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Predictive habitat distribution models in ecology

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Abstract

With the rise of new powerful statistical techniques and GIS tools, the development of predictive habitat distribution models has rapidly increased in ecology. Such models are static and probabilistic in nature, since they statistically relate the geographical distribution of species or communities to their present environment. A wide array of models has been developed to cover aspects as diverse as biogeography, conservation biology, climate change research, and habitat or species management. In this paper, we present a review of predictive habitat distribution modeling. The variety of statistical techniques used is growing. Ordinary multiple regression and its generalized form (GLM) are very popular and are often used for modeling species distributions. Other methods include neural networks, ordination and classification methods, Bayesian models, locally weighted approaches (e.g. GAM), environmental envelopes or even combinations of these models. The selection of an appropriate method should not depend solely on statistical considerations. Some models are better suited to reflect theoretical findings on the shape and nature of the species' response (or realized niche). Conceptual considerations include e.g. the trade-off between optimizing accuracy versus optimizing generality. In the field of static distribution modeling, the latter is mostly related to selecting appropriate predictor variables and to designing an appropriate procedure for model selection. New methods, including threshold-independent measures (e.g. receiver operating characteristic (ROC)-plots) and resampling techniques (e.g. bootstrap, cross-validation) have been introduced in ecology for testing the accuracy of predictive models. The choice of an evaluation measure should be driven primarily by the goals of the study. This may possibly lead to the attribution of different weights to the various types of prediction errors (e.g. omission, commission or confusion). Testing the model in a wider range of situations (in space and time) will permit one to define the range of applications for which the model predictions are suitable. In turn, the qualification of the model depends primarily on the goals of the study that define the qualification criteria and on the usability of the model, rather than on statistics alone.

Keywords: Biogeography; Plant ecology; Vegetation models; Species models; Model formulation; Model calibration; Model

Abbreviations: CART, classification and regression trees; CC, climate change; CCA, canonical correspondence analysis; DEM, digital elevation model; ENFA, ecological niche factor analysis; GAM, generalized additive model; GLM, generalized linear model; LS, least squares; PCA, principal component analysis; RDA, redundancy analysis.

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predictions; Model evaluation; Model credibility; Model applicability; GIS; Statistics

1. Introduction

The analysis of species–environment relationship has always been a central issue in ecology. The importance of climate to explain animal and plant distribution was recognized early on (Humboldt and Bonpland, 1807; de Candolle, 1855). Climate in combination with other environmental factors has been much used to explain the main vegetation patterns around the world (e.g. Salisbury, 1926; Cain, 1944; Good, 1953; Holdridge, 1967; McArthur, 1972; Box, 1981; Stott, 1981; Walter, 1985; Woodward, 1987; Ellenberg, 1988). The quantification of such species–environment relationships represents the core of predictive geographical modeling in ecology. These models are generally based on various hypotheses as to how environmental factors control the distribution of species and communities.

Besides its prime importance as a research tool in autecology, predictive geographical modeling recently gained importance as a tool to assess the impact of accelerated land use and other environmental change on the distribution of organisms (e.g. climate – Lischke et al., 1998; Kienast et al., 1995, 1996, 1998; Guisan and Theurillat, 2000), to test biogeographic hypotheses (e.g. Mourell and Ezcurra, 1996; Leathwick, 1998), to improve floristic and faunistic atlases (e.g. Hausser, 1995) or to set up conservation priorities (Margules and Austin, 1994). A variety of statistical models is currently in use to simulate either the spatial distribution of terrestrial plant species (e.g. Hill, 1991; Buckland and Elston, 1993; Carpenter et al., 1993; Lenihan, 1993; Huntley et al., 1995; Shao and Halpin, 1995; Franklin, 1998; Guisan et al., 1998, 1999), aquatic plants (Lehmann et al., 1997; Lehmann, 1998), terrestrial animal species (e.g. Pereira and Itami, 1991; Aspinall, 1992; Augustin et al., 1996; Corsi et al., 1999; Mace et al., 1999; Manel et al., 1999; Mladenoff et al., 1995, 1999), fishes (Lek et al., 1996; Mastrorillo et al., 1997), plant communities (e.g. Fischer, 1990; Brzeziecki et al., 1993; Zimmermann and Kienast, 1999), vegetation types (e.g. Brown, 1994; Van de Rijt et al., 1996), plant functional types (e.g. Box, 1981, 1995, 1996), biomes and vegetation units of similar complexity (Monserud and Leemans, 1992; Prentice et al., 1992; Tchebakova et al., 1993, 1994; Neilson, 1995), plant biodiversity (e.g. Heikkinen, 1996; Wohlgemuth, 1998), or animal biodiversity (Owen, 1989; Fraser, 1998) (see also Scott et al., in press for numerous additional examples of plant and animal species distribution models). Such static, comparative, models are opposed to more mechanistic models of ecosystem processes (Peters, 1991; Jones, 1992; Pickett et al., 1994; Lischke et al., 1998). Since only very few species have been studied in detail in terms of their dynamic responses to environmental change, static distribution modeling often remains the only approach for studying the possible consequences of a changing environment on species distribution (Woodward and Cramer, 1996).

The development of predictive models is coherent with Peters's (1991, p. 274) view of a "more rigorously scientific, more informative and more useful ecology". The use of and theoretical limitations of static models compared with dynamic approaches have been described in several papers (e.g. Decoursey, 1992; Korzukhin et al., 1996; Lischke et al., 1998). Franklin (1995) provides a review of some currently used statistical techniques in vegetation and plant species modeling. Particular aspects of model development (e.g. verification, calibration, evaluation (= validation), qualification) have been covered in more specific papers, with very special attention given in recent years to evaluation and its usefulness for testing ecological models (e.g. Loehle, 1983; Oreskes et al., 1994; Rykiel, 1996). Since then, new statistical techniques for calibrating and testing predictive models have emerged (see e.g. Scott et al., in press).

The aim of this paper is to review the various steps of predictive modeling, from the conceptual model formulation to prediction and application (Fig. 1). We discuss the importance of differentiating between model formulation, model calibration, and model evaluation. Additionally, we

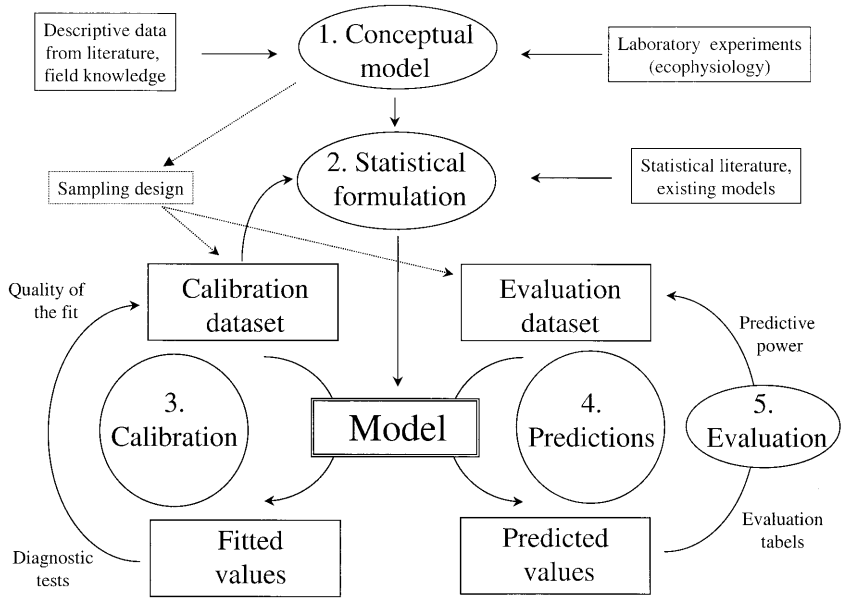

Fig. 1. Overview of the successive steps (1–5) of the model building process, when two data sets – one for fitting and one for evaluating the model – are available. Model evaluation is either made: (a) on the calibration data set using bootstrap, cross-validation or Jack-knife techniques; (b) on the independent data set, by comparing predicted to observed values using preferentially a threshold-independent measure (such as the ROC-plot approach for presence/absence models).

provide an overview of specific analytical, statistical methods currently in use.

2. Conceptual model formulation

The process, which ends with the formulation of an ecological model, usually starts from an underlying ecological concept (e.g. the pseudo-equilibrium assumption in static distribution modeling). We consider it crucial to base the formulation of an ecological model on an underlying *conceptual framework*. Hereafter, we discuss a selection of important conceptual aspects.

2.1. General patterns in the geographical distribution of species

The core theory of predictive modeling of biotic entities originates from major trends published in the field of biogeography. Here, our aim is not to summarize all the patterns and processes of geographic range limitation, which are best provided by specific review papers (e.g. Brown et al., 1996), but to illustrate the link with the conceptual model formulation through examples.

A matter of primary interest is the relative importance of biotic versus abiotic factors at the margins of a species' range. Brown et al. (1996) recalls that "in most ecological gradients, the majority of species appear to find one direction to be physically stressful and the other to be biologically stressful". This was stressed for an elevation gradient (Guisan et al., 1998) and already suggested for latitudinal gradient by Dobzhansky (1950) and McArthur (1972). In a more general way, physical limits are caused by environmental and physiological constraints (i.e. direct and resource gradients in the sense of Austin et al. (1984) and Austin and Gaywood (1994) under suboptimal conditions along these gradients (e.g. too cold, too dry). A discussion on (1) using causal rather than non-causal factors and (2) considering inter-species competition for fitting a static model follows in the next sections and in the final perspectives.

2.2. Generality, reality, and precision

Nature is too complex and heterogeneous to be predicted accurately in every aspect of time and space from a single, although complex, model. Levins (1966) formulated the principle that only any two out of three desirable model properties (generality, reality, precision) can be improved simultaneously (Fig. 2), while the third property has to be sacrificed. This trade-off leads to a distinction of three different groups of models (Sharpe, 1990; Prentice and Helmisaari, 1991; Korzukhin et al., 1996), and its associated constraints are consequential when selecting modeling approaches for specific project goals.

The first group of models (i) focuses on generality and precision. Such models are called analytical (Pickett et al., 1994) or mathematical[2] (Sharpe, 1990), and are designed to predict accurate response within a limited or simplified reality. The Lotka–Volterra equation and their variants (Volterra, 1926; May, 1981), the general logistic growth equation, or the Blackman growth law (Assmann ex Sharpe, 1990) are examples of analytical models. A second group of models (ii) is designed to be realistic and general. They are called mechanistic (e.g. Prentice, 1986a), physiological (e.g. Leersnijder, 1992), causal (e.g. Decoursey, 1992) or process models (e.g. Korzukhin et al., 1996), and they base predictions on real cause–effect relationships. Thus they may also be considered as general, since these relationships are considered as biologically functional (Woodward, 1987). A model of this group is not judged primarily on predicted precision, but rather on the theoretical correctness of the predicted response (Pickett et al., 1994). A third group of models (iii) sacrifices generality for precision and reality. Such models are called empirical (Decoursey, 1992; Korzukhin et al., 1996), statistical (Sharpe and Rykiel, 1991), or phenomenological (Pickett et al., 1994; Leary, 1985). The mathematical formulation of such a model is not expected to describe realistic 'cause and effect' between model parameters and predicted response, nor to inform about underlying ecological functions and mechanisms, being the main purpose to condense empirical facts (Wissel, 1992)[3].

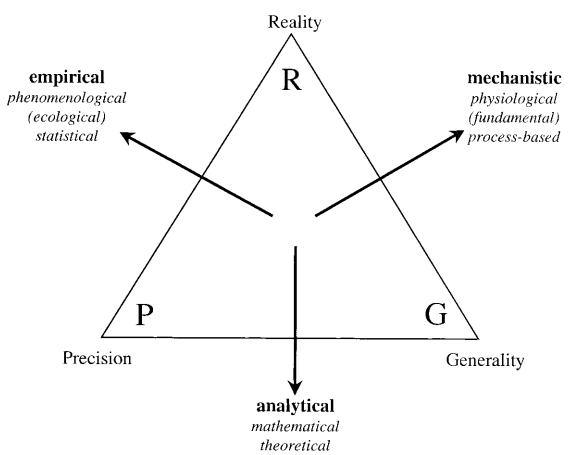

Fig. 2. A classification of models based on their intrinsic properties. After Levins (1966), and Sharpe (1990).

Although Levins' classification is helpful, it is somewhat misleading. In practice it can be difficult to classify a specific model (Korzukhin et al., 1996). Predictive distribution models are generally categorized as empirical models; however, Prentice et al. (1992) argue that their (predictive) global vegetation model, rigorously based on independent physiological data and physiological first principles, is as mechanistic as we would achieve with limited data. Also Korzukhin et al. (1996) point out that process and empirical models can both have either a high or low degree of generality depending on the nature of the object being modeled, and that mechanistic models by their nature do not necessarily have to be imprecise. They conclude that precision, generality and reality are not always mutually exclusive. Similarly, Peters (1991, p.32) notices that, "there is no necessary conflict between precision and generality".

[2] We find this term misleading, since all of the three principal modeling approaches may rely on more or less extensive mathematical formulations.

[3] Several authors do not distinguish clearly between analytical and empirical models (e.g. Loehle, 1983; Wissel, 1992), they use multiple criteria to arrange models along these gradients (e.g. Pickett et al., 1994), or they introduce subclasses to Levins' model classification (Kimmins and Sollins, 1989; Kimmins et al., 1990).

Loehle (1983) recognizes two distinct types of models: calculating tools and theoretical models. The first can be put in the class of empirical models, since "they are intended only to inform us about the configuration of the world" (Peters, 1991, p. 105), whereas the theoretical models are synonymous with the mechanistic models, capable of predicting response from plausible causal relations.

We argue that Levins' classification and trade-offs are nevertheless useful in a conceptual context (see below). They help to focus on one or the other characteristics in model building, depending on the overall goal of the modeling effort. Predictive vegetation models are generally empirical by nature. However, they can be based on physiologically meaningful parameters (e.g. Prentice et al., 1992; Lenihan, 1993), and can thus be described as more mechanistic than models based, say, on topographic parameters only (e.g. Burke et al., 1989; Moore et al., 1991). This difference summarizes the main axis along which most of the predictive vegetation models can be arranged: in most cases it is the trade-off between precision and generality.

2.3. Direct versus indirect predictors

From a mechanistic point of view, it is desirable to predict the distribution of biotic entities on the basis of ecological parameters that are believed to be the causal, driving forces for their distribution and abundance. Such ecological factors are generally sampled from digital maps, since they are usually difficult or expensive to measure. However, they often tend to be less precise than pure topographic characteristics. Most bioclimatic maps are developed by elevation-sensitive spatial interpolations of climate station data (Hutchinson and Bischof, 1983; Daly et al., 1994; Thornton et al., 1997). This introduces spatial uncertainties because of (i) interpolation errors, (ii) lack of sufficient stations data, and (iii) the fact that standard climate stations do not reveal the biologically relevant microclimates. Soil (and nutrient) and geology maps are even more difficult to derive. They are usually generated at very coarse resolution and are often drawn up using vegetation as delineation criteria. On the other hand, available digital elevation models (DEM) tend to be relatively accurate, even in mountainous terrain. Thus, directly derived topographic variables (slope, aspect, topographic position, or slope characteristics) are generated without much loss of precision. It is thus not surprising that predictive vegetation models, developed for mountainous terrain at relatively high spatial resolution, are based partially or completely on topographical factors (Fischer, 1990; Moore et al., 1991; Brzeziecki et al., 1993; Brown, 1994; Guisan et al., 1998, 1999). On the contrary, large-scale predictive models are generally based solely on biophysical parameters, since topography no longer has any predictive power at such coarse resolution (Box, 1981; Prentice et al., 1992; Lenihan, 1993; Huntley et al., 1995; Neilson, 1995).

The distinction between topographic and bioclimatic variables is important in the discussion of precision versus generality. Austin (1980, 1985), Austin et al. (1984), and Austin and Smith (1989) defined three types of ecological gradients, namely *resource*, *direct*, and *indirect* gradients. Resource gradients address matter and energy consumed by plants or animals (nutrients, water, light for plants, food, water for animals). Direct gradients are environmental parameters that have physiological importance, but are not consumed (temperature, pH). Indirect gradients are variables that have no direct physiological relevance for a species' performance (slope, aspect, elevation, topographic position, habitat type, geology; Fig. 3 gives an example for vascular plants). They are most easily measured in the field and are often used because of their good correlation with observed species patterns. Indirect variables usually replace a combination of different resources and direct gradients in a simple way (Guisan et al., 1999).

However, one drawback of using such indirect parameters is that a model can only be applied within a limited geographical extent without significant errors, because in a different region the same topographic position can reveal a different combination of direct and resource gradients. Walter and Walter (1953) called this the "law of relative site constancy" (*Gesetz der relativen Stan-*

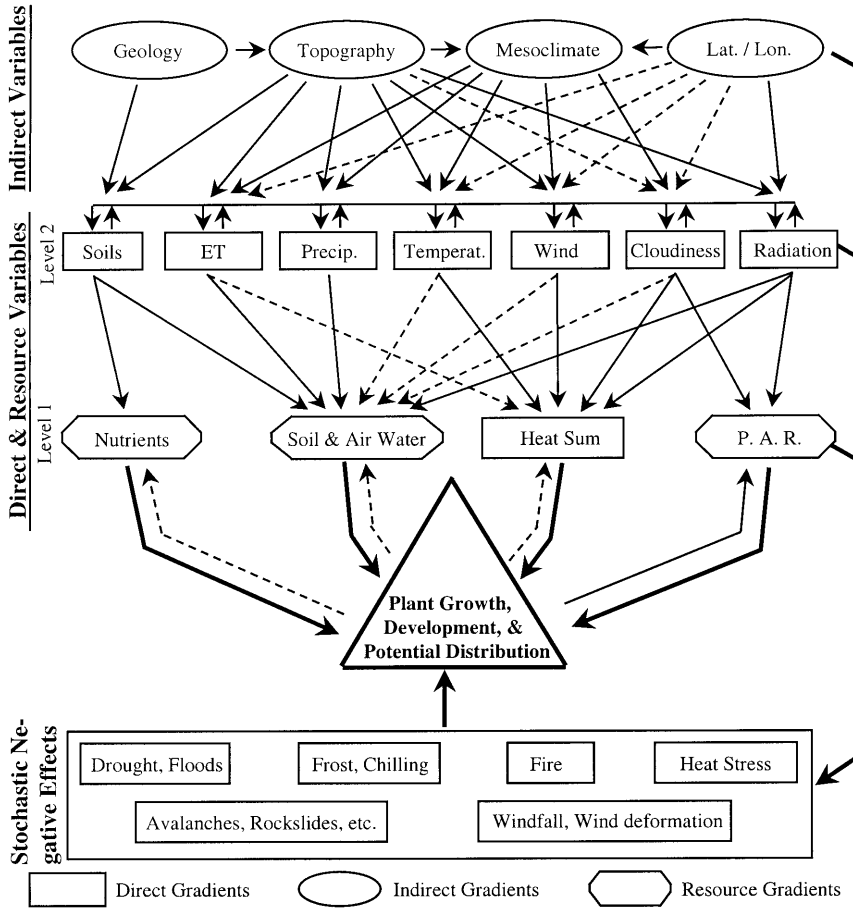

Fig. 3. Example of a conceptual model of relationships between resources, direct and indirect environmental gradients (see e.g. Austin and Smith, 1989), and their influence on growth, performance, and geographical distribution of vascular plants and vegetation.

dortkonstanz). It describes the fact that species tend to compensate regional differences in climatic conditions by selecting comparable microsites by changing their topographic positions. In turn, the use of direct and resource gradients as predictive parameters – in which case predictions are based on what is supposed to be more physiologically 'mechanistic' – ensures that the model is more *general* and applicable over larger areas. Furthermore, direct and resource gradients help to pave the way towards incorporating dynamic aspects of vegetation succession in spatially explicit models, as proposed by Solomon and Leemans (1990) or by Halpin (1994).

2.4. Fundamental versus realized niche

The fundamental niche is primarily a function of physiological performance and ecosystem constraints. As an example, Woodward (1987, 1992) analyzed the mechanistic relationships between climate parameters and plant fundamental response. The realized niche additionally includes biotic interactions and competitive exclusion (Ellenberg, 1953; Malanson et al., 1992; Malanson, 1997). The concept of the ecological niche was clarified by Hutchinson (1957) and recently revisited by several authors in the context of predictive modeling (e.g. Austin et al., 1990; Westman, 1991;

Malanson et al., 1992; de Swart et al., 1994; Rutherford et al., 1995; Franklin, 1995; Leibold, 1995). Differentiating between the fundamental and the realized niche of a species is particularly important because it distinguishes whether a simulated distribution is predicted from theoretical physiological constraints or rather from field-derived observations.

Strict mechanistic models parameterize the fundamental niche and additionally implement rules of competitive behavior to finally result in the predictions of the realized response. As an example, Prentice et al. (1992) based their model primarily on theoretical and physiological constraints, and they add simple rules to cope with succession and dominance. Static predictive models are generally based on large empirical field data sets, thus, they are likely to predict the realized (ecological) niche. This seriously limits applications in changing environmental situations. However, Malanson et al. (1992) demonstrate how empirically fitted response surfaces can be altered on the basis of theoretical and physiological principles to design a more fundamental response.

2.5. Equilibrium versus non-equilibrium

Static distribution models are developed from simple statistically or theoretically derived response surfaces. Thus, they automatically assume equilibrium – or at least pseudo-equilibrium (Lischke et al., 1998) – between the environment and observed species patterns. The non-equilibrium concept is more realistic in ecology (Pickett et al., 1994), because it includes equilibrium as a possible state (Clark, 1991). However, a model based on the non-equilibrium concept must be (i) dynamic and (ii) stochastic. Static distribution models are conceptually unable to cope with non-equilibrium situations, since they do not distinguish between the transient and equilibrium response of species to a stochastically and dynamically changing environment. Hence, considering a state of equilibrium is a necessary assumption for the purpose of large-scale distribution modeling. This limitation is less restrictive for species, or communities, which are relatively persistent or react slowly to variability in environmental conditions (e.g. arctic and alpine).

Such a drawback is compensated by large-scale prediction with less effort, and the advantage that no detailed knowledge of the physiology and behavior of the species involved is necessary. Situations with strong disturbance, human influence, or successional dynamics can thus only be modeled with difficulty (Brzeziecki et al., 1993; Guisan et al., 1999; Lees and Ritman, 1991; Zimmermann and Kienast, 1999). However, it is sometimes possible to include such factors as predictive parameters[4]. The alternative to static, equilibrium modeling is dynamic simulation modeling (Korzukhin et al., 1996; Lischke et al., 1998). However, since such models require intensive knowledge of the species involved, most of these models are developed for well-investigate species and habitats. Only few dynamic models have yet been developed in a spatially explicit way that allow simulations on larger spatial scales (e.g. Urban et al., 1991; Moore and Noble, 1993; Roberts, 1996; He et al., 1999; He and Mladenoff, 1999).

2.6. Species versus community approach

Another major discussion in this field is whether a model is said to be 'gleasonian' or 'clementsian' (Prentice et al., 1992) simulating species either individually or as community assemblages (see also Franklin, 1995). This discussion is embedded in the community-continuum debate (Clements, 1916, 1936; Gleason, 1926; Cooper, 1926; Whittaker, 1967; McIntosh, 1967; Austin, 1985; Austin and Smith, 1989; Collins et al., 1993).

A main argument for species modeling is the paleoecological evidence that plant species assem-

[4] Fischer (1990) identified land-use as the factor with the highest predictive power when modeling community distribution in a human-disturbed landscape. Lees and Ritman (1991) discussed the trade-off between spectral (remotely sensed data) and spatial (environmental GIS data) accuracy to respectively predict disturbed (e.g. rural or urban) versus undisturbed (e.g. rainforest) landscapes. Box (1981) as well as Prentice et al. (1992) included hierarchical rules to cope with succession, by simulating mature stages only.

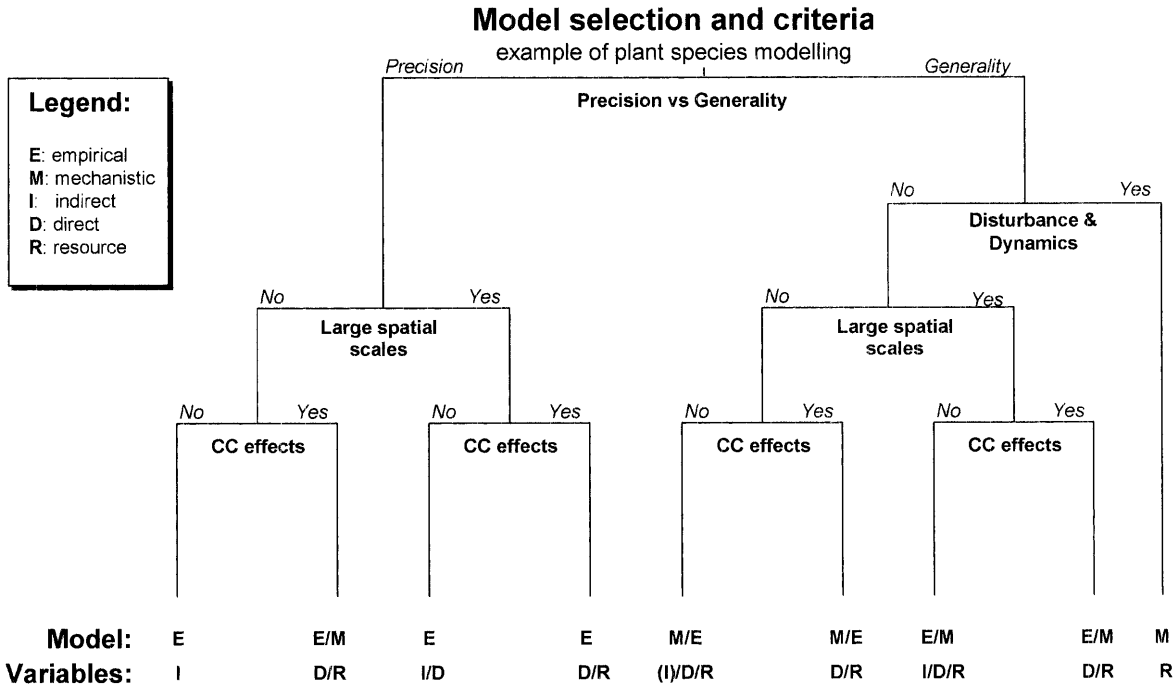

Fig. 4. Criteria for model selection. Examples of considerations for modeling vascular plant species in space and/or time, given a set of possible criteria to reach the project goals, CC: climatic change.

blages have never been stable, mostly due to past variations in climate (Webb, 1981; Prentice, 1986b; Ritchie, 1986). Modern species assemblages do not have long histories (Davis, 1983; Birks, 1993) and therefore, communities are not likely to move as an entity under changing climatic conditions (Birks, 1986; Huntley and Webb, 1988). Hence, modeling species instead of communities comes closer to what is believed to be realistic[5]. An alternative to modeling communities is to simulate a selection of dominant species, and to classify their superimposed distributions afterwards, in order to generate simulated community maps (Lenihan, 1993; Austin, 1998; Guisan and Theurillat, 2000). This approach solves the missing logic of arbitrary a priori classifications. However, when predicting future potential distributions based on static models and scenarios of environmental change (e.g. climatic change), the same limitations apply to species and community models. Both approaches are based on equilibrium assumptions (between observed response and environmental conditions) and lack the possibility of simulating the individualistic behavior of species (i.e. seed dispersal, migration, plasticity, adaptation, etc.).

2.7. Conceptual guidelines

So far we discussed that conceptual considerations based on the overall goal of the study are essential for the design of an appropriate model. Fig. 4 gives an example of possible considerations for modeling the distribution of vascular plants. In general, if high predictive precision is required to model the distribution of biological entities on

[5] Franklin (1995) discusses the different points of view in the context of predictive vegetation mapping. She concludes that: "...communities (and ecotones) are geographic entities, and therefore can be predictively mapped. However, predictive mapping of species distributions presents far fewer definitional uncertainties or abstractions. Often the distribution of species assemblages (plant communities) or functional types... is predicted owing to methodological considerations (lack of sufficient data to model species distributions) rather than strong loyalty to the community concept."

a large spatial scale under present environmental conditions (e.g. Hausser, 1995), then static modeling is a valid and powerful approach. It may also be selected for modeling large-scale potential distributions under environmental change scenarios, but limitations apply, as previously discussed. For modeling at small spatial scales and in complex topography the use of indirect variables may provide better predictions, while for simulations at large spatial scales the use of direct and resource gradients should be the first choice.

3. Sampling design, field survey, spatial scales, and the geographical modeling context

The formulation of the conceptual model leads ideally (i) to the choice of an appropriate spatial scale (reviewed by Wiens, 1989; see also Hengeveld, 1987; Fitzgerald and Lees, 1994a) for conducting the study, and (ii) to the selection of a set of conceptually (e.g. physiologically) meaningful explanatory variables for the predictive model (Fig. 3). Additionally, it may be helpful to design an efficient sampling strategy by identifying those gradients that are believed to play a key role in the model and should thus be considered primarily to stratify the sampling (Mohler, 1983; Austin and Heyligers, 1989, 1991; Wessels et al., 1998). The main environmental gradients in the study area (be it a small catchment or a large area) can be identified in a preliminary exploratory analysis (e.g. Dufrêne and Legendre, 1991; Aspinall and Lees, 1994) and used to define a sampling strategy that is especially designed to meet the requirements of the model objectives (Mohler, 1983).

The gradsect approach – originally proposed by Helman (1983) and later improved by Gillison and Brewer (1985) and by Austin and Heyligers (1989, 1991) – represents a compromise between randomized sampling (distribution and replication) of multiple gradients along transects (stratification) and minimizing survey costs (accessibility). It can easily be designed in a geographical information system (Cocks and Baird, 1991; Neldner et al. 1995; Franklin et al., in press1995) and can thus be adapted to the spatial resolution of any study area. Austin and Heyligers (1991, p.36) provide a detailed list of the general steps that can be used to design a reasonable survey based on the gradsect method.

Designing the sampling according to a random-stratified scheme is another classical approach that can also be set up in a GIS. However, difficulties may arise from studies that involve many environmental gradients and many species, since setting up a multi-gradient stratified sampling is a particularly demanding task (Goedickemeier et al., 1997; Lischke et al., 1998). Individual GIS layers have to be stratified and intersected in order to delineate the polygons from which random samples have to be drawn. Each polygon represents a specific combination of environmental conditions, and each of these combinations (stratum) is usually present in multiple polygons. Next, a given number of polygons per stratum is selected randomly where samples have to be located. Restrictions may be applied, such as excluding polygons of size smaller than a lower threshold and larger than an upper threshold, to ensure the sampling of polygons of similar surface area. Finally, the sample location within the polygon can be selected randomly or systematically (e.g. at the centroid of the polygon)[6].

A quantitative comparison between gradsect, stratified (habitat-specific), systematic and random sampling is given in Wessels et al. (1998) and partly also in Goedickemeier et al. (1997). It shows that the gradsect approach gives comparable results to the stratified sampling for approaching species richness patterns in the study area, and both are superior to systematic and random sampling in their study context. However, if sampling is aimed at building species distribution models, one will want to have all environmental combinations equally sampled, which can be done but is not enforced by the gradsect approach. The use of a stratifying approach, although involving more

[6] To improve on this, multiple locations per polygon can be selected to ensure backup points for cases where the actual environmental characteristics in the field do not correspond to the strata defined from the information available in the GIS (physiography, vegetation, or soil maps, etc.). Each sampling site is then best localized in the field using DGPS (see for e.g. Goedickemeier et al. (1997) or Cherix et al. (1998)).

effort, will provide such a guarantee. Hence, if species richness and biodiversity are the focus, stratifying will require the proportional representation of all habitats in order to ensure sampling of as much as possible of the entire species pool in each habitat. Conversely, if a quantitative analysis between species distribution and environmental descriptors is the focus, one will attempt to sample an equal number of replicates per environmental combination (strata). It is thus fundamental to discuss the use of a particular method in a well-defined ecological context.

If a data set was not collected according to a stratified strategy (as in many observational studies), one may resample a fixed-size subset of observations from the existing data set within each environmental stratum. If there are not enough observations available for a stratum, we suggest to design a complementary field survey that will aim at sampling additional observations in under-represented strata, until the fixed-size number of replicates is reached. The new – resampled – data set is then more valid for statistical, analytical purposes.

The minimum *distance* between two sampling sites should be defined prior to sampling, according to an exploratory spatial autocorrelation study (see Legendre, 1993 for a review). Autocorrelation occurs when sampling points are located so close to each other that the postulate of independence between observations is violated. In such a case, pseudoreplication occurs (see Heffner et al., 1996), i.e. the number of degrees of freedom (d.f.) is lower than $(n - k - 1)$, the usual number of d.f. used for inferences when all observations are independently and identically distributed (i.i.d.), with n the number of sites and k the number of parameters in the model. Hence, in order to avoid spatial autocorrelation, a distance larger than the minimum distance at which autocorrelation occurs has to be chosen (e.g. 150 m for alpine communities; Fischer, 1994). Such a minimum distance criterion can easily be implemented in the design of a random-stratified sampling. If the sampling distance is too low to avoid autocorrelation, then an alternative is to include autocorrelation in the model (Malanson, 1985; Roxburg and Chesson, 1998), through adding an autocorrelative term (Augustin et al., 1996), adding the distance between the observation points (Leathwick, 1998) or smoothing model predictions by a trend surface analysis (TSA; Pereira and Itami, 1991)[7].

The environmental information gathered at the required spatial resolution for the entire study area is best stored in a GIS. Four main sources may be identified for the gathering of such environmental data:

1. field surveys or observational studies;
2. printed or digitized maps;
3. remote sensing data (numerical aerial photographs and satellite images);
4. maps obtained from GIS-based modeling procedures.

Field data (1) can be field measurements (e.g. abiotic characteristics of a site) or a network of meteorological measurements aimed at further interpolating climatic maps (4). Spatial data on geology, soil units, or hydrology most commonly originate from existing printed or digitized maps (2). Land use, rocky surfaces, snow cover, potential moisture or vegetation maps can be derived from aerial photographs or satellite scenes (3). Examples of distribution studies including remote sensing data are Frank (1988), Hodgson et al. (1988), Bagby and Brian (1992), Fitzgerald and Lees (1992), Herr and Queen (1993), Guisan et al. (1998), or Franklin et al. (2000). In certain cases, e.g. in mountainous areas where distortion can be high due to the steep relief, aerial photographs have to be rectified with the help of a DEM (see Guisan et al., 1998; Fig. 5) before they can be properly georeferenced.

In many cases the main prerequisite for spatial modeling is the DEM (Fig. 5). It constitutes the basis for generating new maps of environmental variables and determines the spatial resolution of all derived maps. However, it is important to distinguish between spatial resolution and map

[7] The above discussion is not relevant to those studies which aim to interpolate the sampled property (e.g. a crop biomass), without recourse to any additional environmental information. In such cases, the use of spatial interpolation techniques to design an optimal sampling strategy, as e.g. kriging (Atkinson, 1996), is more appropriate.

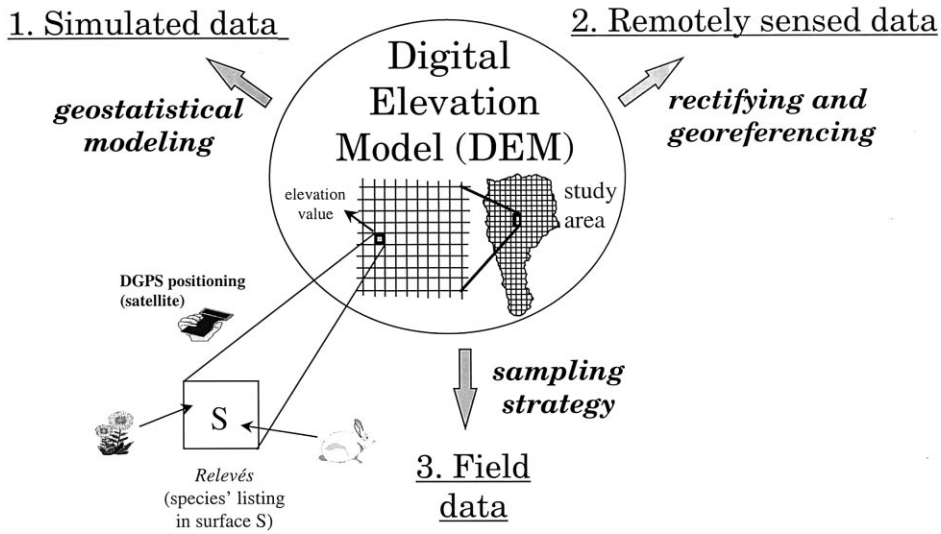

Fig. 5. The central role of the DEM in predictive habitat distribution modeling, as a basis for: (i) generating additional environmental information through geostatistical modeling (e.g. climatic data); (ii) rectifying aerial photographs and satellite images in mountainous areas; (iii) planing field survey (e.g. stratification design).

accuracy. Only rigorous testing of the errors of mapped entities or gradients will allow one to assess map accuracy. Generally, all maps derived from interpolations, calculations or combinations are less precise than the maps from which they originate. Thus, a DEM and its basic derivatives – slope, aspect, topographic position and curvature – are usually the most accurate maps available, though not necessarily those with the highest predictive potential.

Modeling of environmental variables has become more and more powerful. Fractal geometry can for instance be used to characterize vegetation complexity and help to interpret aerial photographs (Van Hees, 1994). Various spatial interpolation techniques and approaches to deal with the spatial context (in the sense of Fitzgerald and Lees, 1994a), such as regional autocorrelation and topographic dependencies, have been employed to generate a multitude of bioclimatic maps (Hutchinson and Bischof, 1983; Daly et al., 1994; Dubayah and Rich, 1995; Kumar et al., 1997; Thornton et al., 1997). These publicly available maps or modeling tools drastically improve the perspective of building physiologically more meaningful models of the environment. Still, the trade-off between modeling accuracy and 'physiological' correctness remains to be evaluated in terms of the overall goal of the model.

Related to the problem of accuracy is the task of selecting an appropriate data set to parameterize the model. Most predictive variables vary along topographical gradients. Depending on the spatial resolution and the techniques used to generate these maps, topographic variables can be used to evaluate the correspondence between digital and field-observed attributes for any location. Selecting a subset of plots that meet criteria of high correspondence between digital and real topography can significantly improve the model parameterization (Zimmermann, 1996; Zimmermann and Kienast, 1999). This way, the influence of mapping errors on the model parameterization can be reduced, although predictive accuracy may not be improved. It is obvious that measuring appropriate additional topographic parameters during the survey is important to make full use of such modeling steps.

4. Statistical model formulation

The statistical formulation has also been called *verification* by some authors (e.g. Rykiel, 1996) and is often presented in the 'Statistical analysis' section of most papers dealing with vegetation or single species modeling. By model formulation, we mean the choice of (i) a suited algorithm for predicting a particular type of response variable and estimating the model coefficients, and (ii) an optimal statistical approach with regard to the modeling context.

Most statistical models are specific to a particular type of response variable and its associated theoretical probability distribution (or density function). As a consequence, the latter has to be tested prior to the selection of an adequate model. This can be done, e.g. for a continuous response variable, by comparing its empirical distribution to the theoretical probability distribution (goodness-of-fit χ test) or their cumulative form (Kolmogorov–Smirnov test). A summary of some available techniques for modeling respectively quantitative (i.e. metric; ratio or interval scale; continuous or discrete), semi-quantitative (i.e. ordinal) or qualitative (i.e. nominal; categorical) response variables are given in Table 1 and illustrated with examples from the literature. Often, more than one technique, that may or may not belong to the same statistical approach, can be applied appropriately to the same response variable (Table 1).

The importance of a correct statistical model formulation is best illustrated with an example. Consider predicting the potential abundance of a species (or ground cover for plant species; see Brown et al., 1995 for a review of models for the spatial distribution of species abundance). Using standard least square (LS) regression in this case might be inadequate for the following reasons. Abundance is often recorded as a discrete variable and its distribution might reasonably follow: (i) a Poisson distribution (Vincent and Haworth, 1983), (ii) a negative binomial distribution (May, 1975; Oksanen et al., 1990; White and Bennetts, 1996), (iii) a canonical log-normal distribution (May, 1975), (iv) a broken-stick distribution (May, 1975) or, in cases where it was directly sampled on a semi-quantitative scale, (v) an ordinal distribution (Guisan et al., 1998; Guisan and Harrell, 2000; Guisan, in press2000), rather than the normal distribution implying the use of LS regression. Often, log-transforming the response variable only solves such situations unsatisfactorily (Vincent and Haworth, 1983); it is more appropriate to use maximum-likelihood (ML) estimation to fit the model, as this technique can deal with any parametric distribution. Thus, if abundance originates for instance from counts of individuals, one would preferably use generalized linear models (GLM; ML-based) with a Poisson or a negative-binomial distribution (Vincent and Haworth, 1983; Nicholls, 1989), rather than LS regression applied to a log-transformation of the response variable (log-linear models)[8]. Table 1 provides an overview of examples of response variables and their corresponding statistical models.

If necessary, the appropriateness of a statistical model can be checked by a series of tests (e.g. Marshall et al., 1995 in the case of LS regression) or graphical methods (e.g. *diagnostic plots*). A quantile–quantile plot (*QQ-plot*) of regression residuals can be used to check whether the assumption about the distribution of errors holds. Similarly, a plot of standardized residuals against fitted values can also help to identify unexpected patterns in the deviance (i.e. variance for GLMs). In such a case, one solution is to reconsider the definition of the deviance in the model[9]. With ordinal regression models, partial residual plots can be used to check the ordinality of the response variable y against each explanatory variable x_i (Guisan and Harrell, 2000).

The formulation of a theoretically appropriate model may fail to provide satisfying results be-

[8] The use of a binomial GLM with logistic link to predict presence/absence of plant communities (e.g. Zimmermann and Kienast, 1999), of plant species (Lischke et al., 1998; Franklin, 1998), or the use of a proportional odds (PO) regression model to predict ordinal abundance (Guisan et al., 1998; Guisan and Harrell, 2000; Guisan, in press2000) are other examples of appropriate model formulations.

[9] Using the e.g. 'quasi' family in the S-PLUS statistical software (see Guisan et al., 1999).

Table 1
Some statistical approaches and models, with literature examples, for three different types of response variables: quantitative (ratio or interval scales), semi-quantitative (ordinal), and qualitative (nominal)

Type of response variable	Probability distribution	Examples of response variable	Statistical approaches	Possible modeling technique	Type of predictions	Examples of habitat modeling studies
Quantitative (continuous)	Gaussian	Percent cover, sp richness, biomass	MULREG	WA, LS, LOWESS, GLM, GAM, Regression tree	Prob.	Huntley et al., 1995; Heikkinen, 1996
			ORDIN	CANOCO	Dist.	Hill, 1991; Gottfried et al., 1998; Guisan et al., 1999
	Poisson	Individual counts, species richness	MULREG	GLM, GAM	Prob.	Vincent and Haworth, 1983; Guisan, 1997
	Negative binomial	Individual counts	MULREG	GLM, GAM	Prob.	–
Semi-quantitative (ordinal)	Discretized continuous	Abundance scale	MULREG	PO model, CR model	Prob.	Guisan, 1997; Guisan et al., 1998; Guisan and Harrell, 2000; Guisan, in press2000
	True ordinal	Phenological stages	MULREG	Stereotype model	Prob.	–
Qualitative (categorical, nominal)	Multinomial	Vegetation units, plant communities	MULREG	Polychotomous logit regression	Prob.	Davis and Goetz, 1990
			CLASSIF	Classification tree	Class	Walker and Moore, 1988; Burke et al., 1989; Moore et al., 1991; Lees and Ritman, 1991
				MLC	Dist.	Frank, 1988
				Rule-based class	Class	Twery et al., 1991; Lenihan and Neilson, 1993; Li, 1995
			DISCR	DFA	Discrim. score	Lowell, 1991
			ENV–ENV	Boxcar, Convex Hull, point-to-point metrics	Degree of confidence	Box, 1981; Busby, 1986; Carpenter et al., 1993; Tchebakova et al., 1993
	Binomial	p/a, relative abundance	MULREG	GLM, GAM, Regression tree	Prob.	Nicholls, 1989; Austin et al., 1990, 1994; Yee and Mitchell, 1991; Lenihan, 1993; Brown, 1994; Van de Rijt et al., 1996; Guisan, 1997; Saetersdal and Birks, 1997; Franklin, 1998; Leathwick, 1998; Zimmermann and Kienast, 1999; Guisan et al., 1999; Guisan and Theurillat, 2000
		p/a	CLASSIF	Classification tree	Class	Franklin, 1998; Franklin et al., 2000

Table 1 (*Continued*)

Type of response variable	Probability distribution	Examples of response variable	Statistical approaches	Possible modeling technique	Type of predictions	Examples of habitat modeling studies
			ENV–ENV	Boxcar, Convex Hull, point-to-point metrics	Degree of confidence	Busby, 1986; Busby 1991; Walker and Cocks, 1991; Shao and Halpin, 1995; Huntley et al., 1995
			BAYES	Bayes formula	Prob.	Skidmore, 1989; Fischer, 1990; Aspinall, 1992; Brzeziecki et al., 1993

cause (i) the data themselves are not good enough, (ii) the resolution of the spatial scale is not appropriate, or (iii) the sampling design was not intended for this purpose. In some cases, the model predictions can be greatly improved by applying a particular category of statistical algorithms. As an example, the use of more empirically based techniques, such as generalized additive models (GAM) instead of LS or GLM, proved to be more satisfying in some studies (e.g. Yee and Mitchell, 1991).

In the following sections, we discuss the main statistical approaches (to modeling) grouped into seven categories (see Table 1): Multiple regression and its generalized forms, Classification techniques, Environmental envelopes, Ordination techniques, Bayesian approaches, Neural networks and a seventh category including other potential approaches or approaches involving several methods (mixed approach).

4.1. Generalized regressions

Regression relates a response variable to a single (simple regression) or a combination (multiple regression) of environmental predictors (explanatory variables). The predictors can be the environmental variables themselves or, in order to prevent multicollinearity in the data, orthogonalized components derived from the environmental variables through multivariate analysis (e.g. partial least square (PLS), Nilsson et al., 1994; Heikkinen, 1996; Birks, 1996, principal component regression (PCR), Brown et al., 1993; Saetersdal and Birks, 1997). One possible multicollinearity diagnostic is the variance inflation factor analysis (VIF; Montgomery and Peck, 1982). It should be preferred to analyze pairwise correlation between predictors, as near linear dependencies may involve more than two predictors. The classical LS regression approach is theoretically valid only when the response variable is normally distributed and the variance does not change as a function of the mean (homoscedasticity). GLMs constitute a more flexible family of regression models, which allow other distributions for the response variable and non-constant variance functions to be modeled. In GLMs, the combination of predictors, the linear predictor (LP), is related to the mean of the response variable through a link function. Using such link functions allows (i) transformation to linearity, and (ii) the predictions to be maintained within the range of coherent values for the response variable. By doing so, GLMs can handle distributions such as the Gaussian, Poisson, Binomial, or Gamma – with respective link functions set e.g. to identity, logarithm, logit and inverse. Contrary to LS-regressions, that could predict biologically unfeasible values (e.g. probabilities higher than 100% or negative values; see Guisan, in press), GLM models yield predictions within the limits of observed values (e.g. presence/absence [1/0] and probability values in between these extremes)[10].

If the response is not in linear relationship with a predictor, a transformed term of the latter can be included in the model. A regression model including higher order terms is called polynomial regression. Second order polynomial regressions simulate unimodal symmetric responses (e.g. Fig. 6a), whereas third order or higher terms allow simulating skewed and bimodal responses, or even a combination of both. Other transformation functions (also called parametric smoothers; see Oksanen, 1997) to simulate more specific response shapes include: (i) β-functions (Austin et al., 1994), (ii) hierarchical set of models (Huisman et al., 1993), or (iii) a set of '*n*-transformed' functions (Usó-Domènech et al., 1997).

Alternative regression techniques to relate the distribution of biological entities to environmental gradients are based on non-parametric smoothing functions of predictors (Fig. 6b)[11]. They include

[10] A Gaussian GLM with identity link is equivalent to a LS regression. Binomial GLMs with logit link are commonly used in distribution modeling under the name of logit regression. The latter also constitute the core of ordinal regression models (Guisan and Harrell, 2000) and polychotomous regression models (Davis and Goetz, 1990).

[11] Thus rising new questions such as: 'is a skewed response curve best integrated in a model by a parametric polynomial (e.g. Ferrer-Castán et al., 1995), a Beta-function (e.g. Austin et al., 1994), a non-linear function (e.g. from a hierarchical set of functions; Huisman et al., 1993) or a smoothed function (e.g. Yee and Mitchell, 1991)?'

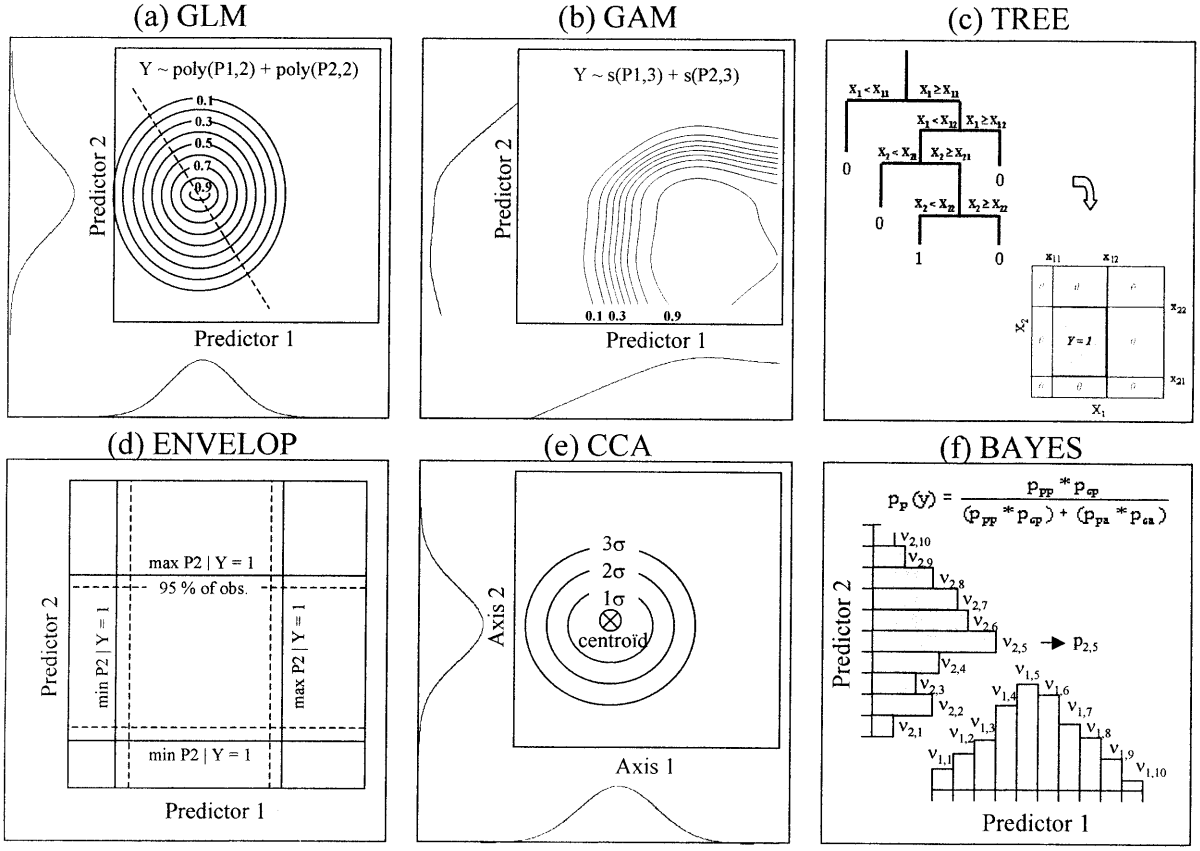

Fig. 6. Examples of response curves for different statistical approaches used to model distribution of plants and vegetation. (a) Generalized linear model with second order polynomial terms; (b) generalized additive model with smoothed spline functions; (c) classification tree; (d) environmental envelope of the BIOCLIM type; (e) canonical correspondence analysis; (f) Bayesian modeling according to Aspinall (1992); p_p = posterior probability of presence of the modeled species, p_{pp} = a priori probability of presence, p_{pa} = a priori probability of absence, p_{cp} = product of *conditional* probability of presence of the various predictor classes, p_{ca} = product of *conditional* probability of absence of the various predictor classes.

running means, locally weighted regression, or locally weighted density functions (Venables and Ripley, 1994). GAMs are commonly used to implement non-parametric smoothers in regression models (Yee and Mitchell, 1991; Brown, 1994; Austin and Meyers, 1996; Bio et al., 1998; Franklin, 1998; Lehmann, 1998; Leathwick, 1998)[12]. This technique applies smoothers independently to each predictor and additively calculates the component response. Alternatively, multidimensional smoothers can be applied (Huntley et al., 1989, 1995), the drawbacks of which are discussed by Friedman and Stuetzle (1981) and Yee and Mitchell (1991).

Furthermore, regression models can be improved by incorporating additional information on ecological processes such as dispersal or connectivity. An example is the recent implementation of autocorrelative functions in a logistic GLM (Augustin et al. 1996; Preisler et al., 1997) as previously suggested by Malanson (1985).

[12] GAMs are sometimes used in an exploratory way, to identify the most probable shape of response curves that are then best fitted with a GLM (e.g. Brown, 1994; Franklin, 1998), but can also be used directly to fit the final model (e.g. Lehmann, 1998; Leathwick, 1998).

4.2. Classification techniques

The category of classification encompasses a broad range of techniques. It includes techniques such as classification (qualitative response; Fig. 6c) and regression (quantitative response) trees (CART; Breiman et al., 1984; e.g. in Moore et al., 1991; Lees and Ritman, 1991; Franklin, 1998; Franklin et al., 2000)[13], rule-based classification (e.g. Twery et al., 1991; Lenihan and Neilson, 1993) and maximum-likelihood classification (MLC; e.g. Franklin and Wilson, 1991). Within some GIS software (ArcInfo, Imagine, GRASS, Ilwis, Idrisi), the latter is generally called 'supervised classification' when it relies on a training data set, and 'unsupervised classification' when no training data set is required. We found no direct examples of the application of linear machines to predict plant or animal distribution, i.e., machine learning multivariate or hybrid decision trees related to CART (Brodley and Utgoff, 1995). However, examples of their use to derive land cover from satellite scenes do exist (J. Franklin, personal communication). All these techniques assign a class of the binary (Fig. 6c) or multinomial response variable to each combination of (nominal or continuous) environmental predictors.

CART, decision tree, and other rule-based classifications are sometimes placed within artificial intelligence (AI) techniques, although not all of these are based on classification techniques (e.g. neural networks; Fitzgerald and Lees, 1992). Some expert systems or decision-tree classifiers are built from interrelating simple rules deduced from previous understanding of the phenomena to be modeled (e.g. from literature, laboratory experiments, expert knowledge). In a more empirical way, algorithms such as CART allow the rules to be induced directly from the observations (Lees and Ritman, 1991).

4.3. Environmental envelopes

Until recently, many large-scale vegetation or species models were based on environmental envelope techniques (e.g. Holdridge, 1967; Box, 1981; Busby, 1991; Carpenter et al., 1993; Shao and Halpin, 1995). Busby (1986, 1991) developed the BIOCLIM model – a fitted, species-specific, p-dimensional environmental envelope (Boxcar) – to model plant species distribution in Australia, using one-by-one degree latitude–longitude grid cells. This approach is based on calculating a minimal rectilinear envelope in a multi-dimensional climatic space (see Fig. 6d for a two-dimensional example). Holdridge (1967) applied the same approach to ecosystems, and Box (1981) to plant functional types.

In an attempt to enclose record sites in the environmental space more tightly than by the BIOCLIM rectilinear envelope, Walker and Cocks (1991) developed the HABITAT model using convex polytope envelopes (convex hull). Interestingly, both models give very similar results although they differ in their classification procedure. A rectilinear envelope can be defined from a very simple classification tree as well (only one dichotomy per predictor), whereas the more complex polytope envelope would need a more detailed tree including more terminal nodes[14]. The DOMAIN model, developed by Carpenter et al. (1993), is more complex. Its approach is not that of classification trees; instead, it is based on a point-to-point similarity metric (measure of multivariate distances) and has proved to be more suitable for applications where available records are limited.

Prentice et al. (1992) developed a more mechanistic version of the environmental envelope model family by fitting only the lower limit of direct and resource gradients in order to predict the predominant plant functional types on a global scale. Thus, these limits represent the minimum requirement for plant growth. Upper limits for functional types along environmental gradients are assumed to be caused by competition rather than by intolerance or environmental constraints. Consequently, the functional types are ranked by their ability to dominate, and a func-

[13] A comparison between classification trees and GLM/GAM can be found in Franklin (1998).

[14] Quantitative comparisons of environmental envelope and classification tree approaches can be found in Walker and Cocks (1991) or Skidmore et al. (1996).

tional type is replaced automatically by a more competitive type, once the latter is simulated.

4.4. Ordination techniques

Most models that use ordination techniques to predict the distribution of species or communities are based on canonical correspondence analysis (CCA; see Hill, 1991; Birks, 1996; Gottfried et al., 1998; Ohmann and Spiess, 1998; Guisan et al., 1999)[15]. In this direct gradient analysis the principal ordination axes are constrained to be a linear combination of environmental descriptors (ter Braak, 1988). The method is based on reciprocal averaging of species and site scores (Hill, 1973). Thus, the assumed distribution of species is Gaussian (Fig. 6e), with an upper and a lower limit of occurrence and an optimum along gradients. This method is appropriate for data sets with many zeros (i.e. absences)[16]. Although the method relies on several postulates (e.g. Gaussian response curves, species having equal ecological tolerance and equal maxima along canonical axes, with the position of the modes distributed uniformly along a much larger range than species tolerances) that may theoretically invalidate its use in many situations, ter Braak (1985) argues that the method is still robust when such postulates are violated.

Redundancy analysis (RDA) – the canonical counterpart of the principal component analysis (PCA) – is less frequently used to simulate environmentally dependent distribution of communities and taxa. The method is similar to LS-regression with linear terms only. However, the deviation of the residuals is calculated perpendicular to the fitted axes, since there is no independent gradient in ordination. Thus, the underlying response model is a linear or monotonic distribution of species along environmental gradients, which limits the applicability of this method to short (truncated) environmental gradients only (Jongman et al., 1995; ter Braak, 1988). Hence, the approach is of limited use on the scale of landscape modeling, where large gradients are usually analyzed.

4.5. Bayesian approach

Models based on Bayesian statistics combine a priori probabilities of observing species (e.g. Skidmore, 1989; Aspinall, 1992; Aspinall and Veitch, 1993) or communities (e.g. Fischer, 1990; Brzeziecki et al., 1993) with their probabilities of occurrence conditional to the value (or class of values) of each environmental predictor (Fig. 6f). Conditional probabilities $p(y|x_i)$ can be for instance the relative frequencies of species occurrence within discrete classes of a nominal predictor. A priori probabilities can be based on previous results or literature. This results in an a posteriori predicted probability of the modeled entity at a given site with known environmental attributes. In vegetation mapping, a posteriori probabilities are calculated for each vegetation unit and the unit with the highest probability is predicted at every candidate site (Fischer, 1990; Brzeziecki et al., 1993).

4.6. Neural networks

The recourse to artificial neural networks (ANN) as used by Fitzgerald and Lees (1992, 1994a,b), Civco (1993), Tan and Smeins (1994), Chen et al. (1995), Lees (1996), Lek et al. (1996) or Manel et al. (1999) is a promising area of predictive habitat distribution modeling. However, most published applications of ANN in ecology are concerned with the field of remote sensing (see Fitzgerald and Lees, 1992) and (non-spatial) predictive assessment of environmental changes (see Spitz and Lek, 1999). Very few examples exist of ANN being used to predict the spatial distribution of species or communities using biophysical descriptors. Fitzgerald and Lees (1992) had recourse to back-propagation neural network to predict the distribution of nine land-use/floristic classes from a mix of remote-sensing (LANDSAT TM bands 2, 4, 7), topographic (elevation, aspect, slope, catchment) and geological data. They obtained results as good as those using a classifica-

[15] A comparison between CCA and GLM modeling is given in Guisan et al. (1999).

[16] Yet, the CCA-approach has mainly been used to predict presence–absence of species at spatial locations.

tion tree applied to the same data (e.g. Lees and Ritman, 1991; Lees, 1996). Lek et al. (1996) showed that neural network models are more powerful than multiple regression models when modeling nonlinear relationships. The full classification procedure in the case of neural network is a complex non-parametric process that is sometimes seen as a 'black art', even by computer scientists (Caudill, 1991). Detailed discussion of the method is the e.g. provided by Hepner et al. (1990) or Benediktsson et al. (1991).

4.7. Other approaches

Other existing techniques are not listed in Table 1. Simple models can be developed directly within a GIS, using overlays of environmental variables, measures of variation, measures of similarity and final rules for combining single probabilities. An example is given in Martinez-Taberner et al. (1992). For each cell of the DEM and for each environmental variable, a modified Jaccard index is used to measure the overlap between the degree of seasonal variation and the environmental tolerance of each species. These values are then considered to be probabilities of occurrence of species as a function of a single environmental predictor. Finally, to calculate an overall probability of occurrence, all predictors are combined using a geometric mean[17].

Examples of distribution modeling exist that have recourse to discriminant function analysis (DFA; e.g. Frank, 1988; Lowell, 1991; Corsi et al., 1999). When modeling vegetation units, individual discriminant functions are produced for each unit, from which a discriminant score is calculated. Further assignment of any candidate site to one of the unit is based on the highest calculated score. This approach relies on similar assumptions as those used for least square regression (independence of predictors, constant variance) except that here, the data for each unit need to be drawn from a multivariate normal population (Huberty, 1994). Interestingly, using a GLM with binomial distribution for a binary response variable (i.e. the logistic regression) can be considered a more flexible way to run a discriminant analysis.

The ecological niche-factor analysis (ENFA) was first suggested by Perrin (1984), developed later by Hausser (1995) and recently implemented in the BIOMAPPER package (Hirzel et al., 2000). It differs from CCA or RDA, in the sense that it considers only one species at a time. Like the environmental envelope approach, it presents the advantage of requiring only presence data, a frequent situation in the case of animal observations where absences are difficult to assess in the field. Using a *marginality* index and up to three *tolerance* indices, ENFA situates the species–environmental envelope within the multidimensional environmental envelope that is defined by considering all mapping units within the study area.

With the MONOMAX approach (Bayes and Mackey, 1991; Mackey, 1993), a suite of algorithms fits a monotonic maximum-likelihood function through iterative processes (which Mackey calls 'dynamic programming'). One severe drawback of this method is that the probability of a response variable can be determined from a maximum of two predictor variables at a time. In turn, a clear advantage of such non-parametric method (also called *distribution-free* method) is that no assumptions about the distribution of the data or the residuals nor about their variance is needed, which makes such a tool particularly suitable for exploratory analyses (Mackey, 1993).

5. Model calibration

This step results in the adjustment of the mathematical model that was selected for the specific data set at hand. Rykiel (1996) defines calibration as "the estimation and adjustment of model parameters and constants to improve the agreement between model output and a data set".

[17] Additional examples of boolean approaches (overlay rules) can be found in Turner and Baumer (1984), Franklin et al. (1986), Scepan et al. (1987), Cibula and Nyquist (1987), Hodgson et al. (1988), Mead et al. (1988), Shaw and Atkinson (1988), Agee et al. (1989), Stoms et al. (1990), Breininger et al. (1991), Bagby and Brian (1992), Chang et al. (1992), Schuster (1994), or Herr and Queen (1993).

Although we agree with this definition, we would like to broaden it to encompass the more global phase of model construction, which includes the selection of explanatory variable.

To enhance the accuracy and predictive power of a model, the number of explanatory variables used must be reduced to a reasonable number (Harrell et al., 1996). Thus, one of the most difficult tasks is to decide which explanatory variables, or combination of variables, should enter the model. Estimating their coefficients, once they are selected, is usually a straightforward task.

The selection of predictors can be made arbitrarily (which we do not recommend), automatically (e.g. by stepwise procedures in LS regression, GLMs, and CCA), by following physiological principles, or by following shrinkage rules (Harrell et al., 1996, 1998). The latter approach seems to be promising in the case of main effect GLM models (i.e., models without interaction terms). Overall, Harrell et al. (1996) suggest than no more than $m/10$ predictors should be included in the final model, where m is the total number of observations or the number of observations in the least represented category in the case of a binary response.

By predictors, we also mean all their possible transformations such as polynomial terms, β-functions (Austin et al., 1994), smoothed empirical functions (GAMs; Yee and Mitchell, 1991), or the use of significant ordination axes (Franklin et al., 1995) as in orthogonalized regressions (e.g. Heikkinen, 1996). In the latter case, however, the biological interpretation of such artificial components as well as the link to a conceptual model might be difficult. Clearly, the selection of a set of *direct* and *resource* gradients (Austin, 1980, 1985) for calibrating a model is particularly promising if ecological significance and interpretability are to be optimized (Prentice et al., 1992).

Variable transformation is closely bound to the primary identification of species' response curves to environmental gradients (see first section). Once their shape is approximated (see e.g. Huisman et al., 1993; Austin and Gaywood, 1994; Austin et al., 1994; Bio et al., 1998), the statistical model attempts to reproduce and formalize this shape (Austin, 1987). As an e.g. Brown (1994) or Franklin (1998) used non-parametric GAMs to explore the response of species to the environmental predictors and then used GLMs to reproduce the identified shapes with adequate parametric terms in the model.

Particular problems arise with skewed responses, as their simulation in LS or GLMs is not easy. Third order and higher polynomials can simulate a skewness in the responses, but they tend to reveal spurious and biologically unfeasible response shapes that are more difficult to interpret (Austin et al., 1990; Hastie and Tibshirani, 1987; Huisman et al., 1993; Austin et al., 1994; Bio et al., 1998). This is specifically true outside the range of values used for calibrating the model (e.g. outside the study area, for evaluating climate change impacts on plant distribution; see Guisan, 1997). Oksanen (1997) concludes that β-functions (Austin et al., 1994) are not appropriate in this case, and that using Huisman's approach of hierarchical models (Huisman et al., 1993) is a preferable alternative, although no clear explanation is given on how to implement such non linear models within, for example, a GLM. Besides, choosing appropriate initial values for the estimation of parameters in non-linear models might also constitute an additional limitation to their common use in further modeling studies (Huisman, personal communication).

Parameter estimation is an objective mathematical operation described in most statistical textbooks and available in any statistical package (SAS, S-PLUS, SPSS, SYSTAT, etc.). The fit of most models is characterized by a measure of the variance reduction (or deviance reduction in the case of maximum-likelihood estimation (MLE) techniques). In GLMs, the model is optimized through deviance reduction, which can easily be converted into an estimated D^2 – the equivalent to R^2 in LS models – by the following formula:

$$D^2 = (\text{Null deviance} - \text{Residual deviance}) / \text{Null deviance}, \quad (1)$$

where the null deviance is the deviance of the model with the intercept only, and the residual deviance is the deviance that remains unexplained by the model after all final variables have been included. A perfect model has no residual devi-

ance and its D^2 takes the value 1. In the case of LS regression, Weisberg (1980) and Nagelkerke (1991) argue that such a measure is not representative of the real fit, unless the number of observations n and the number of predictors p in the model are taken into account (i.e. weighting by the residual degrees of freedom). For this purpose, Weisberg (1980) suggests a new measure that is commonly called the adjusted R^2. It can be defined similarly for GLMs as

$$\text{adjusted } D^2 = 1 - [(n-1)/(n-p)] \times [1 - D^2] \,, \quad (2)$$

where D replaces R in Weisberg's original formula. The value of the adjusted D^2 increases with an increasing number of observations (n) or a decreasing number of parameters (p) in the model.

The adjusted D^2 – or R^2 – is an ideal measure to compare models that include different combinations of variables and interaction terms. Generally, the model for which the deviance reduction is maximal is considered as the best, and further used for prediction purposes. During the variable selection procedure, the deviance reduction associated with each variable is tested for significance at a given confidence level (usually 0.05). The test depends on the method used for estimating the coefficients and the related variance or deviance distribution. For GLMs, McCullagh and Nelder (1989, p. 36) stated: "Once we depart from the Normal-theory linear model we generally lack an exact theory for the distribution of the deviance [...] Usually we rely on the χ^2 approximation for differences between deviances". Additionally, a Student t-test, using the standard error associated with the estimated model coefficients, is necessary to check whether the coefficients differ significantly from zero.

In *tree-based techniques* the model will attempt to predict the data exactly, so that no fit needs to be characterized and the evaluation of the model may take place immediately after the model calibration. With classification and regression trees (CART) this generally results in over-fitted trees (Chambers and Hastie, 1993) with almost as many terminal nodes as there are observations. Hence, the model is not parsimonious and no reduction in complexity has been achieved. Pruning – which is cutting the tree at a certain complexity level to limit the number of terminal nodes – combined with cross-validation (CV), can be used to cut the tree down to a more 'optimal' number of terminal nodes (Breiman et al., 1984; Chambers and Hastie, 1993; see Franklin et al., 2000 for an application). However, if more than one observation is left out at a time, the result of such optimized pruning can be subject to change from one run to the other, since it relies on a random partitioning of the training data set. In this case, we recommend replicating the procedure and choosing the most frequent or average number of terminal nodes.

Walker and Cocks (1991) describe one way to calibrate *environmental envelopes*. Instead of using the same set of environmental parameters for all species (as in BIOCLIM), they propose the selection of a subset using the CART algorithm (Breiman et al., 1984). This subset of predictors is then used to define the multidimensional envelope that best encloses the occurrence of the species. Their HABITAT model uses a refined set of habitat decision rules which divide the global envelope into sub-envelopes of varying sizes in an optimal way (Walker and Cocks, 1991). The proportion of species' occurrence over the total number of observations in each sub-envelope is now used linearly as a measure of degree of membership (not a probabilistic concept; see Zadeh, 1965) of each new site to each sub-envelope of the species. Another approach for calibrating an environmental envelope is proposed by Carpenter et al. (1993). Their DOMAIN model is based on a point-to-point similarity metric (Gower, 1971) between a candidate site and the most similar record site in environmental space. Again, the predictions are not probabilistic, but an expression of the degree of classification confidence.

In *constrained ordination* methods (also called 'direct gradient analysis', or 'direct ordination') like CCA, the model calibration is very similar to linear regression, except that here the goodness-of-fit criterion is to "minimize the ratio of the mean within-species sum-of-squares of the variance to the overall sum of squares" (Hill, 1991). As in regressions, explanatory variables can be

selected stepwise. Posterior to the ordination, each axis can be tested for significance through Monte Carlo permutations. A subset of environmental predictors can also be defined as covariables, which allows the removal of their effect (i.e. 'partial out') from the ordination of the remaining set of explanatory variables (Borcard et al., 1992). This is especially useful in cases where the effects of particular variables are to be singled out from the background variation imposed by other variables (ter Braak, 1988). This is achieved in partial canonical ordination, a method that was first applied by Borcard et al. (1992) and by Borcard and Legendre (1994) to detect hidden spatial gradients that are still unexplained by present ecological gradients. Finally, variables can be declared as 'passive', which means that their vector is plotted with other environmental variables in the resulting ordination bi- or tri-plot, but they are not actually used with other predictors to calculate the linear combination that best explains the system of ordination axes.

An overall measure of the CCA fit is given both by the trace (or total inertia) of the underlying correspondence analysis (CA) and by the proportion of variance in the species' data that is explained by each canonical axis. The trace is the total variance in the species data (i.e. the sum of all eigenvalues). It is measured by the χ^2 of the sample-by-species table (Greenacre, 1984) divided by N, the table's grand total (see ter Braak and Smilauer, 1998). The fit of a particular species by k CCA axes is given cumulatively and expressed as a fraction of the variance of a species. The species variance is calculated as the χ^2 of the sample-by-species table divided by species' column total (for more details, see Greenacre, 1984, or ter Braak and Smilauer, 1998). The reported fits are the regression sums of squares of the weighted regression of the data for the species, expressed as a fraction of the total sum of squares for the species (i.e. in a similar way as D^2 in GLMs), on the $1 - k$ ordination axes. The overall percentage of explained variance is obtained by adding all axes. These measures of the fit are discussed in more detail in ter Braak and Smilauer (1998). In addition, the species–environment correlation can be measured for each axis as the correlation of the respective multidimensional coordinates of the species occurrences in both the species and the environmental space. The latter results from multiple regression predictions of the species coordinates on the environmental variables. A high species–environment correlation does not necessarily mean that a considerable amount of the species data is explained by the environmental variables (ter Braak, 1988), and thus it is not a good measure of the fit (see also Guisan et al., 1999).

Calibrating a *Bayesian model* to predict distribution of species or vegetation units is equivalent to calculating the multivariate state conditional probability of each considered entity, given the values of the environmental predictors (Aspinall, 1992; Brzeziecki et al., 1993). The significance of each habitat attribute for discriminating or not discriminating the occurrence of the modeled entity can be assessed through χ^2 frequency analysis (Aspinall, 1992). The resulting χ scores can be used to decide which predictor should be included in the model. If prior information is available, e.g. about the overall frequency of the modeled entities in the study area, it can be set as the prior probabilities. If no prior information is available, the prior probabilities can be defined as equal and assigned an arbitrary value. Fischer (1993) used prior probabilities using data from a systematic sampling, whereas Brzeziecki et al. (1993) did not distinguish prior probabilities because the training data set lacked any statistical sampling procedure. In Aspinall (1992), prior probabilities are estimates of the probabilities of presence and absence. Both can be set to 0.5 if the assumption of equal probability for presence and absence is chosen. As an alternative, they can be set according to the proportion of all sites in which the entity is present (Aspinall, 1992). Qualitative predictors can be treated as in parallelepiped (PPD) classification (see Binz and Wildi, 1988), by assigning probability 1 if a vegetation type occurs at least once (or another defined threshold) within the qualitative class, and 0 if it never occurs within the respective class (Brzeziecki et al., 1993). These values are then multiplied by the probabilities originating from the Bayes formula. Thus, a zero value for any of the qualitative predictors will set the overall probability to zero.

Discriminant functions are often calibrated using Wilk's λ goodness-of-fit statistic, which provides a similar measure of overall model fit as the R^2 in multiple regression. It is distributed as an F-ratio when the number of units modeled is less than or equal to 4, or when there are only two predictors (Lowell, 1991; Huberty, 1994).

During model calibration, the individual influences of each observation on the model-fitting can usually be evaluated graphically (e.g. in LS, GLMs). In regression analyses, such screening allows the identification of outliers and leverage points, the removal of which (supported by biological reasons) may contribute to improve the fit of the model. In LS regressions, they are derived from the residual calculations (in the case of outliers) and from the hat matrix (in the case of leverage points). Another measure of influence is based on the *Jack-knife* methods (Efron and Tibshirani, 1993). It is performed by fitting the model with n observations but one, leaving out successively one observation at a time. This procedure leads to the calculation of the *empirical influence values* ε for each observation. These values can be plotted as a function of the observation number to detect possible outlying observations. A similar approach can be used for cross-validating the model when no held-back data are available (see Section 7).

6. Model predictions

Once the plant species' or community's multiple response (i.e. its ecological profile) is derived by any of the modeling techniques previously described, its potential distribution within the modeled area can be predicted. Modeling potential distribution of plant species or communities is equivalent to modeling their potential habitat (Schuster, 1994; sensu Whittaker et al., 1973), which led some authors to call such maps 'potential habitat distribution maps' (PHDMs). Potential distribution maps can be defined in several ways, as cartographic representations of:

1. the *probability of occurrence* (e.g. from logistic GLMs; Fig. 7a);
2. the *most probable abundance* (e.g. from ordinal GLM; Fig. 7b);
3. the *predicted occurrence* based on non-probabilistic metrics (e.g. from CCA; Fig. 7c);
4. the *most probable entity* (e.g. from hierarchical considerations, Fig. 7d).

Although GIS are widely used tools in all types of spatially explicit studies, they still lack important statistical procedures for predictive purposes. This is a serious flaw because not all statistically derived models are similarly easy to implement in a GIS environment.

Logistic regression and supervised classification techniques are available in most GIS packages but they remain largely insufficient when applying most of the previously cited methodological steps (e.g. no stepwise selection procedure for logistic regression is available in ArcInfo). Moreover, they do not provide graphical checking of the model fitting (e.g. regression diagnostics), and the final evaluation of the model predictions cannot be made immediately. In turn, models cannot be easily calibrated outside of the GIS, since most statistical packages cannot read GIS-maps directly, and the interchange files are generally huge in size.

GLM models are easy to implement in a GIS, as far as the inverse of their link function can be calculated. Each model is generated by simply multiplying each regression coefficient with its related predictor variable. The results of the calculations are obtained on the scale of the LP so that the inverse link transformation is necessary to obtain probability values on the scale of the original response variable (Guisan et al., 1998, 1999). With binomial GLM, for instance, the inverse logistic transformation is

$$p(y) = \exp(\mathrm{LP})/(1 + \exp(\mathrm{LP})), \quad (3)$$

where LP is the linear predictor fitted by logistic regression. Such transformation is necessary to obtain probability values between 0 and 1. Ordinal GLMs are implemented on the same basis in a GIS (see Guisan and Harrell, 2000).

Implementing classification models in a GIS depends on the specific approach chosen. Supervised classification techniques (using an MLC algorithm) are available in most GIS. Classification

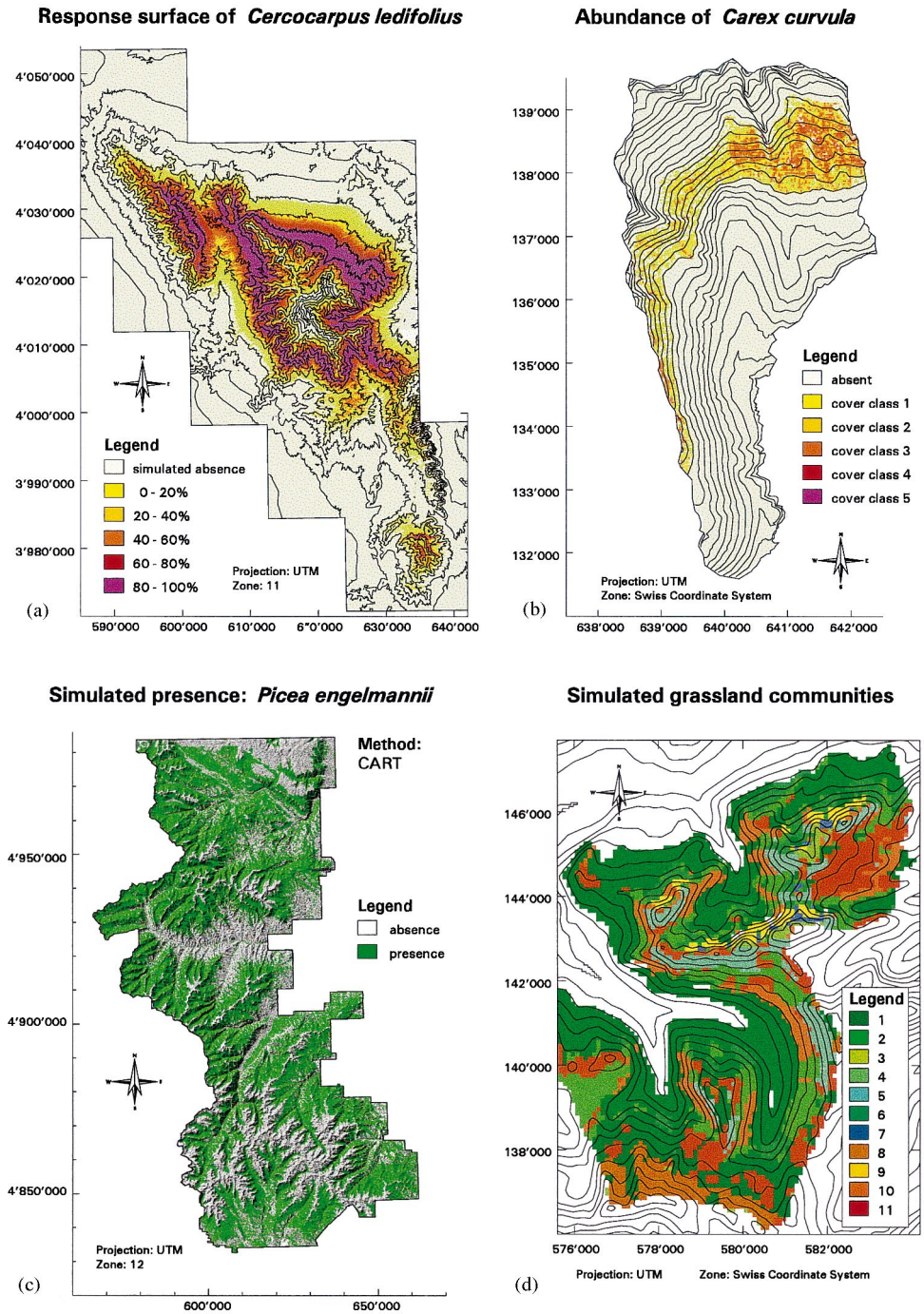

Fig. 7. Predicted maps representing (a) the probability of occurrence of a species (Spring Mountains, Nevada; see Guisan et al., 1999), (b) the distribution of most probable abundance values of a species at each pixel (Belalp area, Swiss Alps; from Guisan, 1997), (c) the potential distribution of a species based on a non-probabilistic metric (CART) (Shoshone National Forest, Wyoming; Zimmermann, N.E. and Roberts, D.W., unpublished data) and (d) the most probable entity (vegetation map; Pays d'En-Haut, Swiss Alps; from Zimmermann, 1996; the legend numbers represent vegetation types).

and regression trees can be implemented by using the CART software (Breiman et al., 1984; CART, 1984) directly linked to a GIS, or by writing a GIS specific macro to reconstruct the tree by using conditional statements (e.g. Lagacherie, 1992). However, the latter solution becomes laborious to implement when trees are complex. Rule-based classifications are the easiest to implement in a GIS, as they can be performed through simple overlay procedures combined with simple conditional statements or written as simple macros.

Many environmental envelope models are calculated by using specific programs that include the display of final maps. In the HABITAT program (Walker and Cocks, 1991), environmental envelopes (convex polytopes in this case) are implemented (i) through a successive splitting of variables (as done by the CART software; what Breiman et al., 1984 call *computer induction*) and (ii) by maximizing a function via iterative processes with constraints (what is called *linear programming* by Breiman et al., 1984). Computer induction aims at (a) identifying a reduced number of parameters for explaining the species' distribution, and (b) dividing the environmental envelope into sub-envelopes with differing probabilities of occurrence of the modeled species.

Linear programming checks if a candidate site lies inside or outside the envelope. Implementing predictions from environmentally constrained ordinations in a GIS is achieved by calculating the main axes from linear combinations of the original environmental predictors (using the *canonical coefficients*). Each axis constitutes a new grid layer in the GIS, and multiple axis layers together define the new canonical space. This allows for the position of each candidate grid cell in the canonical space to be determined and, finally, the calculation of its Euclidean distance to each species centroid. Distances can be grouped by classes of standard deviation units and mapped to draw the potential distribution of each species. Again, such implementation can be facilitated if the whole procedure is written as a custom macro function (e.g. the CANOGEN macro, an implementation of CCA models in ArcInfo, written in the Arc Macro Language; see Guisan et al., 1999).

Bayesian models are implemented in a GIS by combining the environmental layers within Bayes' theorem. Estimates of presence/absence (a priori probabilities) are modified by the conditional probabilities of observing the modeled entity at each site. As an example, Aspinall (1992) implemented the full procedure in a single GIS macro and Brzeziecki et al. (1993) as a FORTRAN program (personal communication).

Models based on discriminant analysis can be implemented in a GIS in the same manner as GLMs, by calculating the discriminant function from the estimated coefficients. However, no inverse link function is needed to transform the predictions back to the scale of the response variable.

7. Model evaluation

Loehle (1983), Oreskes et al. (1994) and Rykiel (1996) discuss the use of the term *validation* when measuring the adequacy between model predictions and field observations, what is called *accuracy assessment* in remote sensing studies. Oreskes et al. recommend that the term validation be no longer used for this specific step. Loehle comments that validation generally implies a logical analysis of models, which we here refer to as 'theoretical model formulation'. To analyze the predictive success of models, we propose to follow Oreskes et al. (1994) and use the term *evaluation*. We believe it to be the most appropriate term, as the model's veracity is not called into question. Models cannot be tested as being true or false, but for providing good testable hypotheses relevant to important problems (Levins, 1966), and for the accurate prediction of biological patterns. Gauging the accuracy of predictions is directly related to the estimation of their apparent error rate. When assessing the predictive power of a statistical model, Van Houwelingen and Le Cessie (1990) showed that their model was too optimistic, at least as regards the three methods they tested. A better assessment can be obtained by using optimism corrections. The latter can be analytical (see Van Houwelingen and Le Cessie, 1990) or empirical (based on CV and bootstrap; see Guisan and

Harrell, 2000). Furthermore, evaluation is related to the measure of adequacy, which depends on the specific purpose of the project, and the domain in which the model is supposed to be applicable (Fieldings and Bell, 1997).

Two main approaches exist for evaluating the predictive power of a model. The first approach is to use a single data set to calibrate the model and then evaluate it by CV (Van Houwelingen and Le Cessie, 1990; Manel et al., 1999; Franklin et al. 2000), *leave-one-out* Jack-knife (JK, a special case of CV; Efron and Tibshirani, 1993, 1993; Manel et al., 1999) or bootstrap (Efron and Tibshirani, 1993, 1993; Guisan and Harrell, 2000) techniques. The second approach is to use two independent data sets, one for calibrating and another for evaluating the model (often called the *training* and *evaluation* data sets; e.g. Brzeziecki et al., 1993; Guisan et al., 1998, 1999; Zimmermann and Kienast, 1999).

Bootstrap, in particular, attempts to correct the error rate for over-optimism rather than to assess the adequacy between predictions (i.e. values predicted at independent sites not used for calibrating the model) and actual observations. Hence, bootstrap and other resampling methods can be used to complement an independent evaluation of the models. As a first step, bootstrap or CV can be used to assess the stability of the model. As a second step – if an independent data set is available – the quality of model predictions can be assessed using appropriate adequacy measures. Manel et al. (1999) using both evaluation approaches, demonstrate the need to evaluate predictive habitat distribution models from independent data, and to use a range of criteria to assess the model performance.

7.1. Jack-knife, cross-validation and bootstrap

When using *a single data set* to calibrate and evaluate the model (Fig. 1), CV, JK or bootstrap techniques are appropriate to evaluate the model and its predictions. This approach should be selected if the data set is too small to be split into separate data sets (in which case JK or bootstrap will be preferred), or if the use of as many observations as possible for the model calibration is preferred. In the latter case, the model is not evaluated outside of its calibration range of applicability and credibility.

Resampling techniques, as e.g. used by Halfon (1985) in ecotoxicology, are very promising but have rarely been used until now for such applications. Bootstrap methods allow one to approach the bias of an estimation by performing multiple re-sampling (with replacement) within the calibration data set, and then to remove it to obtain an unbiased estimate (Efron and Tibshirani, 1993). The bias is the difference between the parameter estimate and the true population value. With GLMs for instance, bias-corrected values of R^2, of the regression coefficients and of intercepts can be estimated this way (Harrell et al., 1996; Guisan and Harrell, 2000). When the difference between apparent and bias-corrected values is too high, called the 'optimism from overfitting' (Harrell et al., 1998), the adequacy of the model should be seriously questioned.

7.2. Evaluation from an independent data set

When using *two independent sets* of data (Fig. 1), the first is used to adjust the model (calibration data) whereas the second is used to evaluate the quality of model predictions. When both data sets result from the splitting of an originally single data set, it is called the split-sample approach (Van Houwelingen and Le Cessie, 1990). This approach is unsuitable for small data sets because there are not enough observations for calibrating and evaluating the model and unsatisfactory predictions may result. In turn, when data sets are sufficiently large, the method becomes particularly attractive because of its simplicity with regard to CV and bootstrap procedures. This approach is optimal if two different data sets are available up front, originating from two distinct sampling strategies, preferably not mixed in one single statistical analysis. As an example, the calibration data set could result from a well-designed random-stratified sampling whereas the evaluation data set would result from a previous observational study. Mixing the observational data with the stratified data would diminish the sampling design and thus impair the fitting of a satisfying model.

Two types of measure can be used in such a case. A first approach is to evaluate the success of the predictions with the same measure of *goodness-of-fit* used for calibrating the model. The evaluation procedure will then measure the fit between predicted and observed values of the *evaluation data set* (and not between fitted and observed values as in the calibration step). In the case of LS regression, this means calculating the coefficient of determination (R^2) between predictions and real field observations. For other statistical methods (like GLM or GAM), however, this solution may be more difficult to implement, if more complex estimation algorithms are involved (e.g. iterative, like ML).

A second approach is to use any discrete measure of association between predicted and observed values (e.g. Fieldings and Bell, 1997; Stehman, 1999; Guisan and Harrell, 2000; see below). However, if the predictions of a statistical model are probabilistic, they need to be transformed back to the scale of the real observations. For binary data, this can be done by truncating probabilities at a given threshold. Instead of applying an arbitrary threshold, this step can be improved by (i) adjusting an optimal threshold that provides the best agreement between predicted and observed values of the calibration data set (Guisan et al., 1998, 1999; Franklin, 1998), or (ii) applying a threshold-independent measure such as the receiver operating characteristic (ROC) plot methodology (Fieldings and Bell, 1997; Manel et al., 1999 or Guisan, in press for examples of its application in ecology). In the first case, the optimized threshold is used to transform probabilistic predictions (from the evaluation data set) back into presence/absence (for binomial models; Guisan et al., 1999) or into an ordered scale (for ordinal models; Guisan and Harrell, 2000). For nominal data, the unit with the highest probability of occurrence can be predicted and compared to real data when evaluating a model (Brzeziecki et al., 1993; Zimmermann and Kienast, 1999). Final comparisons are best set out in a contingency table, also called *confusion matrix* in literature dealing with nominal predictions (such as vegetation units in remote sensing studies). The choice of an appropriate measure of association is dependent upon: (1) the type of the response variable being modeled (Table 1) and (2) the study objectives (Fieldings and Bell, 1997; Stehman, 1999).

Evaluating the predictions of *quantitative* response variables is the simplest case, for (i) they are intrinsically threshold-independent and (ii) they can hardly be weighted (contrary to evaluating predictions of qualitative or binary variables; see below). Pearson's product–moment correlation coefficient can be used if the variable is normally distributed. Otherwise, a non-parametric rank correlation coefficient can be used (Kendall's τ or Spearman's ρ, for instance). The prediction mean squared error (PMSE; see e.g. Gotway et al., 1996) or the G-value (Agterberg, 1984; Gotway et al., 1996) are other measures of prediction accuracy in the case of a quantitative response. G, in particular, is given by the formula

$$G = \left(1 - \left(\sum_{i=1}^{n} [z(x_i) - \hat{z}((x_i))]^2 \Big/ \sum_{i=1}^{n} [z(x_i) - \bar{z}]^2\right)\right) \times 100\% \quad (4)$$

where $Z(x_i)$ is the measured (real) value at a given location i, $Z(x_i)$ is the predicted value, and $\overline{Z}$ is the overall sample mean of the calibration data set. This measure tests the relative improvement of the model, simply using the sample mean of the calibration data set as a model prediction. A value of 100% indicates a perfect fit, while a value of 0% describes no significant improvement using the sample mean alone. Negative values indicate systematic errors in the predictions (Schloeder, personal communication).

For *qualitative* response variables, it is appropriate to compare the predictions to the observations in a contingency table and to apply an adequate measure of association for nominal scale (Agresti, 1990). The resulting contingency tables are 2×2 if presence/absence (binary) data are modeled, or $n \times n$ if habitat or other multinomial units are modeled (i.e. the confusion matrix cited above). Numerous association measures have been proposed such as the proportion of area correctly classified, the percent commission and omission errors (and the resulting percent confusion error), κ (Cohen, 1960; Monserud and Lee-

mans, 1992; Fitzgerald and Lees, 1994b), τ (Ma and Redmond, 1995), or Foody's (1992) κ. They all reveal adequate results given the specific modeling context. When the relative seriousness of possible errors between predicted and observed units vary, weighting the errors is more appropriate. For instance, the weighted κ (Cohen 1968; Naesset, 1996) is a useful extension when a large number of simulated habitat types with varying pairwise dissimilarities are evaluated. The use of (user-defined) cost matrices attributing different weight to two types of prediction errors (omission, commission) can also be appropriate when models are used e.g. in a biological conservation perspective (Fieldings and Bell, 1997)[18]. A similar approach is discussed by Stehman (1999) under the terms *user's accuracy* or *producer's accuracy* for evaluating thematic maps, where certain predicted classes have comparatively greater or lesser importance to the project's objectives.

For *semi-quantitative* response variables, such as semi-logarithmic abundance scales (e.g. cover classes), it is best to compare the predictions and the observations in a contingency table and subsequently apply a measure of association for ordinal scales (Agresti, 1990). Examples of such measures are γ (Goodman and Kruskal, 1979), D_{xy} of Somer, D_{xy} of Kim, D_{xy} of Wilson (Gonzalez and Nelson, 1996; Guisan and Harrell (2000) for an application in ecology) or the weighted κ (Cohen, 1968; Naesset, 1996).

7.3. Assessing error propagation and spatial trends in uncertainties

Another important aspect of model evaluation is the assessment of (i) *error propagation* and (ii) *the distribution of uncertainties*.

Error propagation, resulting from the combination of several heterogeneous data layers within a GIS (e.g. Heuvelink et al., 1989) or from rasterizing vector data (e.g. Bregt et al., 1991), can produce significant noise that affects the interpretation of results (Lagacherie and Holmes, 1996). Although such assessments do not offer an evaluation of model quality, it may help to trace the source of error if model predictions are unsatisfactory.

Aspinall (1992) includes an assessment of uncertainties in a Bayesian model of species distribution. He repeatedly applies the procedure of relative frequency calculation, using a random subset of the data for each run (i.e. a sort of bootstrap), to estimate a standard deviation and a standard error for all conditional probabilities.

Cartographic representation of errors or uncertainties may help to identify areas where additional data sampling is needed to improve the model (Dave Roberts, personal communication) or where ecological processes not taken into account in the model may occur. For instance, a patchy distribution of a significant ecological variable not included in the set of predictors would produce a patchy distribution of high residual errors.

8. Model credibility and applicability

The interpretation of model accuracy is subjective. Consequently, Monserud and Leemans (1992) propose a scale of terms to express this judgment based on the evaluation statistics. Thereafter, the modeled accuracy is classified as *fair* if a κ value of 0.5 is obtained, and as *excellent* if this value lies between 0.85 and 0.99. Such subjective judgment can also include the spatial scale and resolution covered by the model. A model may appear to be satisfying when its predictions partially or totally agree with the observed patterns. However, saying that a model is 'good' or 'bad' is subject to critics, because it is implicit in modeling that perfect truth cannot be attained (Oreskes et al., 1994). Thus, a model should be discussed only in the pre-defined context of its application. Such discussions are particularly important when models are applied in a management context, and when an evaluation is needed to determine their range of applicability. This step was recently summarized by Rykiel (1996) under the terms *credibility* and *qualification*

[18] E.g. if a model is used to design a nature reserve, the failure to correctly predict locations of observed presence (= omission) is more 'costly' for conservation than would be the prediction of false presence (= commission).

of a model. Using Ryckiel's definitions, credibility is based on a subjective confidence level whereas qualification is related to the model applicability and lies mainly in "discovering the domain over which a validated model may properly be used". Both terms converge when a model has been extensively used and tested, and has become widely accepted for scientific and management purposes.

Predictions of static models, even if properly evaluated, have to be considered with regard to their potential for application. Decoursey (1992) divides models into three classes, according to their potential use: (i) screening, (ii) research; and (iii) planning, monitoring; and assessment. Static distribution models mostly belong to the first and second categories. They are fundamentally probabilistic in nature and should remain so. Consequently, their best range of application is for comparative or screening purposes. Examples of applications in literature range from management of rare species (e.g. Miller, 1986; Myatt, 1987; Carey and Brown, 1995), identification of possible 'hot spots' of biodiversity (e.g. Heikkinen, 1996), earlier assessment of potential impact of climate change on plant species (e.g. Lischke et al., 1998; Guisan and Theurillat, 2000), community distributions (e.g. Brzeziecki et al., 1995; Kienast et al., 1995, 1996) or species richness (Kienast et al., 1998; Guisan and Theurillat, 2000), or combinations of these applications (e.g. Carey and Brown, 1995).

As discussed previously, the transfer of the predictive ability of the models into a climatically changeable future environment may be seriously questioned. However, while dynamically-mechanistic models are "more likely to provide more accurate predictions of system behavior under a wide range of conditions" (Jones, 1992), their present reliability and applicability to large geographical areas is still limited (Lischke et al., 1998). Static comparative models can thus be considered an appropriate alternative for obtaining rapid primary impact assessments over large areas (e.g. Brzeziecki et al., 1995; Franklin, 1995; Guisan et al., 1995; Kienast et al., 1995, 1996, 1998; Guisan and Theurillat, 2000).

9. Some research perspectives

When analyzing the literature dealing with static distribution models, some key topics related to their limitations appear repeatedly. Among these, the most important ones in our opinion are: 'accuracy and resolution of input maps', 'biotic interactions', 'causality', 'evaluation data', 'historical factors', 'response curves', 'sampling design', 'spatially explicit uncertainty assessment' and 'spatial autocorrelation'.

9.1. Accuracy and resolution of input maps

Yet, the generation of large-scale climate maps has been greatly improved (Hutchinson and Bischof, 1983; Mitchell, 1991; Daly et al., 1994; Thornton et al., 1997). However, higher accuracy and resolution of biophysical input maps are still considered the primary requirements for improving model predictions. This is especially true for qualitative variables like geology, soil units, or land-use that can act as powerful 'filters' for primary predictions made with quantitative predictors if accurately mapped (Fischer, 1994). The problem of accuracy becomes even more important when models are developed for mountainous terrain with heterogeneous topography, where vegetation is distributed in mosaic-like patterns with sharp transitions from one vegetation type to another (Brown, 1994; Fischer, 1994; Zimmermann and Kienast, 1999). In this respect, progress in GIS-modeling and in remote sensing – particularly (rectified) multi-band aerial photographs (as three-bands infra-red photographs) – could pave the way for obtaining more accurate information (moisture, vegetation index, land-use, etc.).

9.2. Biotic interactions

Biotic interactions, and more particularly competition, represent a challenge for the future of species distribution modeling. This is the key to making species models meet community models. A way of integrating biotic interactions into static distribution models might be the use of integrated systems of simultaneous regression equations or GLMs, as already applied to a few econometric

models (Greene, 1993). The principle of such a system of simultaneous regressions (SSR) is given – in a simplified form – in the series of equations:

$$Y_1 = \alpha_1 + X\beta_1 + Y_{(-1)}\gamma_1,$$

$$Y_2 = \alpha_1 + X\beta_2 + Y_{(-2)}\gamma_2,$$

$$\vdots$$

$$Y_n = \alpha_1 + X\beta_n + Y_{(-n)}\gamma_n, \quad (5)$$

where $X\beta_i$ represents the matrix products for environmental predictors and $Y_{(-i)}\gamma_i$ represents the matrix products for all other Y responses (but the ith one). With this approach, each fitted species' presence or abundance is included as an additional predictor in all other equations until equilibrium is reached in an iterative process. This approach shares some similarities with the loop analysis (LA). The basics of LA were initially proposed by Mason (1954) for computations of electrical circuits and were later adapted by Wright (1968) for analyzing inbreeding systems. Levins (1974, 1975, 1977) further developed it for integrating the simultaneous impact of environment and co-occurring species on the (qualitative) individual species' dynamic behavior. Both LA and SSR require the modeled system to be at or near equilibrium.

9.3. Causality

Related to the accuracy of input maps is the problem of how to develop more mechanistic static models, as claimed by several authors (e.g. Austin et al., 1983; Prentice et al., 1992; Lenihan, 1993). This is particularly necessary if static distribution models are considered to be the first step in building more complex spatio-temporal process models, as suggested by Solomon and Leemans (1990) and others. To achieve this goal, physiology-based parameters, like minimum temperature during the coldest month or site water balance, should preferably be used over physiographic predictors. As noted by Franklin (1995), so far only a few studies (e.g. Hanson et al., 1990; Baker et al., 1991) have investigated this promising area of plant ecology for use in predictive modeling. More collaboration with plant ecophysiologists and dynamic succession modelers is strongly encouraged.

9.4. Evaluation data

Models are often evaluated through CV, using the same data set that was used to parameterize the model. However, this approach remains weak in assessing model credibility and applicability. Spatial models have more serious theoretical limitations than dynamic models, but are clearly an alternative for quickly predicting plant or animal distribution over large spatial scales. In order to assess its predictive power along spatial scales, the performance of a static model should ideally be tested on independent data. If no equivalent test data are available, we propose choosing between two alternatives: (i) to set apart a portion of the calibration data set, or (ii) to use other data sources like vegetation maps to generate independent test data. The first approach may be implemented simultaneously with re-sampling (for calibration) a database that originates from observational studies. The second approach is more often used, but runs the risk of introducing new uncertainties, due to mapping errors, insufficient map resolution and the translation errors which can occur when deriving species distribution from vegetation maps (Brzeziecki et al., 1993; Zimmermann and Kienast, 1999).

9.5. Response curves

This remark is related to techniques that fit multidimensional response surfaces, which can (theoretically) be broken down into individualistic response curves for each explanatory variable. Ideally, the shape of such individualistic response curves should be analyzed systematically before the variable is included in a multivariate model. However, exploring the response of each variable separately may be of limited use in a multiple variable context where interactions between predictors can modify the shape of the response curve. A sound alternative is then to use partial residual diagnostic plots to explore the probable shape of each predictor, since it takes into account all other predictors already included in the

model. An equivalent task is to evaluate whether parameters shall be fitted parametrically (as in GLMs) or non-parametrically (as in GAMs, CART)[19].

9.6. Historical factors

The influence of historical factors on the present day distribution of organisms – in the sense of both biogeographers (history of location) and evolutionary biologists (history of lineage; see Brown et al., 1996) – can be a severe limitation to static distribution modeling. It should thus be assessed whenever it is possible. (1) History of place: a plant or animal can be absent from a site having a high likelihood of presence (i.e. a suitable habitat) due to past geological or climatic events (e.g. glaciations) or due to physical barriers (e.g. high mountains), so that its range never extended into this area. A few pioneer works recently started analyzing this field (see e.g. Birks, 1996; Leathwick, 1998) by including historical factors in static models to test their influence on plant distributions. (2) History of lineage: when simulating large areas, static modelers are encouraged to collaborate with evolutionary biologists and population geneticists to assess the genetic integrity of a species. Is there ecotypic differentiation within the range of a plant species, which would require preferably separate model calibrations for the different ecotypes identified?

9.7. Sampling design

Too many static modeling exercises are still based on field data from observational studies lacking a designed sampling strategy. For future research, we suggest basing field sampling more systematically on strategies such as the gradsect method (Austin and Heyligers, 1989, 1991) or a true random-stratified design (Goedickemeier et al., 1997; Cherix et al., 1998). Alternatively, in order to reduce the sampling bias and to improve the data quality for further statistical analysis we propose the re-sampling of databases containing data from observational studies along environmental gradients (to simulate the gradsect method) or to collect additional data in the field, in order to improve an existing sampling with stratification. A drawback of both alternatives is that the resulting sampling will not truly originate from a random-stratified design.

9.8. Spatially explicit uncertainty assessment

Regression diagnostics and model evaluation allow the assessment of the overall quality of a model. However, such statistics do not reveal details about the spatial distribution of prediction uncertainties. The latter is very helpful for designing additional field campaigns, or for assessing the model credibility and applicability more specifically. We thus propose to map more systematically not only predicted entities, but also their associated uncertainties.

9.9. Spatial autocorrelation

Spatially explicit predictive models are generally built with few or no attention to spatial processes that drive biogeographical patterns. Regression methods are e.g. applied to infer the distribution of biological entities from environmental variables by considering these observations to be independent from each other. Neighborhood relationships between contiguous geographical observation points are rarely investigated at this stage. Such relationships include for instance spatial autocorrelation and other features of spatial variance, which belong to the domain of spatial statistics (see Cressie, 1993; Cressie and Ver Hoef, 1993) and were previously seen as statistical annoyances (Horne and Schneider, 1995). Nevertheless, patchiness due to factors other than biophysical drivers has to be accepted as an ecological reality (e.g. dispersal). Such influences can be included into distribution models through autocorrelative models (Malanson, 1985; Augustin et al., 1996). However, assuming or

[19] The identification of sampling density, sampling lags, and data outliers are helpful when choosing between parametric and non-parametric models. Parametric response curves are somewhat less sensitive to lags and outliers than more data-driven, non-parametric response curves (e.g. spline, loess), since the model expects a predefined function.

measuring spatial autocorrelation in the response variable implies that observations are spatially dependent and, as a result, great care should be taken that the number of degrees of freedom used to test significance of parameters in the model has been corrected accordingly.

Another category of spatial models – called *cellular automaton* – was proposed in recent years to account for neighborhood relationships (and thus spatial correlation) and changing environments (see e.g. Wolfram, 1984; Hogeweg, 1988; Phipps, 1992; Ruxton, 1996; Ruxton and Saravia, 1998). These models are based upon a number of cells on a grid. Each cell is assigned one of several possible states, and inherits its own set of transition rules to change from one state to another. These rules are sensitive to the content of the neighboring cells. Such models were already successfully applied in ecology, e.g. to predict the distribution of plant species in a changing climate (Carey, 1996) or to simulate the migration of plants along corridors in fragmented landscapes (van Dorp et al., 1997).

Finally, we noticed a lack of comparative papers (such as Walker and Cocks, 1991; Skidmore et al., 1996; Manel et al., 1999) in which more than two statistical methods are applied to the *same* data set. Most published static modeling studies use only one of the many statistical techniques that may properly be used, and little information is available on the respective predictive capacity of each approach. The debate is usually restricted to the intrinsic suitability of a particular method for a given data set. When starting a static modeling study the choice of an appropriate statistical method would be much facilitated by having access to publications of comparative papers that show the advantages and disadvantages of using different methods in a particular context.

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