1 · *Species distribution modeling*

Prediction is very difficult, especially about the future.
Niels Bohr

1.1 Introduction

What are predictive maps of species distributions? Why make them? How? Environmental scientists increasingly need to use local measurements to assess change at landscape, regional and global scales, and statistical or simulation models are often used to extrapolate environmental data in space (Miller *et al.*, 2004; Peters *et al.*, 2004). *Species distribution modeling* (SDM) is just one example of this, but an increasingly important one – SDM extrapolates species distribution data in space and time, usually based on a statistical model. Developing a species distribution model begins with observations of species occurrences, and with environmental variables thought to influence habitat suitability and therefore species distribution. The model can be a quantitative or rule-based model and, if the fit is good between the species distribution and the predictors that are examined, this can provide insight into species environmental tolerances or habitat preferences. It also provides the opportunity to make a spatial prediction. *Predictive mapping*, or geographical extrapolation using the model, results in a spatially explicit "wall-to-wall" prediction of species distribution or habitat suitability (Fig. 1.1). Maps of environmental predictors, or their surrogates, must be available in order for predictive mapping to be implemented (Franklin, 1995).

The purpose of this book is to describe the process of species distribution modeling, review the significant advancements that have been made recently in this field, and try to provide guidelines and a framework for choosing data, methods and study design that are appropriate to a given SDM application. This book provides an introduction to SDM for beginners in the field who wish to use such models in environmental analyses while also providing a comprehensive review of current practice

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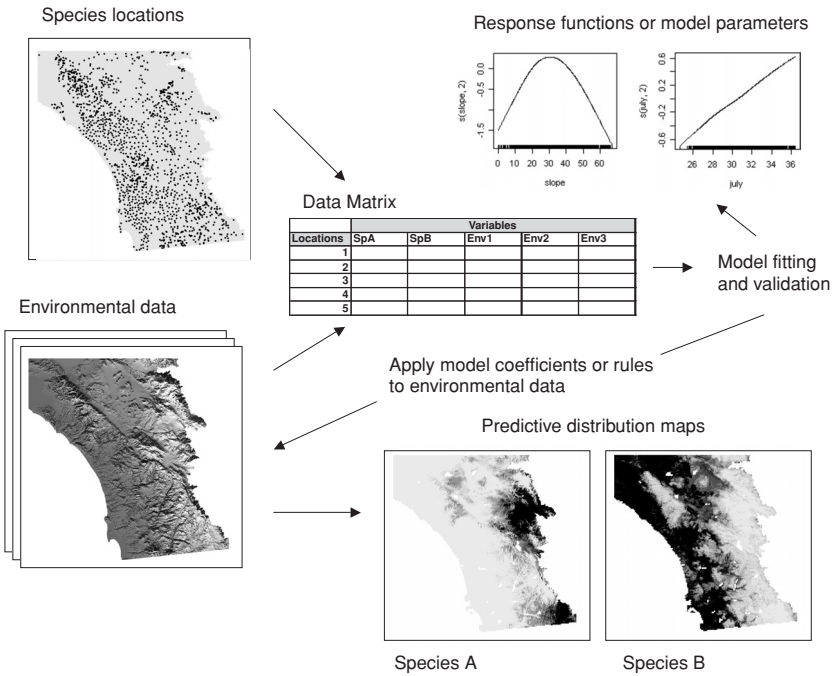


Fig. 1.1. The steps in species distribution modeling and predictive mapping. Spatially explicit (georeferenced) species occurrence data are linked with digital maps of environmental predictors and values of environmental predictors for species locations are extracted. A statistical, machine learning, or other type of model describing the relationship between species occurrence and environmental data is developed. The parameters or response functions are evaluated and these coefficients or decision rules are applied to environmental maps yielding spatial predictions of species distribution or habitat suitability.

for more advanced practitioners. There are a wide variety of applications of SDM ranging from basic to applied science. It is because of this that there are many choices that have to be made about what data and model to use. Given the range of subsequent decisions that will be made on the basis of SDMs, it is important to understand how they are constructed, using what types of applicable data, the assumptions behind them and their limitations. In the remainder of this chapter I will define some key terms, highlight some recent publications that illustrate the growing interest in SDM, outline the process of species distribution modeling along with the organization of the remainder of this book, and review some of the main uses of SDM.

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1.2 What is in a name?

It seems a straightforward question, but what do species distribution models *describe*, and, literally, what do they *predict*? What variable is depicted in the resulting map? (This is discussed further in Chapter 4.) The terminology that has developed in this field was somewhat confusing when I reviewed it in 1995, with individual studies using different terms, and has grown even more complex. *Species distribution models*, of the kind discussed in this book, have been said to describe both (a) the species niche, and (b) the suitability of habitat to support a species.

1.2.1 Niche models

"Species niche model," "ecological niche model" or even "niche-theory model" are terms that have been used to describe SDM. These models have variously been described as estimating the fundamental (potential) niche, realized (actual) niche, the multivariate species niche (Rotenberry *et al.*, 2006), or, when conditioned only on climate variables, the "climatic niche" (Chapter 3 discusses this further).

The original climate niche modeling system (BIOCLIM) actually referred to the "climate profile" of a species or other entity (Busby, 1991). The term climate (or bioclimatic) envelope modeling (Heikkinen *et al.*, 2006) has been used even when envelope methods are not used (see Chapter 8) and when environmental predictors include variables other than climatic, especially when the models are applied to climate change questions. The maps resulting from the application of climatic niche models are often referred to as predictions of (species) geographical *range* (Graham *et al.*, 2004). Some authors even distinguish between ecological niche models, which they define as models of potential distribution, and species distribution models of actual distributions (Peterson *et al.*, 2008).

I prefer the term "species distribution model" to any of the variations on "niche model" (in spite of their widespread use) because SDM more accurately describes the modeling process and resulting model. Although niche theory strongly underpins SDM (Chapter 3), SDMs describe empirical correlations between species distributions and environmental variables. While these models should always be evaluated for "ecological realism," that is, consistency with ecological knowledge of limiting factors and species response curves (Chapter 3), the data rarely allow the true species niche to be fully specified or confirmed. Further,

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these models are frequently used to predict the geographical distribution of a species, rather than to study the characteristics of its distribution in environmental (niche) space.

1.2.2 Habitat suitability models

SDMs are also referred to as habitat suitability models (e.g., Hirzel *et al.*, 2006; Ray & Burgman, 2006; Hirzel & Le Lay, 2008), describing the suitability of habitat to support a species. When used to predict in geographical space, they have been called, among other things, "predictive habitat distribution models" (Guisan & Zimmermann, 2000) and "spatially explicit habitat suitability models" (Rotenberry *et al.*, 2006).

The concept of habitat suitability is closely related to the idea of a resource selection function from wildlife biology (Manly *et al.*, 2002) as noted by Boyce *et al.* (2002), and can be applied to plants and animals. A resource selection function (RSF) is any function (for example, from a statistical model) that is proportional to the probability of habitat use by an organism (Manly *et al.*, 2002). If a resource selection function is proportional to the probability of use, then a SDM could be said to predict the likelihood that an event (species) occurs at a location – that is, *the probability of species presence*. Mackey and Lindenmeyer (2001) presented a very interesting analytical framework for modeling the spatial distribution of terrestrial vertebrates which tend to be mobile and may not occupy all suitable habitat (van Horne, 1983). They refer to the spatial occurrence and abundance of a species as its "distributional behavior" (discussed further in Chapter 3).

A species distribution model, when applied to maps of environmental variables, is said to predict the species potential geographical distribution (potential occurrence at a location); the resulting maps have been called ecological response surfaces (Lenihan, 1993); biogeographical models of species distributions (Guisan *et al.*, 2006), spatial predictions of species distribution (Austin, 2002), predictive maps (Franklin, 1995), predictions of occurrence (Rushton *et al.*, 2004), or predictive distribution maps (Rodriguéz *et al.*, 2007). According to Meyer and Thuiller (2006), one of the most important applications of RSFs is mapping species distributions.

Further, the same methods and spatial modeling principles apply whether the locations of plants, animals, microbes, community properties (e.g., diversity), ecosystem properties (e.g., productivity), or other response variables are being correlated with the mapped distributions of those factors hypothesized to control their geographical patterns. Some theory other than the species niche concept (Chapter 3) would have to

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support such analyses, for example an ecosystem productivity model or community diversity theory. These analyses might also have to rely on different predictors than those typically used in SDM (Chapter 5). Spatial overlay of geographical patterns to examine the suitability of a location for a particular use forms the historical foundation of geographical information science (McHarg, 1969).

The description of SDM that I have used before (Franklin, 1995), "geographical modeling of biospatial patterns in the relation to environmental gradients," while comprehensive, is cumbersome. In this book I will use the terms *species distribution model*, and *predictive [distribution] map*, for simplicity and generality.

1.3 Heightened interest in species distribution modeling

"The quantification of . . . species–environment relationships represents the core of predictive geographical modeling in ecology" (p. 148) (Guisan & Zimmermann, 2000). Species distribution modeling has its roots in ecological gradient analysis (Whittaker, 1960; Whittaker *et al.*, 1973), biogeography (Box, 1981), remote sensing and geographic information science (for review see Franklin, 1995). It has recently experienced explosive growth in the scientific literature, and in practice, especially by governmental and non-governmental organizations charged with biological resource assessment and conservation at larger spatial scales. The level of activity has been greatly enhanced by the development of digital databases for natural history collections, making species location information from specimen records and other sources more widely available (Graham *et al.*, 2004), for example via the Global Biodiversity Information Facility (http://www.gbif.org/). In 1995, I wrote a "comprehensive" review of the state of the art that described only 30 studies. SDM has since been the subject of a number international symposia and workshops resulting in an edited book (Scott *et al.*, 2002) and special features (collections of papers) in journals:

- *Ecological Modelling*, 2002, **157** (2–3) and 2006, **199** (2);
- *Biodiversity and Conservation*, 2002, **11** (12);
- *Journal of Applied Ecology*, 2006, **43** (3);
- *Diversity and Distributions*, 2007, **13** (3).

It is a topic that is, or has been, featured often in *Ecography*, *Ecological Applications*, *Journal of Vegetation Science*, and in a number of other scientific journals. Pick up any recent issue and you will find several

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SDM studies. For example, the October 2008 issue of the journal *Ecological Applications* featured a study distinguishing the factors affecting the establishment piñon–juniper woodland before, versus after, Euro-American settlement in western North America using topo-climatic predictors (Jacobs *et al.*, 2008). Another study in the same issue showed that improved predictions of marine predator (bottlenose dolphin) distributions could be made using models of prey (fish) distributions (Torres *et al.*, 2008). Species distribution modeling methods have even been used to map the human "ecological" niche during the last glacial maximum in Europe (Banks *et al.*, 2008), and the "biophysical environmental space" of wildfire (Syphard *et al.*, 2008; Parisien & Moritz, 2009). These are just a few of the many fascinating SDM studies to pass my desk.

Several review papers, essays and editorials have summarized advances in different aspects of SDM. These advancements include conceptual issues such as a general framework for species distribution modeling (Franklin, 1995; Guisan & Zimmermann, 2000; Mackey & Lindenmayer, 2001; Guisan & Thuiller, 2005; Elith & Leathwick, 2009), links to ecological theory (Austin, 2002, 2007; Hirzel & Le Lay, 2008), modeling methods (Guisan *et al.*, 2002, 2006; Pearce & Boyce, 2006), data and scale issues and statistical model selection (Rushton *et al.*, 2004), use of natural history collections data (Graham *et al.*, 2004), modeling ecological communities (Ferrier & Guisan, 2006), and the influence of spatial autocorrelation on models of species distributions (Miller *et al.*, 2007). Other reviews have focused on applications, including the use of SDMs in land management under uncertainty (Burgman, 2005), and their applicability to conservation planning (Ferrier *et al.*, 2002a, b; Rodriguéz *et al.*, 2007). Each of these topics will be explored in this book.

Further, growing numbers of government agencies and non-governmental organizations have implemented ambitious, large-scale species distribution modeling programs (Iverson & Prasad, 1998; Ferrier, 2002). These projects usually involve modeling the distributions of hundreds (even thousands) of individual species or ecological communities over large regions. Often, these efforts are extensive and influential, affecting regional and global conservation decision making, but they are not necessarily reported in the scientific literature. For example, NatureServe, a non-profit conservation organization that represents an international network of biological inventories (http://www.natureserve.org/), calls their program predictive (or element) distribution modeling and they are using it to model species distributions in South America. They have run training workshops and provided tutorial materials (for developing the statistical models) on their website (http://www.natureserve.org/

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prodServices/predictiveDistModeling.jsp). The American Museum of Natural History, as part of their Remote Sensing and Geographic Information System Facility, has offered short courses in species distribution modeling for conservation biology (http://geospatial.amnh.org/). Clark Labs, in collaboration with Conservation International, an international non-governmental conservation organization, has developed specialized commercial GIS software to implement both species distribution models and project the impacts of land cover dynamics on biodiversity (http://www.clarklabs.org/). It is being used to model the distributions of 16 000 species in the Andes.

It is challenging to try and summarize the wealth of new information being produced in this exciting and dynamic field into a coherent narrative that can guide those who wish to use these methods in their work, but that is the goal of this book. Much recently published research in this area has focused on comparisons of different modeling methods and those comparisons have emphasized different measures of model performance or accuracy. While the findings of that important and useful work will be summarized, this book has a somewhat different emphasis. SDMs are empirical models and they start with data. I will first consider the qualities or characteristics of the data describing environment and species distributions in relation to the question being asked. This is in line with more recent studies that have emphasized the effect of species and environmental data properties on model performance. Trained as a geographer, I will emphasize the spatial nature of the data.

I will also emphasize how research informs the practice of SDM with reference to the published literature, as in the preceding paragraphs. Attribution is very important in science and scholarship, and I have tried to not only give credit where credit is due, but also provide signposts to where to look for those who want to find more detailed information about a particular topic.

1.4 What is species distribution modeling and how is this book organized?

This book is organized according to a framework for modeling species distributions presented by Austin (2002) that has three parts: the ecological, data, and statistical models (model here meaning framework or conceptual model). The ecological model includes the ecological theory applied or hypotheses tested in the study. The data model "consists of the decisions made regarding how the data are collected and how the data will be measured or estimated" (Austin, 2002, p. 102). The

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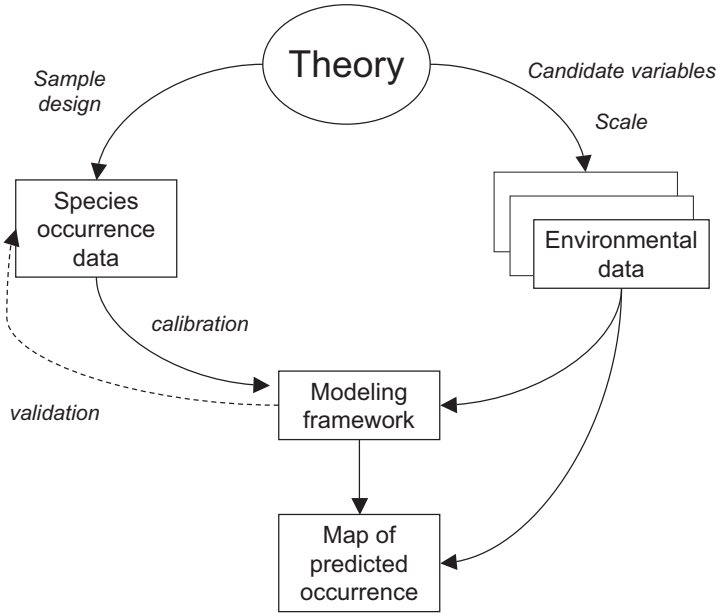


Fig. 1.2. Diagram showing the components of species distribution modeling. Biogeographical and ecological theory and concepts frame the problem, and identify the characteristics of the species and environmental data required to calibrate an appropriate empirical SDM and apply it to produce a map of predicted species occurrence or suitable habitat.

statistical model includes the choice of methods and decisions regarding implementation (calibration and validation).

The following elements are required for modeling and spatial prediction of species distributions and are described in the chapters of this book (Fig. 1.2):

- A theoretical or conceptual model of the abiotic and biotic factors controlling species distributions in space and time, and at difference scales, and the expected form of the response functions (Chapter 3);
- Data on species occurrence (location) in geographical space (a measure of presence, habitat use, abundance, or some other property) (Chapter 4), or expert knowledge about habitat requirements or preferences (Chapter 7);
- Digital maps of environmental variables representing those factors (or their surrogates) determining habitat quality, or correlated with it (Chapter 5). These are generally derived from remote sensing, from

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spatial models of environmental processes, or from some other source, and stored in a GIS.
- A model linking habitat requirements or habitat use (species occurrence) to the environmental variables. The model can be statistical, descriptive, logical, or rule-based (Burgman *et al.*, 2005) (Chapters 6–8);
- Tools for applying the model (rules, thresholds, weights, coefficients) to the values of the mapped environmental variables to produce a new map of the metric of species occurrence – a geographic information system or GIS (Tobler, 1979);
- Data and criteria to validate the predictions and a way to interpret error or uncertainty in the analysis (Chapter 9).

Before discussing the theories supporting and tested using distribution models (Chapter 3), I review the growing number of ways that comprehensive geographical data on species distributions are being collected, assembled and displayed in Chapter 2. These do not all involve extrapolation using a statistical model. This will address the question "why do we need these correlative models at all?" and set the stage for the rest of the book.

The framework and procedures outlined are valid for spatial extrapolation of any ecological variable (e.g., biomass, species richness), and are often applied to spatial prediction in other domains, e.g., predicting the likelihood of deforestation (Ludeke *et al.*, 1990), urban growth, or fire risk, but the emphasis of this book is on individual species distributions. Many decisions regarding theory, data, models, and validation have to be made when developing species distribution models for a particular purpose. Often, the choice of a modeling framework is based on the experience of the practitioners (Burgman *et al.*, 2005; Austin *et al.*, 2006). I propose that the characteristics of the species (their life histories and distributions), the scale of the analysis, and the data available for modeling, determine the best modeling framework in any particular application. I will attempt to summarize this into a framework for implementation of SDM in Chapter 10.

1.5 Why model species distributions?

Why model habitat relations and make spatial predictions of species distributions? One reason is to *understand* the relationship between a species and its abiotic and biotic environment based on observations for the

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purpose of ecological inference, or to test ecological or biogeographical hypotheses about species distributions and ranges. Determining how pattern and scale influence the distribution and abundance of organisms is the focus of much of ecology (Elton, 1927; Scott *et al.*, 2002). When testing ecological (e.g., Jones *et al.*, 2007) and phylogenetic hypotheses (e.g., Peterson & Holt, 2003), the model describing species–habitat relationships or species niche may be the result of interest and spatial predictions from the model may not be needed. Even for applied problems, e.g., for wildlife management, ecological restoration (habitat manipulation, species translocation), species reintroductions or impact assessment, SDMs can be used to predict the value or suitability of habitat at discrete unsurveyed locations, or for a different time period. This does not necessarily require a map of predictions – a wall-to-wall spatial prediction for every location in a region.

However, species distribution models are now being widely used to interpolate or extrapolate from point observations over space, similar to forecasting through time, in order to *predict* the occurrence of a species for locations where survey data are lacking – that is, most locations on the earth's surface. This yields a predictive *map*. Maps of habitat suitability, or a predicted species distribution, are useful to test hypotheses about species range characteristics, niche partitioning or niche conservatism. Predictive distribution maps are also required for many aspects of resource management and conservation planning including biodiversity assessment, reserve design, habitat management and restoration, population, community and ecosystem modeling, ecological restoration, invasive species risk assessment, and predicting the effects of climate change on species and ecosystems. Further, a model calibrated for current conditions can be used to project potential species distributions at another point in time in order to predict the impacts of environmental change on species distributions. These are the kinds of potential uses that are usually enumerated at the outset of any one of the hundreds of papers now published on SDM. Examples of the primary applications are summarized here in order to provide a broad sense of the myriad uses of this methodology.

1.5.1 Reserve design and conservation planning

Regional to global scale conservation planning activities that require "biodiversity assessment," i.e., knowing the distribution of species, communities, species richness or other community attributes, on the landscape (e.g., Scott *et al.*, 1993; Li *et al.*, 1999; Rodrigues *et al.*, 2004;

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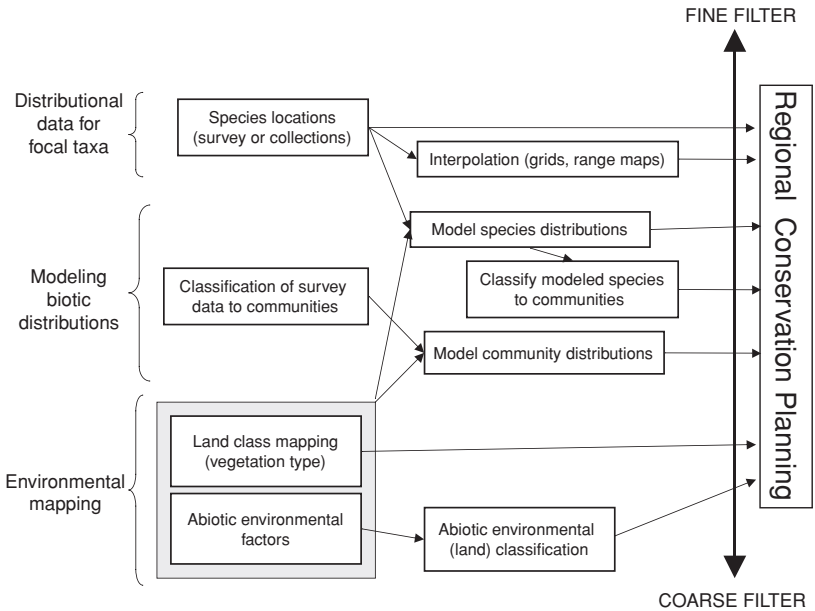


Fig. 1.3. Conceptual diagram (modified from Ferrier, 2002), showing how species distribution modeling, and specifically spatial prediction, supports regional conservation planning. Ferrier considers those entities (species, communities, other elements of biodiversity and the environment) for which good distributional data exist to be surrogates for the spatial distribution of biodiversity as a whole. These surrogates are used to ensure that conservation areas are designed to represent as many elements of biodiversity as possible. Species and community distribution modeling can be important tools in this framework, but so can direct interpolation of species locations (Chapter 2) and land classification systems, depending on data availability.

Kremen *et al.*, 2008; Thorn *et al.*, 2009), have made extensive use of SDM. Maps of species distributions or habitat suitability are required to prioritize or target areas for protected status, to assess threats to those areas, and to design reserves. To give just one of many examples, an impressive implementation was carried out by scientists at state agencies in Australia who developed models and spatial predictions for more than 4000 species of vascular plants, vertebrates, and ground-dwelling arthropods based on over a quarter of a million location records in a 100 000 km^2 region, and made important conceptual and methodological advancements along the way (Ferrier, 2002; Ferrier *et al.*, 2002b). Figure 1.3, modified from Ferrier (2002), illustrates how species distribution modeling supports regional biodiversity conservation planning.

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1.5.2 Impact assessment and resource management

Once a reserve is designed, or wherever land is managed at least in part to achieve conservation goals or manage wildlife populations, land management planning, or managing desirable species, may require predicting the impact of an activity on the habitat of a focal species or for related resource management decisions (for some recent examples, see Bradbury *et al.*, 2000; Nams *et al.*, 2006; Traill & Bigalke, 2006; Lopez-Lopez *et al.*, 2007; Massolo *et al.*, 2007; Newton-Cross *et al.*, 2007). In other words, an impact assessment or risk assessment is required (Rushton *et al.*, 2004; Burgman *et al.*, 2005). SDM can be used to develop spatially explicit predictions of habitat suitability or quality (Wu & Smeins, 2000; Gibson *et al.*, 2004). This can be compared to the expected spatial distribution of the impact such as land use change (for example, Wisz *et al.*, 2008a). For example, in one of the first published applications of SDM, Kessell (1976, 1978, 1979) modeled the potential distribution of many plant and animal species in support of wildland fire management in Glacier National Park, USA.

One specific use of SDM for resource and land management has been to designate so-called critical habitat for species that have legally protected status, e.g., under the US Endangered Species Act or similar legislation in Europe, Canada and elsewhere. In these studies, the results of an SDM are used to define the location and extent of habitat required for the protection or recovery of the focal species (Carroll *et al.*, 1999; Turner *et al.*, 2004; Carroll & Johnson, 2008; Thomaes *et al.*, 2008). In aquatic or marine ecosystems SDMs have been used to designate essential fish habitat as legally mandated by environmental legislation (Valavanis *et al.*, 2004).

1.5.3 Ecological restoration and ecological modeling

SDMs are increasingly being used to determine suitable locations for species reintroductions by associating maps of environmental factors with information on their historical ranges or habitat preferences using a model (Pearce & Lindenmayer, 1998; Schadt *et al.*, 2002; Carroll *et al.*, 2003; Hirzel *et al.*, 2004; Martínez-Meyer *et al.*, 2006).

In another exciting area of applied conservation biology, population viability analysis (PVA), a species-specific modeling framework used to forecast extinction risk (Beissinger & McCullough, 2002), has been widely used to predict the consequences of habitat loss and other threats for species of conservation or management concern (Brigham *et al.*, 2003;

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Akçakaya *et al.*, 2004; Henle *et al.*, 2004; Melbourne *et al.*, 2004). Population viability analysis often requires spatially explicit information about the distribution of habitat (location, size and quality of suitable habitat patches), and this can be derived using a SDM for the species under consideration (Akçakaya, 2000). PVA can incorporate landscape dynamics (Pulliam *et al.*, 1992; Lindenmayer & Possingham, 1996; Akçakaya & Atwood, 1997; Kindvall *et al.*, 2004), such as changing carrying capacities of habitat patches through time. SDMs may be used, in this case, to provide the initial conditions (spatial distribution of suitable habitat) or to provide maps of suitable habitat as different time steps whose changes are driven by landscape dynamics resulting from natural disturbance, land use change or climate change (Akcakaya *et al.*, 2004, 2005; Keith *et al.*, 2008).

Another form of ecological modeling, landscape modeling of plant community dynamics (e.g., forest succession), can require spatially explicit information on the distribution of potential habitat for the plant species comprising the community (He & Mladenoff, 1999; Mladenoff & Baker, 1999; Franklin, 2002; Franklin *et al.*, 2005). This information is typically generated using species distribution models. Again, this provides initial conditions for simulation models that explore the multiple impacts of natural and anthropogenic disturbance on ecological communities at large spatial scales (Syphard *et al.*, 2006; 2007; Xu *et al.*, 2007; Scheller *et al.*, 2008). For example, how do fire, logging, and climate change synergistically affect the distribution of late-successional forest patches on the landscape, and therefore on the distribution of old growth dependent species? Further, the initial distribution of species habitat provided by SDMs can then be modified by a landscape simulation model to provide dynamic habitat information to a PVA model (Akçakaya, 2001; Larson *et al.*, 2004) as described above.

1.5.4 Risk and impacts of invasive species including pathogens

Invasive species can have major economic and ecological impacts, and an important and growing use of SDMs is to determine locations where an invasive species is likely to establish (Peterson & Vieglais, 2001; Peterson, 2003; Andersen *et al.*, 2004). Two basic approaches are used – the first is to predict the geographic potential of an invasive species in a new region based on information about its habitat preferences in its native range (often using climate variables), and the second is to use information on where it has established in its new range to identify locations not yet

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invaded that may be at risk (Beerling *et al.*, 1995; Peterson & Robins, 2003; Underwood *et al.*, 2004; Mau-Crimmins *et al.*, 2006; Mohamed *et al.*, 2006; Roura-Pascual *et al.*, 2006; Herborg *et al.*, 2007; Loo *et al.*, 2007). Careful use of both kinds of distribution data (native range and invaded areas) can be very informative, indicating the degree to which invading species are restricted to the environmental conditions in which they are found in their native range during invasion (e.g., Broennimann *et al.*, 2007; Broennimann & Guisan, 2008). Some studies have specifically modeled factors associated with fitness of the invading species (Ficetola *et al.*, 2009). Multiscale environmental variables, including land use and other predictors in addition to climate, have been found to be important in predicting potential invasions (Meentemeyer *et al.*, 2008a; Ibáñez *et al.*, 2009).

In an inverted approach, Richardson and Thuiller (2007) modeled the current climatic distributions of South Africa's biomes, and then predicted the global distributions of regions with similar climates, thus identifying potential source areas for species likely to invade South Africa's biomes. While there are many factors involved in making an exotic, introduced species invasive (Rejmanek & Richardson, 1996), spatial prediction of the invasive species potential distribution based on environmental correlates with its established distribution is one tool for determining risk and targeting areas for monitoring and management.

If the species whose potential habitat is being predicted is a pest or disease organism that affects plants, animals or humans, or its vector or host, then spatial prediction of its potential distribution serves public health goals and supports epidemiological studies. This is another growing application of SDM (Kelly & Meentemeyer, 2002; Levine *et al.*, 2004; Saathoff *et al.*, 2005; Peterson, 2006; Raso *et al.*, 2006; Fleming *et al.*, 2007; Zeilhofer *et al.*, 2007; Menke *et al.*, 2007).

Predicting the potential location of alien species invasion, including pathogens, presents special challenges for SDM methods because the historical range or current distribution of the taxon may not fully represent the environments into which it might spread. An invasive species (a) can occupy environments outside its native range owing to competitive release, facilitation or genetic adaptations; or (b) may occupy a more restricted set of environmental conditions in a new location due to competition or dispersal limitations. Because of the ecological and economic importance of invasive species, the application of SDM and other approaches (such as genetic analysis or explicit consideration of dispersal) to risk analysis is an active area of research.

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1.5.5 Effects of global warming on biodiversity and ecosystems

Changes in natural systems attributable to anthropogenic climate change are now well documented (Walther *et al.*, 2002; Root *et al.*, 2003; Parmesan, 2006; Rosenzweig *et al.*, 2008). Species distribution modeling has been used to project the potential effects of anthropogenic global warming on species distributions and ecosystem properties for more than a decade (Neilson *et al.*, 1992; Lenihan & Neilson, 1993; Mackey & Sims, 1993; Iverson & Prasad, 1998; Rehfeldt *et al.*, 2006; Iverson *et al.*, 2008). However, more recently the use of species distribution modeling for this purpose (Thomas *et al.*, 2004) has received a lot of attention, as well as some criticism (Thuiller *et al.*, 2004a; Akçakaya *et al.*, 2006; Botkin *et al.*, 2007). In this subsection I will expand more on this use of SDM than on previous applications because of the importance of, and growing interest in, understanding the effects of anthropogenic climate change on natural systems.

Although the relationship between climate and species ranges is well established (Woodward, 1987), as is the relationship between climate change and species range shifts based on paleoecological studies (Huntley & Webb, 1988; Webb, 1992), using SDMs to predict the impact of global warming on species distributions requires a number of assumptions. It must be assumed that species distributions tend to be in equilibrium with the climate and this assumption does not account for time lags (Lenihan, 1993). Species distribution modeling, as it is defined in this book, is a "static" approach to modeling species geographical response to climate change – it does not take into account species ability to move on the landscape (dispersal or migration), or typically does so in simple ways – usually assuming "all or nothing" dispersal or migration into new suitable habitat, or limited dispersal to contiguous suitable habitat (Peters *et al.*, 2004; Araújo *et al.*, 2006; Heikkinen *et al.*, 2006; Midgley *et al.*, 2006; Thuiller *et al.*, 2006). Static SDM usually does not account for species interactions such as competition or predation, for evolutionary adaptation, or for a number of other potentially confounding factors, and thus could either over- or under-estimate species range shifts. Nevertheless, this tool for projecting the impacts of global warming in conjunction with other methods is continually being modified, improved and applied (Heikkinen *et al.*, 2006; Pearson *et al.*, 2006; Thuiller *et al.*, 2006; Lawler *et al.*, 2009).

However, it is worth discussing some of the controversy in the literature surrounding the use of SDMs to project the impacts of climate

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change on biodiversity. Controversy is a natural part of the scientific process, and it is important that practitioners state their assumptions and methods clearly so that their studies are replicable. In one study, already mentioned (Thomas *et al.*, 2004), the authors developed species distribution models for over 1000 species in half a dozen regions of the world. They then estimated the proportion of those species "committed to extinction" by using the species area relationship and assuming that loss of habitat area would be related to extinction risk in a predictable way. They concluded that 15%–37% of the species they studied would be committed to extinction caused by anthropogenic global warming by 2050, depending on the climate projections they used (e.g., Gallagher *et al.*, 2008) and the assumptions they made in their analysis. These estimates also varied by region and taxonomic group of species.

Thuiller *et al.* (2004a) responded that, although Thomas *et al.* had made an effort to measure the uncertainties in their estimates associated with different climate projections, there were additional sources of uncertainty in their approach that had not been accounted for (see also Botkin *et al.*, 2007). Specifically, they noted that the original study had been based on projections from a variety of SDM modeling approaches applied to different subsets of the data (species within regions). Thuiller *et al.* conducted additional analyses, based on a different dataset, using four different SDM methods for each species, but with the same species-area approach and assumptions used in the Thomas *et al.* study. They demonstrated that, for the region and taxonomic group that they modeled (over 1000 plant species in Europe), uncertainty in the estimated proportion of species committed to extinction varied as much due to the SDM method used as to the different climate change projections.

Buckley and Roughgarden (2004) also questioned the findings of the Thomas *et al.* study because they contested that the species–area relationship had been incorrectly applied. They also argued that extinction risk is unevenly distributed with respect to range size. They concluded that, while species are vulnerable to extinction due to climate change, it is premature to conclude that the risk due to climate is equal to or greater than that due to land use change (as Thomas *et al.* stated). Botkin *et al.* (2007) also discussed the limitations to the use of the species-area method of forecasting changes in biodiversity under global warming. Additionally, Botkin *et al.* specifically questioned the ability of static, equilibrium SDMs to predict future distribution, positing that changing species interactions and adaptations would result in systematic underestimation of future distributions by SDMs. Akçakaya *et al.* (2006) further

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argued that the responses of most species to climate change are too poorly understood (e.g., Austin, 1992) to estimate extinction risks solely from SDMs applied to climate change scenarios. They recommend that using multiple models to address the interactions among potential habitat shifts, landscape structure (dispersal barriers caused by land use patterns, landscape patterning caused by altered disturbance regimes), and demography for a range of species functional groups is a way to develop guidelines for assigning degrees of threat to species (see Keith *et al.*, 2008). For example, SDMs can be combined with realistic rates (Fitzpatrick *et al.*, 2008), or simple models (Iverson *et al.*, 1999, 2004a), of species migration to evaluate the potential impacts of climate change. Transplant experiments (Ibáñez *et al.*, 2009) can be explicitly combined with an SDM approach to projecting species range changes under climate change scenarios.

At the same time, the assumptions and conclusions of the original study were being debated in the scientific literature, some scientists also expressed concern that misrepresentation of that study in the media could be damaging to biodiversity conservation in the political arena. Specifically, exaggeration of the threat of climate change to biodiversity could result in conservationists being accused of "crying wolf." Some media reports were highly inaccurate, stating that the study predicted that a million species could be extinct by 2050 (Ladle *et al.*, 2004). However, coauthors of the original study voiced the opinion that the publicity about the extinction risk posed by climate change was worth the inaccuracies in reporting in some outlets (Hannah & Phillips, 2004). They felt that the benefits of connecting species extinctions to climate change for the public and policy makers outweighed the costs of errors in reporting the details.

Another study modeling the response of just two species to climate change focused on the use of regional, rather than global climate models as a more appropriate data source for predicting shifts in species distributions, especially in mountainous terrain (Kueppers *et al.*, 2005). The species were endemic oaks in California and this brought a response from Carmel and Flather (2006) that ignoring dispersal or colonization rates might actually underestimate the negative impacts of climate change on species distributions. Specifically, those authors cited the documented lack of regeneration of oaks on abandoned agricultural land in California over the last 60 years. Kueppers *et al.* (2006) responded that the limitations of species distribution models that use a climatic envelope approach (described in Chapter 8) are well documented, but that they remain an

https://doi.org/10.1017/CBO9780511810602.003 Published online by Cambridge University Press

important tool for estimating the first-order effects of climate change on species potential distributions (Pearson & Dawson, 2003).

I present these debates because I think they represent a healthy exchange of ideas in the scientific literature, and illustrate the importance of SDMs in the toolbox for predicting the impacts of land use and climate change on species distributions. I consider these arguments to be simply "growing pains" in the development of methodologies to address an important issue. One thing ecologists do agree on is that assessing the consequences of anthropogenic climate change for biodiversity is an important task on which scientific talent and resources should be focused (Thuiller, 2007).

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