

Predicting reptile distributions at the mesoscale: relation to climate and topography

Antoine Guisan^{1,3*} and Ulrich Hofer² ¹Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland, ²Department of Vertebrates, Natural History Museum, Bernastrasse, Berne, Switzerland and ³Swiss Center for Faunal Cartography, Terreaux, Neuchâtel, Switzerland

Abstract

Aim To explore the respective power of climate and topography to predict the distribution of reptiles in Switzerland, hence at a mesoscale level. A more detailed knowledge of these relationships, in combination with maps of the potential distribution derived from the models, is a valuable contribution to the design of conservation strategies.

Location All of Switzerland.

Methods Generalized linear models are used to derive predictive habitat distribution models from eco-geographical predictors in a geographical information system, using species data from a field survey conducted between 1980 and 1999.

Results The maximum amount of deviance explained by climatic models is 65%, and 50% by topographical models. Low values were obtained with both sets of predictors for three species that are widely distributed in all parts of the country (*Anguis fragilis*, *Coronella austriaca*, and *Natrix natrix*), a result that suggests that including other important predictors, such as resources, should improve the models in further studies. With respect to topographical predictors, low values were also obtained for two species where we anticipated a strong response to aspect and slope, *Podarcis muralis* and *Vipera aspis*.

Main conclusions Overall, both models and maps derived from climatic predictors more closely match the actual reptile distributions than those based on topography. These results suggest that the distributional limits of reptile species with a restricted range in Switzerland are largely set by climatic, predominantly temperature-related, factors.

Keywords

Predictive models, GLM, reptiles, vertebrates, climate, topography, Switzerland.

INTRODUCTION

Predictive habitat modelling, i.e. the use of a statistical model to predict the locations of suitable habitat for a given species (see Guisan & Zimmermann, 2000 for a review), became very popular in recent years, as a powerful method to test ecological hypotheses about the distribution of organisms (e.g. Birks, 1996; Mourell & Ezcurra, 1996; Leathwick, 1998) and to assess the possible impacts of

environmental changes (e.g. climate change) on these distributions (e.g. Guisan & Theurillat, 2000; Teixeira & Arntzen, 2002). However, although the distribution of many plant and animal species was modelled in the last years (e.g. for animal species: Pereira & Itami, 1991; Aspinall, 1992; Augustin *et al.*, 1996; Mastroiillo *et al.*, 1997; Corsi *et al.*, 1999, 2000; Manel *et al.*, 1999; Mladenoff *et al.*, 1999; see Guisan & Zimmermann, 2000), we found few papers in the literature which predicted reptiles' distributions. Among the rare examples are the predicted maps included in the atlas of Australian Elapid snakes (Longmore, 1986, see Nix, 1986) and the model of herpetofaunal diversity patterns in Texas (Owen, 1989). The recent book on predicting species occurrences (Scott *et al.*, 2002) does

*Correspondence: Antoine Guisan, Institute of Ecology, University of Lausanne, Biology Building, CH-1015 Lausanne, Switzerland.
E-mail: antoine.guisan@ie-bsg.unil.ch

not include any case study on reptiles, whereas many studies deal with plants, birds and mammals.

As a basic postulate, it is assumed with this type of modelling that, within a time frame of interest and considering a certain spatial scale, species' distributions are in equilibrium with their surrounding environment (Guisan & Theurillat, 2000). This is clearly inherent to the statistical methods that are used, as they all rely on fitting a relationship between the response variable – the distribution of the biological entity of interest – and a combination of environmental predictors (Guisan & Zimmermann, 2000). Potential habitat distribution maps are clearly drawn for a given time frame, usually small as regards geological scales, and several maps can be drawn at successive times to assess some dynamic behaviour. Hence, considering successive maps in time can give insights on temporal features of plant and animal species distributions, but without truly incorporating the underlying mechanistic ecological processes. Sometimes, ecological theories can even be suggested or evaluated from combining different models (e.g. on competition; Leathwick & Austin, 2001; Anderson *et al.*, 2002; Austin, 2002), or an ecological hypothesis can be verified by testing the shape of the ecological response curves (e.g. Oksanen & Minchin, 2002).

Generalized linear models (GLM), for instance, are robust tools in this respect. They allow one to test hypotheses in addition to being easily implemented within a geographical information system, to derive potential habitat distribution maps (e.g. Guisan *et al.*, 1999). Owen (1989) had recourse to least square multiple regression to model reptile richness (species' counts), which today might be best modelled by specifying a Poisson distribution in a GLM (Vincent & Haworth, 1983; Jones *et al.*, 2002). Similarly, species' abundance would be best simulated by a zero-inflated Poisson distribution (Barry & Welsh, 2002).

Austin (1980) discusses the ecological causality of various types of predictors commonly used to predict plant or animal distributions (see also Austin, 2002). They divide these predictors into three categories: (i) *indirect* predictors, having no causal relationship with the physiology of the target organism, (ii) *direct* predictors, which have a direct physiological effect on the organism, and (iii) *resource* predictors, which directly constitute a resource that can be assimilated by the organism. Topography, for example, usually has an indirect effect on plant or animal distribution by determining microclimate, of which some parameters, e.g. monthly minimum temperature, have a direct effect on species survival and can thus impose strong distributional limits. Recently, Austin (2002) proposed a new terminology where all types of predictors are ranged along a gradient from distal (indirect) to proximal (direct, resource).

With the modelling approach presented in this paper, we explore the respective power of climate (usually direct predictors) and topography (mostly indirect predictors) to predict reptile distributions at the mesoscale. Hereafter, the term mesoscale is used as a synonym for regional scale (according to Leser, 1977) to characterize areas about the size of the Swiss territory (c. 41,000 km²) or greater, which

corresponds to geographical scales in the order of 1 : 1,000,000. Local scale is used here to characterize areas equal to or smaller than the biogeographical regions of Switzerland (Gonseth *et al.*, 2001; usually < 10,000 km²), which corresponds to geographical scales in the order of 1 : 100,000 or less.

Specifically, we are interested in the amount of variation in the presence/absence pattern of species that can be explained by each of the two sets of predictors. We consider a more detailed knowledge of these relationships, in combination with maps of the potential distribution derived from the models, a valuable contribution to the design of conservation strategies. If climate and/or topography largely explain a species' distribution at the mesoscale, then any species-specific conservation measures must be implemented within these distributional limits. Of major concern, however, will be species with a substantial part of unexplained variation in their actual distribution pattern, as they possibly show a strong response to environmental components that can be manipulated within a conservation program, e.g. the density and accessibility of key resources.

MATERIAL AND METHODS

Patterns of reptiles' distribution in Switzerland

Switzerland covers 41,293 km² and consists essentially of two mountain chains with a west-east extension, the *Jura* (its highest peak reaching 1607 m) in the north and the *Alps* (its highest peak, the Mont-Blanc, reaching 4807 m) in the south, separated by a lowland corridor about 50 km broad, generally referred to as the *Swiss Midlands* and ranging from about 360–900 m in elevation (Gonseth *et al.*, 2001; Fig. 1a). Reptiles occur up to about 2800 m (Hofer *et al.*, 2001). Of the thirteen species considered native (Table 1), six are found in most or all parts of the country (*Anguis fragilis*, *Lacerta agilis*, *L. vivipara*, *Podarcis muralis*, *Coronella austriaca* and *Natrix natrix*), two are absent from the Midlands (*Vipera aspis*, *V. berus*), and five have a very limited distribution restricted to the Rhone valley and/or the southern foothills of the Alps (*L. viridis*, *Elaphe longissima*, *Coluber viridiflavus*, *N. maura*, *N. tessellata*). The autochthonous status of recent populations of another two species, *Emys orbicularis* and *P. sicula*, is doubtful.

For eight species, Switzerland includes parts of their overall range limit. Although most taxa respond to the dispersal barriers imposed by the mountain chains, in particular the Alps, the distribution patterns of some adequately sampled reptile species raise the question of what factors potentially restrict their present-day range extensions. *V. aspis*, for example, is absent from the Midlands and the eastern half of the Swiss Alps, despite an apparently favourable climate in the former and suitable habitat in the latter subregion. Likewise, *L. viridis* and *E. longissima* never left the Rhone valley to successfully colonize the adjacent Midlands, although introductions show that both species are capable of locally maintaining stable populations at higher elevations outside the Rhone valley.

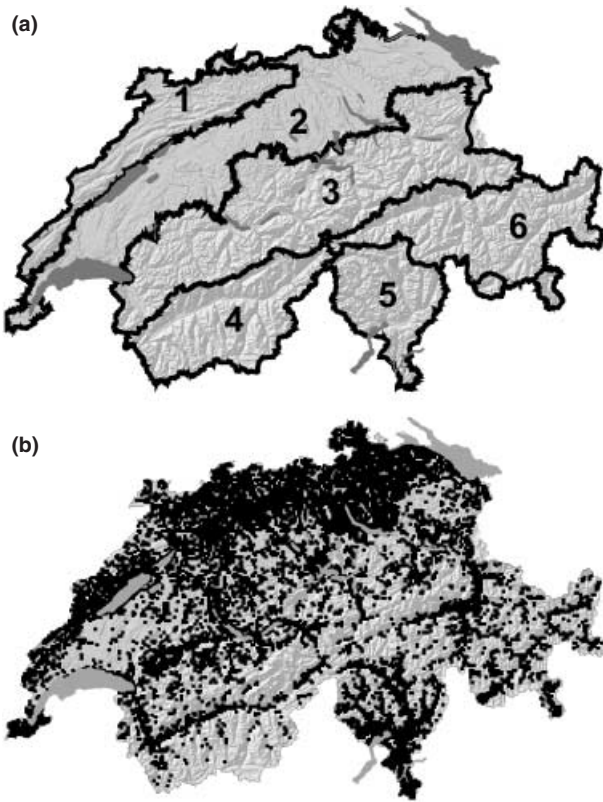


Figure 1 Biogeographical division of Switzerland and sample locations. (a) The major landscapes referred to are (see Gonseth *et al.*, 2001): (1) Jura mountains, (2) Midlands, (3) Northern Alps, (4) Western Internal Alps (Rhone valley), (5) Southern Alps, (6) Eastern Internal Alps. (b) Geographical distribution of the 10,138 km² that contain at least one observation of the 13 autochthonous reptile species in Switzerland.

Table 1 List of the thirteen reptile species native to Switzerland whose distributions are modeled by GLM

Acronym	Scientific name	Common name
AF	<i>Anguis fragilis</i> L. 1758	Slow worm
CA	<i>Coronella austriaca</i> Laurenti 1768	Smooth snake
CV	<i>Coluber viridiflavus</i> Lacépède 1789	European whip snake
EL	<i>Elaphe longissima</i> Laurenti 1768	Aesculapian snake
LA	<i>Lacerta agilis</i> L. 1758	Sand lizard
LB	<i>Lacerta bilineata</i> Daudin 1802	Green lizard
LV	<i>Lacerta vivipara</i> Jacquin 1787	Common lizard
NM	<i>Natrix maura</i> L. 1758	Viperine snake
NN	<i>Natrix natrix</i> L. 1758	Grass snake
NT	<i>Natrix tessellata</i> (Laurenti 1768)	Dice snake
PM	<i>Podarcis muralis</i> Laurenti 1768	Wall lizard
VA	<i>Vipera aspis</i> L. 1758	Asp viper
VB	<i>Vipera berus</i> L. 1758	Adder

Distributional data

The data base of the Swiss Amphibian and Reptile Conservation Programme (KARCH) provided the basis for the

models presented in this paper. The data base contains > 43,000 observations pertaining to the 13 reptile species for which models were fitted. The majority of the data originate from regional mapping projects with slightly different sampling protocols.

For each species, the distributional data were aggregated at a square kilometer (quadrat) resolution (or grain). The pooled distributions resulted in a set of presence/absence data covering a total of 10,138 different km², each one containing observations of one to nine different species. Species not found in a given square kilometer were considered absent, because one could suppose a quasi-exhaustive sampling for most squares. Although we are aware that this might be too strong an assumption, this approach nevertheless remains better than generating pseudo-absences (as done, e.g. in Zaniewski *et al.*, 2002), as shown by similar studies on rare plant species (O. Broennimann and A. Guisan, unpubl. results). The distribution of all 10,138 km² is given in Fig. 1. We calibrated the models using a subset of 6000 randomly selected squares. With the remaining 4138 km² we subsequently evaluated the predictions of the models on a quasi-independent basis.

Environmental predictors

All topographical predictors used in this study were derived from the Swiss digital elevation model (DEM) at a resolution of 25 m × 25 m (DHM25, OFT, 2002). Slope angle and slope aspect were derived from elevation in the ArcInfo[®] (ESRI Inc., Redlands, CA, USA) geographical information system (in-built functions). Aspect is a circular rather than a continuous variable. We, therefore, split it into four disjunct classes, namely north (0°–45° and 315°–360°), east (45°–135°), south (135°–225°) and west (225°–315°). Topographical position indices were calculated at each cell of a DEM aggregated to a resolution of 100 m, by calculating the difference between the elevation of the cell and the mean elevation calculated for all cells of a moving rectangular window centred on the cell of interest. Such indices are a flexible way to define the relative position of a location along a topographical gradient (ridge top, middle slope or valley; Guisan *et al.*, 1999). Two topographical positions were considered, with windows' sides respectively set to 3 × 3 and 5 × 5 pixels. Using such resolution and window size implies that these indices reflect rather the general shape of the relief (e.g. mountain side) than micro-topographical variations.

The climate maps were obtained from the Swiss Federal Research Institute WSL in Birmensdorf (N.E. Zimmermann and F. Kienast), at the resolution of 25 m × 25 m, by interpolating climatic measurements made throughout the network of meteorological weather stations on the DEM (using mainly smoothing splines). The climatic predictors are described in Table 2.

All predictors were then aggregated to the resolution of 1 km × 1 km in ArcInfo[®], by specifying: (i) the *mean* as the operation to perform on aggregated values of elevation, slope, the two topographical positions, and all climatic

Name	Description	Unit
(A) Climatic predictors		
<i>Tjul.mea</i>	Average temperature of July – mean of subpixels	°C
<i>Tjul.min</i>	Average temperature of July – minimum of subpixels	°C
<i>Pjul.mea</i>	Amount of precipitation for July – mean of subpixels	mm
<i>Pjul.min</i>	Amount of precipitation for July – minimum of subpixels	mm
<i>Pyea.mea</i>	Yearly amount of precipitation – mean of subpixels	mm
<i>Pyea.min</i>	Yearly amount of precipitation – minimum of subpixels	mm
<i>Wbud.mea</i>	Water budget: pyea-potential evapotranspiration – mean of subpixels	mm
<i>Wbud.min</i>	Water budget: pyea-potential evapotranspiration – minimum of subpixels	mm
<i>Rjul.mea</i>	Amount of solar radiation for July – mean of subpixels	kJ
<i>Rjul.min</i>	Amount of solar radiation for July – minimum of subpixels	kJ
<i>Dgd3.mea</i>	Degree-days above 3.0 °C – mean of subpixels	°C
<i>Dgd3.min</i>	Degree-days above 3.0°C – minimum of subpixels	°C
(B) Topographical predictors		
<i>Alt25.mea</i>	Elevation – mean of subpixels	m
<i>Slo25.mea</i>	Slope angle – mean of subpixels	Degree
<i>AspN.per</i>	North aspect – sum of subpixels	%
<i>AspE.per</i>	East aspect – sum of subpixels	%
<i>AspS.per</i>	South aspect – sum of subpixels	%
<i>AspW.per</i>	West aspect – sum of subpixels	%
<i>Tp3 × 3.mea</i>	Topographical position rect. windows 3 × 3 – mean of subpixels	–
<i>Tp5 × 5.mea</i>	Topographical position rect. windows 5 × 5 – mean of subpixels	–

predictors; (ii) the *minimum* operation in addition for some climatic predictors; and (iii) the *sum* as the operation to perform on the 0/1 aggregated values of the four aspect classes. This step resulted in three series of predictors, ended with the suffix 'mea', 'min' or 'sum', respectively (Table 2).

Statistical analyses

Generalized linear models (McCullagh & Nelder, 1989; see Guisan *et al.*, 2002) were used to fit the different models in the S-Plus® software (Insightful Corp.). GLMs are an extended form of the classical multiple regression, where model coefficients are estimated by a Maximum-Likelihood (ML) algorithm (or an approximation of it, as, e.g. the reiterated Least-Squares) instead of the classical Least Squares. All GLMs were fitted by specifying a binomial distribution and a logistic link function, as similarly carried out for other presence-absence data in ecological studies (e.g. Guisan *et al.*, 1999; Manel *et al.*, 1999; Guisan & Hofer, 2001).

Two series of models were fitted: (i) models including only topographical predictors, and (ii) models including only climatic predictors. In both cases, models were first fitted with a linear and a quadratic term specified for all quantitative predictors. For each species, final models included only those terms, quadratic or linear, which satisfied two criteria: (i) to be significant at the 0.05 confidence level from a chi-square test of deviance reduction (the deviance is similar to the variance in the case of ML methods), and

(ii) to explain at least 1% of the deviance. The latter can be considered a very strict criterion since, with a large data set as in our case, a reduction of deviance of 1% is always highly significant. This makes a permutation test unnecessary in most of the cases (i.e. it provides as strong a result). In addition, such a rigorous deviance reduction criterion and the large size of the data set both contribute to limit inference problems potentially caused by autocorrelation in the reptile occurrence data (which usually contributes to lower the effective degrees of freedom). We did not further investigate autocorrelation aspects in this study. For each species, a final model was fitted with the significant terms only.

Evaluating model predictions

Assessing the predictive ability of a model is a crucial step for allowing its proper use in ecological applications, especially when conservation issues are a main objective. As a result, many recent papers discussed this particular aspect of the model building process (e.g. Fieldings & Bell, 1997; Corsi *et al.*, 2000; Guisan & Zimmermann, 2000; Pearce & Ferrier, 2000; Manel *et al.*, 2001), from which some reasonable guidelines for optimally evaluating model prediction success emerge.

Manel *et al.* (1999, 2001 and Guisan & Zimmermann (2000), amongst others, support the primary use of an independent data set to evaluate the predictive ability of a model. If the original data set cannot be split into subsets for

Table 2 List of climatic and topographical predictors used to model reptile distributions in Switzerland. Mean (*.mea*), minimum (*.min*) or percentage (*.per*) values were calculated for each predictor in each square kilometre quadrat, by aggregating 25 m × 25 m subpixels (original resolution of maps; 1600 subpixels per km²). The water budget is calculated by removing the predicted potential evapotranspiration to the annual precipitation. Degree-days above 3.0 °C: the number of days throughout the year with a mean temperature >3 °C

calibration and evaluation, resampling techniques, such as Jackknife or cross-validation, provide an alternative approach for evaluating the model (e.g. Jaberger & Guisan, 2001).

As a very large data set formed the basis of this study, we could use a quasi-independent data set for evaluation, obtained by randomly splitting the original data set (*split-sample* approach; see e.g. Guisan *et al.*, 1999). This approach was also more appropriate in our case than Jackknifing, because resampling techniques are slow with very large data sets. However, as both data sets still cover the same study area, the data sets cannot be considered fully independent. Hence, they should preferably be mentioned as quasi-independent data sets. A fully independent data set should also concern a distinct geographical area.

Two measures were used to compare predictions with field observations: (1) the Kappa statistics (Cohen, 1960), by detecting the optimal threshold (i.e. the one providing the maximum Kappa) for cutting the probabilistic predictions into presence-absence on the calibration (i.e. training) data set and using this optimal threshold for calculating Kappa on the evaluation (i.e. test) data set (Guisan *et al.*, 1999); (2) the threshold-independent Receiver Operating Characteristic (ROC) approach (Fieldings & Bell, 1997), by calculating the area under the roc curve (AUC) as the measure of prediction success. The AUC measure takes values between 0.5 and 1, which can make it difficult to compare to other adequacy measures that take values between 0 and 1. Hence,

we also calculated the *Gini coefficient* AUC' – a modified version of AUC – which takes values between 0 and 1 (Copas, 1999):

$$\text{AUC}' = 2(\text{AUC} - 0.5).$$

RESULTS

For all species except *C. austriaca*, both climatic and topographical models could be fitted. In *C. austriaca*, modelling had to be restricted to climatic predictors, because no topographical predictor explained at least 1% of the deviance (our second selection criterion). The amount of deviance explained by climatic models ranged from 5.7 to 64.9% (Table 3, Fig. 2), for topographical models from 0 to 49.6% (Table 4, Fig. 2). Low values ($\leq 11\%$) were obtained by both sets of predictors for three species that are widely distributed in all parts of the country (*A. fragilis*, *C. austriaca*, and *N.atrix*), and, with respect to topographical predictors, for two species where we anticipated a strong response to aspect and slope, *P. muralis* and *V. aspis*.

The maxima were reached in two snakes with widely differing distributions. For *N. tessellata*, in Switzerland largely restricted to low elevation stream- and lakesides on the southern foothills of the Alps, combinations of climatic predictors explained almost 65% of the deviance. For *V. berus*, with most of its populations found along southern-facing slopes at higher elevations in the Alps, combinations

Table 3 Selected climatic predictors and their proportion of explained deviance. All predictors retained in a model explained at least 1% of deviance and were at least significant at the 0.01 confidence level. The name of species is given in Table 1 and the description of predictors is given in Table 2. Values of explained deviance adjusted for the number of predictors and the number of observations, hence a realistic estimate of model fit, are set in bold

	Af	Ca	Cv	El	La	Lb	Lv	Nm	Nn	Nt	Pm	Va	Vb
<i>Tjul.me</i>	7	2.5	31.1	20.4	5.3	11.9	16.2	36.6	–	47.5	6.1	2.7	48.3
<i>Tjul.min</i>	–	1.9	3.2	8.2	19.6	9.5	6.2	3.1	–	–	–	5.4	–
<i>Pjul.me</i>	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pjul.min</i>	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyea.me</i>	1.6	–	–	–	1.7	–	–	–	–	7.5	1.3	2.3	2.4
<i>Pyea.min</i>	–	1.4	16.7	6.5	–	15	2	11.1	–	2.1	5	–	2.9
<i>Wbud.me</i>	1.7	–	–	4.6	2	7.5	–	11.2	–	1.4	7.4	10.3	–
<i>Wbud.min</i>	–	–	–	–	–	–	–	–	–	2	1.4	3.8	–
<i>Rjul.me</i>	–	–	1.7	–	–	–	–	–	–	–	–	–	–
<i>Rjul.min</i>	–	–	–	–	–	–	–	–	–	3.2	–	1.2	–
<i>Dgd30.me</i>	–	–	–	–	–	–	–	–	–	11.04	1.2	–	1.8
<i>Dgd30.min</i>	–	–	–	–	–	–	–	–	–	–	–	–	–
% Expl dev. (D^2)	10.3	5.8	52.7	39.7	28.6	43.9	24.4	62.0	11.0	64.9	21.2	25.7	55.4
Adjusted D^2 (%)	10.2	5.7	52.6	39.6	28.5	43.8	24.3	61.9	11	64.9	21.1	25.6	55.4
No. of occurrences	1982	645	205	232	2067	408	1499	39	1207	87	1139	740	403
<i>Kappa cal</i>	0.28	0.18	0.56	0.43	0.49	0.58	0.46	0.49	0.22	0.65	0.41	0.38	0.62
<i>Threshold</i>	0.35	0.15	0.25	0.20	0.40	0.20	0.45	0.25	0.25	0.30	0.25	0.20	0.45
<i>Kappa eva</i>	0.28	0.11	0.60	0.43	0.50	0.57	0.46	0.43	0.23	0.49	0.45	0.38	0.59
<i>AUC cal</i>	0.71	0.70	0.95	0.94	0.82	0.95	0.82	0.99	0.72	0.98	0.82	0.86	0.96
<i>AUC eva</i>	0.71	0.65	0.95	0.94	0.84	0.95	0.83	0.99	0.72	0.96	0.82	0.85	0.95
<i>AUC' cal</i>	0.42	0.40	0.90	0.88	0.64	0.90	0.64	0.98	0.44	0.96	0.64	0.72	0.92
<i>AUC' eva</i>	0.42	0.30	0.90	0.88	0.68	0.90	0.66	0.98	0.44	0.92	0.64	0.70	0.90

cal = measured on the calibration data set, *eva* = measured on the evaluation data set, *Threshold* = probability threshold used to cut predictions into presence-absence, *no. of occurrences* = number of occurrences for the species.

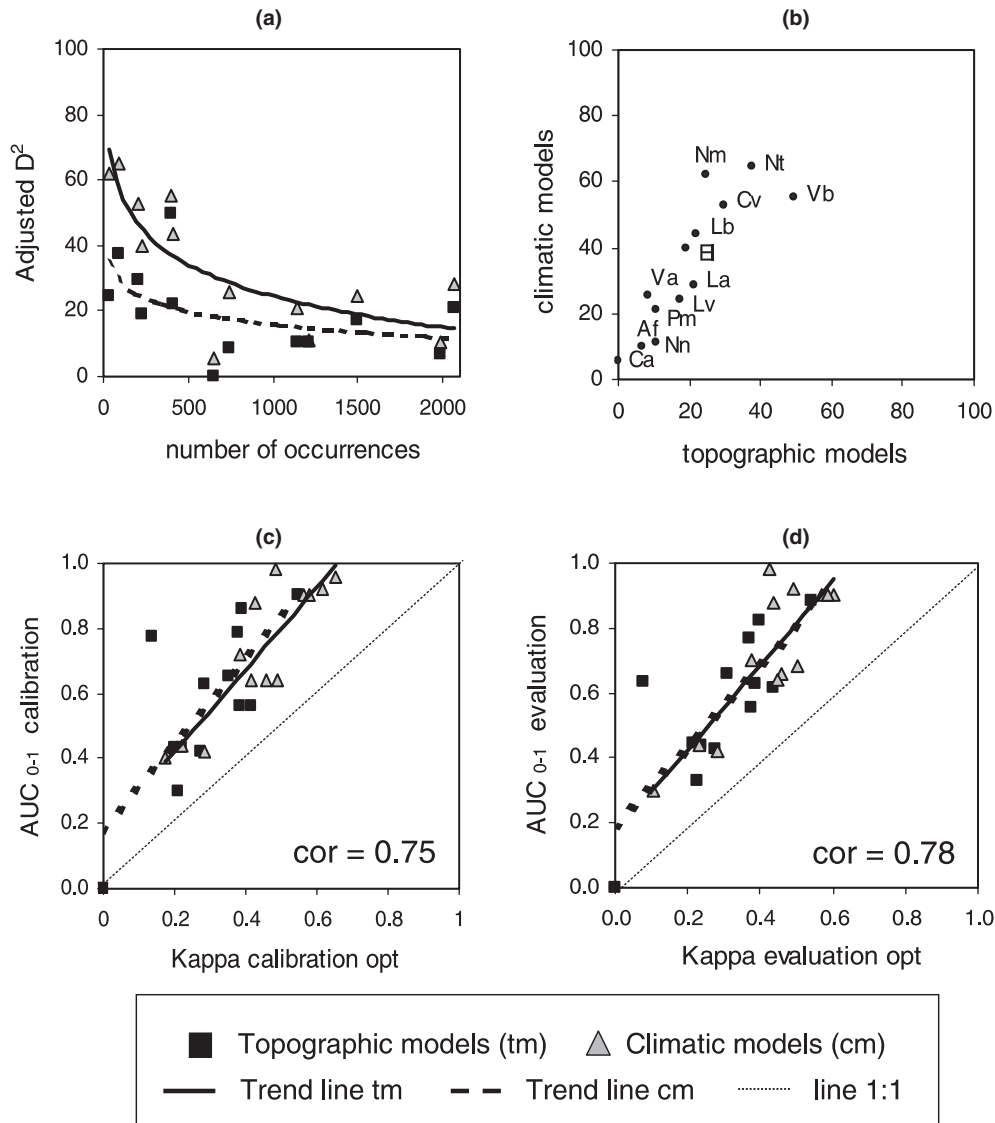


Figure 2 Model adjustment and evaluation. Points refer to species. (a) Adjusted D^2 (corrected % deviance explained) as a function of the number of occurrences; (b) Adjusted D^2 of topographical models versus climatic models; (c) Optimal Kappa versus re-scaled AUC (taking values between 0 and 1), as measured on the calibration data set; (d) Kappa (calculated by cutting probabilistic predictions at optimal threshold) vs. re-scaled AUC₀₋₁, as measured on the evaluation data set.

of topographical predictors accounted for nearly 50% of the explained deviance. Whereas in the latter species, climate explained the distribution only slightly better than topography (55.5%), topographical predictors accounted for substantially less deviance (37.7%) than climate in *N. tessellata*, as in all other species whose distribution is restricted to the southern parts of the country. Yet, the two species exemplify the overall result of the models: computed as the mean of relative differences between adjusted- D^2 across all species, climate explains 44% more deviance than topography. This is illustrated by Fig. 2b, where, with one exception, the species points fall above the 1 : 1 line into the upper triangle.

A further evaluation of the models by Kappa and AUC confirms this trend (Fig. 2c, d). Additionally it shows that Kappa and AUC (re-scaled to 0–1), the two measures of evaluation used in this study, are in good agreement (Pearson correlation of 0.78 for climate models, Fig. 2c, d), as similarly observed by Manel *et al.* (2001).

Overall, throughout the territory of Switzerland (mesoscale), the maps derived from climatic predictors more closely match the actual reptile distributions than those based on topography. Examples of potential habitat distribution maps are given for two species with distinct distribution patterns in Switzerland, the Green lizard, *L. viridis*, and the Adder, *V. berus* (Figs 3 and 4).

Table 4 Selected topographical predictors and their proportion of explained deviance. See legend of Table 3 for an explanation of column and row names. No topographical predictor explained more than 1% of the deviance in the case of *Coronella austriaca* (Ca). Values of explained deviance adjusted for the number of predictors and the number of observations, hence a realistic estimate of model fit, are set in bold

	Af	Ca	Cv	El	La	Lb	Lv	Nm	Nn	Nt	Pm	Va	Vb
<i>Alt25.mea</i>	7	–	4.2	2.6	19	1.2	12.2	19.3	7.9	8.5	4.3	4.3	46.5
<i>Slo25.mea</i>	–	–	24.4	16.4	1.1	20.6	3.9	1.6	–	23.4	6.3	3.4	1.9
<i>Aspn.per</i>	–	–	1	–	1.1	–	–	–	1	–	–	1	–
<i>Aspe.per</i>	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Asps.per</i>	–	–	–	–	–	–	1.3	2.7	1.7	4.5	–	–	–
<i>Aspw.per</i>	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Tp3x3.mea</i>	–	–	–	–	–	–	–	1.3	–	1.4	–	–	1.3
<i>Tp5x5.mea</i>	–	–	–	–	–	–	–	–	–	–	–	–	–
% expl dev. (D2)	7.0	–	29.6	19.0	21.2	21.9	17.4	24.9	10.6	37.8	10.6	8.7	49.7
Adjusted D2 (%)	7.0	–	29.6	19	21.1	21.8	17.3	24.8	10.5	37.7	10.6	8.6	49.6
No. of occurrences	1982	645	205	232	2067	408	1499	39	1207	87	1139	740	403
Kappa cal	0.21	–	0.38	0.28	0.42	0.35	0.38	0.14	0.22	0.39	0.27	0.20	0.55
Threshold	0.35	–	0.10	0.15	0.40	0.20	0.35	0.05	0.30	0.15	0.25	0.20	0.35
Kappa eva	0.23	–	0.37	0.31	0.44	0.39	0.38	0.08	0.24	0.40	0.28	0.21	0.54
AUC cal	0.65	–	0.89	0.81	0.78	0.83	0.78	0.89	0.72	0.93	0.71	0.72	0.95
AUC eva	0.66	–	0.88	0.83	0.81	0.82	0.78	0.82	0.72	0.91	0.71	0.72	0.94
AUC cal	0.30	–	0.78	0.63	0.56	0.65	0.56	0.77	0.43	0.86	0.42	0.43	0.90
AUC eva	0.33	–	0.77	0.66	0.62	0.63	0.55	0.63	0.44	0.82	0.43	0.44	0.89

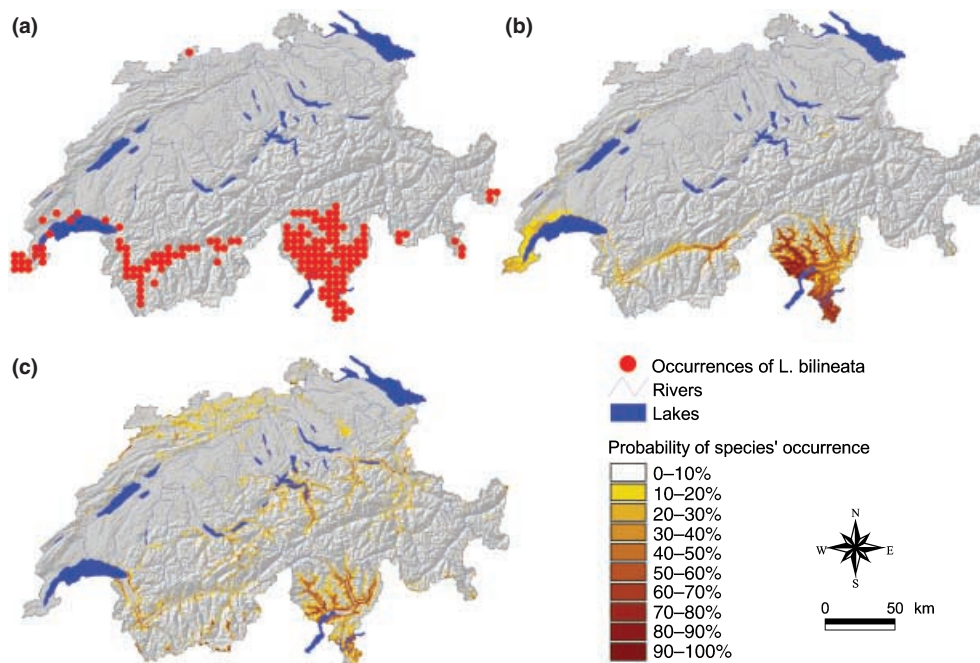


Figure 3 Distribution of *Lacerta bilineata* in Switzerland. (a) Documented distribution (by square of 5×5 km, 1980–99), (b) predicted distribution by climatic model (square kilometre resolution), (c) predicted distribution by topographical model (square kilometre resolution).

DISCUSSION

Statistically speaking, models fitted with climatic predictors proved superior to those fitted with topographical predictors. This is demonstrated here by (i) a better fit and (ii) higher values obtained from the independent evaluations. From a

biogeographical viewpoint, the greatest difference between climatic and topographical models lies in the potential distributions they predict for the same set of species. Maps calculated from climatic predictors reflected more realistic distributions than those calculated from topographical predictors, as shown by maps (b) and (c) in Figs 3 and 4. The

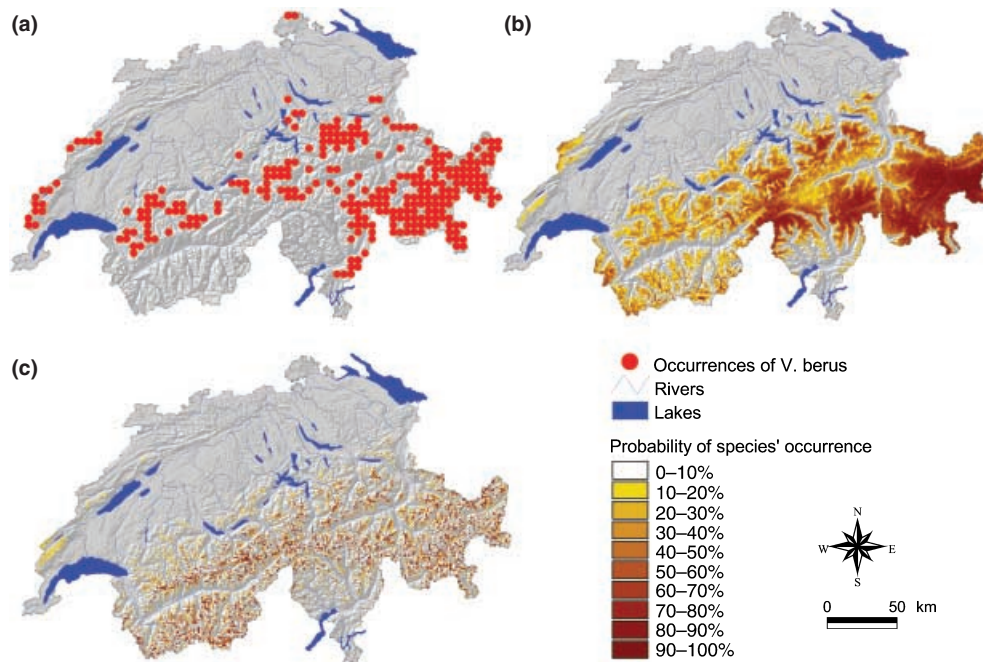


Figure 4 Distribution of *Vipera berus* in Switzerland. (a) Documented distribution (by square of 5×5 km, 1980–99), (b) predicted distribution by climatic model (square kilometre resolution), (c) predicted distribution by topographical model (square kilometre resolution).

maps based on topography also appear less smooth than those based on climate, which typically results from topography varying along shorter distances than climate, providing more contrasted values between adjacent cells.

According to Austin (1980, 2002), topography is usually considered an indirect predictor (i.e. distal), whereas climate is considered a direct or even a resource predictor (i.e. proximal). However, climatic predictors are often derived from topographical predictors, which can give rise to error propagation (Elith *et al.*, 2002). For this reason, topography has been shown to predict species distribution more efficiently than climate in some particular cases (e.g. Guisan *et al.*, 1999; Franklin *et al.*, 2000 in the case of plant species). Where climate remains relatively constant over the study area, it can be adequately reflected by topographical surrogates (Austin, 2002). Such climatic regularity is usually observed at local scales, where the lapse rate of temperature change along elevation remains constant throughout the study area.

As stated above, climate explained the twelve reptile distribution patterns more efficiently than topography at the mesoscale. Topography is certainly a proxy for important environmental features other than climate (e.g. soil), nevertheless at our study scale it explained less variance than climate alone. A possible explanation is that, relative to climate, these features are of secondary importance to the reptile species considered. Alternatively, the integrity of such additional environmental features and their possible combinations might not be kept when aggregating topographical data to the square kilometre resolution, which results in their effect remaining contained in the unexplained variance.

Nowadays, resolution (grain) and scale (relating here to the extent of the study area) can be considered quasi-independently in a geographical information system, i.e. one can conduct a study on a large scale at a very high resolution. Hence, improving the quality (e.g. accuracy) and resolution of environmental maps should theoretically allow their use as predictors in studies of various geographical extents. However, two potential limitations need to be discussed here. First, resolution is directly related to the vital domain of a species. As a result, high resolution (small grain) might not be appropriate for modelling species for which individuals have large spatial needs and require various habitat types in a close vicinity (e.g. bats; see Jaberg & Guisan, 2001). In such cases, a larger pixel size is more appropriate and high-resolution data would need to be aggregated into lower resolution pixels. Second, distinct predictors can explain the spatial variance in the distribution of a species when different extents are considered. A modelling study conducted on a large extent can reveal environmental drivers that best characterize the overall species range, whereas a second, nested analysis conducted on a smaller extent can reveal other features that best characterize habitat at a population or homerange level (Patthey, 2003). This is not in contradiction with the fact that some predictors, such as climate, can remain important at all scales. Hence, using more direct climatic (and other) predictors should allow a better testing of models at different scales (using a same resolution).

Our results further suggest that the distributional limits of most reptile species with a restricted range in Switzerland are strongly associated with climatic, predominantly

temperature-related factors. This interpretation is supported by distribution patterns where the Alps cannot obviously be the single limit to dispersal: a raise in elevation of 200–300 m from the shoreline of Lake Geneva (375 m a.s.l.) to the adjacent Midlands appears sufficient to prevent range extensions of *L. viridis* and *E. longissima*, two species which colonize steep south-facing slopes up to 1700 m in the Rhone valley and on the southern foothills of the Alps. *Vipera berus* seems to be temperature-limited in the opposite sense, in that the species is absent from most parts of the country below 1000 m a.s.l. and exhibits a patchy distribution in the western Alps. Monney (1996) suggested competitive exclusion by *V. aspis* as a possible explanation for the patchy distribution and lower limit of elevational distribution of *V. berus* in the western Alps. This view is not supported by our model results, which indicate a low probability (< 20%) of occurrence of *V. berus* at lower elevations over the entire mountain chain, whether *V. aspis* is present (western Alps) or absent (eastern Alps) as a potential competitor.

In two taxa with a large part of unexplained variation in their distribution pattern, *P. muralis* and *V. aspis*, temperature may well be of considerable importance, although at a scale below the resolution of the environmental predictors used in this approach. Many examples of local distribution in regions with a relatively harsh climate suggest that these species owe their presence to patches where aspect and slope in combination with an appropriate substrate quality provide a particularly favourable microclimate. Small size and low density of this specific patch type may ultimately prevent *V. aspis* from colonizing the Swiss Midlands, a hypothesis that may be further explored by a GLM approach based on a set of predictors reflecting such landscape properties.

For three widespread species present in all parts of the country, *A. fragilis*, *N. natrix* and *C. austriaca*, the GLM approximation of the distribution pattern proved particularly poor. A possible explanation is a strong response to key resources, e.g. anuran prey and suitable oviposition sites in the case of *N. natrix*. Relative to climatic factors, the local availability of these resources may be of overriding importance in limiting the dispersal of this snake species. However, the exploration of resource-related hypotheses by a GLM approach at the mesoscale would require GIS-based data on resource densities that so far are not available for Switzerland. In the absence of these data, such hypotheses must be tested at a local scale, by experimental manipulations of resource densities in the field.

In all, our modelling approach to reptile distributions in Switzerland identified six species where the distribution is strongly associated with climate at the mesoscale ($\geq 40\%$ of variance explained); to be successful, conservation measures of any type must be implemented within the distributional limits set by climatic factors, temperature in particular. For the remaining taxa, neither climate nor topography allows a straightforward interpretation of the distribution patterns at the mesoscale. The available knowledge on the ecology of these species and the outcome of previous conservation measures suggest two general types of distributional

response, of which the first one could be readily explored by a new GLM approach: (a) a response dominated by climatic and/or topographical factors at a local scale, probably best exemplified by *P. muralis* and *V. aspis*, where the current status might be improved by a protection of favourable patches or small areas; (b) a strong response to resource availability, probably best exemplified by *N. natrix*, where appropriate conservation measures might significantly improve the current status of a species.

ACKNOWLEDGMENTS

The Swiss Amphibian and Reptile Conservation Program (KARCH) is indebted to many persons for supplying their personal data, in particular to Eugen Kramer, Jean-Marc Pillet and Josef Zoller, and to colleagues for assisting the compilation of the Swiss reptile data base, namely Jean-Claude Monney and Goran Dusej. Niklaus E. Zimmermann and Felix Kienast at the Swiss federal institute for forest, snow, and landscape research (WSL) kindly provided the climatic maps. Further on, we would like to thank the Swiss Federal Offices of Forest, Snow and Landscape (OFEFP) and of Topography (OFT) for making geographical data available. Finally, our warmest thanks go to Julie Warrillow who kindly accepted to make the linguistic revision, and to Louis-Felix Bersier and an anonymous reviewer for their valuable comments.

NOMENCLATURE

Gasc *et al.* (1997).

REFERENCES

- Anderson, R.P., Peterson, A.T. & Gomez-Laverde, M. (2002) Using niche-based GIS modelling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos*, **98**, 3–16.
- Aspinall, R. (1992) An inductive modeling procedure based on Bayes' theorem for analysis of pattern in spatial data. *International Journal of Geographical Information Systems*, **6**, 105–121.
- Augustin, N.H., Muggleston, M.A. & Buckland, S.T. (1996) An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology*, **33**, 339–347.
- Austin, M.P. (1980) Searching for a model for use in vegetation analysis. *Vegetatio*, **42**, 11–21.
- Austin, M.P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modelling*, **157**, 101–118.
- Barry, S. & Welsh, A.H. (2002) Generalized additive models and zero inflated count data. *Ecological Modelling*, **157**, 179–188.
- Birks, H.J.B. (1996) Statistical approaches to interpreting diversity patterns in the Norwegian mountain flora. *Ecography*, **19**, 332–340.
- Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational Psychology Measurement*, **20**, 37–46.
- Copas, J. (1999) The effectiveness of risk scores: the logit rank plot. *Applied Statistics*, **48**, 165–183.

- Corsi, F., Duprè, E. & Boitani, L. (1999) A large-scale model of wolf distribution in Italy for conservation planning. *Conservation Biology*, **13**, 150–159.
- Corsi, F., de Leeuw, J. & Skidmore, A.K. (2000) Modeling species distribution with GIS. *Research techniques in animal ecology: controversies and consequences* (ed. by L. Boitani and T.K. Fuller), pp. 389–434. Columbia University Press, New York.
- Elith, J., Burgman, M.A. & Regan, H.M. (2002) Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecological Modelling*, **157**, 313–329.
- Fieldings, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Franklin, J., McCullough, P. & Gray, C. (2000) Terrain variables used for predictive mapping of vegetation communities in Southern California. *Terrain analysis: principles and applications* (ed. by J.P. Wilson and J.C. Gallant). John Wiley, New York.
- Gasc, J.-P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H., Oliveira, M.E., Sofianidou, T.S., Veith, M. & Zuidervijk, A. (eds) 1997. *Atlas of amphibians and reptiles in Europe*. Societas Europaea Herpetologica & Muséum National d'Histoire Naturelle (IEGB/SPN), Paris, 496 p.
- Gonseth, Y., Wohlgemuth, T., Sansonnens, B. & Buttler, A. (2001) Régions biogéographique de Suisse - Explications et divisions standards. *Cahier de l'Environnement*, Swiss Federal Office of the Environment, Forest and Landscape (OFEFP), Berne, Switzerland.
- Guisan, A. & Hofer, U. (2001) Modéliser le domaine de distribution potentiel des espèces. *Les reptiles de Suisse* (ed. by U. Hofer, J.-C. Monney and G. Dusej). Birkhäuser Verlag, Basel.
- Guisan, A. & Theurillat, J.-P. (2000) Equilibrium modeling of alpine plant distribution and climate change: how far can we go? *Phytocoenologia*, **30**, 353–384.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Guisan, A., Weiss, S.B. & Weiss, A.D. (1999) GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology*, **143**, 107–122.
- Guisan, A., Edwards, T.C. Jr & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species' distribution: setting the scene. *Ecological Modelling*, **157**, 89–100.
- Hofer, U., Monney, J.-C. & Dusej, G. (2001) *Les reptiles de Suisse. Die Reptilien der Schweiz. I rettili della Svizzera*. Birkhäuser Verlag, Basel.
- Jaberg, C. & Guisan, A. (2001) Modelling the influence of landscape structure on bat species distribution and community composition in the Swiss Jura Mountains. *Journal of Applied Ecology*, **38**, 1169–1181.
- Jones, M.T., Niemi, G.J., Hanowski, J.M. & Regal, R.R. (2002) Poisson regression: a better approach to modeling abundance data? *Predicting species occurrences: issues of accuracy and scale*, Chapter 35 (ed. by J.M. Scott, P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson), pp. 411–418. Island Press, Covelo, CA.
- Leathwick, J.R. (1998) Are New-Zealand's *Nothofagus* species in equilibrium with their environment. *Journal of Vegetation Science*, **9**, 719–732.
- Leathwick, J.R. & Austin, M.P. (2001) Competitive interactions between tree species in New Zealand old-growth indigenous forests. *Ecology*, **82**, 2560–2573.
- Leser, H. (1977) *Feld- und Labormethoden des Geomorphologie*. Gruyter, Berlin.
- Longmore, R. (ed.) (1986) *Atlas of elapid snakes of Australia. Number 7*. Australian Flora and Fauna Series, Australian Government Publishing Service, Canberra.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman and Hall, London.
- Manel, S., Dias, J.-M. & Ormerod, S.J. (1999) Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. *Ecological Modelling*, **120**, 337–347.
- Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921–931.
- Mastrorillo, S., Lek, S., Dauba, F. & Belaud, A. (1997) The use of artificial neural network to predict the presence of small-bodied fish in a river. *Freshwater Biology*, **38**, 237–246.
- Mladenoff, D.J., Sickley, T.A. & Wydeven, A.P. (1999) Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. *Ecological Application*, **9**, 37–44.
- Monney, J.-C. (1996) *Biologie comparée de Vipera aspis L. et de Vipera berus L. (Reptilia, Ophidia, Viperidae) dans une station des Préalpes bernoises*. PhD dissertation, University of Neuchâtel, Neuchâtel, Switzerland, 174 p.
- Mourell, C. & Ezcurra, E. (1996) Species richness of Argentine cacti: a test of biogeographic hypotheses. *Journal of Vegetation Science*, **7**, 667–680.
- Nix, H. (1986) A biogeographic analysis of Australian elapid snakes. *Atlas of elapid snakes of Australia* (ed. by R. Longmore), pp. 4–15. Australian Flora and Fauna Series 8. Australian Government Publishing Service, Canberra.
- OFT (2002) *Digital height model level 2, product information*. Federal Office of Topography (OFT), Wabern, Switzerland.
- Oksanen, J. & Minchin, P.R. (2002) Continuum theory revisited: what shape are species responses along ecological gradients? *Ecological Modelling*, **157**, 119–129.
- Owen, J.G. (1989) Patterns of herpetofaunal species richness: relation to temperature, precipitation and variance in elevation. *Journal of Biogeography*, **16**, 141–150.
- Patthey, P. (2003) *Habitat and corridor selection of an expanding red deer (Cervus elaphus) population*. PhD Thesis, University of Lausanne, Lausanne, Switzerland.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- Pereira, J.M.C. & Itami R.M. (1991) GIS-based habitat modelling using logistic multiple regression: a study of the Mt Graham Red Squirrel. *Photogrammetric Engineering and Remote Sensing*, **57**, 1475–1486.

- Scott, J.M., Heglund, P.J., Haufler, J.B., Morrison, M., Raphael, M.G., Wall, W.B. & Samson, F. (eds) (2002) *Predicting species occurrences: issues of accuracy and scale*. Island Press, Covelo, CA.
- Teixeira, J. & Arntzen, J.W. (2002) Potential impact of climate warming on the distribution of the Golden-striped salamander, *Chioglossa lusitanica*, on the Iberian Peninsula. *Biodiversity and Conservation*, **11**, 2167–2176.
- Vincent, P.J. & Haworth, J.M. (1983) Poisson regression models of species abundance. *Journal of Biogeography*, **10**, 153–160.
- Zaniewski, A.E., Lehmann, A. & Overton, J.McC. (2002) Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, **157**, 261–280.

BIOSKETCHES

Antoine Guisan is Assistant Professor at the Institute of Ecology, University of Lausanne, where he mainly teaches plant biogeography and spatial modeling. His key fields of interest are the study of plant species – including endangered and invasive species – and diversity distribution, the improvement of predictive habitat distribution models and their use for assessing climate change impacts on species distribution. An important focus is on alpine landscapes.

Ulrich Hofer is lecturer at the Universities of Berne and Basel, and at the Swiss Federal Institute of Technology. His current research interests are in conservation biology and community ecology of Swiss and tropical reptiles and amphibians. It includes the study of individual and population-level responses to conservation measures, especially to changes in resource abundance and availability.