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Species distribution models in conservation biogeography: developments and challenges

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EDITORIAL

Species distribution models in conservation biogeography: developments and challenges

Janet Franklin

INTRODUCTION

Species distribution modelling (SDM) associates georeferenced observations of a biotic response variable – typically species occurrence or abundance – with multiple environmental predictors using a broad array of statistical learning methods (Elith & Leathwick, 2009; Franklin, 2010b; Elith & Franklin, 2013). A model estimated from observations can then be applied to digital maps of predictors resulting in a spatial prediction of the response variable, for example probability of species occurrence or habitat suitability. Species distribution modelling has deep roots in spatial decision support for land management (Hoffer, 1975; Kessell, 1976; Strahler, 1981), weed or pest species risk assessment (Sutherst & Maywald, 1985; Busby, 1991) and studies of climate impacts on the biota (Busby, 1986; Nix & Busby, 1986). On the order of a thousand papers a year are currently being published that use SDM methods, dramatically increased from about ten per year in the 1980s (Peterson & Soberón, 2012).

Species distribution modelling (sometimes called environmental or bioclimatic niche modelling) relies on ecological theory of processes that mediate species distributions and abundance – especially niche theory (Austin, 2002). In fact, burgeoning applications of SDM appears to have driven a renaissance in niche theory development and articulation (e.g. Godsoe, 2010). Species distribution modelling also relies on, and lies at the foundation of, three decades of development in geographic information science (GIScience) and remote sensing. It is obvious that SDM requires geospatial data for spatial prediction, but it has also driven developments in the field of GIScience. Environmental and terrain modelling has been identified as one of the three major subdomains in GIScience, with the most cited literature in that area including papers by M. F. Hutchinson, I. D. Moore, A. K. Skidmore, M. P. Austin and A. Guisan (see Figure 2 in Goodchild, 2010); this classic literature is directly related to species distribution modelling.

Diversity and Distributions is a journal of conservation biogeography. Its mission is to publish papers that apply biogeographical principles, theories and methods (those addressing the distributional dynamics of taxa and assemblages) to problems concerning the conservation of biodiversity. The study of biological invasions is considered a key component of conservation biogeography, and the journal is an important forum for research on biogeographical aspects of biological invasions (Richardson, 2004; Richardson & Whittaker, 2010). *Diversity and Distributions* has seen a steeply increasing trend in the number of submissions and published studies that use SDM as a method of analysis. Of the 579 papers published between January 2008 and June 2013 (queried 23 June 2013), for example, 100 (and an additional 16 accepted and posted on EarlyView) used SDM in some capacity – that is, they developed empirical models of species-environment correlations that were used to make a spatial prediction. Those papers addressed problems ranging from forecasting risk of future biological invasions, pathogen spread and climate change impacts, to spatial conservation planning and historical biogeography (Fig. 1). They span taxonomic groups, habitats and geographical regions (Appendix S1).

This editorial serves as an introduction to a virtual issue of *Diversity and Distributions* that compiles key papers on species distribution modelling published in the journal (Table 1; Appendix S2). Papers selected for the virtual issue include contributions that both address pressing conceptual and methodological issues and provide key examples of the use of SDM for biodiversity assessment, conservation planning, risk analysis for invasive species and forecasting global change impacts. I selected those papers that have a high rate of citation relative to time since publication (empirical evidence that they are influential and useful; Table 1) or more recently published papers that are particularly creative in their use of SDM to support conservation biogeography (my subjective judgment or prediction that they will become influential). Another aim of the editorial is to suggest some profitable avenues of research relating to SDMs, both 'nuts and bolts' work on the philosophical underpinnings and technical aspects of such modelling, but also how SDMs could and should be used in advancing the aims of conservation biogeography.

The following sections describe the articles in the Virtual Issue and their linkages by grouping them into three areas: (1) those that address vexing methodological issues in SDM ranging from variability among modelling methods to sample size and sample design, (2) those that use SDM in innovative and rigorous ways to 'interpolate' species distributions in space, for example for biodiversity inventory, prospecting and conservation planning and (3) those that combine SDM with other data and methods in thoughtful ways to 'extrapolate' species distributions to different places or time periods to forecast impacts of environmental change on species

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Figure 1 Word cloud based on the titles and keywords of the 116 papers listed in Appendix S1 deleting the most common words which were as follows: **species**; **distribution**(s); **model**(s)(ing)(ling); **predict**. Developed using Wordle (http://www.wordle.net).

Table 1 Papers included in the virtual issue in chronological order of publication date. Number of citations (CITE#) based on Web of Science queried 13 May 2013

Paper	CITE#	Topic
(Dark, 2004)	62	Application invasives: spatial autoregressive model contrasting invasive versus non-invasive non-native plant species
(Thuiller *et al.*, 2006)	79	Application climate change: temperate areas of Europe predicted to lose tree functional diversity while boreal areas gain
(Elith & Leathwick, 2007)*	61	Methods: examine effect of background sample and multivariate response on SDM performance
(Osborne *et al.*, 2007)	48	Methods: Local regression methods may perform better for interpolation but global methods for extrapolation
(Guisan *et al.*, 2007)*	111	Methods: Effect of change in spatial grain on SDM performance
(Tsoar *et al.*, 2007)	141	Methods: compared six presence-only SDM methods
(Jiménez-Valverde *et al.*, 2008)	129	Concepts and methods: best models for realized versus potential distribution, performance as a function of prevalence, inaccuracy of SDMs
(Wisz *et al.*, 2008)*	203	Methods: Sample size effect on presence-only SDM methods
(Marmion *et al.*, 2009)	118	Methods: compared five consensus methods for SDM
(Puschendorf *et al.*, 2009)	31	Application pathogens: predict potential pathogen distribution from climate data
(Beaumont *et al.*, 2009)	75	Application invasives: predict invasive plant species distributions from native versus entire distribution
(Williams *et al.*, 2009)	31	Application new occurrences: compared SDM methods for predicting undiscovered populations of rare plant species
(Franklin, 2010a)	46	Concepts and methods: SDMs have been linked to other models to forecast impacts of environmental change on biodiversity
(Platts *et al.*, 2010)	11	Application conservation planning: predict distribution of forest plant taxa in biodiversity hotspot for conservation prioritization
(Elith *et al.*, 2011)	154	Methods: describes MaxEnt in statistical terms; links species and data characteristics to implementation decisions
(Dubuis *et al.*, 2011)	7	Application conservation: compared statistical models of species richness to estimates from stacked SDMs
(Václavík & Meentemeyer, 2012)	12	Application invasives: SDMs of invasive pathogen from different stages of invasion
(Hof *et al.*, 2012)	5	Application climate change: incorporate predator and prey distribution predictions into SDM forecast of climate change impacts
(Junker *et al.*, 2012)	2	Application conservation: changes in human impacts variables predict changes in suitable habitat for great apes
(Naujokaitis-Lewis *et al.*, 2013)	1	Application climate change: linked SDM-population models are sensitive to model uncertainty

*Papers initiated from, and using datasets compiled for, a working group at the National Center for Ecological Analysis and Synthesis (NCEAS), Santa Barbara, California, USA 'Testing Alternative Methodologies for Modelling Species' Ecological Niches and Predicting Geographic Distributions', led by A.T. Peterson and C. Moritz.

distributions or risk of biological invasions. I conclude with prospects and priorities for future research on modelling species distributions in support of conservation biogeography research.

METHODOLOGICAL ISSUES

Methodological papers included in the virtual issue tended to focus on challenges that face modellers who must rely on presence-only observations of species occurrences, such as those available from natural history collections and increasingly from global databases that compile those collections information and other observations. This group of papers also addressed methodological issues of spatial dependence and non-stationarity, sample design, data resolution, sample size and consensus forecasting. Tsoar *et al.* (2007) compared six presence-only modelling methods, and while they did find systematic differences in performance among methods, also found that differences among species tended to be consistent across models. Osborne *et al.* (2007) showed that local regression methods are appropriate for interpolation of species distributions in space, while global methods are more appropriate for extrapolation to different places or time periods. Dark (2004) also demonstrated that spatial (auto-)regression models were more effective at identifying correlates of distribution of invasive species than non-spatial models.

Elith & Leathwick (2007) examined the effect of background sample design on model performance for presence-only models, finding that target group background performed better than a random sample, a conclusion borne out by subsequent studies. Guisan *et al.* (2007) found that a tenfold (single order of magnitude) change in spatial grain of data did not greatly affect SDM performance; there was only a slight trend towards lower performance at the coarser scale. Wisz *et al.* (2008) described how SDM performance degrades with smaller sample sizes. Consensus forecasting is one way of dealing with SDM uncertainty (Araújo & New, 2007). Marmion *et al.* (2009) evaluated five methods for calculating or deriving a consensus prediction from multiple SDMs and found that simple averaging, or accuracy-weighted averaging, of the probabilities estimated by different methods for the same data were the best-performing consensus methods.

Elith *et al.* (2011) provided an explanation of a widely used SDM algorithm for presence-only data (MaxEnt) in statistical terms and showed how the characteristics of species and species data affect model implementation decisions. They demonstrated that lack of absence data means that species prevalence cannot be estimated, sample selection bias has a strong effect on presence-only models (and there are ways to select background sample with same bias as presences), and that the way the extent of the region is defined (that the background sample is drawn from) also has big effect on these models.

Conceptual papers included in the Virtual Issue address the importance of establishing a strong conceptual framework for matching methods with data and questions (Jiménez-Valverde *et al.*, 2008) and ways to use SDM in combination with other tools for forecasting or extrapolation (Franklin 2010a).

INTERPOLATING SPECIES DISTRIBUTIONS IN SPACE USING SDM

Species distribution modellings have proven to be powerful tools for conservation biogeography, especially when they are used for 'interpolation' – to fill in the geographical gaps in our knowledge of species distributions. This approach is effective when observations of species distributions are sparse, and correlations of those distributions with mapped environmental gradients are strong. Interpolation using SDM is very useful tool for biodiversity inventory, biodiversity prospecting (designing biodiversity surveys – predicting new occurrences), gap analysis, prioritizing areas for conservation (reserve design) and environmental impact analysis (determining how human activities including resource management might affect critical habitat for species of conservation concern).

Several recent examples of effective use of SDM to fill in the geographical gaps in species distributions are included in the virtual issue (Table 1). Platts *et al.* (2010) used SDMs to make spatial predictions of plant species richness for a biodiversity hotspot and suggested that because models are most uncertain for species of conservation concern, they should be developed iteratively with targeted fieldwork. Williams *et al.* (2009) took the next step in their study – several SDM methods were compared for their ability to predict the distributions of rare plant species, and further field surveys based on those predictions yielded discovery of new populations. Dubuis *et al.* (2011) compared direct statistical modelling of plant species richness as the response variable versus 'stacking' predictions from individual species models and concluded that both direct estimation (unbiased with correct response curve shape, but low accuracy) and the stacked approach (overestimating richness but yielding information about community composition) are complimentary and useful for conservation planning. Puschendorf *et al.* (2009) used SDM methods to predict the potential distribution of amphibian chytrid fungus in Costa Rica, a disease that threatens amphibians globally. Their study identified climatic (topographic) refuges where this pathogen, and therefore infectious outbreak, may be less likely; this information could be used for spatial conservation planning aimed at preserving amphibian diversity.

EXTRAPOLATING SPECIES DISTRIBUTIONS ACROSS SPACE OR TIME

Species distribution modellings are no longer enough on their own when we want to extrapolate, for example, the effects of future global (climate, land use) change on the biota, and risk of invasive species, although extrapolation has come to be their primary mode of application and has included studies remarkably broad in scope (Warren *et al.*, 2013). Species distribution modellings are limited in their ability to forecast to novel environments by their empirical nature and equilibrium assumption, especially if naively applied with inadequate data. If used with explicit consideration of these limitations, however, they can be an important part of a methodological toolkit used to address pressing forecasting needs (Franklin, 2010a).

There are three ways SDMs can be more effectively used for extrapolation. (1) Data or information from more mechanistic or process-based studies or models (population, ecophysiology, community dynamics) can be incorporated during conceptual and statistical formulation (see Table 9.1 in Franklin, 2010b), for example deriving explanatory variables, variable selection, model estimation, specifying interactions and response curve shape (Elith *et al.*, 2010). (2) SDMs can be linked with process models (Franklin, 2010a). This is sometimes called hybrid modelling (Dormann *et al.*, 2012), but often the output from one model is used as the input to another, without feedback, so 'linked' or 'coupled' modelling is more descriptive. (3) Predictions from SDMs can be compared with process-based models and much can be learned from where and how they agree and disagree, in light of their respective assumptions (for example Kearney *et al.*, 2010; Serra-Diaz *et al.*, In Press).

In the virtual issue, Hof *et al.* (2012) used the first approach to extrapolation, informing their SDM with information about important biotic interactions affecting the distribution and abundance of the focal species (predator–prey dynamics). Naujokaitis-Lewis *et al.* (2013) used the second approach, linking SDM and population models to forecast climate change impacts in a study of Hooded Warbler to examine uncertainty due to different Global Climate Models (GCMs). Population viability estimates were sensitive to GCM effect on vital rates, but more sensitive to direct habitat loss projected from SDM. Thuiller *et al.* (2006) contrasted the predicted changes in plant species richness under climate change when assuming no dispersal versus unlimited dispersal from current distributions to bracket the range of outcomes likely to be generated using process models that more explicitly simulated dispersal.

The problem of extrapolation to predict risk of invasive species was addressed by Beaumont *et al.* (2009) who found that including data from the entire (native and non-native) distribution of invasive species may better characterize its fundamental niche and better forecast potential for invasion in space and time, for example, under climate change (but see Webber *et al.*, 2011). Václavík & Meentemeyer (2012) used temporally explicit data on the invasion of a plant pathogen and demonstrated that SDMs calibrated at the early stages of invasion tend to underestimate the potential range compared with those calibrated with data from later stages. Dark (2004) sought to understand the environmental correlates of the distributions of invasive versus non-invasive non-native plant species in California (many of which are well established); she found the same factors to be important in both cases (lower elevations, higher road density and higher native plant species richness), pointing to the importance of species traits in determining whether an alien species is invasive or not.

Finally, a broad-reaching study recently published in *Diversity and Distributions* by Junker *et al.* (2012) modelled habitat suitability for African great ape taxa using environmental and human impact variables representing conditions in the 1990s. They projected these models to the 2000s based on updated human impact variables (population density, proximity to roads, etc.) and estimated losses of suitable habitat ranging from 11% to 59% for different taxa. While they cautioned that the coarse spatial scale of the analysis meant that it is informative to broad-, but not fine-scale conservation planning, their temporal extrapolation was short-term and well justified and was based on actual, observed changes in the driving variables (rather than modelled projections). This is an exemplary use of SDM for extrapolation over a limited time horizon in support of conservation biogeography.

PROSPECTS AND PRIORITIES FOR THE FUTURE

Because forecasting species distributions in novel or non-analogue environments is so central to conservation biogeography in an era of rapid global change (Sala *et al.*, 2000), research that develops and tests innovative ways of forecasting impacts of global change – climate change, land use change, invasive species including emerging infectious diseases, altered disturbance regimes – on biodiversity should be of great interest to *Diversity and Distributions*. Hindcasting distributions to address historical and phylogeographical questions can also inform conservation biogeography (e.g. Porto *et al.*, 2013; Smith *et al.*, 2013). Molecular methods can provide genetic information about historical demography and dispersal dynamics of taxa (Scoble & Lowe, 2010; Duckett *et al.*, 2013). Incorporating information about diversity below the species level may be particularly important for identifying genetically and geographically structured populations that may differ in their potential for genetic adaptation to environmental change (Hamann & Aitken, 2013) or for invading new regions (Thompson *et al.*, 2011). In addition to genetically distinct populations, understanding factors driving the distributions of species' functional types or traits (McGill *et al.*, 2006; Kearney & Porter, 2009), as well as community properties such as taxonomic or phylogenetic diversity, effectively links ecological theory to conservation biogeography (e.g. Slik *et al.*, 2009; Dubuis *et al.*, 2011; Syphard *et al.*, 2013). Shifts in disturbance regimes that play out at large spatial scales may have important implications for conservation biogeography (Reside *et al.*, 2012; Syphard *et al.*, 2013).

Moving forward, *Diversity and Distributions* is interested in publishing those studies that use insights from phylogeography and palaeodistribution dynamics, draw in cutting-edge work on genetics, and build on key developments in invasion, population and community ecology, to address critical information needs in conservation biogeography. These studies are likely to be multiscale and multidisciplinary, interfacing with climate and land change science, so that drivers of species distributions can be characterized at relevant scales. Species distribution modelling can be part of a methodological toolkit to address these information needs. Its limitations are well known, but solutions to those limitations are also being described in the growing literature on this topic. Often overcoming those limitations involves collecting additional data about species, ecological communities and habitat (Elith & Franklin, 2013).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species distribution modelling (SDM) papers published in *Diversity and Distributions* Jan 2008 – May/Jun 2013.

Appendix S2 Virtual Issue – Species Distribution Models in Conservation Biogeography: Developments and Challenges.