ELSEVIER

Ecological Modelling 157 (2002) 313–329

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Mapping epistemic uncertainties and vague concepts in predictions of species distribution

Jane Elith *, Mark A. Burgman, Helen M. Regan

School of Botany, The University of Melbourne, Parkville 3010, Australia

Abstract

Most habitat maps are presented as if they were a certain fact, with no indication of uncertainties. In many cases, researchers faced with the task of constructing such maps are aware of problems with the modelling data and of decisions that they make within the modelling process that are likely to affect the output, but they find it difficult to quantify this information. In some cases they attempt to evaluate the modelled predictions against independent data, but the summary statistics have no spatial component and do not address errors in the predictions. It is proposed that maps of uncertainty would help in the interpretation of these summaries, and to emphasize patterns in uncertainty such as spatial clustering or links with particular covariates. This paper reviews the aspects of uncertainty that are relevant to habitat maps developed with logistic regression, and suggests methods for investigating and communicating these uncertainties. It addresses the problems of subjective judgement, model uncertainty and vague concepts along with the more commonly considered uncertainties of random and systematic error. Methods for developing realistic confidence intervals are presented along with suggestions on how to visualize the information for use by decision-makers.

Keywords: Epistemic and linguistic uncertainty; Generalized linear models; Logistic regression; Vagueness; Confidence intervals; Prediction; Visualization; Model

1. Introduction

Predictions from models of species-habitat associations are commonly interpreted as measurements of the 'suitability' of sites for the species of interest, and can be used as the basis for land-use decisions and conservation planning strategies (e.g. Corsi et al., 1999; Jarvis and Robertson, 1999; Manel et al., 2001; NSW NPWS, 1998). In many cases, researchers faced with the task of constructing such habitat maps are acutely aware of deficiencies in the modelling data and of decisions that they make within the modelling process that are likely to affect the output. Visualizations of uncertainty could be stored as part of the suite of maps relevant to the species in a geographic information system (GIS) and used to inform decision-makers of regions that are prone to extreme error or that appear particularly well-modelled. But in general, habitat suitability maps are presented as precise digital representations that give the impression of certainty. Even though

* Corresponding author. Tel.: +61-3-8344-4572; fax: +61-3-9347-5460
E-mail address: j.elith@botany.unimelb.edu.au (J. Elith).

0304-3800/02/$ - see front matter
PII: S0304-3800(02)00202-8

levels of uncertainty may be quantified with prediction intervals, uncertainty is rarely factored into the decision-making processes to which the maps contribute. This deprives the users of information that could be crucial to their interpretation of the data, particularly if circumstances suggest the decision-maker should not be risk-neutral. In the long term it increases the risk that conservation effort will be misdirected and ineffective. Mapped confidence intervals are also essential for analyses of the propagation of uncertainty into other models—for example, where habitat maps are used as an input to a population viability analysis (Akçakaya et al., 1995; Burgman et al., 1993; Possingham et al., 1993; Elith and Burgman, 2002).

Generalized linear models (GLMs) are being used with increasing frequency for habitat modelling, but there appear to be very few examples where there is anything but a brief discussion of the uncertainties in predictions. The objectives of this paper are to review the aspects of uncertainty that are relevant to habitat maps developed with GLMs applied to presence-absence data, and to outline and illustrate methods for investigating and communicating these uncertainties. Many of the ideas will be more broadly applicable to other types of habitat models. If methods can be developed for clearly communicating prediction uncertainties to end-users it is likely that decisions will become more sensitive to uncertainty. Moreover, a clear representation of the source and location of most uncertainty will help focus efforts to areas where a lack of information is a hindrance to decision-making.

2. Classifying uncertainty

In a broad sense, uncertainty refers to a lack of sureness or confidence about something. It is sometimes thought of as being synonymous with 'error', where error includes not only 'mistakes' and 'faults' but also the statistical concept of 'variation' (Heuvelink, 1998). Recently Regan et al. (2002) developed a taxonomy of uncertainty that identifies the main sources of uncertainty in biological systems and outlines appropriate methods for dealing with each type. Their work provides a useful framework for considering uncertainties in models of species distribution. They propose that uncertainty falls broadly into two main groups: epistemic uncertainty (uncertainty about a determinate fact) and linguistic uncertainty (uncertainty that arises because our natural language is vague, ambiguous, and context dependent, and because the precise meaning of words can change in time). Both linguistic and epistemic uncertainty can be present in modelled predictions.

The following exploration of classes of uncertainty uses the taxonomy developed by Regan et al. (2002) and outlines sources that are most common in modelled predictions, including measurement error, systematic error, natural variation, model uncertainty, subjective judgement, and vagueness (see Table 1).

3. Epistemic uncertainty

3.1. Measurement error

Measurement error arises from imperfections in measuring equipment and observational techniques, and imprecision in computer processes. It results in apparently random variation around a mean value. Some of the uncertainties in species records are due to measurement error. A whole population is rarely sampled, some individuals may be unintentionally sampled more than once, individual observers may make different observations in identical circumstances, and locations may be recorded inaccurately or rounded inconsistently. This is true for presence-absence records, for counts, and for estimates of continuous variables such as cover.

Measurement error also contributes to uncertainty in predictor variables. Models and predictions are usually made on variables stored as GIS layers. These are commonly produced by interpolation of field-based measurements, interpretation of aerial photos or satellite images, or modelling of physical processes. Uncertainty exists in the base data and is propagated as the data are summarized, classified, modelled and interpolated. Whilst some of this uncertainty is model uncer-

Table 1
Summary of some classes of uncertainty, with examples

Uncertainty	Brief explanation	Ideas for dealing with it, with examples
Epistemic		
Measurement error	Imperfect measurements or techniques produce random variation in result, e.g. available equipment may not record location precisely	Provide bounds, confidence intervals (e.g. Stoms et al., 1992; Crosetto et al., 2000)
Systematic error	Methods produce biased data, e.g. sampling is close to roads	Recognise and remove bias (e.g. Cawsey et al., 2002)
Natural variation	Real systems change in ways that are difficult to predict and hard to characterise	Represent response with a probability distribution, e.g. in GLMs
Model uncertainty	Models are simplifications of real processes, and several models may fit the data	In explanatory variables: produce multiple realizations of the variable (e.g. Goovaerts, 2001). In GLM: allow >1 model (e.g. Wintle et al., 2002b)
Subjective judgement	Experts estimate facts or classifications	Assign degrees of belief or imprecise probabilties (e.g. Ho and Smith, 1997)
Linguistic		
Vagueness	Nature does not arrange itself into strict classes, so sharp boundaries and homogenous classes do not represent reality	Use fuzzy sets (e.g. Davis and Keller, 1997b; Roberts, 1996), supervaluational approach (Fine, 1975; Regan et al., 2002)
Ambiguity	Words can have more than one meaning	Clarify meaning (e.g. Meyer and Printzen, 2000)
Underspecificity	Data may have unwanted generality, e.g. location not precisely reported	Provide narrowest bounds (e.g. Lynn et al., 1995)
Compounded	Several types of uncertainty can be present in one set of data or model	Use Monte Carlo simulations to combine realizations of uncertainties in the constituent parts (e.g. Davis and Keller, 1997a; Stoms et al., 1992)

tainty because a model (such as kriging, nearest neighbour and so on) has been used to interpolate expected values, measurement error is represented by uncertainty at the actual measured or mapped points. Other sources of measurement error in predictor variables include translation of vector data into raster format, and uncertainty about the exact location of polygon boundaries for data such as tenure classes that are, in principle at least, sharply defined (Burrough, 1986). Information on the likely magnitude of errors in such data products is hard to find and, if it exists as metadata accompanying the GIS layer, is usually a brief summary statement for the whole layer.

3.2. Systematic error

Systematic error results from bias in measuring equipment, sampling procedures or GIS operation. It is not random, is difficult to recognize except on theoretical grounds, and can only be corrected by more careful consideration of the relevant theory and experimental methods, by double sampling or by post-hoc correction factors. However, systematic error is difficult to treat and post-hoc correction factors may indeed introduce further biases if the direction and magnitude of the error is unknown.

Uncertainty in species data is partly systematic error. Where data are used beyond their original intention, or when there are constraints on time or money, errors are especially prone to bias. For instance, sampling is commonly close to roads, and may be focussed in some vegetation types or landscapes, or biased away from ecotones. In these cases efforts are sometimes made to supplement the existing data with records in poorly sampled strata (Cawsey et al., 2002) or to adjust modelling methods to cope with incomplete coverage (Augustin et al., 1998). However, the effect of the uncorrected biases are difficult to predict and are not well researched. Mobile and cryptic species are difficult to detect, and tend to be underestimated by common field survey techniques (Lindenmayer et al., 2001; Wintle et al., 2002a). A species may be consistently overlooked in part of its range because of disturbance or successional dynamics, or because of incorrect identification where there is partial overlap with sister species.

In some cases systematic error is present in species data but is not detrimental to the purpose of the modelling. For example, predictions may be required for ranking sites according to the relative likelihood of species presence. If the species data were systematically biased in the same direction in each case, it is possible that the model predictions will be poorly calibrated but will still have good discrimination. The relative rank of sites is of interest here, rather than absolute estimates of the likelihood of species presence. In such cases careful model evaluation is required to investigate the nature of the bias and its effect on predictions (Pearce and Ferrier, 2000).

Predictor variables can be biased. As the grain at which data are recorded becomes coarser, units that exist at a finer grain are subsumed into more prevalent ones, leading to a bias against unusual classes (e.g. rare vegetation classes). Alternatively, mapping may be biased towards classes with unusual and noticeable properties, such as those with greater reflectivity, e.g. a lake, road or grassland. Uncertainty that appears to be random at one scale may be shown to be biased at another. It may also be spatially clustered, such as errors in a digital elevation model (DEM) which may be globally small but locally large and spatially correlated (Holmes et al., 2000).

Spatial autocorrelation (SA) is the tendency of neighbouring units to have more similar (positive SA) or more different (negative SA) characteristics than expected for randomly associated pairs of observations (Legendre, 1993). This is a potentially widespread problem for modelled distributions. Neighbours may be similar because of a patchy resource, and careful modelling of the relationship between the resource and the species will successfully describe the distribution of the species. However, many species are also influenced by their neighbours through contagious biotic processes such as reproduction, mortality, predator–prey interactions, disturbances, social organization and so on. In these cases spatial autocorrelation occurs, and if it is not accounted for in the model, parameter estimates will be biased (Fox et al., 2002) and standard errors will be underestimated.

3.3. Natural variation

Natural variation exists in systems that change (for example, with respect to space or time) in ways that are difficult to predict. Regan et al. (2002) comment that it ‘is not a source of epistemic uncertainty per se—it is just that the true value of the parameter in question is changing as a result of changes in independent variables. It is often regarded as a source of uncertainty because the true value of the quantity of interest is usually extraordinarily difficult to measure or predict across the full range of temporal and spatial values’.

Species data exhibit natural variation, and it is unlikely that this variation would ever be fully characterized. Models that are used to predict habitat suitability are usually incomplete because they do not incorporate all of the underlying mechanisms for variation. Knowing that a species currently occurs in a few locations and in a couple of habitat types is not enough information to predict occurrence without error in other locations. Such predictions would require knowledge of all the underlying causal mechanisms of species occurrence at very refined temporal and spatial scales and full understanding of the dynamics of the species, its interactions with other species, and its reliance on ecological factors. Fielding and Bell (1997), Austin (2002) and Guisan and Zimmerman (2000) discuss further cases of biotic variation including intra- and inter-specific interaction, the spatial structure of historical events, the effect of individual variability on site selection for cryptic advantage, and issues related to scale.

If all causes of variation were known and could be quantified, prediction would be certain and 'present' or 'absent' would be the only necessary predictions from presence-absence data. Since it is impracticable (if not impossible) to make error-free predictions, usually predictions are made in terms of the chance of occurrence. 'Natural variation' summarises the uncertainty of the prediction as the chance that the response takes a particular value, or as a distribution of possible values for the response at a particular time and place that arise as a consequence of a species' response to its environment.

The usual way to deal with incomplete knowledge of the natural variation in a dependent variable is to construct a probability distribution for the quantity in question that encompasses the full range of possible values. For instance, logistic regression specifies the distribution of the response as binomial, and the logit link has a variance function of $\mu(1-\mu)$, where μ is the estimated response (McCullagh and Nelder, 1989, and Guisan et al., 2002). This variance function contributes to the estimated confidence intervals around predictions (see later). In other words, the confidence intervals encompass uncertainty due to natural variation.

3.4. Model uncertainty

Model uncertainty arises, in the case of GLMs, because models are used to represent biological or physical processes. This type of uncertainty does not refer to the uncertainty in parameter estimates, but rather addresses the simplifying assumptions and the abstraction of ecological processes required by any model. It is widely recognized that parsimony is an important goal in model building (McCullagh and Nelder, 1989). Within reason, simpler models have wider applicability and are generally better overall predictors of species presence than more complex models because they are less likely to be fitted to the peculiarities of a particular sample of species data. However, there is a trade-off between under-fitted models, in which bias is large and precision is overestimated, and over-fitted models, which may be free of bias but have needlessly imprecise parameter estimates (see, for example, Chatfield (1995) and the discussion of the tradeoff between bias and variance in Burnham and Anderson (1998) and Hastie et al. (2001)).

While effort is usually dedicated to developing the 'best' model for a species, in reality the final model is only one of many possible models. Decisions about how to select a model, which predictors should be included in the initial candidate set, whether factors are included with all available levels or as binary subsets, how to test for collinearity between predictors and how to decide which variables in a collinear set should be retained, what form the response is allowed to take (linear, quadratic, smoothed and so on), how to handle interactions, whether to transform predictors to an orthogonalized dimension, how to deal with spatial autocorrelation and overdispersion, and how to define the link and variance functions, are all embedded in the final model. In reality there are a suite of competing models for the spatial distribution of a species, and selection of one model should not imply that it is the correct one. Some modelling approaches such as Bayesian Model Averaging (BMA) that specifically allow for more than one model are discussed in a later section.

3.5. Subjective judgement

Another type of epistemic uncertainty arises when subjective judgement is used to interpret data. For example, Pausas et al. (1995) used subjective estimates from three field biologists to develop a variable that indicated how prone particular tree species were to developing hollows. Similarly, field records of 'suitable' or 'unsuitable' habitat can be made instead of records of species presence or absence, but they rely on an expert's interpretation of the environment and its effect on the species. A degree of uncertainty accompanies the expert's judgement. The uncertainty is epistemic because the experts estimate a determinate fact based on experience, knowledge of environmental systems, and anecdotal observation.

4. Linguistic uncertainty

4.1. Vagueness

Vagueness is a type of linguistic uncertainty that arises because natural and scientific language allows borderline cases. For instance, the number of mature plants in a population may be uncertain because some individuals, such as older juvenile plants, are apparently neither mature nor are they not mature—they are borderline cases and it is not clear whether they should be counted or not. In cases such as these, the uncertainty arises because there is no precise fact that defines what constitutes a mature plant. Before the number of mature plants can be counted, it is necessary to decide what is meant by the term 'mature plant' (such as individuals that have reproduced, are capable of reproduction, have reached a certain age or size, or have achieved a specific social status). Typically, vagueness is dealt with by using arbitrary sharp boundaries to define terms (such as, a mature plant has a stem diameter >5 cm). But such an approach submerges the ecological reality and leads to a tension between the original meaning of the vague term and the technical term created with the sharp delineation (see Regan et al. 2000). Vagueness can be found in concepts with a natural numerical ordering (such as seedling, juvenile, mature that can be ordered according to age or size) but also in concepts without a numerical order, such as vegetation classes. Most ecologists now accept the individualistic continuum view of vegetation (McIntosh, 1967; Whittaker, 1967), in which vegetation types or communities are understood to be intrinsically arbitrary subdivisions of continuous patterns. Vegetation classes mapped as polygons are an arbitrary quantification of a vague concept.

Vagueness is often referred to in the GIS literature as classification fuzziness (e.g. Davis and Keller, 1997a), but Regan et al. (2002) recommend the term 'vagueness' on the grounds that it does not prejudice the selection of a method for dealing with it. Use of the term 'fuzziness' may lead to the adoption of fuzzy measures, which are just one of a set of potentially useful tools (see Regan et al. 2002, and Table 1).

4.2. Ambiguity

Ambiguity arises because some words have more than one meaning, and it is not clear which meaning is intended. Regan et al. (2002) use the example of 'cover', which could refer to projective foliage cover (which excludes gaps in the canopy from its measure) or to crown cover (which is determined by the perimeter of the crown and thus includes gaps). Ambiguity can be a problem in modelling when records from a number of sources are being used and the original researcher is not accessible for, or cannot help with, clarification of the record.

4.3. Underspecificity

Underspecificity is present where there is unwanted generality in data. For example, historic records of species locations are often very general, e.g. 'north-east of Melbourne'. While the species location is actually more precise than this (at least for immobile species), the choice of language to describe locality obscures the information and renders the record underspecific. In this way it can be considered as a source of linguistic uncertainty. The recording of information in this underspecific manner can be regarded as information loss if the original data on which the record is based was more precise than this general description. However, historically observers may have considered that there was no precise locality (i.e. the actual observation represents the species existing north-east of Melbourne). In many instances, when historical data have been recorded in this way, they are too general to be useful in quantitative applications.

Underspecificity can also arise as a result of epistemic uncertainty. Today observations of species location are likely to be recorded to within a few meters of the true location with a global positioning system. The current trend is to think of location in terms of precise coordinates, so if it is recorded generally (e.g. the location is within a 100 km radius of specified coordinates) the underspecificity is due to epistemic uncertainty.

5. Compounded and interrelated uncertainties

This list of possible sources of uncertainty is not complete. But the elements are rarely acknowledged explicitly, despite their pervasive presence. It is clear that some data will carry uncertainty from several different sources. For instance, there are a number of factors that influence prediction success. A prediction of habitat suitability can be realized as false because: (i) the model on which the predictions are based is an incomplete representation of the system; (ii) the data on which the prediction is based are subject to measurement error, systematic error, model uncertainty (in the case of interpolated GIS data) and subjective judgment; (iii) the ecological system is subject to spatial and temporal variation as well as variation in other parameters and processes making it difficult to predict species occurrence across the full parameter space; (iv) underspecificity in historical records may be so general that it swamps predictions.

Incomplete knowledge of the ecological system and errors in observations will always lead to uncertainty in predictions. Models used to predict species presence are based on observations of current distribution, and in a strict sense, predictions are estimates of the probability that the species currently occupies a site. Within a recovering or an expanding population it is not always clear whether some of the current absence records are actually records of unsaturated but suitable habitat (Capen et al., 1986). Furthermore, some observations of presence may be recorded in habitat unsuitable for the persistence of a population. Van Horne (1983) pointed out that density and demographic success are not necessarily closely related. Individuals of a species may not congregate in the most suitable locations because of behavior, intraspecific competitive exclusion, or dispersal dynamics. As a result of such processes, population sinks may have high population densities, but they may be of relatively limited value in contributing to the likelihood of persistence of a species. Buckland and Elston (1993) suggest that different models may be needed to estimate presence and suitability.

Temporal uncertainty (Davis and Keller, 1997a) is likely to affect both species data (often collected over a number of years but modelled as if they are current) and predictor variables (e.g. vegetation classes interpreted from old images). Age of data can also present problems where there is a mismatch between the year(s) when species data were collected and the year(s) represented in GIS layers for disturbance events. In some cases these uncertainties could be interpreted as natural variation (the habitat is broadly suitable but knowledge is not detailed enough to model temporal fluctuations). In others it could be viewed as measurement error (the aim is to model current distribution but old and inaccurate data are used).

Linguistic uncertainty only adds to the mix. For example, an estimate of the number and cover of mature woody shrubs of a rare species on a rocky outcrop is likely to be uncertain because of vagueness (there are borderline cases between ‘mature plants’ and ‘not mature plants’) and ambiguity in the definition of cover, and also because of epistemic uncertainties: measurement error (some plants may not be counted), systematic error (shrubs on the steepest slopes are more difficult to sample and less likely to be included in the count), and temporal variation (the number of shrubs changes in time). The errors will have both a random and a systematic component.

Definition of the source of the variation is important in as much as it clarifies the problem and points to ways to correct the errors or account for the resulting uncertainty in predictions. Any attempt at quantifying uncertainty cannot address all uncertainties, but in many cases modellers have an appreciation of the deficiencies in their data and of the decisions they have made that are likely to influence predictions. This can be a starting point for dealing with uncertainty.

6. Quantifying uncertainty in predictions

6.1. Confidence intervals: dealing with epistemic uncertainty

One way to begin to quantify uncertainty is to estimate confidence intervals around predictions.

The usual confidence intervals for predictions from a GLM express the uncertainty associated with parameter estimation in the final model. In the case of linear regression with normal errors, confidence intervals for one particular value of the response ('prediction intervals') are wider than those for the mean response because an extra term is used to describe the added variability of an individual's response over the group's mean response (Kleinbaum et al., 1998). The prediction intervals are allowing for natural variation in the response of the new individual. The situation is different for logistic regression, because the fitted values for any individual must be either 0 or 1. That is, no extra individual variability is possible. Therefore the only possible confidence interval is that for the fitted logistic regression line (Hosmer and Lemeshow, 1995).

The simplest and most commonly used interval estimate for a fitted value in logistic regression is a Wald statistic confidence interval for the logit, but other parametric intervals are available for special situations (Table 2). These confidence intervals encompass uncertainty from a number of sources. For example, species data are a sample and may not be sufficient to estimate parameters (see Harrell et al., 1996; Miller, 1990; Steyerberg et al., 1999), and species data may be sparse in part of the environmental space. These have elements of measurement error and systematic error. The intervals are also affected by the specification of a particular error distribution for the response. In the case of logistic regression, this influences the weights which are used in calculation of the residual deviance, which are in turn used to calculate the likelihood of the parameter estimates. This uncertainty can be attributed to natural variation. Any uncertainties that influence the precision of parameter estimation will be included in the confidence intervals. Since the standard error of parameter estimates depends on the curvature of the log-likelihood function at its maximum (Agresti, 1996), uncertainties that decrease this curvature will increase the Wald CIs.

There are other sources of uncertainty that contribute to the confidence intervals, but their contribution actually misrepresents the truth. For example, selection algorithms such as stepwise, forward or backward selection lead to selection biases because a variable will tend to be selected if its parameter is overestimated (Chatfield, 1995; Miller, 1990). This results in parameter estimates that are biased high and standard errors that are biased low, resulting in falsely narrow confidence intervals (Harrell, 2001). In the statistical literature this is categorized as model uncertainty (e.g. see Chatfield, 1995; Draper, 1995) because it reflects the fact that the true model is not known and that selection procedures have been employed to find a 'good' model. However, it could be argued that it is more broadly due to measurement and systematic uncertainty in the data, because these lead to inaccurate parameter estimates. Regardless of its classification, such uncertainty affects the usual confidence intervals but is not properly represented (that is, it makes them narrower rather than wider) and needs to be investigated in other ways.

Confidence intervals can also be estimated with bootstrap methods (Buckland and Elston, 1993; Davison and Hinkley, 1997; Efron and Tibshirani, 1993). There are different types of bootstrap confidence intervals (for example, percentile, BCa, bootstrap t-interval (Efron and Tibshirani, 1993)) and these are calculated on bootstrap samples generated under two approaches to Monte Carlo sampling (Hall, 1992) (Table 2). Bootstrapped confidence intervals account for different sources of uncertainty depending on the approach taken, and particular methodologies need to be analyzed to understand what is represented in the final estimate of uncertainty.

6.2. Widening the bounds for epistemic uncertainty: model uncertainty

In all of the above cases, confidence intervals will be too narrow because they do not properly deal with uncertainty about the model or uncertainty in the species and/or covariate data. However, a treatment of model uncertainty is no trivial matter. The best (or closest) representation of the system is extremely difficult to determine. This is the 'structural uncertainty' of Draper (1995) and Chatfield (1995) and is a separate issue from the uncertainty in the parameter values on which a model relies. It is likely to have a substantial effect

Table 2
Particulars of confidence intervals (CIs) and their estimation

Estimate	Description	Comments	References
Wald CI	Two-sided $1-\alpha$ interval CI is: logit $\pm z_{1-\alpha/2} s$ where z is critical value from normal distribution and s is the estimated large-sample standard error (ASE)	ASE is estimated from information in the variance–covariance matrix. Wald CI easy to calculate in most advanced statistical packages	Agresti (1996); Collett (1991); Harrell (2001)
Other parametric CIs	e.g. score and LR-based CIs	May be more appropriate in some situations	Harrell (2001); Hauck (1983); Doganaksoy and Schmee (1993)
Robust covariance estimates	e.g. 'sandwich' estimator, bootstrapped CIs. Consider these in conditions where usual matrix based on Fisher information matrix is not valid: e.g. if model incorrect because non-independence, lack of fit	These address systematic uncertainty and model uncertainty and attempt to account for them within the Cis	Huber (1967); Harrell (2001)
Bootstrap CIs—non-parametric	Do not rely on any assumption about the model. Each of many resamples is generated by sampling with replacement vectors of data from the original sample.	For regression models resampling is usually from residuals, and GLMs require special methods for scaling and sampling the errors.	Efron and Tibshirani (1993); Davison and Hinkley (1997); Buckland and Elston (1993)
Bootstrap CIs—parametric	Considers the predictors to be fixed and generates a sample according to the model.	Has the disadvantage that datasets generated from a poorly-fitted model may not have the statistical properties of original data—for example, in cases of unmodelled overdispersion	Buckland and Elston (1993), Harrell (2001), Davison and Hinkley (1997)

on model predictions and therefore on the confidence intervals (Buckland et al., 1997; Burnham and Anderson, 1998; Chatfield, 1995; Draper, 1995). For example, a model that mis-specifies the dependence of the probability of presence on explanatory variables may have confidence intervals of an appropriate width but in the wrong place (Miller, 1995)—that is, the entire interval may be shifted away from the true value because of systematic uncertainty. Some methods for exploring the problem include model checking (goodness-of-fit tests, calibration tests, tests on the residuals including testing for the presence of spatial autocorrelation (Bio 2000; Pearce and Ferrier 2000; Fox et al., 2002)) and testing the predictions against independent data (Fielding and Bell, 1997). These produce useful summary statistics for the particular locations where species records have been collected, but cannot be mapped over an entire geographic area. Nevertheless, they are essential as part of the suite of model testing tools.

Bayesian methods (BMA) avoid selecting a single best model by averaging over a number of plausible competing models. Each model contributes to the prediction proportionally to the support it receives from the observed data and prior knowledge. Several approaches have been advocated—see, for example, Draper (1995) on model expansion, Madigan and Raftery (1994) on Occam's window, and Madigan and York (1995) on Markov chain Monte Carlo techniques. Bayesian methods have been applied to GLMs for prediction and for estimation of confidence intervals (e.g. see Raftery et al. 1997; Wintle et al., 2002b). Alternatively, Buckland et al. (1997) and Burnham and Anderson (1998) present less complex non-Bayesian methods that assign a weight to each model in proportion to their relative penalized likelihood, or in proportion to the number of times it is selected in many bootstrap resamples. Any of these methods could be implemented as part of a strategy for investigating the effect of model uncertainty on predictions and their confidence intervals. All of them will only encompass the set of models initially considered, so that ignorance or lack of data that leads to problems such as omission of important variables will still be unrepresented in the confidence intervals.

6.3. Widening the bounds for epistemic and linguistic uncertainty in model inputs

Model inputs (species and covariate data) may include many types of epistemic and linguistic uncertainty. There is an expanding research effort addressing uncertainty in the GIS field, and it is remarkable that few of the concepts about uncertainty or of the methods for dealing with it have been applied to ecological modelling. Two relatively early publications (Burrough, 1986; Lodwick et al., 1990) present detailed summaries of sources of possible errors in GIS and provide examples and discussions of many of the error classes of Regan et al. (2002), including measurement error, natural variation, model uncertainty, systematic error and linguistic uncertainty.

Uncertainty in model inputs is not explicitly accounted for in the usual confidence intervals of GLMs. However, it could be argued that a portion of it is indirectly incorporated because data error is likely to make parameter estimation less precise. A recent analysis of input uncertainty on prediction uncertainty in GLMs applied to wetland plant species showed that confidence intervals due solely to input uncertainty can be very wide (van Horssen et al., 1999).

Sensitivity analyses (e.g. Crosetto et al., 2000; Stoms et al., 1992) allow users to quantify the uncertainties in species data and explanatory variables and to explore the extent of their effect on predictions. They require information on the type, magnitude and spatial distribution of error in the input. The GIS literature provides a range of methods for defining the uncertainty in point, line, raster and vector data—see, for example, Fisher (1991), Holmes et al. (2000), Stoms et al. (1992), De Genst et al. (1999) and Hunter et al. (1999). In many modelling situations, however, there is no definite information available about errors associated with covariate data, and the only option is to make informed guesses about error type and extent. This is clearly far from ideal and runs the risk of misrepresenting the true uncertainty in the data (Heuvelink, 1998), but is preferable to making no attempt at characterizing the input error. Examples of studies where expert knowledge has been used to quantify at least some of the error include Stoms et al. (1992), Davis and Keller (1997b) and Thorsen et al. (2001). The 'informed guess' could be based on available data-for instance, in the case of subjective judgement, where experts have been used to classify data, the extent and frequency of disagreement in the classifications could be simulated in new realizations of the data.

Errors can be treated in a variety of ways from a mathematical perspective—for example, they can be represented by intervals, probability distributions, degrees of belief, fuzzy sets and so on. See Regan et al. (2002) for a discussion of the appropriate treatment for the different sources of uncertainty, Davis and Keller (1997b) for an example using fuzzy sets, and Stoms et al. (1992) for an application of probability distributions.

Monte Carlo methods (Hammersley and Handscomb, 1964; Manly, 1997) are commonly used within sensitivity analyses to create likely realizations of the input data and apply the modelling process to each realization (e.g. see Crosetto et al., 2000; Lodwick et al., 1990; McKenney et al., 1999; Stoms et al., 1992). The results are then summarized for the statistic of interest. For GLMs, methods need to be developed for establishing confidence intervals that combine parameter uncertainty, model uncertainty and input uncertainty, or combinations of these. Conceptually, bootstrap confidence intervals can offer an appealing solution, but care is needed in establishing the correct philosophy for generating bootstrap resamples where there are potentially many realizations of the species data, the covariate data and the model form (see, for example, Buckland and Elston (1993); Buckland et al. (1997)). Alternatively, the analytical method of Burnham and Anderson (1998) and Buckland et al. (1997) could be extended to deal with more than model uncertainty. The method involves calculation of a weighted term that sums the variance of a prediction from each model and the deviation of each prediction from the weighted average prediction (see their equation 4.10 and example 4.3.1) for that set of covariate data. It could be used to expand Wald confidence intervals in logistic regression as shown in Appendix 1.

6.4. Dealing with non-statistical uncertainty

It is often suggested that probabilistic tools and Monte Carlo simulations cannot deal with vagueness (Colyvan, 2002). There are some elegant examples in the GIS literature of methods for dealing with vague concepts such as vegetation classes, forest types or soil types with fuzzy classification (e.g. Davis and Keller, 1997b; Fisher et al., 1997). These demonstrate that non-probabilistic methods can be developed to explore this type of uncertainty. If habitat suitability is an inherently vague concept, then statistical tools will not address the uncertainty associated with the vagueness. Statistical tools are useful for dealing with the epistemic components of habitat suitability metrics. It is likely that a combination of statistical and non-probabilitistic methods are necessary to address the full suite of uncertainty in ecological methods (Regan et al., 2002).

7. Visualizing data uncertainty

An important component of communicating the uncertainty in predictions to the decision-maker is summarizing and visualizing it in ways that highlight the information that is useful in the particular context. A planner may need to define a threshold at which it will be assumed that the species is present, and would be helped by having mapped information on the certainty of predictions, particularly in areas where land-use will change contingent on his/her decisions. It has been demonstrated that visualizations of data reliability can help to inform even novice users (Evans, 1997). These are usually prepared and displayed within a GIS, but can be displayed in other interactive computer software (e.g. Evans, 1997; Ehlschlaeger et al., 1997). There is a growing body of research in the GIS literature on visualization techniques; key references include Beard et al. (1991) and Hearnshaw and Unwin (1994).

Techniques available for mapped visualizations fall into two broad classes: static maps and dynamic maps. Static maps include simple comparisons between the separate sets of maps of the predictions and their upper and lower bounds (or the predictions and the range of the confidence interval), or single maps that depict both the data and its uncertainty (e.g. Lindenmayer et al., 1995). In the second case the uncertainty could be visualized by saturation of the colour, by fuzziness, or a third dimension (Davis and Keller, 1997a; Goodchild et al., 1994; Van der Wel et al., 1998). Another option is to summarize the data into groups by determining cutoffs. For example, classes could be formed representing a small chance of occurrence with low uncertainty, a small chance of occurrence with high uncertainty and so on, and this summary could be visualized. The interpretation of the simple parametric confidence intervals for logistic regression requires some care, because the intervals around 0.5 tend to be wider than the intervals around predictions closer to 1 or 0.

Dynamic visualizations or animations can be useful for viewing a set of static maps. A simple application is that of a 'dynamic map pair', for example where a color map of predicted probabilities and one of associated uncertainties (e.g. a grey-scale map of the ranges of the confidence intervals) are toggled (Van der Wel et al., 1998). The speed of the toggle can generally be selected interactively. The animation produces an impression of the uncertainty surrounding predictions (e.g. see Evans 1997). Alternatively, many realizations of predictions could be animated. If Monte Carlo simulations were used to generate many realizations of the response and explanatory data, and these were then used to produce many realizations of predicted species occurrence, these realizations could be visualized in an animation. The particular animation method chosen (with options such as: are transitions between images smoothed? is each image given equal time?) may affect how the viewer interprets the data, and it is important to choose a method that can be theoretically justified from the data (Ehlschlaeger et al., 1997; Van der Wel et al., 1998). Animations are reported to draw the user's eye to the more uncertain areas by the apparent motion of the images in those areas compared with the more constant colour of less variable regions (Bastin et al., 1999). See Buttenfield et al. (1991) for a bibliography on animation of spatial data.

A mixture of graphs and maps could be used to help the modeller to investigate patterns in the data. Where confidence intervals are particularly wide, it would be interesting to know what environment exists in that region. If graphs of the response to each variable with confidence intervals were linked to a static map of uncertainties in prediction across the study area (Fig. 1) so that clicking on the map at the site of interest activated a pointer at the realized value for each variable, this may help to indicate what contributes to the uncertainty in the prediction. There is plenty of scope in this area to develop useful technology.

A combination of maps and species observations is also likely to be useful in exploring a model visually, particularly if independent observations are available. Observations that are poorly fitted could be highlighted (e.g. all records that are more than, say, 0.3 from the numerically closest confidence bound; or all records which are discrepant with the estimated probability at selected thresholds). This could be used alongside summaries of

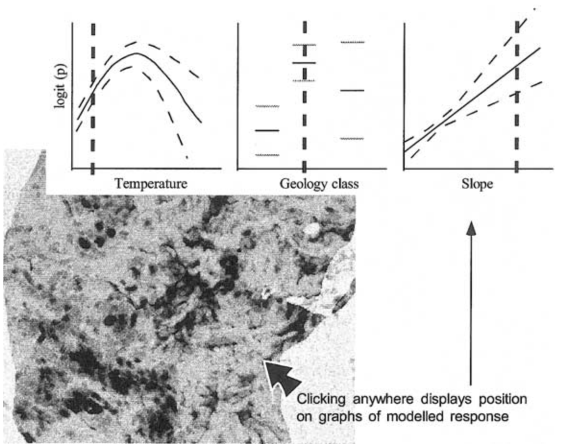

Fig. 1. Visualization of uncertainty in predictions linked to graphs of responses. The heavy vertical lines on the response functions show the position in environmental space corresponding to the geographical position in the greyscale map of prediction uncertainty. The responses are graphed as solid black lines; the surrounding dotted lines are 95% confidence intervals. We envisage an interactive link.

the model performance such as area under the receiver operating characteristic (ROC) curve (Hanley and McNeil, 1982; Zweig and Campbell, 1992) or Cohen's kappa statistic (Cohen, 1960).

8. Conclusion and directions for future research

At the end of an important statistical paper on model uncertainty, Draper (1995) concluded 'A greater acknowledgement of model uncertainty often has the consequence of widening one's uncertainty bands... this is an unpopular turn of events, at least in the short run'. He was making the point that it is difficult to deal with uncertainty, but in the long run it is better to address and treat the uncertainty in an attempt to include the true values within a model's predictions than to ignore uncertainty and miss the true values completely. Others express the same sentiment as their efforts in dealing with uncertainty result in wider confidence intervals (e.g. Buckland et al., 1997; Chatfield, 1995; Davis and Keller, 1997a). Part of the problem is that uncertainty has many dimensions, making it difficult to think about in relation to GLMs. This paper attempts to make some of these dimensions explicit and to trace the uncertainty from its source to the modelled predictions. Graphical displays of predictions that deal with uncertainty (say, in the form of prediction estimates with confidence intervals) are a necessary part of a model assessment toolbox. Relatively few published ecological models developed with GLMs present predictions with any indication of their uncertainty. Exceptions include the work of Buckland and colleagues (Buckland et al., 1997; Buckland and Elston, 1993; Elston and Buckland, 1993) who present confidence intervals around estimates of range, and Lindenmayer et al. (1995) who present upper and lower 95% confidence limits alongside estimated probabilities of presence. Only one study was found that included an analysis of the contribution of uncertainties in data to final estimates (van Horssen et al., 1999), and this paper apparently ignored parameter uncertainty in the confidence intervals. Most work on model evaluation to date has focussed on summary statistics calculated across all point estimates (Fielding and Bell, 1997; Manel et al., 2001). Recognition and treatment of uncertainty would help in the interpretation of these summaries, and to emphasize patterns in uncertainty such as spatial clustering or links with particular covariates.

Sensitivity analysis of predictions of species occurrence allows the decision-maker to explore the impact of various sources of uncertainty on prediction estimates. It is also important to understand and quantify the uncertainty associated with less commonly considered sources of error, such as the components of linguistic uncertainty, when predictions are going to be used as input into other models such as PVAs or reserve selection algorithms (e.g. Akçakaya et al., 1995; Ferrier et al., 2000; Freitag et al., 1996), or where predictions are guiding decisions about species reintroductions (Yanez and Floater, 2000) or sites at risk from invasive species (Buchan and Padilla, 2000). Bastin et al. (1999) present an example of an integrated software system that allows decision-makers to explore visually the range of likely realizations of fuzzy data and to interpret the results that are particularly relevant to their context. It reflects the current momentum related to dealing with uncertainty (in GIS, risk assessment, and conservation biology) which provides an opportunity for spatial modellers to develop an appropriate approach for their discipline.

It would be particularly useful to develop some studies that address the full range of issues associated with uncertainties in predictions from GLMs, and consider the results in the light of other summaries of model performance and with respect to their impact on management decisions. At the moment the relatively small amount of work that has been done is scattered throughout the literature, but is difficult to analyze as a whole. A framework needs to be developed that will enable prediction uncertainty to be traced back to its various sources, quantified, and communicated to decision-makers.

Acknowledgements

We are indebted to a number of people for sharing their thoughts and ideas with us and for commenting on earlier drafts of the manuscript. Thanks to Brendan Wintle, Julian Fox, Michael McCarthy, Mark Colyvan, Simon Jones, Karin Reinke,William De Genst and the reviewers. Jane Elith was funded for part of this work by a generous bursary from the Australian Fellowship of University Women, SA Inc. Helen Regan completed part of this work while a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (grant no. DEB-0072909), the University of California, and the Santa Barbara campus.

Appendix A: Expanding confidence intervals to represent more of the true uncertainty

1) An outline of the situation: many predictions can potentially be generated because there may be many possible realizations of the value of any predictor variable at any site, giving many realizations of the modelling data set (Section 6.3) and perhaps several alternative plausible models (Section 6.2). Predictions will be made with each model applied to each realization of the modelling data set. The final set of all predictions for any given site will include a weight for each prediction. Perhaps each realization of the modelling data set is viewed as equally likely and thus the prediction for each realization will be given an equal weight, with the total weights summing to one. Superimposed over this, predictions arising from alternative models could be weighted according to some sort of penalized likelihood statistic, such as the Akaike Information Criterion (AIC).
2) For estimation of confidence intervals begin with the calculation of predictions and their standard error and hence variance, $\hat{v}$, for each of the m realizations of the modelling data and the n models (producing $m \times n = j$ predictions for the response at each site), retaining these on the logit scale (i.e., on the scale of the additive predictors).
3) For a prediction $\theta_i$that is one of the j possible predictions for the response at site i with a weight w_i, and an averaged prediction $\theta_a$which is a weighted average of the j predictions, the expanded standard error of the average $\hat{s}(\hat{\theta}_a)$ is estimated as:

$$\hat{s}(\hat{\theta}_a) = \sum_{i=1}^{j} \hat{w}_i \sqrt{\hat{v}(\hat{\theta}_i) + (\hat{\theta}_i - \hat{\theta}_a)^2}$$

4) Use this standard error to determine the two-sided $1 - \alpha$ confidence interval for the logit as $\hat{\theta}_a \pm z_{1-\alpha/2}\hat{s}(\hat{\theta}_a)$, and translate these to the response (probability) scale by substituting $\hat{\theta}_a$ and its bounds as θ into:

$$\text{Probability of presence} = \frac{\exp(\theta)}{1 + \exp(\theta)}$$

References

Agresti, A., 1996. An Introduction to Categorical Data Analysis. Wiley, New York, 290 pp.

Akçakaya, H.R., McCarthy, M.A., Pearce, J.L., 1995. Linking landscape data with population viability analysis-management options for the Helmeted Honeyeater *Lichenostomus melanops cassidix*. Biol. Conserv. 73, 169–176.

Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol. Model. 157 (2–3), 101–118.

Augustin, N.H., Borchers, D.L., Clarke, E.D., Buckland, S.T., Walsh, M., 1998. Spatiotemporal modelling for the annual egg production method of stock assessment using generalized additive models. Can. J. Fish. Aquat. Sci. 55, 2608–2621.

Bastin, L., Wood, J., Fisher, P.F., 1999. Visualization of fuzzy spatial information in spatial decision-making. In: Lowell, K., Jaton, A. (Eds.), Spatial Accuracy Assessment: Land Information Uncertainty in Natural Resources. Third International Symposium on Spatial Accuracy Assessment in Natural Resources and Environmental Sciences. Ann Arbor Press, Michigan, pp. 151–156.

Beard, M.K., Buttenfield, B.P., Clapham, S.B., 1991. Visualization of Spatial Data Quality. NCGIA Technical Paper 91-

26, National Center for Geographic Information and Analysis; Maine, USA. Available at http://www.ncgia.ucsb.edu/Publications/Tech_Reports/91/91-26.pdf
Bio, A.M.F., 2000. Does vegetation suit our models? Data and model assumptions and the assessment of species distribution in space. PhD, published, Utrecht University.
Buchan, L.A.J., Padilla, D.K., 2000. Predicting the likelihood of Eurasian watermilfoil presence in lakes, a macrophyte monitoring tool. Ecol. Appl. 10, 1442–1455.
Buckland, S.T., Elston, D.A., 1993. Empirical models for the spatial distribution of wildlife. J. Appl. Ecol. 30, 478–495.
Buckland, S.T., Burnham, K.P., Augustin, N.H., 1997. Model selection: an integral part of inference. Biometrics 53, 603–618.
Burgman, M.A., Ferson, S., Akçakaya, H.R., 1993. Risk Assessment in Conservation Biology. Chapman and Hall, London, 314 pp.
Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: a Practical Information—Theoretic Approach. Springer-Verlag, New York, 353 pp.
Burrough, P.A., 1986. Data quality, errors, and natural variation. In: Principles of Geographical Information Systems for Land Resources Assessment. Clarendon Press, Oxford, pp. 103–135.
Buttenfield, B.O., Weber, C.R., MacLennan, M., Elliott, J.D., 1991. Bibliography on Animation of Spatial Data: a Guide to Literature, Video and Movie Media. Technical Paper 91-22, National Center for Geographic Information and Analysis, Maine, USA.
Capen, D.E., Fenwick, J.W., Inkley, D.B., Boynton, A.C., 1986. Multivariate models of songbird habitat in New England forests. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. Based on an International Symposium held at Stanford Sierra Camp, Fallen Leaf Lake, California. The University of Wisconsin Press, Wisconsin, pp. 171–175.
Cawsey, M. et al., 2002. Prediction of vegetation cover of the central Lachlan region of New South Wales, Australia: a case study in the practical use of statistical modelling. Biodivers. Conserv., in press.
Chatfield, C., 1995. Model uncertainty, data mining and statistical inference. J. R. Stat. Soc. Ser. A Stat. 158, 419–466.
Cohen, J., 1960. A coefficient of agreement for nominal scales. Educ. Psychol. Meas. 20, 37–46.
Collett, D., 1991. Modelling Binary Data. Chapman and Hall, London, 369 pp.
Colyvan, M., 2002. Is probability the only coherent approach to uncertainty? Risk Anal., in press.
Corsi, F., Duprè, E., Boitani, L., 1999. A large-scale model of wolf distribution in Italy for conservation planning. Conserv. Biol. 13, 150–159.
Crosetto, M., Tarantola, S., Saltelli, A., 2000. Sensitivity and uncertainty analysis in spatial modelling based on GIS. Agric. Ecosyst. Environ. 81, 71–79.
Davis, T.J., Keller, C.P., 1997. Modelling and visualizing multiple spatial uncertainties. Comput. Geosci. 23, 397–408.
Davis, T.J., Keller, C.P., 1997. Modelling uncertainty in natural resource analysis using fuzzy sets and Monte Carlo simulation: slope stability prediction. Int. J. Geogr. Inf. Sci. 11, 409–434.
Davison, A.C., Hinkley, D.V., 1997. Bootstrap Methods and their Application. Cambridge University Press, Cambridge, 582 pp.
De Genst, W., Canters, F., Jacquet, W., Vermeersch, S., 1999. Development of a technique to decompose heterogeneous mapping units in a categorical map of the biotic environment using correlated categorical data. Int. J. Geogr. Inf. Sci. 13, 591–614.
Doganaksoy, N., Schmee, J., 1993. Comparisons of approximate confidence intervals for distributions used in life analysis. Technometrics 35, 175–184.
Draper, D., 1995. Assessment and propagation of model uncertainty. J. R. Stat. Soc. Ser. B Stat. Med. 57, 45–97.
Efron, B., Tibshirani, R.J., 1993. An Introduction to the Bootstrap. Chapman and Hall, London, 436 pp.
Elith, J., Burgman, M.A., 2002. Habitat models for PVA. In: Brigham, C.A., Schwartz, M.W. (Eds.), Population Viability in Plants. Springer-Verlag, in press.
Elston, D.A., Buckland, S.T., 1993. Statistical modelling of regional GIS data: an overview. Ecol. Model. 67, 81–102.
Ehlschlaeger, C.R., Shortridge, A.M., Goodchild, M.F., 1997. Visualizing spatial data uncertainty using animation. Comput. Geosci. 23, 387–395.
Evans, B.J., 1997. Dynamic display of spatial data reliability: does it benefit the map user? Comput. Geosci. 23, 409–422.
Ferrier, S., Pressey, R.L., Barrett, T.W., 2000. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. Biol. Conserv. 93, 303–325.
Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
Fine, K., 1975. Vagueness truth and logic. Synthese 30, 265–300.
Fisher, P.F., 1991. First experiments in viewshed uncertainty: the accuracy of the viewshed area. Photogramm. Eng. Remote Sensing 57, 1321–1327.
Fisher, P.F., Abrahart, R.J., Herbinger, W., 1997. The sensitivity of two distributed non-point source pollution models to the spatial arrangement of the landscape. Hydrol. Process. 11, 241–252.
Fox, J.C., Ades, P.A., Burgman, M.A., 2002. Autocorrelation and binary ecological models. Ecol. Model., submitted for publication.
Freitag, S., Nicholls, A.O., Van Jaarsveld, A.S., 1996. Nature reserve selection in the Transvaal, South Africa: what data should we be using? Biodivers. Conserv. 5, 685–698.
Goodchild, M.F., Buttenfield, B., Wood, J., 1994. Introduction to visualizing data validity. In: Hearnshaw, H.M., Unwin,

D.J. (Eds.), Visualization in Geographic Information Systems. Wiley, New York, pp. 158–167.

Goovaerts, P., 2001. Geostatistical modelling of uncertainty in soil science. Geoderma 103, 3–26.

Guisan, A., Zimmerman, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.

Guisan, A., Edwards Jr, T.C., Hastie, T., 2002. Generalized linear and generalized additive models of species distributions: setting the scene. Ecol. Model. 157, 89–100.

Hall, P., 1992. The Bootstrap and Edgeworth Expansion. Springer-Verlag, New York, 352 pp.

Hammersley, J.M., Handscomb, D.C., 1964. Monte Carlo Methods. Methuen & Co, London, 178 pp.

Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143, 29–36.

Harrell, F.E., 2001. Regression Modeling Strategies with Applications to Linear Models, Logistic Regression and Survival Analysis. Springer Verlag, New York, 568 pp.

Harrell, F.E., Lee, K.L., Mark, D.B., 1996. Multivariate prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. Stat. Med. 15, 361–387.

Hastie, T., Tibshirani, R., Friedman, J.H., 2001. The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Springer-Verlag, New York, 533 pp.

Hauck, W.W., 1983. A note on confidence bands for the logistic response curve. Am. Stat. 37, 158–160.

Hearnshaw, H.M., Unwin, D.J., 1994. Visualization in Geographical Information Systems. Wiley, Chichester, UK, 243 pp.

Heuvelink, G.B.M., 1998. Error Propagation in Environmental Modelling with GIS. Taylor and Francis, London, 127 pp.

Ho, C.H., Smith, E.I., 1997. Volcanic hazard assessment incorporating expert knowledge—application to the Yucca mountain region, Nevada, USA. Math. Geol. 29, 616–627.

Holmes, K.W., Chadwick, O.A., Kyriakidis, P.C., 2000. Error in a USGS 30-meter digital elevation model and its impact on terrain modeling. J. Hydrol. 233, 154–173.

Hosmer, D.W., Lemeshow, S., 1995. Confidence interval estimates of an index of quality performance based on logistic regression models. Stat. Med. 14, 2161–2172.

Huber, P.J., 1967. The behaviour of maximum likelihood estimates under nonstandard conditions. In: Proceedings of the Fifth Berkeley Symposium in Mathematical Statistics, pp. 221–233.

Hunter, G.J., Qiu, J., Goodchild, M.F., 1999. Application of a new model of vector data uncertainty. In: Lowell, K., Jaton, A. (Eds.), Spatial Accuracy Assessment: Land Information Uncertainty in Natural Resources. Third International Symposium on Spatial Accuracy Assessment in Natural Resources and Environmental Sciences. Ann Arbor Press, Michigan, pp. 203–208.

Jarvis, A.M., Robertson, A., 1999. Predicting population sizes and priority conservation areas for 10 endemic Namibian bird species. Biol. Conserv. 88, 121–131.

Kleinbaum, D.G., Kupper, L.L., Muller, K.E., Nizam, A., 1998. Applied Regression Analysis and Other Multivariable Methods, 3rd ed.. Duxbury Press, California, 798 pp.

Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659–1673.

Lindenmayer, D.B., Ritman, K., Cunningham, R.B., Smith, J.D.B., Horvath, D., 1995. A method for predicting the spatial distribution of arboreal marsupials. Wildlife Res. 22, 445–456.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Incoll, R.D., Pope, M.L., Tribolet, C.R., Viggers, K.L., Welsh, A.H., 2001. How effective is spotlighting for detecting the greater glider (*Petauroides volans*)? Wildlife Res. 28, 106–109.

Lodwick, W.A., Monson, W., Svoboda, L., 1990. Attribute error and sensitivity analysis of map operations in geographical information systems: suitability analysis. Int. J. Geogr. Inf. Sys. 4, 413–428.

Lynn, H., Mohler, C.L., DeGloria, S.D., McCulloch, C.E., 1995. Error assessment in decision—tree models applied to vegetation analysis. Landscape Ecol. 10, 323–335.

Madigan, D., Raftery, A.E., 1994. Model selection and accounting for model uncertainty in graphical models using Occam's window. J. Am. Stat. Assoc. 89, 1535–1546.

Madigan, D., York, J., 1995. Bayesian graphical methods for discrete data. Int. Stat. Rev. 63, 215–232.

Manel, S., Ceri Williams, H., Ormerod, S.J., 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38, 921–931.

Manly, B.F.G., 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, 2nd ed.. Chapman and Hall, London, 399 pp.

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, 2nd ed.. Chapman and Hall, London, 261 pp.

McIntosh, R.P., 1967. The continuum concept of vegetation. Bot. Rev. 33, 130–187.

McKenney, D.W., Mackey, B.G., Zavitz, B.L., 1999. Calibration and sensitivity analysis of a spatially distributed solar radiation model. Int. J. Geogr. Inf. Sys. 13, 49–65.

Meyer, B., Printzen, C., 2000. Proposal for a standardized nomenclature and characterization of insoluble lichen pigments. Lichenologist 32, 571–583.

Miller, A.J., 1990. Subset Selection in Regression. Chapman and Hall, London, 229 pp.

Miller, A.J., 1995. Discussion of the paper by Chatfield: model uncertainty, data mining and statistical inference. J. R. Stat. Soc. Ser. A Stat. 158, 460.

NSW NPWS, 1998. Eden Fauna Modeling—a report undertaken for the NSW CRA/RFA Steering Committee Project number NE 24/EH, New South Wales National Parks and Wildlife Service; Canberra.

Pausas, J.G., Braithwaite, L.W., Austin, M.P., 1995. Modelling habitat quality for arboreal marsupials in the south coastal forests of New South Wales, Australia. Forest Ecol. Manage. 78, 39–49.

Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133, 225–245.

Possingham, H.P., Lindenmayer, D.B., Norton, T.W., 1993. A framework for the improved management of threatened species based on population viability analysis. Pacific Conserv. Biol. 1, 39–45.

Raftery, A.E., Madigan, D., Hoeting, J.A., 1997. Bayesian model averaging for linear regression models. J. Am. Stat. Assoc. 92, 179–191.

Regan, H.M., Colyvan, M., Burgman, M.A., 2000. A proposal for fuzzy IUCN categories and criteria. Biol. Conserv. 92, 101–108.

Regan, H.M., Colyvan, M., Burgman, M.A., 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecol. Appl. 12, 618–628.

Roberts, D.W., 1996. Landscape vegetation modelling with vital attributes and fuzzy systems theory. Ecol. Model. 90, 175–184.

Steyerberg, E.W., Eijkemans, M.J.C., Habbema, J.D.F., 1999. Stepwise selection in small data sets: a simulation study of bias in logistic regression analysis. J. Clin. Epidemiol. 52, 935–942.

Stoms, D.M., Davis, F.W., Crogan, C.B., 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. Photogramm. Eng. Remote Sensing 58, 843–850.

Thorsen, M., Refsgaard, J.C., Hansen, S., Pebesma, E., Jensen, J.B., Kleeschulte, S., 2001. Assessment of uncertainty in simulation of nitrate leaching to aquifers at catchment scale. J. Hydrol. 242, 210–227.

Van der Wel, F.J.M., Vandergaag, L.C., Gorte, B.G.H., 1998. Visual exploration of uncertainty in remote-sensing classification. Comput. Geosci. 24, 335–343.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. J. Wildlife Manag. 47, 893–901.

van Horssen, P.W., Schot, P.P., Barendregt, A., 1999. A GIS-based plant prediction model for wetland ecosystems. Landscape Ecol. 14, 253–265.

Whittaker, R.H., 1967. Gradient analysis of vegetation. Biol. Rev. 49, 207–264.

Wintle, B.A., Burgman, M.A., Kavanagh, R.P, 2002a. The magnitude and management consequences of false negative observations in surveys of arboreal marsupials and large forest owls, in preparation.

Wintle, B.A., McCarthy, M.A., Kavanagh, R.P., Burgman, M.A., 2002b. The use of Bayesian model averaging to better represent uncertainty in predictions derived from ecological models. Conserv. Biol., submitted for publication.

Yanez, M., Floater, G., 2000. Spatial distribution and habitat preference of the endangered tarantula, *Brachypelma klaasi* (Araneae: Theraphosidae) in Mexico. Biodivers. Conserv. 9, 795–810.

Zweig, M.H., Campbell, G., 1992. Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. Clin. Chem. 39, 561–577.