be expected in locations characterized by source-sink dynamics.

APPLICABILITY OF SDMS

The SDMs can be used to tackle many issues in conservation biology and applied ecology (Table 1). Here, we only discuss two related issues that are currently much debated in the literature: climate change projections and conservation planning. The former can also have strong implications for the latter.

Projecting SDMs into future climates

Since the development of finer scale climate change scenarios in the past decade, numerous SDM studies have extrapolated the likely impacts of global change on species

distribution (e.g. Bakkenes *et al.* 2002; Peterson *et al.* 2002; Midgley *et al.* 2003) and community assemblages (Leathwick *et al.* 1996; Guisan & Theurillat 2000). The application of SDMs to climate change analyses was highlighted by a recent, massive study assessing global species extinction risk (Thomas *et al.* 2004). Results from this analysis reveal the potentially substantial impact of climate change on species extinctions, according to a range of future scenarios.

Nevertheless, SDMs have some limitations in this context. First, because SDMs of many species are likely to be based on the realized rather than the fundamental species niche, projections into future climate, where biotic interactions may have changed (e.g. because of different migration rates), are likely to generate mistakes (Davis *et al.* 1998). The degree of prediction errors should be related in some way to a species capacity to occupy its full fundamental niche in the current and future climate. For most species, it is unknown how much its fundamental niche is represented by its realized niche, although we expect it should relate to its competitive and dispersal abilities. In principle, the same limitation exists when projecting SDMs to other areas with different floras or faunas, testing the transferability of models in space may already provide a useful assessment on the validity of these future projections.

An alternative approach would be to base predictive models on fundamental (i.e. physiological) responses obtained from field or laboratory experiments, and constrain these by general rules of biotic interactions, dispersal behaviour and populations dynamics, in order to obtain more realistic predictions of species distribution under changing environments. This fundamental-constrained approach is supported – but also complicated – by the fact that most species seem to be generalists rather than specialists (Huntley *et al.* 1997), and thus most species are involved in generalist interactions with a large number of other species in any given ecosystem. In addition, and as a direct consequence of the individualistic behaviour of species, the effects of interacting species in one locality are supplanted by the effects of other species as an assemblage changes across the focal species geographical range (Huntley *et al.* 2004). Furthermore, a legitimate question is whether such fundamental knowledge will ever be available for many species in the wild. Thus, other alternatives should also be explored and the robustness of current SDMs should be properly assessed, whenever possible, to provide as realistic estimates of climate change impact as possible.

Second, in most projections, species dispersal is inappropriately taken into consideration, relying either on a ‘no dispersal’, an ‘unlimited dispersal’ scenarios, or both (e.g. Thomas *et al.* 2004; Thuiller 2004). With ‘no dispersal’, a species can only loose habitat as climate changes, whereas in the ‘unlimited dispersal’, all habitats

that become suitable can be colonized, two rather unlikely extreme situations. As migration capabilities of organisms depend on both dispersal characteristics and fecundity, they must be accounted for each species individually when deriving projections. The simplest approach is to attribute an estimate of migration rate per unit of time according to the dispersal agent of the selected species. For instance, Williams *et al.* (in press) for the Cape Proteaceas assumed a dispersal to be a maximum of 1 min per decade for ant- and rodent-dispersed Protea species. They also assumed a dispersal maximum of three cells per decade for wind-dispersed species based on empirical measurements. Dispersal events were assumed to occur on average every decade, anticipating decadal fires that provide the only dispersal opportunities to fire-adapted species. Such an approach is easily implemented within SDMs and could be used to assess risk in global change analyses. A second, and much more complicated, approach couples a landscape model simulating habitat fragmentation and dispersal events with SDMs (e.g. Carey 1996). Schwartz *et al.* (2001) and Iverson *et al.* (2004) developed such an approach merging SDM (regression tree analysis, RTA) with SHIFT, a cellular automaton. The RTA was used to devise prediction rules from current species–environment relationships, which were then used to replicate the current distribution and predict the potential future distributions. RTA predictions represent the potential ‘environmental envelope’ shift required by species, while the migration SHIFT model predicts the more realistic shifts based on colonization probabilities from varying species abundances within a fragmented landscape.

Third, uncertainty provided by the combination of different analyses, spatial resolutions, scales, modelling techniques and evaluation methods was greater than the variability of using different climate change scenarios (Thuiller 2004). Such a challenge demonstrates that different analyses using different models and resolutions are not comparable, because the way in which models are constructed varies and this strongly influences the model outputs (Thuiller *et al.* 2004c). Overpredictions or overparameterization greatly affect models and could explain why two SDMs calibrated on the same species could produce different projections in the future (Thuiller 2004). Better understanding of the behaviour of models and better evaluations of their predictive power are both necessary to facilitate such projections (Boone & Krohn 2002). Recent developments, combining different algorithms within a common framework and exploring the central tendency (consensus) of model projections, may lead to improve agreement between projected and observed shifts (Thuiller 2004; Araújo *et al.* 2005b; Gelfand *et al.* 2005).

Finally, although major issues remain concerning the application of SDMs to climate change research, they currently represent one of the only tools for assessing the impacts of forecasted climate change on a wide range of species, independent of the trophic level considered (Huntley *et al.* 2004). Mechanistic models (Chaine *et al.* 2000), while very appealing at the species level, are often too data-hungry to be of general use in nature management and biodiversity assessment.

SDMs in conservation planning

A major role of conservation planning is to design reserve networks that protects biodiversity *in situ*. Research within the field of conservation planning has focused on the development of theories and tools to design reserve networks that protect biodiversity in an efficient and representative manner (Williams & Araujo 2000; Araujo *et al.* 2002; Ferrier 2002; Cabeza *et al.* 2004). Predicted species distribution data from SDMs are commonly used for conservation planning because the alternatives (e.g. survey data) are often incomplete or biased spatially (Austin 1998; Andelman & Willig 2002). However, there may be considerable uncertainty associated with the use of predicted species distribution data, particularly given the variety of approaches available to generate predictions for use in conservation planning (Wilson *et al.* 2005). These approaches range from using the probabilistic data directly to using a threshold – identified *a priori* or *a posteriori* – to convert the probabilistic data into presence–absence data. Wilson *et al.* (2005) recently assessed the sensitivity of conservation planning outcomes to different uses of predicted species distribution data and showed that the resulting reserve networks differed, and had different expected species representation. They concluded that efforts should be directed towards producing the most reliable predictions for use in conservation planning, and to find the reserve network that is most robust to the uncertainty in the predictions.

The need to rely on robust predictions from SDMs in conservation planning is emphasized when SDMs and reserve selection algorithms are used together to investigate the pertinence of reserve networks under future global climate change. For instance, Araújo *et al.* (2004) assessed the ability of existing reserve-selection methods to secure species in a climate-change context using modelled species distribution from SDMs. They concluded that opportunities exist to minimize species extinctions within reserves, but that new approaches are needed to account for impacts of climate change on species; particularly for those projected to have temporally non-overlapping distributions. Such achievement was recently carried out in the Cape Floristic Region, where SDMs coupled with very simple dispersal

model and reserve-selection methods were used to identify minimum-dispersal corridors allowing species migration across reserve networks under climate change and land transformation scenarios (Williams *et al.* in press).

The SDM-based approaches to conservation assessment should also be compared with recently proposed alternative, like generalized dissimilarity modelling (GDM; Ferrier *et al.* 2004), which focus on emergent properties of biodiversity (richness and compositional turnover) rather than distribution of individual species. The latter is for instance suggested to be better suited to lesser known, yet highly diverse, biological groups (Ferrier *et al.* 2004).

NEW CHALLENGES FOR SDM RESEARCH

Although many recent applications of SDMs relate to climate change and conservation assessments, their use in theoretical ecology and evolution is resurfacing. Many of the prevailing challenges facing SDM research involve the inclusion of ecologically relevant parameters and an improved assessment of errors and uncertainties to yield more robust predictions. We discuss some additional challenges below.

Migration process

Including migration processes more systematically into SDMs would provide interesting tools to address ecological questions such as rarity phenomena (do rare species have lower dispersal or colonization capabilities than common species?) or, in a context of climate change, to provide more realistic projections of future species distributions (will species be able to migrate fast enough to track changes?). Although such analyses require species-specific data on dispersal, they are particularly promising in a context of global climate change (see also Collingham & Huntley 2000; Collingham *et al.* 2000). Two important aspects that should not be neglected in future dispersal SDMs are the possibility to model stochastic long-distance dispersal events and the effect of barriers to dispersal.

More dynamics

The SDMs are not often explicitly related to population dynamics theory and models, although existing studies show that much can be gained by linking these disciplines (Dullinger *et al.* 2004). SDMs can be improved by incorporating theoretical information from population dynamics, but can also lend support to population studies. In the first case, knowledge of a species population dynamics may help determine the maximum amount of deviance that can possibly be explained by the SDM of a given species (e.g. 50%), for instance because of year-to-year stochastic fluctuations and dispersal limitations

in a source-sink system (i.e. a proportion of commission or omission 'errors' can have biological causes). In the second case, SDMs could provide great support to metapopulation studies. For instance, in a simplified patch-matrix landscape, spatially explicit metapopulation models require: (i) a better definition of patches (i.e. criteria that make them suitable) and their location in the landscape (Ferrier *et al.* 2002); and (ii) a more realistic estimation of ecological distances between patches, for improving the estimation of dispersal success (Ferrier *et al.* 2002).

Incorporating biotic interactions

There is an ongoing debate concerning the inclusion of interspecific interactions into SDMs, particularly in a global change and conservation contexts (Davis *et al.* 1998; Pearson & Dawson 2003). Recent SDM studies indirectly support the role of competition in shaping species distributions on the landscape scale (Leathwick & Austin 2001; Anderson *et al.* 2002). However, it is unclear whether the use of the occurrence of a species in the model of another species truly reflects a biotic interaction, or simply reflects the absence of an important environmental predictor in the model. Furthermore, even if species interactions exist, is it critical that they be included in SDMs? This point is at the heart of controversies involving null models in community ecology, and also raises the issue of whether, for example, a neutral model considering individuals with equivalent ecological requirements and no competition is sufficient to describe species patterns (Bell 2001; Hubbell 2001). The latter also relates to the question of scale, because some processes might apply at coarser resolutions but not at finer ones.

Nevertheless, it would be interesting to test relationships across various scales. At broad extent and coarse resolution, we expect competition or facilitation should have a lesser effect on species distribution than at more local extent and finer resolution (Huston 2002; Pearson & Dawson 2003), although local abundance may still be strongly affected at larger scale. Finally, one should be aware that interactions other than competition and facilitation – usually the only ones explicitly mentioned in most SDM studies – also play an important role in driving species distributions (e.g. predators for prey, herbivores for plants, pathogens, parasites, mutualists).

Modelling functional groups and communities

Going one step further, spatial predictions for individual species could theoretically be analysed at higher levels of ecological complexity, for instance: (i) whether some functional groups of species can be better modelled than others (Boone & Krohn 2002; Huntley *et al.* 2004), and the

likely ecological reasons for such patterns; and (ii) for reconstructing species assemblages and biological communities in a bottom-up approach (Leathwick *et al.* 1996; Guisan & Theurillat 2000; Ferrier *et al.* 2002).

For instance, Segurado & Araújo (2004) found a significant interaction between species group (defined by prevalence, occupancy, extent of occurrence, niche position and breadth) and model performance. Other research, assessing the relationship between species niche properties (niche position, niche breadth and range size) and bioclimatic gradients, found that stress-tolerant species do not occupy broad environmental ranges, and that functional attributes of species vary with species niche position (e.g. leaf characteristics, phenology or dispersal mode; Thuiller *et al.* 2004b).

Still very few studies have attempted to reconstruct community assemblages from individual species predictions. New alternative approaches attempt now to build species assemblages in a single process, such as classification trees fitted to multiple species (De'Ath 2002), or GDM (Ferrier *et al.* 2004). A major challenge here will be to incorporate assembly rules (e.g. Keddy 1992) in these reconstructions, particularly when attempting to predict future assemblages.

CONCLUSION

While tremendous progress has been made on many aspects related to the building and evaluation of SDM, future efforts should now focus on the development of standardized, robust, modelling frameworks. Important concepts requiring deeper examination include: (i) exploring other views of the relationship between niche concepts and species distribution, such as source-sink dynamics and dispersal limitation; (ii) assessing how close the modelled species are to equilibrium; and (iii) exploring the degree to which competition can explain the limits of species range along environmental gradients. Although requiring more data on species biology, these findings will also provide a better framework for evaluating models, e.g. by identifying biological causes of errors in predictions. Possible methodological improvements include: (iv) assessing how different scales may be considered in SDMs, depending upon species behaviour, dispersal ability, extent of the study area, and the very nature of the data; and (v) developing enhanced frameworks for assessing errors and uncertainties in SDMs. Integration of these elements may be facilitated within a Bayesian hierarchical framework.

One challenging use of SDMs is for forecasting the likely impact of global change on species distribution. Here, competition and scale are critical parameters. Future changes in biotic interactions may undermine the validity of projections based on the realized niche, while input climate change scenarios are still too coarse in spatial scale to provide

accurate patterns of distributional changes at the local scale. Incorporating additional information on species dispersal and population dynamics will be required for assessing whether species will be able to track habitat shifts at a sufficient pace. Two other related challenges facing SDMs are their use in the design and evaluation of reserve networks and the reconstruction of current and future patterns of communities from individual species predictions and assembly rules.

To conclude, SDMs should thus become: (i) better rooted in ecological theory, (ii) more dynamic and (iii) multispecific. To achieve this, we urge spatial modellers, biogeographers, community ecologists, population biologists and ecophysiologists to work in more concerted ways.

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