Predicting 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.


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
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

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

<table>
<thead>
<tr>
<th>Type of use</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>Quantifying the environmental niche of species</td>
<td>Austin <em>et al.</em> (1990), Vetaas (2002)</td>
</tr>
<tr>
<td>Suggesting unsurveyed sites of high potential of occurrence for rare species</td>
<td>Pearce &amp; Lindenmayer (1998)</td>
</tr>
<tr>
<td>Supporting conservation planning and reserve selection</td>
<td>No published example found</td>
</tr>
<tr>
<td>Modelling species assemblages (biodiversity, composition) from</td>
<td>No published example found</td>
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<tr>
<td>individual species predictions</td>
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</tr>
<tr>
<td>Building bio- or ecogeographic regions</td>
<td></td>
</tr>
<tr>
<td>Improving the calculation of ecological distance between patches</td>
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<td>in landscape meta-population dynamic and gene flow models</td>
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</table>
types of influence on species distribution are best manipulated in a geographical information system (GIS).

The procedure of SDM building ideally follows six steps (modified from Guisan & Zimmermann 2000; see Table 2): (i) conceptualization, (ii) data preparation, (iii) model fitting, (iv) model evaluation, (v) spatial predictions, and (vi) assessment of model applicability.

Many important decisions are made during the initial conceptual phase, which can be split into two subphases: (i) theory and data: define an up-to-date conceptual model of the system to be simulated based on sound ecological thinking and clearly defined objectives (Austin 2002; Huston 2002), setting multiple working hypotheses (e.g. pseudo-equilibrium; Guisan & Theurillat 2000; see next section), assessing available and missing data and the relevance of environmental predictors for the focal species and the given scale (Thuiller et al. 2004a), identifying an appropriate sampling strategy for collecting new data (Hirzel & Guisan 2002) or for complementing existing sets, and choosing the appropriate spatio-temporal resolution and geographic extent for the study. (ii) Modelling methods: identify the most appropriate method(s) for modelling the response variable (e.g. ordinal GLM for semi-quantitative species abundance; Guisan & Harrell 2000) and identifying both the framework (e.g. resampling techniques vs. truly independent observations) and the statistics needed for evaluating the predictive accuracy of the model (Pearce & Ferrier 2000; Fielding 2002).

In current practice, however, few decisions are made at the very start of a study, because of the lack of knowledge of the target organism or of the study area and related data. For instance, the choice of an appropriate resolution might depend on the size of the species home range and the way the species uses resources in the landscape. The choice of the geographical extent might also depend on a prior knowledge of environmental gradients in the study area (to ensure including complete gradients; Austin 2002; Van Horn 2002); or, for animal species, males/females, or summer/winter habitats might need separate models (Jaberg & Guisan 2001). Answers to these questions usually require either the collection of preliminary field observations, running sensitivity analyses, or conducting experiments to, for example, quantify the fundamental range of tolerance of an organism to predictors (e.g. Kearney & Porter 2004).

Many other features – methodological, statistical or theoretical – need to be additionally controlled or considered at each step of SDM building (Table 2). Solid criteria need to be used for detecting potential problems, such as overfitting (when number of predictors > number of observations), overdispersion (i.e. greater dispersion than expected from the probability distribution) or multicolinearity (i.e. high correlations between several predictors). Careful consideration of these factors must be made to ensure successful predictions (Table 2). For more details on the different steps of SDM building, we refer readers to Guisan & Zimmermann (2000).

ECOLOGICAL THEORY AND ASSUMPTIONS BEHIND SDMS

Species distribution models – and their output habitat suitability maps – have been used with relatively good success to investigate a variety of scientific issues (Table 1). However, despite the rapid improvement of methods,
<table>
<thead>
<tr>
<th>Feature to consider</th>
<th>Possible problem</th>
<th>Detection criterion</th>
<th>Examples of proposed solution</th>
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<tbody>
<tr>
<td><strong>Conceptualization</strong></td>
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<tr>
<td>Type of organism</td>
<td>Mobile species in unsuitable habitats</td>
<td>Radio-tracking; continuous time field observations</td>
<td>Neighbourhood focal functions; choice of grain size</td>
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<td></td>
<td>Sessile species (e.g. plants) in unsuitable habitats</td>
<td>Lack of fitness (e.g. no sexual reproduction)</td>
<td>Use fitness criteria to select species observations to be used in model fitting</td>
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<td></td>
<td>Species not observed in suitable habitats</td>
<td>Knowledge of species life strategy (e.g. dispersal)</td>
<td>Interpret the various types of errors</td>
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<tr>
<td></td>
<td>Low detectability species</td>
<td>Field knowledge, literature</td>
<td>Correct test for detectability</td>
</tr>
<tr>
<td></td>
<td>Sibling species or ecotypes of a same species</td>
<td>Genetic analyses</td>
<td>Test niche-differentiation along environmental gradients</td>
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<td></td>
<td>Invasive species</td>
<td>Mostly commission errors</td>
<td>Fit models in the area of origin</td>
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<tr>
<td>Type of predictors</td>
<td>Direct or indirect predictors?</td>
<td>Ecophysiological knowledge</td>
<td>Avoid indirect predictors</td>
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<tr>
<td>Designing the sampling</td>
<td>Selecting sampling strategy</td>
<td>Simulation tests with virtual species in a real landscape</td>
<td>Random-stratified sampling</td>
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<td>Incorporating ecological theory</td>
<td>Linear or unimodal response of species to the predictors?</td>
<td>Partial plots, smoothing curves</td>
<td>GAM or quadratic terms in GLM</td>
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<td></td>
<td>Skew unimodal response curves</td>
<td>Skewness test</td>
<td>HOF, beta functions in GLM, GAM, fuzzy envelope models</td>
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<td></td>
<td>Bimodal response curves</td>
<td>Smoothing curves, partial plots</td>
<td>GAMs, ³ third order polynomials or beta-functions in GLMs</td>
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<td><strong>Data preparation (data model)</strong></td>
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<td>Species data</td>
<td>Bias in natural history collections (NHC)</td>
<td>Cartographic and statistical exploration</td>
<td>Various ways of controlling bias</td>
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<td></td>
<td>Heterogeneous location accuracy in NHC</td>
<td>Only detectable if recorded in the database</td>
<td>Selecting only observations of known accuracy below threshold</td>
</tr>
<tr>
<td>Scale (grain/extent)</td>
<td>No absences</td>
<td>Type of data base and source (metadata)</td>
<td>Generating pseudo-absences</td>
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<td></td>
<td>Different grain sizes for the various predictors</td>
<td>GIS exploration</td>
<td>Aggregating all GIS layers at the limiting grain</td>
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<td>Truncated gradients within the considered extent</td>
<td>Preliminary exploration of species response curves</td>
<td>Enlarging the extent of study area to cover full gradients</td>
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<td><strong>Model fitting</strong></td>
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<tr>
<td>Type of data</td>
<td>No absence</td>
<td>Type of data base and source (metadata)</td>
<td>Using profile methods</td>
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<td></td>
<td>Multicolinearity</td>
<td>Variance Inflation Factor (VIF)</td>
<td>Removing correlated predictors; orthogonalization</td>
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<td>Spatial auto-correlation (SAC)</td>
<td>Non-independence of the observations</td>
<td>SAC indices</td>
<td>Sampling strategies to avoid SAC; correcting inference tests and possibly incorporating SAC in models</td>
</tr>
<tr>
<td>Type of statistical model</td>
<td>Overdispersion</td>
<td>Residual degrees of freedom &gt; residual deviance</td>
<td>Quasi-distribution in GLMs and GAMs; scaled deviance</td>
</tr>
<tr>
<td>Model selection</td>
<td>Which approaches and criteria?</td>
<td>–</td>
<td>AIC-based model averaging; cross-validation; shrinkage</td>
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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 under-estimating 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, Mac Arthur 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 \( \geq 1 \)); (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 Grinellian 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://biogeography.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 fulfill 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).
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 multicolinearity 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-

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

<table>
<thead>
<tr>
<th>Tool</th>
<th>Reference</th>
<th>Methods implemented</th>
<th>URL</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAYES</td>
<td>Aspinall (1992)</td>
<td>BA</td>
<td>ArcView extension available at the discretion of the author</td>
</tr>
<tr>
<td>BIOMAPPER</td>
<td>Hirzel et al. (2002)</td>
<td>ENFA</td>
<td><a href="http://www.unil.ch/biomapper">http://www.unil.ch/biomapper</a></td>
</tr>
<tr>
<td>BIOMOD</td>
<td>Thuiller (2003)</td>
<td>GLM, GAM, CART, ANN</td>
<td>At the discretion of the author</td>
</tr>
<tr>
<td>ECOSPAT</td>
<td>Unpublished data</td>
<td>GLM, GAM</td>
<td><a href="http://www.ecospat.unil.ch">http://www.ecospat.unil.ch</a>; at the discretion of the author</td>
</tr>
<tr>
<td>GDM</td>
<td>Ferrier et al. (2002)</td>
<td>GDM</td>
<td>At the discretion of the author</td>
</tr>
<tr>
<td>MAXENT</td>
<td>Phillips et al. (2005)</td>
<td>ME</td>
<td>At the discretion of the author</td>
</tr>
<tr>
<td>SPECIES</td>
<td>Pearson et al. (2002)</td>
<td>ANN</td>
<td>At the discretion of the author</td>
</tr>
<tr>
<td></td>
<td><strong>Coupled with cellular automata</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Disperse</td>
<td>Carey (1996)</td>
<td>CE</td>
<td>At the discretion of the author</td>
</tr>
<tr>
<td>Shift</td>
<td>Iverson et al. (1999)</td>
<td>CART</td>
<td>At the discretion of the author</td>
</tr>
</tbody>
</table>

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.
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) resampling 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; Iverson 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
extrapolated the likely impacts of global change on species scenarios in the past decade, numerous SDM studies have since the development of finer scale climate change planning. The former can also have strong implications for the literature: climate change projections and conservation discussing two related issues that are currently much debated in 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 climatic parameters, using 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

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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 Proteaceae 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 (Chuine 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 & Araújo 2000; Araújo 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 comparison 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 ecophysio- logists to work in more concerted ways.

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