






UNIL | Université de Lausanne

Faculté de biologie et de médecine

Département d'écologie et évolution

SPECIES DISTRIBUTION MODELS FOR CONSERVATION-ORIENTED STUDIES IN SWITZERLAND: FILLING DATA AND TOOL GAPS

Thèse de doctorat ès sciences de la vie (PhD)

présentée à la

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de l'Université de Lausanne

par

Ramona Maggini

Biologiste diplômée de l'Université de Lausanne

Jury

Prof. Nouria Hernandez, Président
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Directeur de thèse	Monsieur Prof. Antoine	**Guisan**
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Experts	Monsieur Dr Niklaus	**Zimmermann**
	Monsieur Dr Marc	**Dufrêne**

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Madame Ramona Maggini

Biologiste diplômée de l'Université de Lausanne

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FOR CONSERVATION-ORIENTED STUDIES IN SWITZERLAND:
FILLING DATA AND TOOL GAPS**

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pour Le Doyen
de la Faculté de Biologie et de Médecine

Prof. Nouria Hernandez

Nouria Hernandez.

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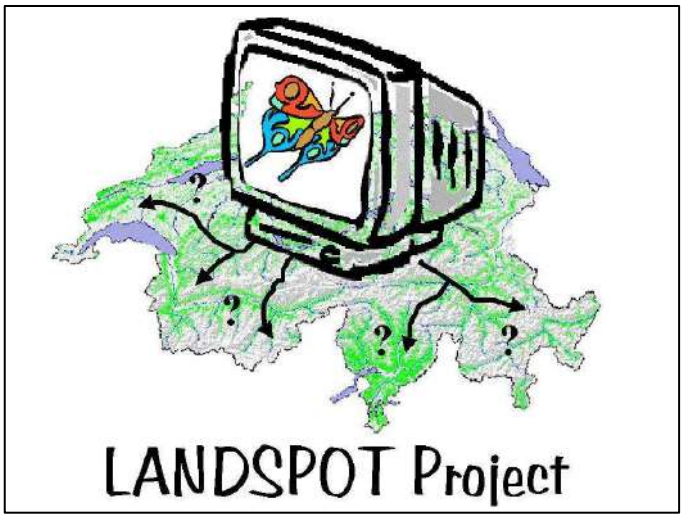

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« … J'ai l'infini à ma portée,

je le vois, je le sens, je le touche,

je m'en nourris et je sais que

je ne pourrais jamais l'épuiser.

Et je comprends mon irrépressible

révolte lorsque je vois supprimer la nature :

on me tue mon infini. »

Robert Hainard

A Ayleen et Nathan,

mes yeux sur le futur.

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SUMMARY

Species distribution models (SDMs) represent nowadays an essential tool in the research fields of ecology and conservation biology. By combining observations of species occurrence or abundance with information on the environmental characteristic of the observation sites, they can provide information on the ecology of species, predict their distributions across the landscape or extrapolate them to other spatial or time frames. The advent of SDMs, supported by geographic information systems (GIS), new developments in statistical models and constantly increasing computational capacities, has revolutionized the way ecologists can comprehend species distributions in their environment. SDMs have brought the tool that allows describing species realized niches across a multivariate environmental space and predict their spatial distribution. Predictions, in the form of probabilistic maps showing the potential distribution of the species, are an irreplaceable mean to inform every single unit of a territory about its biodiversity potential. SDMs and the corresponding spatial predictions can be used to plan conservation actions for particular species, to design field surveys, to assess the risks related to the spread of invasive species, to select reserve locations and design reserve networks, and ultimately, to forecast distributional changes according to scenarios of climate and/or land use change.

By assessing the effect of several factors on model performance and on the accuracy of spatial predictions, this thesis aims at improving techniques and data available for distribution modelling and at providing the best possible information to conservation managers to support their decisions and action plans for the conservation of biodiversity in Switzerland and beyond. Several monitoring programs have been put in place from the national to the global scale, and different sources of data now exist and start to be available to researchers who want to model species distribution. However, because of the lack of means, data are often not gathered at an appropriate resolution, are sampled only over limited areas, are not spatially explicit or do not provide a sound biological information. A typical example of this is data on 'habitat' (sensu biota). Even though this is essential information for an effective conservation planning, it often has to be approximated from land use, the closest available information. Moreover, data are often not sampled according to an established sampling design, which can lead to biased samples and consequently to spurious modelling results. Understanding the sources of variability linked to the different phases of the modelling process and their importance is crucial in order to evaluate the final distribution maps that are to be used for conservation purposes.

The research presented in this thesis was essentially conducted within the framework of the Landspot Project, a project supported by the Swiss National Science Foundation. The main goal of the project was to assess the possible contribution of pre-modelled 'habitat' units to model the distribution of animal species, in particular butterfly species, across Switzerland. While pursuing this goal, different aspects of data quality, sampling design and modelling process were addressed and improved, and implications for conservation discussed. The main 'habitat' units considered in this thesis are grassland and forest communities of natural and anthropogenic origin as defined in the typology of habitats for Switzerland. These communities are mainly defined at the phytosociological level of the alliance. For the time being, no comprehensive map of such communities is available at the national scale and at fine resolution. As a first step, it was therefore necessary to create distribution models and maps for these communities across Switzerland and thus to gather and collect the necessary data. In

order to reach this first objective, several new developments were necessary such as the definition of expert models, the classification of the Swiss territory in environmental domains, the design of an environmentally stratified sampling of the target vegetation units across Switzerland, the development of a database integrating a decision-support system assisting in the classification of the relevés, and the downscaling of the land use/cover data from 100 m to 25 m resolution.

The main contributions of this thesis to the discipline of species distribution modelling (SDM) are assembled in four main scientific papers. In the first, published in Journal of Biogeography different issues related to the modelling process itself are investigated. First is assessed the effect of five different stepwise selection methods on model performance, stability and parsimony, using data of the forest inventory of State of Vaud. In the same paper are also assessed: the effect of weighting absences to ensure a prevalence of 0.5 prior to model calibration; the effect of limiting absences beyond the environmental envelope defined by presences; four different methods for incorporating spatial autocorrelation; and finally, the effect of integrating predictor interactions. Results allowed to specifically enhance the GRASP tool (Generalized Regression Analysis and Spatial Predictions) that now incorporates new selection methods and the possibility of dealing with interactions among predictors as well as spatial autocorrelation. The contribution of different sources of remotely sensed information to species distribution models was also assessed. The second paper (to be submitted) explores the combined effects of sample size and data post-stratification on the accuracy of models using data on grassland distribution across Switzerland collected within the framework of the Landspot project and supplemented with other important vegetation databases. For the stratification of the data, different spatial frameworks were compared. In particular, environmental stratification by Swiss Environmental Domains was compared to geographical stratification either by biogeographic regions or political states (cantons). The third paper (to be submitted) assesses the contribution of pre-modelled vegetation communities to the modelling of fauna. It is a two-steps approach that combines the disciplines of community ecology and spatial ecology and integrates their corresponding concepts of habitat. First are modelled vegetation communities per se and then these 'habitat' units are used in order to model animal species habitat. A case study is presented with grassland communities and butterfly species. Different ways of integrating vegetation information in the models of butterfly distribution were also evaluated. Finally, a glimpse to climate change is given in the fourth paper, recently published in Ecological Modelling. This paper proposes a conceptual framework for analysing range shifts, namely a catalogue of the possible patterns of change in the distribution of a species along elevational or other environmental gradients and an improved quantitative methodology to identify and objectively describe these patterns. The methodology was developed using data from the Swiss national common breeding bird survey and the article presents results concerning the observed shifts in the elevational distribution of breeding birds in Switzerland.

The overall objective of this thesis is to improve species distribution models as potential inputs for different conservation tools (e.g. red lists, ecological networks, risk assessment of the spread of invasive species, vulnerability assessment in the context of climate change). While no conservation issues or tools are directly tested in this thesis, the importance of the proposed improvements made in species distribution modelling is discussed in the context of the selection of reserve networks.

RESUME

Les modèles de distribution d'espèces (SDMs) représentent aujourd'hui un outil essentiel dans les domaines de recherche de l'écologie et de la biologie de la conservation. En combinant les observations de la présence des espèces ou de leur abondance avec des informations sur les caractéristiques environnementales des sites d'observation, ces modèles peuvent fournir des informations sur l'écologie des espèces, prédire leur distribution à travers le paysage ou l'extrapoler dans l'espace et le temps. Le déploiement des SDMs, soutenu par les systèmes d'information géographique (SIG), les nouveaux développements dans les modèles statistiques, ainsi que la constante augmentation des capacités de calcul, a révolutionné la façon dont les écologistes peuvent comprendre la distribution des espèces dans leur environnement. Les SDMs ont apporté l'outil qui permet de décrire la niche réalisée des espèces dans un espace environnemental multivarié et prédire leur distribution spatiale. Les prédictions, sous forme de carte probabilistes montrant la distribution potentielle de l'espèce, sont un moyen irremplaçable d'informer chaque unité du territoire de sa biodiversité potentielle. Les SDMs et les prédictions spatiales correspondantes peuvent être utilisés pour planifier des mesures de conservation pour des espèces particulières, pour concevoir des plans d'échantillonnage, pour évaluer les risques liés à la propagation d'espèces envahissantes, pour choisir l'emplacement de réserves et les mettre en réseau, et finalement, pour prévoir les changements de répartition en fonction de scénarios de changement climatique et/ou d'utilisation du sol.

En évaluant l'effet de plusieurs facteurs sur la performance des modèles et sur la précision des prédictions spatiales, cette thèse vise à améliorer les techniques et les données disponibles pour la modélisation de la distribution des espèces et à fournir la meilleure information possible aux gestionnaires pour appuyer leurs décisions et leurs plans d'action pour la conservation de la biodiversité en Suisse et au-delà. Plusieurs programmes de surveillance ont été mis en place de l'échelle nationale à l'échelle globale, et différentes sources de données sont désormais disponibles pour les chercheurs qui veulent modéliser la distribution des espèces. Toutefois, en raison du manque de moyens, les données sont souvent collectées à une résolution inappropriée, sont échantillonnées sur des zones limitées, ne sont pas spatialement explicites ou ne fournissent pas une information écologique suffisante. Un exemple typique est fourni par les données sur 'l'habitat' (sensu biota). Même s'il s'agit d'une information essentielle pour des mesures de conservation efficaces, elle est souvent approximée par l'utilisation du sol, l'information qui s'en approche le plus. En outre, les données ne sont souvent pas échantillonnées selon un plan d'échantillonnage établi, ce qui biaise les échantillons et par conséquent les résultats de la modélisation. Comprendre les sources de variabilité liées aux différentes phases du processus de modélisation s'avère crucial afin d'évaluer l'utilisation des cartes de distribution prédites à des fins de conservation.

La recherche présentée dans cette thèse a été essentiellement menée dans le cadre du projet Landspot, un projet soutenu par le Fond National Suisse pour la Recherche. L'objectif principal de ce projet était d'évaluer la contribution d'unités 'd'habitat' pré-modélisées pour modéliser la répartition des espèces animales, notamment de papillons, à travers la Suisse. Tout en poursuivant cet objectif, différents aspects touchant à la qualité des données, au plan d'échantillonnage et au processus de modélisation sont abordés et améliorés, et leurs implications pour la conservation des espèces discutées. Les principaux 'habitats' considérés dans cette thèse sont des communautés de prairie et de forêt d'origine naturelle et anthropique telles que définies dans la typologie des habitats de Suisse. Ces communautés sont principalement définies au niveau phytosociologique de l'alliance. Pour l'instant aucune carte de la distribution de ces communautés n'est disponible à l'échelle nationale et à résolution fine. Dans un premier temps, il a donc été nécessaire de créer des modèles de distribution de ces communautés à

travers la Suisse et par conséquent de recueillir les données nécessaires. Afin d'atteindre ce premier objectif, plusieurs nouveaux développements ont été nécessaires, tels que la définition de modèles experts, la classification du territoire suisse en domaines environnementaux, la conception d'un échantillonnage environnementalement stratifié des unités de végétation cibles dans toute la Suisse, la création d'une base de données intégrant un système d'aide à la décision pour la classification des relevés, et le « downscaling » des données de couverture du sol de 100 m à 25 m de résolution.

Les principales contributions de cette thèse à la discipline de la modélisation de la distribution d'espèces (SDM) sont rassemblées dans quatre articles scientifiques. Dans le premier article, publié dans le Journal of Biogeography, différentes questions liées au processus de modélisation sont étudiées en utilisant les données de l'inventaire forestier de l'Etat de Vaud. Tout d'abord sont évalués les effets de cinq méthodes de sélection pas-à-pas sur la performance, la stabilité et la parcimonie des modèles. Dans le même article sont également évalués: l'effet de la pondération des absences afin d'assurer une prévalence de 0.5 lors de la calibration du modèle; l'effet de limiter les absences au-delà de l'enveloppe définie par les présences; quatre méthodes différentes pour l'intégration de l'autocorrélation spatiale; et enfin, l'effet de l'intégration d'interactions entre facteurs. Les résultats présentés dans cet article ont permis d'améliorer l'outil GRASP qui intègre désormais de nouvelles méthodes de sélection et la possibilité de traiter les interactions entre variables explicatives, ainsi que l'autocorrélation spatiale. La contribution de différentes sources de données issues de la télédétection a également été évaluée. Le deuxième article (en voie de soumission) explore les effets combinés de la taille de l'échantillon et de la post-stratification sur le la précision des modèles. Les données utilisées ici sont celles concernant la répartition des prairies de Suisse recueillies dans le cadre du projet Landspot et complétées par d'autres sources. Pour la stratification des données, différents cadres spatiaux ont été comparés. En particulier, la stratification environnementale par les domaines environnementaux de Suisse a été comparée à la stratification géographique par les régions biogéographiques ou par les cantons. Le troisième article (en voie de soumission) évalue la contribution de communautés végétales pré-modélisées à la modélisation de la faune. C'est une approche en deux étapes qui combine les disciplines de l'écologie des communautés et de l'écologie spatiale en intégrant leurs concepts de 'habitat' respectifs. Les communautés végétales sont modélisées d'abord, puis ces unités de 'habitat' sont utilisées pour modéliser les espèces animales. Une étude de cas est présentée avec des communautés prairiales et des espèces de papillons. Différentes façons d'intégrer l'information sur la végétation dans les modèles de répartition des papillons sont évaluées. Enfin, un clin d'œil aux changements climatiques dans le dernier article, publié dans Ecological Modelling. Cet article propose un cadre conceptuel pour l'analyse des changements dans la distribution des espèces qui comprend notamment un catalogue des différentes formes possibles de changement le long d'un gradient d'élévation ou autre gradient environnemental, et une méthode quantitative améliorée pour identifier et décrire ces déplacements. Cette méthodologie a été développée en utilisant des données issues du monitoring des oiseaux nicheurs répandus et l'article présente les résultats concernant les déplacements observés dans la distribution altitudinale des oiseaux nicheurs en Suisse.

L'objectif général de cette thèse est d'améliorer les modèles de distribution des espèces en tant que source d'information possible pour les différents outils de conservation (par exemple, listes rouges, réseaux écologiques, évaluation des risques de propagation d'espèces envahissantes, évaluation de la vulnérabilité des espèces dans le contexte de changement climatique). Bien que ces questions de conservation ne soient pas directement testées dans cette thèse, l'importance des améliorations proposées pour la modélisation de la distribution des espèces est discutée à la fin de ce travail dans le contexte de la sélection de réseaux de réserves.

1 INTRODUCTION

Biodiversity is the diversity of all living organisms on Earth. It encompasses all the plants, animals and micro-organisms, their genes and their habitats within terrestrial, marine or freshwater ecosystems[1]. Biodiversity is both intrinsically valuable and essential for our existence. Humankind development has largely impacted our biodiversity by an unsustainable and irrational use of natural resources, by compromising the functioning of ecosystems, by inducing the degradation, fragmentation and ultimately the loss of species habitat trough direct actions or indirect impacts of human activities.

The Convention on Biological Diversity[2], one of the three conventions resulting from the Earth Summit in Rio in 1992, is the first binding international law that deals with the protection of biodiversity. The three main goals of the convention are the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits from the use of genetic resources. An international strategy to implement the Convention was adopted in 2002 asking the Parties to commit themselves to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level. 2010 was thus the occasion for a comprehensive evaluation of the status of our biodiversity. Unfortunately, the International Year of Biodiversity was not the occasion for celebrating, but more the chance for raising awareness about the irreversible global decrease of biodiversity despite our efforts for stopping its loss.

The last update of the IUCN Red List of Threatened Species reveals that 17,291 species out of the 47,677 assessed are threatened with extinction[3]. It is estimated that the current species extinction rate is between 1,000 and 10,000 times higher than it would naturally be[4]. In Switzerland, more and more species are becoming threatened: 36% of the assessed species, flora and fauna confounded, are currently included in a Red List[5]. Furthermore, 224 species have disappeared or have become extinct over the last 150 years. Only 2.19% of the national territory is actually covered by federally-designated protected areas established with the purpose of biodiversity conservation. A further 4% of the national territory is protected for the conservation of target animal groups but overall, the protected areas are too small and too isolated to be effective in conserving biodiversity (FOEN, 2010).

An effective conservation of biodiversity requires a comprehensive knowledge of the single species, habitats and ecosystems composing it and their interrelations. Ecology (from the Greek *oikos*, "house", and *logos*, "study of") is the scientific discipline studying the relation of living organisms to each other and their surroundings[6]. The knowledge provided by ecology is essential information to conceive effective conservation actions.

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[1] http://www.cbd.int/convention/guide/ (last access: 17.04.2011)

[2] http://www.cbd.int/ (last access: 17.04.2011)

[3] http://iucn.org/about/work/programmes/species/red_list/?4143/Extinction-crisis-continues-apace (last access: 17.04.2011)

[4] http://iucn.org/about/work/programmes/species/red_list/about_the_red_list/ (last access: 17.04.2011)

[5] http://www.bafu.admin.ch/biodiversitaet/10372/10393/index.html?lang=fr (last access: 17.04.2011)

[6] http://en.wikipedia.org/wiki/Ecology (last access: 17.04.2011)

1.1 ECOLOGY AND ECOLOGICAL MODELLING

Throughout the centuries, naturalists have observed, described and collected a multitude of species and made detailed observations concerning their habitat. In the begining, habitat was simply defined as the place where an animal lives and was described in a qualitative way. These natural history studies were replaced in the mid-1950s by the new discipline of quantitative ecology (Stauffer, 2002). Habitat is still considered as the physical area used by an animal, but a functional relationship is assumed between the resources present in that area and animal performance (Morrison and Hall, 2002). The aim is thus to measure and quantify the direct or indirect use of these resources. This introduces an important notion in ecology that is the concept of *niche*. According to Grinnell (1917, cited in Morrison and Hall, 2002), the niche is the sum of the environmental features (i.e. habitat requirements) that allow a species to persist and reproduce. Statistical analysis that were employed to perform the first habitat analysis in the 1960s were t-test, ANOVA, Chi-square, correlation and simple linear regression (Stauffer, 2002). The significant improvement in computer power and statistical methods in the 1970s determined an increase in the number of studies employing multivariate methods such as discriminant function analysis, principal components analysis and factor analysis (Stauffer, 2002). These multivariate approaches allowed the first assessments of the niche of a species as described by Hutchinson (1957). The Hutchinsonian niche is characterized by an hypervolume defined by n axes (environmental factors) in which every point corresponds to a state of the environment that allows the species to survive and reproduce (Hutchinson, 1957). By correlating the occurrence of an organism with a set of environmental variables it is thus possible to describe its niche and hence to predict its pattern of occupancy in different areas (Van Horne, 2002). This vision of the niche and the advent of new regression methods, opened the way to the development of the discipline of species distribution modelling (SDM) during the 1980s (Stauffer, 2002; Elith and Leathwick, 2009). By combining observations of species occurrence or abundance with information on the environmental characteristic of the sites, species distribution models (SDMs) provide information on the ecology of species, predict their distributions across landscapes and can extrapolate these in space and time (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Elith and Leathwick, 2009).

The advent of SDM, supported by geographic information systems (GIS) and the constantly increasing computational capacity, has revolutionized the way ecologists can comprehend species distribution in their environment. SDMs have brought the tool that allows describing species realized niches across a multivariate environmental space. GIS can store, visualize and query a huge amount of spatially explicit data and have thus brought the capacity to put in relation species observations with key environmental drivers stored in the form of numeric layers. GIS have allowed translating the realized niche described through statistical models into spatial predictions. This simple operation certainly represents a major step forward in ecology and especially in conservation planning. Indeed, predictions, in the form of probabilistic maps showing the potential distribution of the species, are used to inform and support many decisions in conservation. Given the very high number of species that compose the biodiversity that we ought to conserve, it is absolutely impossible to directly monitor every single species in space and time in order to assess its current status, especially across large geographical areas. SDMs and predictions based on adequate sampling and point observations offer therefore an irreplaceable mean to inform every single unit of a territory about its biodiversity

potential. This information can in turn be used to assess the distribution and to plan conservation actions for particular species, to design field surveys, to assess the risks related to the spread of invasive species, to select reserve locations and design reserve networks, and ultimately, to forecast distributional changes according to scenarios of climate and/or land use change (Guisan and Thuiller, 2005; Elith and Leathwick, 2007; Elith and Leathwick, 2009).

Generalized linear models (GLMs; McCullagh and Nelder, 1989) allowed pioneering regression based SDMs (Guisan et al., 2002; Elith and Leathwick, 2009). In order to understand the significant advantages brought by GLMs, it is worth to get back to simple linear regression and briefly trace the development of regression methods with their corresponding innovations. Simple linear regression (SLR; Hastie et al., 2009) is the simplest regression model that ecologists have been and are often still using:

$$\text{SLR: } Y = ß_0 + ß_1X_1 + \varepsilon, \text{ where } ß_0 = \text{intercept}, ß_1 = \text{slope}, \varepsilon = \text{error}$$

Parameters are estimated by the method of the ordinary least squares (OLS) which minimize the difference between observed and predicted values. The goodness-of-fit of a OLS regression is typically assessed using the coefficient of determination (R^2), which is calculated as the ratio between the explained and the total variance and corresponds to the square of a Pearson correlation coefficient (r) between observed and predicted values. In SLR, the modelled variable Y is theoretically expected to be normally distributed. A SLR could for instance model the negative relationship between plant biomass (Y) and altitude (X). This is a simple example; the problem is that the ecological relationships are typically multiple and not necessarily linear.

To solve these two problems, statisticians have extended the SLR into a multi-dimensional space with Multiple Linear Regression (MLR; Hastie et al., 2009), further allowing for second or third order relationships.

$$\text{MLR: } Y = ß_0 + \Sigma ß_i X_i^n + \varepsilon, \ldots, ß_i = \text{slope of predictor i}, \ n = \text{order of predictor i}$$

Such a multiple relationship could represent plant biomass as a function of mean annual temperature, rainfall and solar radiation. This represents a huge step forward, but the response variable Y is still expected to be normally distributed.

With Generalized Linear Models (GLM; McCullagh and Nelder, 1989), statisticians have built a more general framework to model responses that can follow different distribution families (e.g. normal, Poisson, binomial,…), by transforming Y with a link function that changes according to the desired distribution:

$$\text{GLM: } f(Y) = ß_0 + \Sigma ß_i X_i^n + \varepsilon, \ldots, f = \text{link function}$$

Parameters are here estimated according to the method of maximum-likelihood. In addition to normally distributed Y, with GLMs ecologists can finally efficiently model species richness or population abundances which are two positive and discrete distributions best modelled with a Poisson distribution. With a binomial model, presence and absence data can be fitted with what is also called a logistic regression (McCullagh and Nelder, 1989). Once again this represents an important progress, but the shape of the relationships is still restricted to X, X^2 or X^3.

A significant step forward was made possible by the advent of Generalized Additive Models (GAM; Hastie and Tibshirani, 1990) that brought an innovative and elegant solution to the restricted shapes of the relationships. By replacing the polynomial relationship by a smooth function that is fitting each predictor with a local smoother within a back fitting algorithm, GAMs provide an efficient method to explore the shape of the relationship without restrictions and pre-defined distributions:

$$\text{GAM: } g(Y) = ß_0 + \Sigma s(X_i) + \varepsilon, \ldots, \text{ s = smooth functions}$$

GAMs are therefore offering all the advantages of GLMs with in addition the capacity to fit different shapes of relationships. This is particularly useful when dealing with skewed or multimodal response curves or those characterized by a plateau. Of course this comes with a cost, typically the increased computing time and the impossibility to write the resulting relationship as proper mathematical equations. Instead, the resulting GAM response shapes can be described step by step in tables subsequently exported from the statistical package where they were fitted to be used to make spatial predictions in a geographic information system (GIS). GAM is the modelling procedure chosen in the Generalized Regression Analysis and Spatial Prediction package (GRASP: Lehmann et al., 2002b) that has been used throughout the present work. In GRASP, response shapes are described in so called 'lookup tables'.

While statistical methods have a central role in SDMs, models are also extremely dependent on the quality, quantity and resolution of the data. In the past, ecologists have built their knowledge on careful observations of species distribution in the field and this essential work has allowed preparing atlas maps of species distribution, which represent important reference information. However, most data found in museum and herbarium collections have been collected without any defined sampling strategy; data were simply collected wherever and whenever the organism of interest was observed in the field. This lack of strategy produce what is known as "presence-only" data (Elith and Leathwick, 2007). Proper "presence-absence" data can only be derived from more elaborated field sampling where sampling units are clearly defined (e.g. vegetation plots, square kilometres, river reach of a given length) and where species presence is effectively assessed within the sampling unit. In order to achieve this, several successive visits of the sampling units may be necessary for species that are not easily detectable. Surveying several time the same sampling unit allow defining a probability of detection for a given species that can be combined to distribution model in order to obtain better estimations of its potential distribution (Kéry et al., 2010). This approach is particularly important with faunistic groups that are characterized by highly mobile species which absences are more difficult to assess in any sampling unit. The timing of the survey is also important. There are periods in which species are more easily observable than other, like for example the breeding period for birds or the flowering season for plants.

Of course, the quality of the spatial predictions issued from SDM is also directly dependent on the resolution and the quality of the maps describing the environmental variables used as predictors. Developments in SDM were accompanied by significant and rapid advances in physical geography that provided essential data such as the digital elevation model (DEM) representing the earth's surface (Elith and Leathwick, 2009). Elevation was widely used in SDM in order to account for the natural elevational distribution of species and biodiversity. However, elevation is an indirect predictor of the elevational distribution of a species which is rather determined by temperature (Austin, 2002). The use

of more ecologically relevant variables such as temperature was made possible with the advent of interpolation techniques allowing estimating climatic parameters between weather stations and thus providing continuous maps (Elith and Leathwick, 2009). Important improvements were also made possible by the availability of remotely sensed data. Pre-classified images, raw spectral information or indices like the normalized difference vegetation index (NDVI) can help in recognizing different types and densities of terrestrial vegetation or informing on the productivity (approximated by the chlorophyll content) of crops and marine areas (Turner et al., 2003; Xie et al., 2008).

1.2 FROM SPECIES DISTRIBUTION MODELS TO CONSERVATION TOOLS

Maps produced by species distribution models allow identifying the most endangered species according to their restricted or very fragmented distributions. If produced at fine resolution, these maps may provide goods estimates of the extent of occurrence (EO) and the area of occupancy (AO) of a species, which are measures employed by the International Union for the Conservation of Nature in order to define the level of threat of the species (IUCN, 2001) and selective criteria for the inclusion in the Red List of endangered species. As an example, this kind of modeling approach in order to estimate EOs was adopted within the framework of the Swiss Red list for Orthoptera (Monnerat et al., 2007). More generally, the spatial distribution of favourable habitat allows identifying new areas to put under protection, the best path for a corridor or the best location for stepping stones and ultimately the best design for a reserve network in order to connect biodiversity hotspots. When dealing with rare species, maps obtained by distribution modelling can designate new areas to prospect (Guisan et al., 2006a) or suggest favourable areas for re-introduction (Carroll et al., 2009). In the case of invasive species, these areas suggest the probable seats of invasion and path of propagation (Thuiller et al., 2005; Broennimann et al., 2007).

The quality of species distribution maps is highly dependent on the quality of the model, the data and the predictors used to produce it. A model used for conservation purposes should have a number of characteristics. The model should not only be statistically efficient, but also ecologically interpretable and meaningful (Austin, 2002; Lehmann et al., 2002a; Guisan et al., 2006b; Austin, 2007). High validation statistics are not sufficient, it is important to look at response curves and at the resulting maps since small differences in the statistical assessment can often correspond to significantly different spatial predictions. The nature and resolution of the environmental predictors used for modelling is also very important. Models based on direct and proximal predictors are the most robust and widely applicable (Austin, 2002). Direct predictors are physiologically limiting factors such as temperature or resources that can be consumed such as light, water or nutrients. Indirect predictors have no physiological effect on the species but are often employed in replacement of direct variables because they are correlated with them and more easily obtainable (Austin, 2002). A good example would be altitude or longitude in replacement of temperature. Extreme attention has to be paid to the spatial resolution at which base data and predictors are sampled and the resolution at which distribution maps are created (Shriner et al., 2006; Guisan et al., 2007a; Pearman et al., 2008). At coarse resolution AOs, are indeed largely over-estimated and can prevent the categorization of a species as critically endangered (Gaston and Fuller, 2009). Coarse resolution can also prevent the

detection of species shifts along environmental or spatial gradient (Pearman et al., 2008). Modelling techniques represent themselves an important source of uncertainty. According to the technique or algorithm employed, predictive performance, predictions and resulting range sizes can differ significantly (Elith et al., 2006; Pearson et al., 2006). Similarly, the use of different settings within a same modelling technique can lead to significantly different results (Araújo and Guisan, 2006). A main issue is the selection criteria employed to select the predictors (Burnham and Anderson, 2002). The inclusion of predictor interactions or accounting for spatial autocorrelation can also significantly affect the final result (Dormann et al., 2007; Elith et al., 2008). Models results are also largely affected by the size of the sample used to fit the model as well as by its prevalence (Manel et al., 2001; Wisz et al., 2008). The sampling of the data in the field is therefore of primary importance to obtain valuable models. A minimum amount of data is necessary even though conclusions differ concerning the optimal sample size (e.g. Stockwell and Peterson, 2002; McPherson et al., 2004; Guisan et al., 2007b). Moreover, stratified sampling and in particular environmentally stratified sampling allows insuring that all environmental combinations will be sampled and that samples will not be biased towards the more frequent combinations and this will further improve modelling results (Hirzel and Guisan, 2002).

Historically, reserves were primarily created to preserve areas of natural, recreational and scenic value and were located in remote, unproductive areas often non representative of the regional biodiversity (Margules and Pressey, 2000). A more systematic approach for the selection of reserves was developed only afterwards. In particular, Margules and Pressey (2000) proposed a framework for a systematic conservation planning composed of six main stages: 1) compilation of the existing data and choice of biodiversity surrogates; 2) clear identification of the conservation goals; 3) review of the existing conservation areas; 4) selection of new additional conservation areas; 5) implementation of the conservation actions; and 6) maintainance of the required values of conservation and development of key indicators. Since it is very difficult to effectively quantify biodiversity (from genotypes, to species, to ecosystems), different surrogates have been used in the literature, especially in the context of reserve selection. Examples are umbrella species (species whose conservation is expected to confer protection to a large number of co-occurring species), indicator taxa, species assemblages, environmental or habitat diversity (Cabeza and Moilanen, 2001; Margules et al., 2002; Roberge and Angelstam, 2004). The effectiveness of umbrella species in ensuring the conservation of co-occurring species is however controversial, since these co-occurring species may be limited by ecological factors that are not relevant for umbrella species (Roberge and Angelstam, 2004). Furthermore, it has been shown that in some cases these do not perform better than species chosen at random within the region of study (Andelman and Fagan, 2000). Different algorithms have been developed for the selection of reserves on the basis of these surrogates. The main goal is to maximize the representation of biodiversity by selecting reserves that contain as many species as possible. There are actually two main possibilities for maximizing representativity, and these imply to either solve the ‘minimum area’ or the ‘maximum coverage’ paradigm (Cabeza and Moilanen, 2001). The minimum area paradigm aims at selecting reserves that represent all natural features a given number of times with a minimum number of sites, surface and/or cost, whereas the maximum coverage paradigm selects the combination of reserves that maximizes the representation of natural features given a limit of cost or area (Cabeza and Moilanen, 2001). Since the 1980s, different heuristic algorithms were thus developed aiming at selecting representative and efficient networks of reserves according to the

principle of complementarity. Subsequently, developments were directed towards other important issues such as the integration of the notion of persistence, the assessment of the effect on network selection of different data sets, and the prioritization of implementation of conservation actions between the selected sites (Cabeza and Moilanen, 2001). More recently, important concerns were raised by climate change and the ability of existing reserve selection methods to ensure species long term persistence (Araújo et al., 2004).

1.3 USEFUL DATA AVAILABLE IN SWITZERLAND, IN EUROPE AND WORLDWIDE TO MODEL BIODIVERSITY

1.3.1 The Swiss data rich case

An important source of information for biodiversity in Switzerland is the network of specialized national databases that is coordinated by the Swiss Federal Office for the Environment (FOEN). These databases are hosted by the following institutions:

- the Swiss Centre for the Cartography of Fauna (CSCF[7]): all faunistic groups except Amphibians, Reptiles and Birds.
- the Swiss Centre for the Coordination of the Protection of Amphibian and Reptiles (KARCH[8]): Amphibians and Reptiles
- the Swiss Ornithological Institute (Vogelwarte[9]): Birds
- the Swiss Centre of Floristic Network (CRSF[10]): Plants

Since 2001 the Swiss Federal Office for the Environment (FOEN) has also put in place the Swiss Biodiversity Monitoring (BDM[11]) to monitor biodiversity of common and widespread species overall but also within the different landscapes and habitat types of Switzerland. Species diversity in landscapes is assessed by sampling 520 square kilometres on a regular grid placed at a random origin (Z7 indicators: vascular plants, breeding birds and butterflies). Additional 1600 10-m^2 sampling sites evenly distributed across the territory are also considered for the assessment of species diversity in the different habitats (Z9 indicators: vascular plants, molluscs and mosses). In parallel to the monitoring of biodiversity, FOEN is also managing the establishment of new red lists of endangered species on 28 different faunistic and floristic groups[12]. Here the sampling strategy is adapted to each group and aims at revisiting sites were species have been observed in the past.

With this wealth of information, Switzerland can pretend to be a data rich country. However, despite this richness in data no comprehensive fine scale map was elaborated until now to describe the distribution of vegetation communities and these are essential information in order to assess landscape

[7] http://www.cscf.ch (last access: 17.04.2011)
[8] http://www.karch.ch (last access: 17.04.2011)
[9] http://www.vogelwarte.ch (last access: 17.04.2011)
[10] http://www.crsf.ch (last access: 17.04.2011)
[11] http://www.biodiversitymonitoring.ch (last access: 17.04.2011)
[12] http://www.bafu.admin.ch/biodiversitaet/10372/10393/index.html?lang=en (last access: 17.04.2011)

biodiversity value and potential. The best available data in this regard is the Swiss Atlas of the vegetation worth of protection by Hegg et al. (1993) which is a photo interpretation of existing vegetation communities for each square kilometre in the country. More recently a consortium of several scientists at the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) predicted vegetation types at a 1 km^2 resolution from existing co-variables (i.e. landuse data, existing vegetation maps, biotope inventories, bioclimatic maps) using expert knowledge[13]. The predicted distribution of habitat types was then used to predict the distribution of more than 3000 animal species with another set of expert models[14].

WSL also holds other very important databases such as the National Forest Inventory (NFI). The first NFI survey was made between 1983-1985, the second between 1993-1995 and the third between 2004-2007. A continuous survey started in 2009 and will continue until 2017[15]. WSL also host the national inventory of fungi[16].

On top of this increasing amount of biodiversity information, Switzerland has also a good set of basic spatially explicit information layers to describe the environment. The Swiss Federal Office for the Environment (FOEN) is responsible for establishing national inventories of habitats of particular interest such as alluvial zones, mires and dry grasslands[17]. These layers are made available as GIS vector coverages and can be linked to several attributes derived from field observations.

The Swiss Federal Statistical Office (FSO[18]) is responsible for producing the Swiss land use statistics[19]. These statistics are available for 1979/85, 1992/97 and the processing of the statistics 2004/09 are still in progress. Statistics are obtained by interpretation of aerial photographs and by assigning one of the 74 predefined categories of land use/cover to the lower-left corner of each cell of a 100m-grid overlaid to the photo. This is therefore not a comprehensive map indicating the predominant land use/cover for each hectare square but rather a statistical survey based on points.

The Swiss Federal Office of Topography (Swisstopo[20]) has a very long tradition of excellence in producing national topographic maps at various scales from 1:25'000 to 1:1'000'000. These maps are available in digital format in raster and vector modes. The vector mode is particularly interesting because each element of the topographic map can be obtained separately (digital landscape model of Switzerland), as for instance the land cover information (primary surfaces, VECTOR25). Swisstopo is also producing the national digital elevation model at 25m resolution (DHM25) from which can bederived many different topographic information (slope, aspect, topographic indices,…). More recently, Swisstopo has integrated the production of geological maps as well and the beta version of

[13] http://www.wsl.ch/land/products/biomod/ehabmaps.html (last access: 17.04.2011)
[14] http://www.wsl.ch/land/products/biomod/epotential.html (last access: 17.04.2011)
[15] http://www.lfi.ch (last access: 17.04.2011)
[16] http://www.wsl.ch/dienstleistungen/inventare/pilze_flechten/swissfungi/index_DE (last access: 17.04.2011)
[17] http://www.bafu.admin.ch/schutzgebiete-inventare/index.html?lang=en (last access: 17.04.2011)
[18] http://www.bfs.admin.ch/bfs/portal/en/index.html (last access: 17.04.2011)
[19] http://www.bfs.admin.ch/bfs/portal/fr/index/dienstleistungen/geostat/datenbeschreibung.html (last access: 17.04.2011)
[20] http://www.swisstopo.ch (last access: 17.04.2011)

the first geology portal[21] for Switzerland has just been launched at the beginning of this month, i.e. April 2011.

The Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) is also producing important environmental layers such as the climate surfaces[22] which are obtained by interpolation at a 25 m resolution of data recorded by weather stations over the baseline period 1960-1990. More recently, WSL also regionalized the projections of the IPCC climate scenarios for Switzerland and made available maps of different climatic variables such as mean annual temperature, precipitation, etc. WSL has also developed land cover/use change scenarios in collaboration with socio-economic experts (Bolliger et al., 2007).

1.3.2 The European unifying case

At a European level, large efforts have been made to bring together the available data from all the member countries, notably through the new INSPIRE directive[23] establishing an Infrastructure for Spatial Information in the European Community. This new infrastructure guarantees a much better access to existing data and metadata and especially to those that were publicly funded. Among existing important European datasets, the European Environment Agency has implemented the Corine Land Cover (CLC)[24] database that is based on the interpretation of satellite images in 1990, 2000 and 2006. Polygons with a minimum mapping unit size of 25 ha are classified in 44 different land cover classes. An interesting derived product from Corine Land Cover is the Eururalis project[25] that aims at predicting the outcomes of four contrasting scenarios of development inspired from IPCC scenarios on climate change, on European rural land cover in 2000, 2010, 2020 and 2030.

Climatic layers presenting spatial interpolation of monthly average (1961-1990) of key climatic variables have been developed also at a European scale by Hulme et al. (1995) and at the International Institute for Applied Systems Analysis (IIASA[26]) at a 1km resolution.

European research projects such as PRUDENCE (Prediction of Regional scenarios and Uncertainties for Defining EuropeaN Climate change risks and Effects)[27] and ENSEMBLES[28] have produced regional climate models according to the IPCC main scenarios on a 50 km, respectively 25 km, grid across Europe. The base model reproduces the 1961-1990 period and the scenarios cover the 2071-2100 period.

The European Commission has also promoted project such as Fauna Europea[29] which aims at assembling a database of the scientific names and distribution of all European land and fresh-water animals. Other collaborative projects exist aiming at gathering data on more specific groups. The

[21] http://www.geologieportal.ch (last access: 17:04.2011)
[22] http://www.wsl.ch/staff/niklaus.zimmermann/progs.html (last access: 17.04.2011)
[23] http://www.ec-gis.org/inspire (last access: 17.04.2011)
[24] http://etc-lusi.eionet.europa.eu/CLC2006 (last access: 17.04.2011)
[25] http://www.eururalis.eu (last access: 17.04.2011)
[26] http://www.iiasa.ac.at/ (last access: 17.04.2011)
[27] http://prudence.dmi.dk (last access: 17.04.2011)
[28] http://ensembles-eu.metoffice.com/index.html (last access: 17.04.2011)
[29] http://www.faunaeur.org (last access: 17.04.2011)

Society of European mammalogists[30] was at the origin of the Atlas of European Mammals published in 1999 now widely used as a reference work. The European Bird Census Council (EBCC) is an association of expert ornithologists co-operating in a range of ways to improve bird monitoring and its major piece of work is the Atlas of European Breeding Birds[31]. The Mapping European Butterflies (MEB) project was initiated in order to fill the gaps in our knowledge concerning European butterflies and its first results was the Distribution Atlas of European Butterflies presented to the public in March 2002[32]. The Atlas of Amphibians and Reptiles in Europe[33] was produced on the initiative of the Society of European herpetologists (SEH). Finally, the Atlas Florae Europaeae (AFE)[34] is a collaborative long-term project of European botanists for mapping the distribution of vascular plants in Europe. The resolution of these atlases is usually relatively coarse, typically based on a 50 km grid. More recently, the Biodiversity Information System for Europe (BISE[35]) was launched as a single entry point for data and information to strengthen decision-making on biodiversity.

1.3.3 The global case

It is worth mentioning also global sources of spatial data as these are becoming more and more available at relatively fine scales, while computers speed will soon allow processing global data as we are now processing national ones. The quantity of data becoming available at global scale is increasing almost every day. Here are presented a selection of the most important datasets in relation to their use for biodiversity assessment.

GlobCover[36] is a project led by the European Space Agency (ESA) that aims at producing a global land cover map in 22 classes from the Envisat MERIS fine resolution data (300m). Products are now available for two periods: end 2004 - mid 2006 and 2009. Another important global database is WorldClim[37] which is a set of global climate layers (grids) with a spatial resolution of a square kilometre that can be used for mapping and spatial modelling. Most of the global covers rely on the digital elevation model made available by NASA at a 90 m resolution. This global DEM has been elaborated from data collected during a short mission (11 days) in February 2000 by a modified radar system on board of the Space Shuttle Endeavour (SRTM[38]). In the field of climate change, the projections of the Intergovernmental Panel on Climate Change (IPCC) are becoming available for instance through the NCAR's GIS Initiative data portal providing Climate Change Scenarios at 1.4 degree resolution[39]. A recent initiative deserves to be mentioned here: the Global Earth Observation System of Systems (GEOSS)[40]. This 'system of systems' proactively links together existing and planned observing systems around the world in nine societal benefit areas. It aims at empowering the international community to protect itself against natural and human-induced disasters, understand the

[30] http://www.european-mammals.org (last access: 17.04.2011)
[31] http://www.ebcc.info/atlas.html (last access: 17.04.2011)
[32] http://www.mapeurbutt.de/index.htm (last access: 17.04.2011)
[33] http://www.seh-herpetology.org/atlas/atlas.htm (last access: 17.04.2011)
[34] http://www.fmnh.helsinki.fi/english/botany/afe (last access: 17.04.2011)
[35] http://biodiversity.europa.eu (last access: 17.04.2011)
[36] http://ionia1.esrin.esa.int/ (last access: 17.04.2011)
[37] http://www.worldclim.org (last access: 17.04.2011)
[38] http://www2.jpl.nasa.gov/srtm (last access: 17.04.2011)
[39] http://www.gisclimatechange.org (last access: 17.04.2011)
[40] http://www.earthobservations.org/geoss.shtml (last access: 17.04.2011)

environmental sources of health hazards, manage energy resources, respond to climate change and its impacts, preserve water resources, improve weather forecasts, manage ecosystems, promote sustainable agriculture and conserve biodiversity[40]. A variety of data is accessible via the GEO Portal[41] provided by ESA.

Biodiversity data at global scale is also becoming increasingly available. The predominant initiative in this respect is certainly the Global Biodiversity Information Facility (GBIF[42]) that aims at facilitating the global dissemination of primary biodiversity data, so that people from all countries can access and use this information. This mission is particularly important in order to make available data hold in museums and herbariums. Another very important actor on global knowledge on biodiversity is certainly the International Union for Conservation of Nature (IUCN[43]), especially through its Species Survival Commission that rely on a network of 7,500 volunteer experts around the world for addressing issues related to wildlife health, species conservation and reintroduction. IUCN is also responsible for the development of the Red Lists of threatened species, which are the world's most comprehensive inventory of the global conservation status of plant and animal species. Unfortunately, IUCN raw data is still not very well organized and probably far from being made available worldwide. The WWF has also developed its spatial databases in order to assess global biodiversity through the definition of ecoregions[44]. WWF defines an ecoregion as a "large unit of land or water containing a geographically distinct assemblage of species, natural communities, and environmental conditions".

Finally, the United Nations Environment Programme (UNEP) has also several initiatives that are strongly based on spatially explicit data at global scale. The Global Resource Information Database network (GRID[45]) is for instance specialized in providing raw and value-added environmental information at all spatial scales. In collaboration with UNEP, the World Conservation Monitoring Centre (WCMC[46]) evaluates and highlights the many values of biodiversity and puts biodiversity knowledge at the centre of decision-making.

1.4 GENERAL AIM

In the last decade the discipline of distribution modelling has benefited from important developments (Guisan and Zimmermann, 2000; Guisan et al., 2002; Guisan and Thuiller, 2005; Araújo and Guisan, 2006; Guisan et al., 2006b; Moisen et al., 2006; Elith and Leathwick, 2009). Such modelling relies on statistical models relating observations of species, communities or biodiversity to environmental predictors, and projecting the fitted relationship into geographical space to produce distribution maps that are to be used for conservation management (Lehmann et al., 2002a; Figure 1.1).

[41] http://www.geoportal.org/web/guest/geo_home?cache_control=0 (last access: 17.04.2011)
[42] http://data.gbif.org (last access: 17.04.2011)
[43] http://www.iucn.org/ (last access: 17.04.2011)
[44] http://www.panda.org/ecoregions (last access: 17.04.2011)
[45] http://www.grid.unep.ch/data/ (last access: 17.04.2011)
[46] http://www.unep-wcmc.org (last access 17.04.2011)

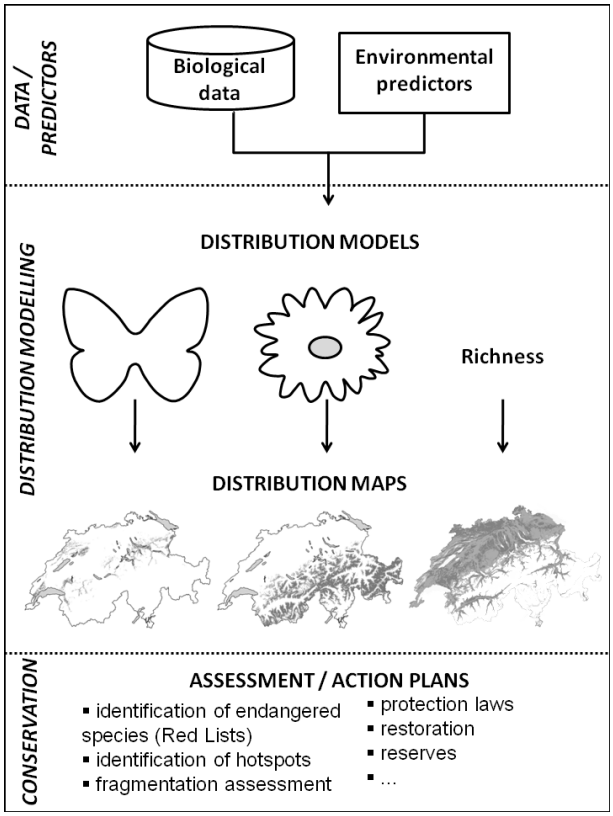

Figure 1.1 The discipline of distribution modelling put in relation species observations or richness with environmental predictors and projects the fitted relationship into geographical space to produce distribution maps that are to be used for conservation management.

By assessing the effect of several factors on model performance and on the accuracy of spatial predictions, this thesis aims at improving techniques and data available for distribution modelling and at providing the best possible information to conservation managers to support their decisions and action plans for the conservation of biodiversity in Switzerland and beyond. As discussed in the previous chapter, several monitoring programs have been put in place and different sources of data now exist and start to be available to researchers. However, because of the lack of means, data are often not gathered at an appropriate resolution**,** are sampled only over limited areas, are not spatially explicit or do not provide a sound biological information. A typical example of this is data on "habitat" (sensu biota). This is essential information for an effective conservation management, but has often to be approximated from land use, the closest available information. Moreover, data are often not sampled according to an established sampling design, which can lead to biased samples and consequently to spurious modelling results. Understanding the sources of uncertainty linked to the different phases of the modelling process and their importance is crucial in order to evaluate the final distribution maps that are to be used for conservation purposes.

1.5 SPECIFIC QUESTIONS

The research presented in this thesis was conducted within the framework of the Landspot Project, a project supported by the Swiss National Science Foundation (grant no. 3100-063147 obtained by Prof.

Antoine Guisan). The main goal of the project was to assess the possible contribution of pre-modelled "habitat" units (*sensu* biota) to model the distribution of animal species, in particular butterfly species, across Switzerland. While pursuing this goal, different aspects of a modelling process were addressed and improved and implications for conservation discussed (Figure 1.2):

- Data and sampling design
- Distribution modelling
- Potential for conservation.

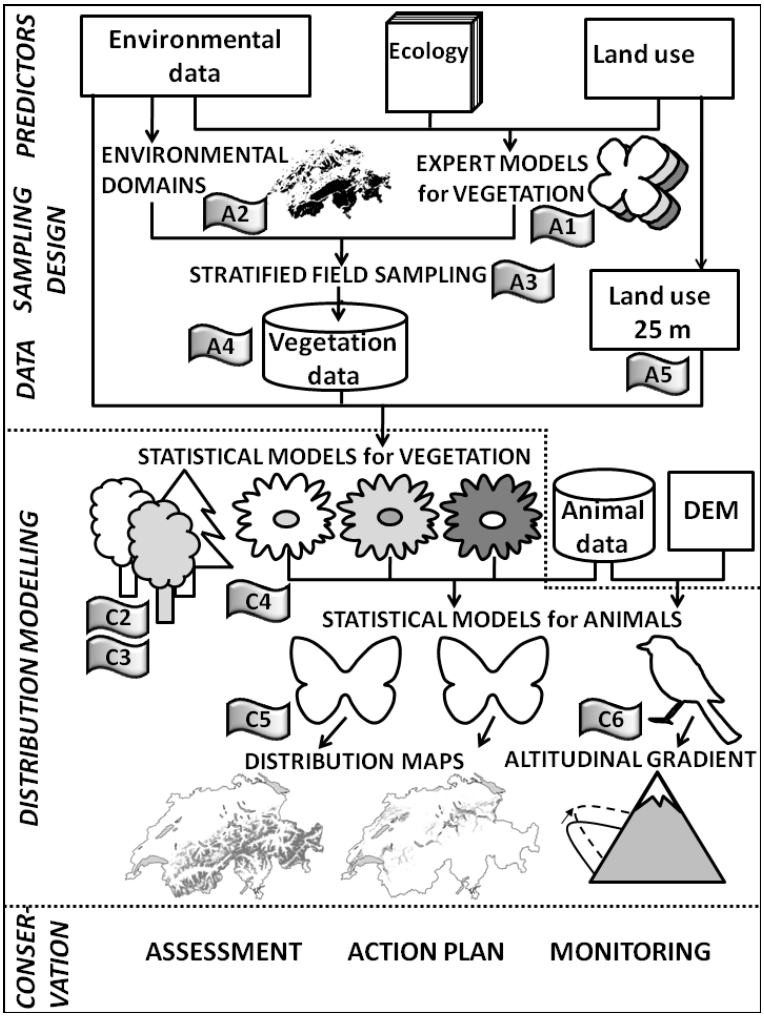

Figure 1.2 Flowchart of the analyses performed and presented within the manuscript. C2-C6: Chapter 2- Chapter 6. A1-A5: Annex1-Annex 5.

1.5.1 Data and sampling design

The main "habitat" units considered in this thesis are grassland and forest communities of natural and anthropogenic origin as defined in the typology of Delarze et al. (1998) for Switzerland. These communities are mainly defined at the phytosociological level of the alliance. For the time being, no

comprehensive map of such communities is available at the national scale and at fine resolution. As a first step, it was therefore necessary to create distribution models for these communities across Switzerland and in order to do so it was thus indispensable to collect the necessary data.

Field survey is succinctly described in Annex 3. Assessing the contribution of these vegetation communities for the modelling of fauna implicitly means comparing them to model obtained using land use, which is the information that was generally used in replacement until now. The survey in the field was thus centred on the same points evaluated by the Federal Statistical Office while producing the Swiss land use statistics (OFS, 1992/97). Furthermore, in order to be more efficient in the field, the sampling of grasslands was based on maps of the potential distribution of the target vegetation communities obtained trough expert modelling. The environmental requirements of the units described in the typology (Delarze et al., 1998) were translated into an expert system (table) that was subsequently implemented in a GIS using spatial information relative to the main environmental drivers as well as potentially favourable land use categories. The expert system for grassland communities is presented in Annex 1 (A1.1). An expert system was subsequently developed for forest communities as well and is also presented in Annex 1 (A1.2). Sampling design was further improved by stratifying it by the Swiss Environmental Domains (SED). SED are the results of an environmental classification of the Swiss territory according to key climatic, topographic and geologic variables influencing both natural and anthropogenic processes at various scales. Classification takes place in the environmental space where sites that have similar environmental characteristics are grouped together. The resulting domains are defined regardless of their geographical location and possibly results in entities that are scattered across the geographic space. Stratifying in a balanced way (i.e. 'equal' in Hirzel and Guisan, 2002) by the environmental domains ensures that all combinations of environmental conditions are effectively surveyed and that the sample is not biased towards more frequent combinations. The first version of SED (Annex 2) was developed in collaboration with Dr Anthony Lehmann (previously at CSCF and presently at UNEP/DEWA/GRID-Europe and University of Geneva[47]) and their first application was made within this thesis, as described in Annex 3.2. Relevance of the Swiss Environmental Domains for reporting statistics and performing environmental analysis has been recognised by the Swiss Federal Office for the Environment (FOEN) that commissioned the production of an official version. A report with their description and some applications was recently published in the FOEN series 'Environmental studies' (available on the FOEN website[48]). Field survey for grassland communities was conducted during two field seasons and covered the entire Swiss territory. The database storing the 638 grassland relevés is presented in Annex 4. In the same database was implemented a decision-support system that helps in classifying the relevés according to the list of the species and according to the expected dominance of each species within the community (dominant vs accompanying species).

A main duty of the Landspot project was to produce maps of the potential distribution of fauna species at high resolution. All the predictors available in numeric form in the GIS as well as the available data for modelling were gathered or produced at a resolution of 25 m. In order to meet these requirements,

[47] http://www.unige.ch/climate/Team/Lehmann.html (last access 17.04.2011)

[48] http://www.bafu.admin.ch/publikationen/publikation/01564/index.html?lang=en&show_kat=/publikationen (last access 17.04.2011)

the land use information provided by the Swiss Federal Statistical Office (FSO/Geostat) had thus to be downscaled from 100 to 25 m. The methodology employed for the downscaling combine spatial interpolation techniques and an expert system with the possible correspondences between the categories of the national topographic base maps 1:25,000 (Swisstopo: Vector25, primary surfaces) and the categories of land use (FSO/Geostat: land use statistics). The methodology and the resulting high-resolution map of land use are described in Annex 5.

1.5.2 Species distribution modeling

Generalized additive models (GAMs) are semi-parametric regression models that estimate response curves with local smoothing functions (Hastie and Tibshirani, 1990). This is considered by some authors a significant and important progress compared to GLMs (Generalized linear models; McCullagh and Nelder, 1989) since species only rarely present bell-shaped or linear response curves along environmental gradients (Austin and Smith, 1989; Austin, 2002). GAMs allow a wide range of response curves to be fitted (Yee and Mitchell, 1991) and thus constitute a powerful explanatory and predictive tool (Austin, 1999; Guisan et al., 2002). The use of GAMs for species distribution modelling was made easier through the development of GRASP (Generalized Regression Analysis and Spatial Predictions), a collection of S-Plus functions with a graphical user interface (Lehmann et al., 2002b). GRASP is the tool that was used and improved throughout this thesis in order to fit the models and produce spatial predictions. Following the nomenclature adopted in GRASP, ROC is the abbreviation used throughout this thesis to refer to the Area Under the Curve (AUC) of a Receiver Operating Characteristic plot (Fielding and Bell, 1997).

Main contributions of this thesis to the discipline of species distribution modelling (SDM) are assembled in four main scientific papers:

1) In the first, presented in Chapter 2 and published in Journal of Biogeography (33: 1729–1749), different issues related to the modelling process itself are investigated. First is assessed the effect of five different stepwise selection methods on model performance, stability and parsimony, using data of the forest inventory of State of Vaud. In the same paper are also assessed: the effect of weighting absences to ensure a prevalence of 0.5 prior to model calibration; the effect of limiting absences beyond the environmental envelope defined by presences; four different methods for incorporating spatial autocorrelation; and finally, the effect of integrating predictor interactions. Results presented in this paper allowed to specifically enhance GRASP that now incorporates new selection methods and the possibility of dealing with interactions among predictors as well as spatial autocorrelation (Lehmann, 2005). The contribution to species distribution modelling of different sources of remotely sensed information was also assessed and results presented in a separate chapter (Chapter 3).

2) The second paper, presented in Chapter 4, explores the combined effects of sample size and data stratification on the accuracy of models using data on grassland distribution across Switzerland collected within the framework of the Landspot project and supplemented with other important vegetation databases. For the stratification of the data, different spatial frameworks were compared. In particular, environmental stratification by Swiss Environmental Domains is compared to geographical stratification either by biogeographical regions (Gonseth et al., 2001) or political states (cantons).

3) The third paper, presented in Chapter 5, assess the contribution of pre-modelled vegetation communities to the modelling of fauna. It is a two-steps approach that combines the disciplines of community ecology and spatial ecology and integrates their corresponding concepts of "habitat". First are modelled vegetation communities *per se* and then these "habitat" units are used in order to model animal species habitat. A case study is presented with grassland communities and butterfly species. Different ways of integrating vegetation information in the models of butterfly distribution are also evaluated.

4) Finally, a glimpse to climate change is given in the paper presented in Chapter 6 and published in Ecological Modelling (222: 21–32). This paper proposes a conceptual framework for analysing range shifts, namely a catalogue of the possible patterns of change in the distribution of a species along elevational or other environmental gradients and an improved quantitative methodology to identify and objectively describe these patterns. The methodology was developed using data from the Swiss national common breeding bird survey (MHB; Schmid et al., 2004).

1.5.3 Potential of SDM for conservation

The overall objective of this thesis is to improve species distribution models as potential inputs for different conservation tools (e.g. red lists, ecological networks, risk assessment of the spread of invasive species, vulnerability assessment in the context of climate change). While no conservation issues or tools are directly tested in this thesis, the importance of the proposed improvements made in species distribution modelling is discussed at the end of this work.

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2 IMPROVING GENERALIZED REGRESSION ANALYSIS FOR THE SPATIAL PREDICTION OF FOREST COMMUNITIES

Ramona Maggini[1 *], Anthony Lehmann[2], Niklaus E. Zimmermann[3] and Antoine Guisan[1]

[*] Address for correspondence: Fax: +41 21 692 42 65, Ramona.Maggini@unil.ch

[1] Department of Ecology & Evolution (DEE), Biophore Building, University of Lausanne, CH-1015 Lausanne, Switzerland

[2] Swiss Centre for Faunal Cartography (CSCF), Terreaux 14, CH-2000 Neuchâtel, Switzerland

[3] Swiss Federal Research Institute WSL, Zürcherstr. 111, HL-C43, CH-8903 Birmensdorf, Switzerland

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2.1 ABSTRACT

Aim This study uses data from temperate forest communities to assess: 1) five different stepwise selection methods with generalized additive models; 2) the effect of weighting absences to ensure a prevalence of 0.5; 3) the effect of limiting absences beyond the environmental envelope defined by presences; 4) four different methods for incorporating spatial autocorrelation; 5) the effect of integrating an interaction factor defined by a regression tree on the residuals of an initial environmental model.

Location State of Vaud, Western Switzerland.

Methods Generalized Additive Models (GAMs) were fitted using the GRASP package (Generalized Regression Analysis and Spatial Predictions - www.cscf.ch/grasp).

Results Model selection based on cross-validation appears to be the best compromise between model stability and performance (i.e. parsimony) among the five tested methods. Weighting absences returns

models that are performing better than models fitted with the original sample prevalence. This seems mostly due to the impact of very low prevalence values on evaluation statistics. Removing zeroes beyond the range of presences on main predictor gradients changes the set of selected predictors and potentially their response curve shape. Moreover, removing zeroes slightly improves model performance and stability when compared to the baseline model on the same dataset. Incorporating a spatial trend predictor significantly improves model performance and stability. Even better models are obtained when including local spatial autocorrelation. A novel approach to include interactions proves to be an efficient way to account for interactions between all predictors at once.

Main conclusions Models and spatial predictions of 18 forest communities were significantly improved by either using: i) cross-validation as model selection method, ii) weighted absences, iii) limited absences, iv) predictors accounting for spatial autocorrelation, or v) a factor variable accounting for interactions between all predictors. The final choice of model strategy should depend on the nature of available data and on the specific study aims. Statistical evaluation is useful to search for the best modelling practice. However, one should not forget to consider the shapes and interpretability of response curves, as well as the resulting spatial predictions in his final assessment.

Keywords Forest communities, potential distribution modelling, generalized regression analysis, spatial predictions, stepwise selection methods, cross-validation, spatial autocorrelation, predictor interactions, GAM, ROC.

2.2 INTRODUCTION

In recent years, predictive distribution modelling benefited from important developments (see Guisan & Zimmermann, 2000; Scott *et al.*, 2002; Segurado & Araújo, 2004). Such modelling relies on statistical models relating observations of species, communities or diversity to environmental predictors, and projecting the fitted relationship into geographical space to produce distribution maps. Their use spans now fields as diverse as biogeography, spatial ecology, conservation biology and environmental management (Guisan & Thuiller, 2005), yielding significant advances in hot topics such as climate change impacts (e.g. Thuiller, 2004, Araújo *et al.*, 2006), rare species distribution (e.g. Guisan *et al.*, 2006), spread of invasive species (e.g. Peterson, 2003), habitat loss and fragmentation (e.g. Opdam & Washer, 2004), biodiversity analysis from museum-based data (e.g. Graham *et al.*, 2004), richness hotspots (e.g. Lehmann *et al.*, 2002a; Moser *et al.*, 2005) and reserve network design (e.g. Ferrier *et al.*, 2002). Pearson *et al.* (2006) have studied the uncertainty of predictions based on nine of the most widely used modelling techniques. Understanding uncertainty is indeed critical as these methods are becoming important tools in basic and applied ecological research, and their development and use is likely to intensify in future years. Other crucial issues pertaining to the model fitting stage itself remain unresolved, as illustrated hereafter for a particular family of regression models.

Generalized additive models (GAMs) are semi-parametric regression models (Hastie & Tibshirani, 1990). Response curves in GAMs are estimated with smooth functions, allowing a wide range of response curves to be fitted (Yee & Mitchell, 1991). This is considered by some authors as an important progress since species only rarely present bell-shaped or linear response curves along

environmental gradients (Austin & Smith, 1989; Austin, 2002). GAMs constitute powerful explanatory and predictive tools (Austin, 1999; Overton *et al.*, 2002) and many applications in the field of distribution modelling have been increasingly reported in the literature (see Guisan *et al.*, 2002 and Lehmann *et al.*, 2002b).

The use of GAMs was made easier through the development of GRASP (Generalized Regression Analysis and Spatial Predictions), a collection of S-Plus functions with a graphical user interface (Lehmann *et al.*, 2002c). A wide range of GRASP applications have been published, spanning different groups and ecosystems including terrestrial vegetation (Cawsey *et al.*, 2002), wetlands (Clarkson *et al.*, 2004), submerged vegetation (Schmieder & Lehmann, 2004), fern diversity (Lehmann *et al.*, 2002a; Zaniewski *et al.*, 2002), amphibians (Joly *et al.*, 2001; Ray *et al.*, 2002), birds (Suarez-Seoane *et al.*, 2002), butterflies (*Luoto et al.*, 2006), aquatic invertebrates (Castella *et al.*, 2001) and coral reef habitats (Garza-Pérez *et al.*, 2004).

Model selection is a complex issue (Burnham & Anderson, 2002) which is central to ecological modelling (Johnson & Omland, 2004). Burnham & Anderson (2002) classify the different methods of selection in three categories: i) optimization of model criteria (e.g. AIC, BIC), ii) tests of hypotheses (e.g. Chi, F), and iii) ad hoc methods (e.g. cross-selection). The Akaike's Information Criterion (AIC; Akaike, 1973) is based on an empirical log-likelihood function that estimates the relative distance between the fitted model and the observed data (Burnham & Anderson, 2002). The log-likelihood value is penalised by the number of parameters in the fitted model. The Bayesian Information Criterion (BIC; Schwarz, 1978) is similar to AIC, but is additionally penalised by the number of observations. Chi- and F-statistics test the significance of change in explained deviance when adding or dropping a term from the model. Selection based on cross-validation (Stone, 1977) appears as a powerful alternative.

It is generally agreed that a model validation based on a comparison of observed and predicted values made on the training dataset (i.e. resubstituition) is not satisfactory, and four alternative strategies are commonly used (Fielding & Bell, 1997; Guisan & Zimmermann, 2000). Validation on a fully independent dataset (e.g. Guisan *et al.*, 1998; Araújo *et al.*, 2005a; Randin *et al.*, 2006) is the most appealing procedure, but may not always be possible for two reasons. First, adequate data for independent validation may be difficult to collect and modellers usually prefer to use all available data to fit their model (e.g. Araújo *et al.*, 2005b). Second, because truly replicated datasets are rare, it is often hard to discern whether a model is being truly validated or whether the calibration and validation datasets are simply being compared (Araújo *et al.*, 2005a). Jackknife has also been used (e.g. Jaberg & Guisan, 2001; Maggini *et al.*, 2002), but for large datasets it is asymptotically equivalent to measures of agreement on the training dataset. K-fold cross-validation (e.g. Franklin *et al.*, 2000) and bootstrap methods (e.g. Efron & Tibshirani, 1993; Guisan & Harrell, 2000) are often seen as the best compromise, because they allow assessing model stability without losing information to calibrate the final model.

Besides variable selection and model evaluation, a variety of factors can influence model performance, such as sample size, prevalence, the environmental range of data, or the type of predictor variables used. Sample size (Pearce & Ferrier, 2000; Stockwell & Peterson, 2002) and species prevalence (i.e. frequency of species' occurrences in the dataset; Fielding & Bell, 1997; Manel *et al.*, 1999b, 2001) are

known to have a major impact on models performance. For example, McPherson *et al.* (2004) found that by gradually increasing sampling prevalence, errors shifted from omission (under-prediction of true presences) to commission (over-prediction), with the best compromise occurring at a prevalence of 0.5 (see also Liu *et al.*, 2005). In practice, one solution to adjust sample prevalence towards this value is to weight absences (e.g. Guisan *et al.*, 2005; Lehmann *et al.*, 2005).

Modelling the environmental niche of eucalyptus species with GAMs, Austin & Meyers (1996) found that zero values beyond the environmental range of a species ("naughty noughts") could reduce the explanatory power of the model and distort the response curve shapes. Models were improved by restricting the data to a suitable range. Thuiller *et al.* (2004) reached a similar conclusion concerning the distortion of response curves, especially towards the upper and lower edges of environmental gradients. However, restricting the data can also reduce model generality by removing true absences that provide relevant ecological information (Thuiller *et al.*, 2004).

Interactions between predictors constitute another important issue that has recently received increasing attention (Austin, 2002). One reason for their past neglect might be the level of complexity of the procedure, which requires testing all interactions during model selection (Moisen & Frescino, 2002; Van den Berg *et al.*, 2003). A novel approach for regression models (Hastie & Pregibon, unpublished) consists in fitting a regression tree on the residuals of an initial environmental model. This allows identifying significant interaction terms and updating the initial model with this additional information coded as a factor variable. We are not aware of any published example of this approach in ecology or biogeography.

In recent years, different methods have been developed to incorporate the spatial structure of the data into models (Wagner & Fortin, 2005). Legendre (1993) proposed a framework for partitioning the variance within a regression model in distinct components: pure spatial, pure environmental, shared spatial-environmental and unexplained variance. Analytical techniques are mainly based on partial regression and trend surface analysis, or a combination of the two. A partial regression analysis using detrending techniques was used by Lobo *et al.* (2001) and Nogués-Bravo & Martinez-Rica (2004) in the context of species-richness modelling. Pereira & Itami (1991) used a Bayesian combination of an environmental model and trend model calibrated separately. Local spatial autocorrelation terms can also be incorporated as predictors in regression equations, giving place to autoregressive models (Lichstein *et al.*, 2002). Augustin *et al.* (1996) used a Gibbs sampler, implemented within an autologistic model, to estimate the presence/absence of red deer in neighbouring unsurveyed squares. Leathwick (1998) and Dirnböck & Dullinger (2004) included a spatial autocorrelation term defined as the presence/absence of the species of interest in adjacent plots within multiple search radii. Araújo *et al.* (2002) modelled probabilities of occurrence for breeding passerine birds using contagion, i.e. the number of occupied grid cells among a set of neighbouring cells, as predictor variable. The same measure of aggregation was used by Segurado & Araújo (2004) for modelling probabilities of occurrence of amphibians and reptiles.

The present study tests several methodological alternatives, some of which are current practice, while others consist of novel developments. We used data on the presence-absence of forest communities in western Switzerland to fit GAMs and assess: 1) five different stepwise selection methods; 2) the effect of weighting absences to ensure a prevalence of 0.5; 3) the effect of limiting absences beyond the

environmental envelope defined by presences; 4) four different methods for incorporating spatial autocorrelation; and 5) the use of a novel approach to include predictor interactions.

2.3 METHODS

2.3.1 Study area

The study area is the *Canton de Vaud*, a state of Western Switzerland. Its total area is 3,212 km^2 and its altitude ranges from 372 m (*Lake Geneva*) to 3209 m (summit of *Les Diablerets*). The Canton encompasses all main landscapes of Switzerland, being limited in the West by the Jura Mountains and in the East by the Alps, with the densely populated Plateau in-between. The climate is mostly temperate, with highly fluctuating atmospheric conditions on the forefront of the Alps. Mean annual precipitation is 1500 mm, with significant spatial variation. Mean annual temperature is 8.5 °C in the Plateau, 6 C° in the Jura Mountains and 5.2 C° in the Alps (OFT, 1990).

Forests cover 31.8 % (approx. 1,020 km^2) of the study area. Beech (*Fagus sylvatica* L.) is the dominant tree of climax montane and sub-montane forests, defining three different phytosociological units successively distributed along an elevational gradient (Delarze *et al.*, 1998): *Galio-Fagenion*, *Lonicero-Fagenion*, *Abieti-Fagenion*, from low to mid-elevations respectively. Two additional units of beech forest are less frequent and confined to driest areas: *Cephalanthero-Fagenion*, *Luzulo-Fagenion*. Within deciduous forests, other relatively important units are ash-alder woods (*Fraxinion*), oak forests (*Quercion pubescenti-petraeae*) and oak-hornbeam forests (*Carpinion*). At higher elevation, coniferous forests dominate. They are mainly represented by silver-fir forests (*Abieti-Piceion*) and spruce forests (*Vaccinio-Piceion*). Larch-arolla pine forests (*Larici-Pinetum cembrae*) and mountain pine forests (*Erico-Pinion mugo*) are rather rare in this humid part of the Alps.

2.3.2 Forest data

Data were obtained from the forest phytosociological atlas of State of Vaud (PhytoVD; © SFFN-Vaud). Data collection was conducted between 1988 and 1999. This forest inventory is based on a regular grid sampling of one plot every 400 m inside forested areas. Supplementary plots were later added to complement the sampling with missing or under-sampled forest units, yielding a total of 11,210 plots. Plots were circular with a 10 m radius. Complete cover-abundance releves including herbaceous, shrub and tree strata were sampled in each plot and classified into phytosociological units (Clot & Delarze, 1998). For our purpose, original phytosociological units were recoded in the Swiss habitat classification system (Delarze *et al.*, 1998), leading to 18 forest communities for modelling (Table 2.1). Units recorded in less than 10 plots were discarded because such low values prevent proper modelling by regression.

Table 2.1 Forest communities selected for modelling, together with their numerical code and their phytosociological name as defined in Delarze et al. (1998). N = number of positive observations; Prevalence = community prevalence.

FOREST TYPE	FOREST UNIT	CODE	PHYTOSOCIOLOGICAL UNIT	N	Prevalence
Bushy formations	Alpine green alder scrub	Y539	*Alnenion viridis*	80	0.00714
Alluvial forests	White willow and grey alder gallery forests	Y6123	*Salicion albae, Alnion incanae*	28	0.00250
	Ash-alder wood	Y614	*Fraxinion*	613	0.05468
Beech forests	Beech forest on limestone	Y621	*Cephalanthero-Fagenion*	695	0.06200
	Acidophilus beech forest with woodrush	Y622	*Luzulo-Fagenion*	70	0.00624
	Neutrophilus beech forest	Y623	*Galio-Fagenion*	2870	0.25602
	Bittercress beech forest	Y624	*Lonicero-Fagenion*	1544	0.13773
	Subalpine beech forest	Y625	*Abieti-Fagenion*	2641	0.23559
Other broad-leaved forests	Ravine ash-sycamore forest	Y631	*Lunario-Acerion*	167	0.01490
	Mixed lime forest	Y632	*Tilion platyphylli*	127	0.01133
	Oak-hornbeam forest	Y633	*Carpinion*	457	0.04077
	Oak wood 1	Y634	*Quercion pubescenti-petraeae*	457	0.04077
	Oak wood 2	Y636	*Quercion robori-petraeae*	30	0.00268
Thermophile pine forest	Spring heath pine forest	Y642	*Erico-Pinion sylvestris*	57	0.00508
Coniferous forests of high altitude	Silver-fir forest	Y661	*Abieti-Piceion*	970	0.08653
	Spruce forest	Y662	*Vaccinio-Piceion*	353	0.03149
	Larch-arolla forest	Y663	*Larici-Pinetum cembrae*	24	0.00214
	Mountain pine forest	Y665	*Erico-Pinion mugo*	10	0.00089

2.3.3 Predictors

We tested different types of predictors, namely climatic, geological and topographic predictors (Table 2.2). All predictors were organized in a GIS database at their original 25 m resolution (ArcView v.3.3; ESRI, Redlands, USA).

Climatic predictors obtained from the Swiss Federal Research Institute WSL, are a spatial subset of those used by Zimmermann & Kienast (1999). Mean annual temperature (*mat*) was calculated by averaging mean monthly temperatures over the year. Winter precipitation (*wiprec*) is the sum of mean monthly precipitation over winter months (December-February). Winter precipitation is used as surrogate for snow cover and its possible influence on tree distribution. Mean potential direct solar radiation during growing season (*mgsr*) is calculated by averaging mean monthly solar radiation over growing season period (March to October). Site water balance (*swb*) is a predictor that integrates the difference between monthly precipitation and potential evapotranspiration (calculated according to the

formula of Turc, 1963) over a soil bucket for a full water year. Soil storage capacity depends on soil properties and topographical position (see Zimmermann & Roberts, 2001).

The geological predictors used were: calcareous content of parent material (*CaCO3*); parent material permeability (*permea*), and soil potential for forestry (*aptsoil*). Geological information is used in replacement of soil information (incomplete in Switzerland). The digital layer for *CaCO3* was derived from the geotechnical map of Switzerland (OFS, 2003) using an expert classification (J.Ayer, University of Neuchâtel). A semi-quantitative variable representing the proportion of calcareous content within each type of parent material was created (class 1 = low content to class 4 = high content). The same procedure was adopted to create the permeability layer *permea* (class 1 = low permeability to class 3 = high permeability). The layer for soil potential for forestry (class 1 = low potential to class 4 = high potential) was derived from the digital soil suitability map of Switzerland (OFS, 2003).

Topographic predictors were: slope angle (*slope*), northness (*nness*, cosine transformation of aspect), distance to river (*distriv*) and alluvial zone (*alluv*). Slope and aspect were derived from the digital elevation model at the 25 m resolution. The distance between sampling plots and the nearest river was determined from the hydrographical map of Canton de Vaud (Swisstopo: http://www.swisstopo.ch) and was log-transformed. Alluvial zones were determined using a combination of *flow accumulation* and *cost distance* functions in ArcView. The hydrological network is very dense in Switzerland; the predictor *distriv* was therefore always significantly retained during exploratory modelling, even for units that are not especially linked with river banks. This predictor was therefore tested only for forest units that are linked to this type of environment, i.e. *Salicion albae-Alnion incanae* (Y6123), *Fraxinion* (Y614) and *Alnenion viridis* (Y539). The same strategy was adopted for *alluv*, which was tested for alluvial forests of unit Y6123 and Y614.

Table 2.2 Environmental predictors used in the modelling experiments. WSL= Swiss Federal Institute for Forest, Snow and Landscape Research; OFS = Swiss Federal Statistical Office; CSCF = Swiss Center for Faunal Cartography; SWISSTOPO = Federal Office of Topography.

NAME	DEFINITION	RANGE within study area	SOURCE
CLIMATE			
MAT	Mean annual temperature: annual mean of monthly temperatures	-374 – 1024 (C°)*100	WSL
MGSR	Mean growing season solar radiation: average of mean monthly solar radiation over growing season (March-October)	2736 -27394 (KJ/m2/day)	WSL
WIPREC	Mean winter precipitation: average of mean monthly rainfalls over winter time (December -February)	1894 – 6275 (mm)*10	WSL
SWB	Site water balance: estimation of water amount available for plants during a year obtained by integrating monthly precipitation and potential evapotranspiration over time, and considering soil storage capacity	-4222 – 1894 1/10(mm/year)	WSL

NAME	DEFINITION	RANGE within study area	SOURCE
GEOLOGY			
CaCO3	Calcareous content of parent material derived by expert knowledge (J.Ayer, University of Neuchâtel) from the Swiss geotechnical map	4 classes	OFS transformed by CSCF
PERMEA	Rock permeability derived by expert knowledge (J.Ayer, University of Neuchâtel) from the Swiss geotechnical map	3 classes	OFS transformed by CSCF
APTSOIL	Soil potential for forestry extracted from the Swiss soil suitability map	4 classes	OFS
TOPOGRAPHY			
SLOPE	Slope angle derived from the DEM at 25m resolution	0 – 8014 (°)*100	SWISSTOPO (DEM)
NORTHNESS	South-North gradient of aspect obtained by cosine function	-1000 – 1000 cos(rad)*1000	SWISSTOPO (DEM)
ALLUV	Alluvial zones defined using *flow accumulation* and *cost distance* functions on DEM and rivers	2 classes	SWISSTOPO (DEM and rivers)
DISTRIV	Logarithmic distance to rivers	0 – 365 (log(m) + 1)*100	SWISSTOPO (rivers)

In order to assess the effects of spatial autocorrelation on models, two different predictors were prepared: *trend* accounted for spatial autocorrelation of observed forest communities at the landscape level, and *AR* (autoregressive term) accounted for spatial autocorrelation of observed forest units at the local level. *Trend* was created in ArcGIS v.9.0 (ESRI, Redlands, USA) by a polynomial (cubic) interpolation and resulted in a smooth surface capturing coarse-scale patterns of presence. The local autoregressive term (*AR*) was defined as the kernel density of each forest unit in a circle of 1 km radius. The kernel density was calculated on a data subset (N = 5,202) including exclusively plots located on the regular grid (pixel = 400 m). This was made in order to avoid bias introduced by the supplementary irregularly spaced plots.

In order to include interactions between predictors entering the model, a new predictor *interact* was defined as follows. A regression tree was fitted with the residuals of a baseline regression model as response variable and the same environmental variables used to fit the baseline model as predictors, limiting the length of the tree to a maximum number of 15 leaves by a standard pruning procedure. The sequences of environmental predictors along branches specify the interactions so that the terminal nodes of the tree finally represent the classes of the new *interact* predictor (qualitative factor).

2.3.4 Statistical models

Models were fitted with generalized additive models (GAMs; Hastie & Tibshirani, 1990) and were calibrated using the GRASP v.3.2 package (Lehmann *et al.*, 2002c; www.cscf.ch/grasp) for S-Plus (v.6.2; Insightful Corp., Seattle, USA). GRASP was specifically enhanced to meet the requirements of this study and now incorporates new selection methods and the possibility of dealing with interactions among predictors as well as spatial autocorrelation (Lehmann *et al.*, 2005). The response variables were forest communities, defined as binary variables. The presence of a given forest unit in a plot

automatically determined the absence of other forest units. A binomial probability distribution was selected for the response and the link function was set to logit. Five bidirectional methods of selection were tested from full models. Three degrees of freedom were given to each smoothed environmental predictor.

All models and predictions were evaluated: i) statistically, using the area under the curve of a Receiver Operating Characteristic plot (ROC; Fielding & Bell, 1997) on the training dataset (resubstituition), a 5-fold cross-validated ROC (CVROC), the percentage of explained deviance (D^2; Guisan *et al.*, 2002) and the number of degrees of freedom used (DFU); and ii) visually, looking at response curves and spatial predictions. Wilcoxon-signed rank tests were used to compare validation statistics between pairs of experiments. Predictor contribution is calculated as a percentage of the sum of model contributions as defined in GRASP. For each predictor, model contribution is defined by the possible range of variation on the linear predictor scale.

2.3.5 Modelling Experiments

Different modelling experiments were planned to test various modelling alternatives (Table 2.3) and to provide an improved modelling framework. Experiments were conducted using 11,210 plots. A model was calibrated for each forest unit in each experiment (for a total of 18 models per experiment).

A first group of experiments (E0-E4) tested methods for selecting predictors: E0) CROSS, a newly developed method in GRASP called *cross-selection* (Stone, 1977); E1) AIC: Akaike's Information Criterion (Akaike, 1973); E2) BIC: Bayesian Information Criterion (Schwarz, 1978); E3) F-test (p-value = 0.05), testing the scaled change in explained deviance between two models, and E4) BRUTO, which is a new alternative in S-Plus (T. Hastie; http://www.stats.ox.ac.uk/pub/MASS4/Software.html). With CROSS, a CVROC statistic is calculated at each step of the selection procedure (Lehmann *et al.*, 2005). The selection stops when no more predictors can be added or removed according to a BIC information criterion. CROSS then selects the model showing the highest value of CVROC. This method is assumed to select the most stable model, as cross-validation in effect perturbs the training dataset while validating predictions on independent subsets. BRUTO fits a GAM using a backfitting procedure that identifies significant predictors and the optimal degree of smoothing for each of them (Hastie & Tibshirani, 1990). All subsequent modelling experiments were based on the *cross-selection* method, because it was judged to be the best compromise between model stability and performance. Hereafter, cross-selected models will be referred to as E0 baseline models.

Experiment E5 tested the effect of weighting absences. An overall prevalence of 0.5 was obtained by giving the presences a weight of 1, and the absences a weight defined by the ratio of the number of presences on the number of absences. A model was then fitted using these weights, hereafter referred to as E5 baseline models. Results were compared to E0 baseline models.

In experiment E6 we tested the effect of limiting absences beyond the environmental envelope defined by presences. An environmental model was selected by removing absences outside the community range along the key environmental gradients (Austin & Meyers, 1996). Absences were limited to 50 on each side of the presence range along mean annual temperature (*mat*) and soil water budget (*swb*). Results were compared to E0 baseline models.

Following experiments were performed by weighting absences in order to avoid the potential effect of prevalence on the different statistics used.

The fourth thematic group of experiments (E7-E10) tested different ways of dealing with spatial autocorrelation. In experiment E7, first-order spatial autocorrelation was incorporated in models by adding a *trend* predictor (Legendre, 1993). To explore second-order patterns, we used an autoregressive model (Borcard & Legendre, 1994; review by Lichstein *et al.* 2002) by adding an autoregressive term (*AR*) accounting for local spatial autocorrelation. The integration in models of the *AR* term was carried out in three different ways. In experiment E8, the local term of spatial autocorrelation was added to the list of predictors retained by the E5 baseline model and the entire set of predictors submitted to a new selection procedure (*AR* tested). In E9, the term was forced to enter the E5 model (i.e. no stepwise selection). Finally, in E10, the term was regressed against residuals of the E5 model with a Gaussian model. The idea was to account for residual spatial autocorrelation still present in the data after accounting for the spatial information contained in environmental predictors. Spatial predictions were then obtained by adding the linear predictor contributions of the E5 environmental model to the predictions of its residuals (E10 model). Resulting values were then transformed into the scale of the response. Results were compared to E5 baseline models.

Finally, in experiment E11 we used a novel approach to include predictor interactions (T. Hastie and D. Pregibon, unpublished). A regression tree was first created from residuals of the E5 baseline model, using the same environmental predictors as classification criteria. Sequences of predictors along branches were then used to define significant interactions that were forced into the baseline model as a new predictor of factor type (*interact*). Results were compared to E5 baseline models.

Table 2.3 Modelling experiments conducted on forest communities in the State of Vaud.

EXPERIMENTS	
SELECTION METHODS	
E0	Environmental model: habitat ~ climate + geology + topography; **selection test: CROSS**
E1	Environmental model: habitat ~ climate + geology + topography; **selection test: AIC**
E2	Environmental model: habitat ~ climate + geology + topography; **selection test: BIC**
E3	Environmental model: habitat ~ climate + geology + topography; **selection test: F**
E4	Environmental model: habitat ~ climate + geology + topography; **selection test: BRUTO**
WEIGHTS (compared to E0)	
E5	Environmental model with **weighted absences**
LIMITS (compared to E0)	
E6	Environmental model with **limited absences** on *mat* and *swb*
SPATIAL AUTOCORRELATION (compared to E5)	
E7	Spatial model: habitat ~ environmental predictors + **trend (tested)**; with weighted absences
E8	Spatial model: habitat ~ environmental predictors + **AR (tested)**; with weighted absences. AR = autoregressive term = kernel density of Y in 1 km radius
E9	Spatial model: habitat ~ environmental predictors + **AR (forced)**; with weighted absences
E10	Environmental model: habitat ~ environmental predictors + $\boldsymbol{\varepsilon}_{ENV}$; with weighted absences. Spatial model: $\boldsymbol{\varepsilon}_{ENV}$ **~ AR**

EXPERIMENTS	
INTERACTIONS (compared to E5)	
E11	Environmental model: habitat ~ environmental predictors + ε_{ENV} ; with weighted absences. Interaction factor: ε_{ENV} ~ Reg Tree (environmental predictors) Interaction model: habitat ~ environmental predictors + **interaction factor (forced)**

In order to compare the effects of the different modelling experiments, statistical evaluation criteria (ROC, CVROC, D^2) and the number of degrees of freedom used (DFU) were calculated for each model and presented as boxplots grouped by experiments.

A supplementary comparison between experiment E0 and E5 was made by: i) re-adjusting without weights the models that have been selected with weights (E5.U), and ii) applying weights when re-adjusting models that have been selected without weights (E0.W). Similarly, an additional comparison was performed between experiment E0 and E6 by: i) re-adjusting on the full dataset the models that have been selected on the limited dataset (E6.F), and conversely ii) re-adjusting models selected in E0 to the limited dataset of E6 (E0.L).

2.3.6 Spatial predictions

Spatial predictions were built in ArcView v.3.3. Models were exported from S-Plus as lookup tables (Lehmann *et al.*, 2002c) and interpreted in ArcView by an Avenue script made available with the GRASP package. Lookup tables describe each response curve point by point.

2.4 RESULTS

Detailed results of all experiments can be examined at *www.cscf.ch/grasp/improve*. A synthesis of these results is presented in the following sections.

2.4.1 Selection methods (E0-E4)

Visual examination of boxplots of ROC and D^2 values reveals very small differences in the results of experiments E0-E4, suggesting that all selection algorithms performed very similarly (Figure 2.1). However, a Wilcoxon-signed rank test revealed significant differences among selection algorithms (Table 2.4) in favour of greedy methods (AIC, F test). We are particularly interested in differences in CVROC, which is an indicator of model stability and predictability (on "pseudo-independent" observations), and in DFU, indicator of model size. According to the CVROC evaluation, the best performance was obtained with CROSS. Based on DFU, best performances (i.e. lowest values) were obtained for BIC, BRUTO and CROSS procedures respectively. The difference between BRUTO and CROSS, however, was not significant.

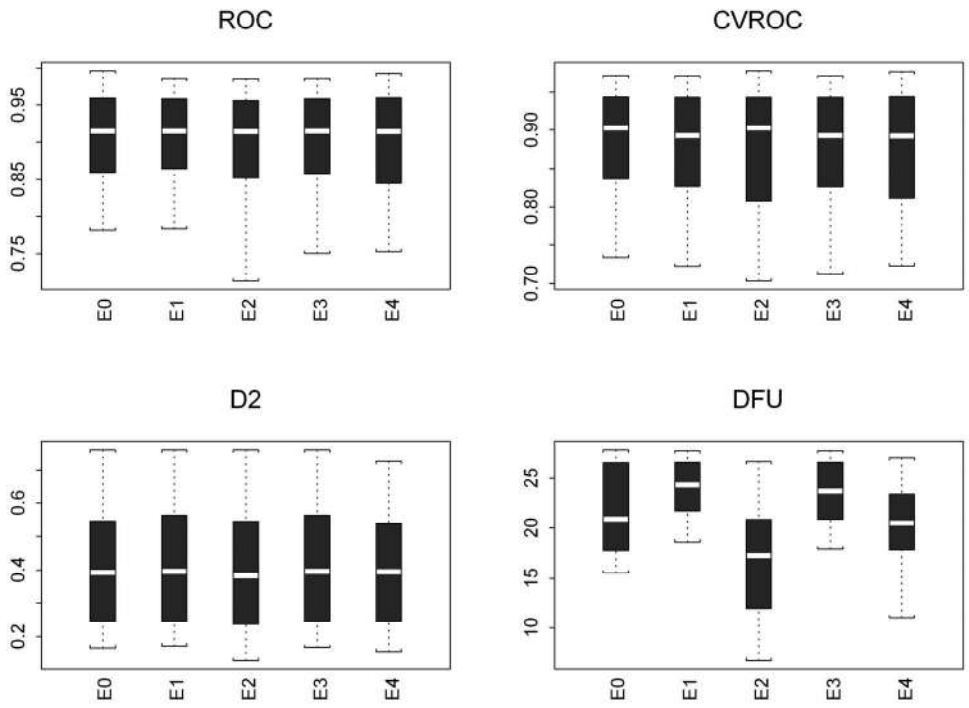

Figure 2.1 ROC, CVROC, explained deviance (D2) and degrees of freedom used (DFU) for models in experiments E0-E4 (E0: CROSS; E1: AIC; E2: BIC; E3: F test; E4: BRUTO).

Table 2.4 Significance of the Wilcoxon-signed rank test (ns>0.1; *<0.1; **<0.05; ***<0.01) based on ROC, CVROC, D2, and DFU values of the 18 models of experiments E0-E4 (E0: CROSS; E1: AIC; E2: BIC; E3: F test; E4: BRUTO).

	ROC				CVROC				D2				DFU			
	E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
E0	ns	***	ns	ns	***	**	***	**	*	***	**	**	**	***	*	ns
E1	-	***	*	ns	-	ns	*	ns	-	***	*	***	-	***	*	***
E2	-	-	***	**	-	-	ns	ns	-	-	***	ns	-	-	***	***
E3	-	-	-	ns	-	-	-	ns	-	-	-	***	-	-	-	***

2.4.2 Weighted absences (E5)

Models calibrated with weighted zeroes (prevalence = 0.5) performed better than E0 baseline models in explaining deviance (D^2) and in predicting correctly presences/absences (ROC; Figure 2.2). They were also more stable when cross-validated (CVROC). Wilcoxon-signed rank tests confirmed these results by showing highly significant differences ($p<0.01$). Reciprocal comparison, however, showed that ROC and CVROC values calculated for E0 models re-adjusted with weights (E0.W) were not significantly different from values calculated for E5 models. Similarly, evaluation statistics for E5 models re-adjusted without weights (E5.U) were not significantly different from evaluation values for E0 models.

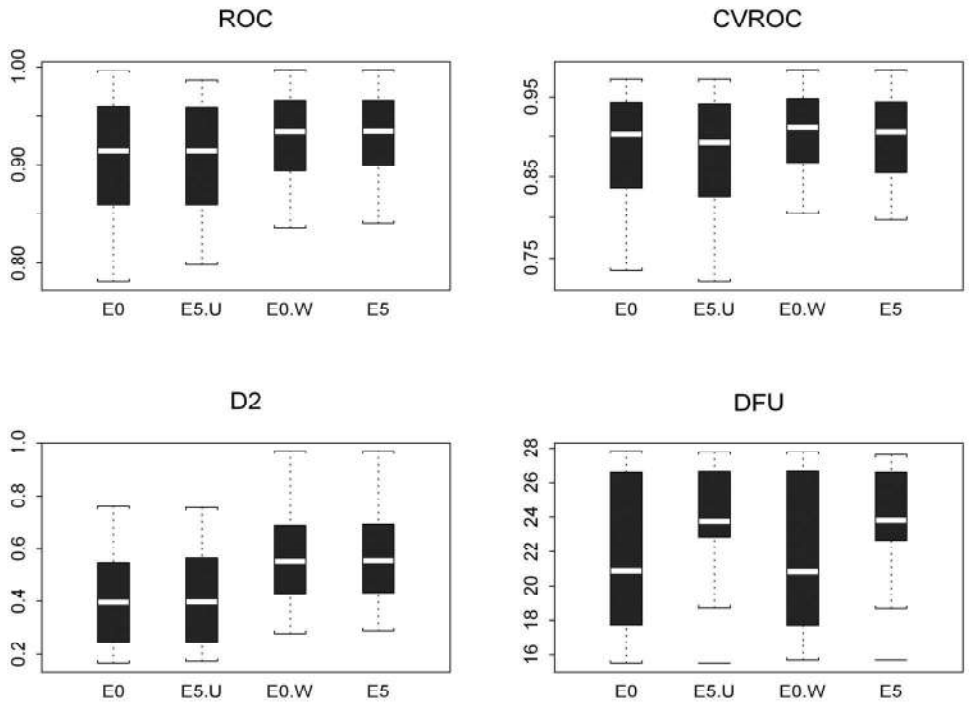

Figure 2.2 ROC, CVROC, explained deviance (D2) and degrees of freedom used (DFU) for models in experiment E0 (baseline environmental models) and E5 (weights). E5.U: E5 models re-adjusted without weights (unweighted); E0.W: E0 model re-adjusted with weights.

A more detailed analysis showed that ROC statistics are sensitive to extreme prevalence values (Figure 2.3). This result was obtained by recalibrating the E0 models at different prevalence values by applying different weights on absences.

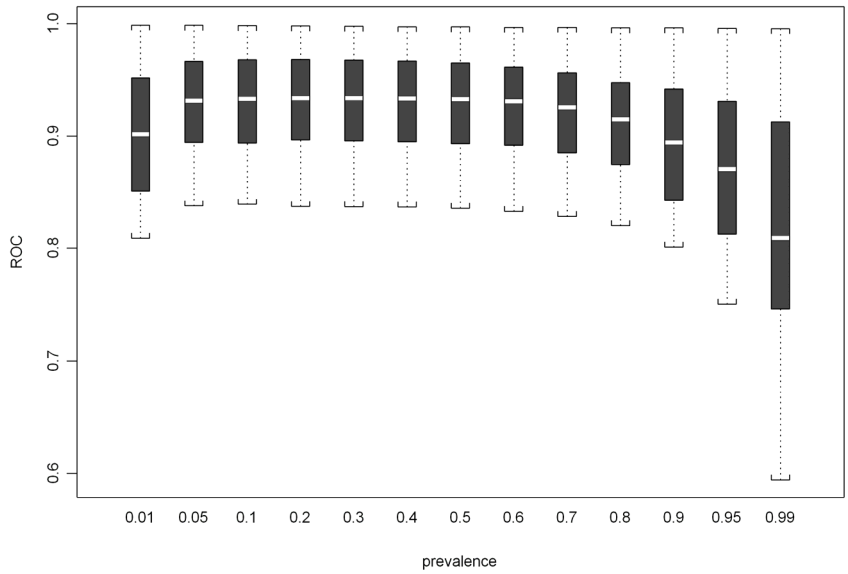

Figure 2.3 ROC evaluation statistics calculated on the E0 models (baseline environmental models) at different prevalence values set by applying different weights on absences.

Weighting zeroes also influenced the selection procedure. The set of predictors retained in models generally differed (in 14 cases out of 18) from the set retained in E0 baseline models. This was also supported by the number of degrees of freedom used in models (Figure 2.2). The shape of predictor response curves generally remained unchanged (Figure 2.4). In spatial predictions, weighting zeroes increased the average probability of occurrence of all forest units and suitable zones were more clearly depicted than in predictions resulting from experiment E0 (Figure 2.5).

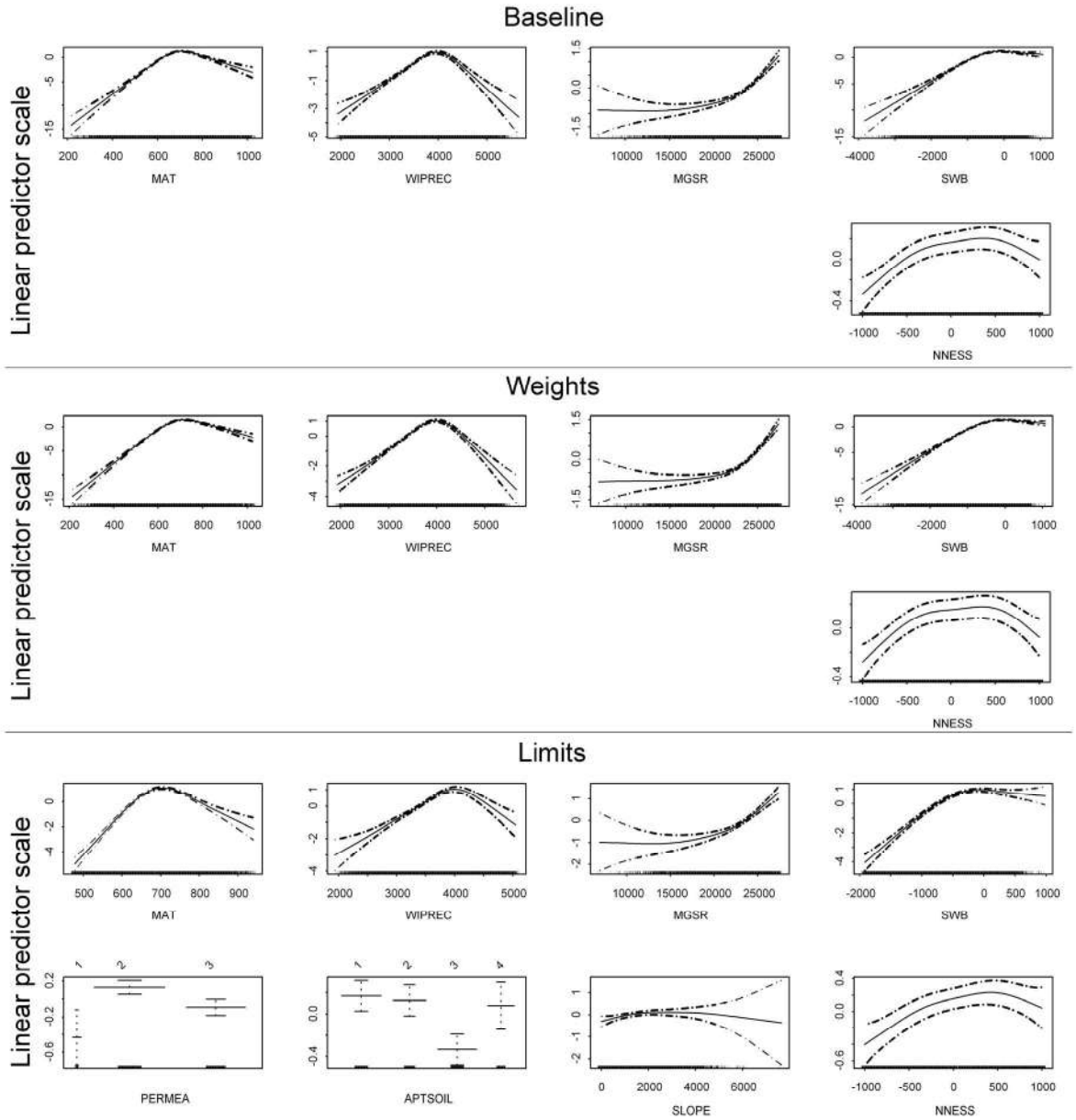

Figure 2.4 Y624 (Bittercress beech forest) response curves for predictors retained in the E0 baseline model, the E5 model (weighted absences) and the E6 model (limited absences).

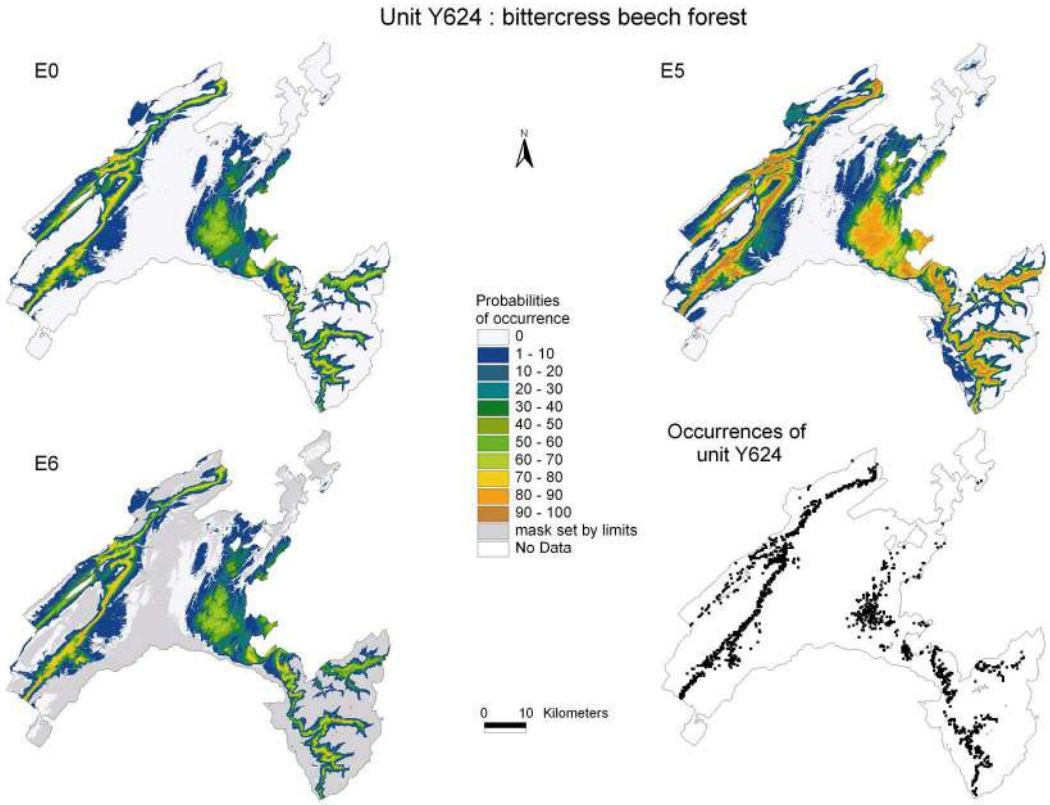

Figure 2.5 Spatial predictions of bittercress beech forest (unit Y624) obtained from the E0 baseline model, the E5 (weighted absences) and the E6 model (limited absences).

2.4.3 Limits on absences (E6)

Limiting zeroes did not seem to improve performance or stability of E0 baseline models (Figure 2.6): ROC, D^2 and CVROC values were indeed significantly lower ($p<0.01$) than values obtained for E0. However, reciprocal comparison showed that E6 models re-adjusted on the full dataset (E6.F) have ROC ($p<0.0.1$) and CVROC ($p<0.05$) values that are significantly higher than E0 values. Conversely, E0 models re-adjusted on the limited dataset (E0.L) give ROC ($p<0.1$) and CVROC ($p<0.05$) values that are significantly lower than E6 models.

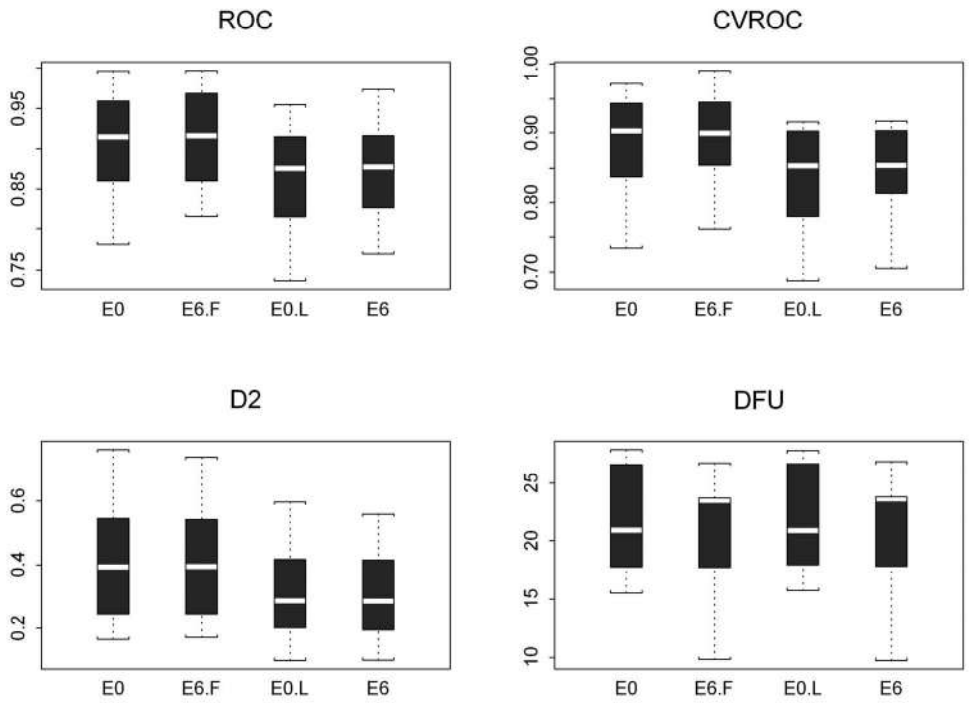

Figure 2.6 ROC, CVROC, explained deviance (D2) and degrees of freedom used (DFU) for models in experiments E0 (baseline environmental model) and E6 (limits). E6.F: E6 models re-adjusted on the full dataset; E0.L: E0 models re-adjusted on the limited dataset.

The number of selected predictors changed with the use of limits (in 14 cases out of 18), however, response curve shapes remain unexpectedly unchanged compared to baseline models (e.g. unit Y624, Figure 2.4). Setting limits around presences restricts spatial predictions within the environmental envelope defined by limited *mat* and *swb*. Outside these limits, predictions are not extrapolated and are shown in grey on predictions maps, whereas inside the limits they remain unchanged compared to baseline predictions (see Figure 2.5). We also found that modelling with limited absences was less time-consuming.

2.4.4 Spatial autocorrelation (E7-E10)

When included in the stepwise procedure with all other environmental predictors, *trend* was always retained in the final model (E7). Performance and stability of models was significantly higher ($p<0.01$) compared to E5 baseline models (Figure 2.7). E9 models (*AR* forced) performed better and were more stable than E5 models; they also performed better but were less stable than E8 (*AR* tested) models. Higher values of ROC and D^2 and lower values of CVROC suggest a probable overfitting of E9 models. In E8, the *AR* term was retained in most cases, except for larch-arolla forests (unit Y663) and mountain pine forests (unit Y665). These two units are quite rare in the study area (only 24 and 10 plots respectively) and are scattered across the higher mountains (Alps). Models calibrated in E8 used significantly fewer degrees of freedom than all other models.

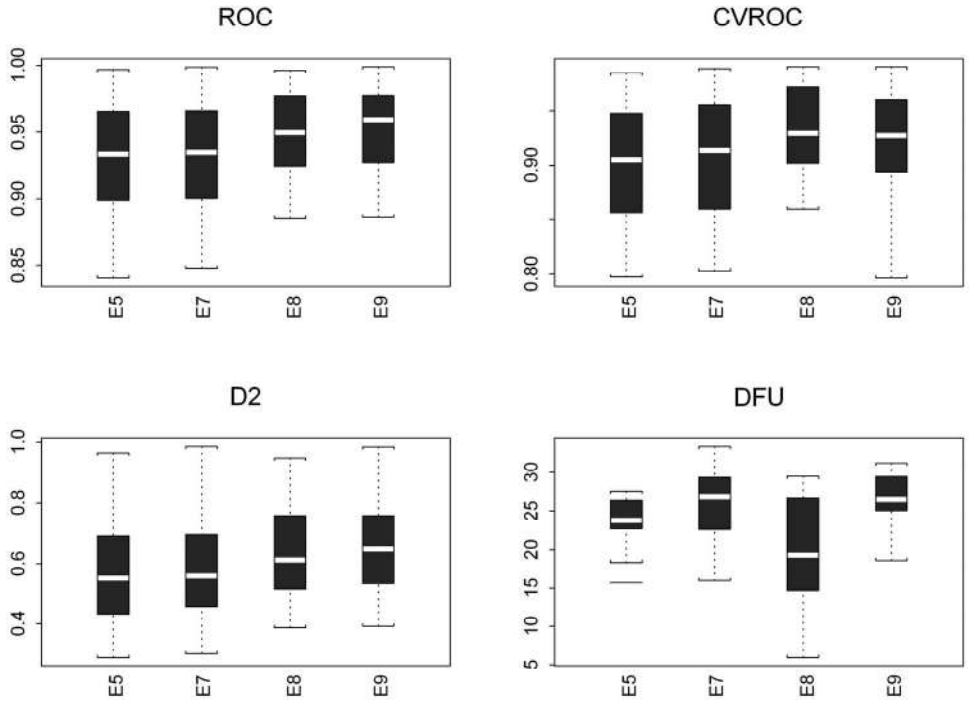

Figure 2.7 ROC, CVROC, explained deviance (D2) and degrees of freedom used (DFU) for experiments E7-E9 incorporating spatial autocorrelation in models (E7: trend; E8: AR tested; E9: AR forced) and reference experiment E5 (baseline environmental model).

Concerning experiment E10, where *AR* term is regressed against residuals of E5, no calculation of D^2, ROC or CVROC was possible since two different models were calibrated separately. However, the contribution of the *AR* term can be appreciated on the maps of spatial predictions (Figure 2.8). From an expert perspective, the overall shape of the predicted distribution according to environmental variables seems locally enhanced with finer structures in densely occupied areas. Predictions for E8 models (provided that the *AR* term was retained) and E9 models (*AR* forced) are much patchier around observations.

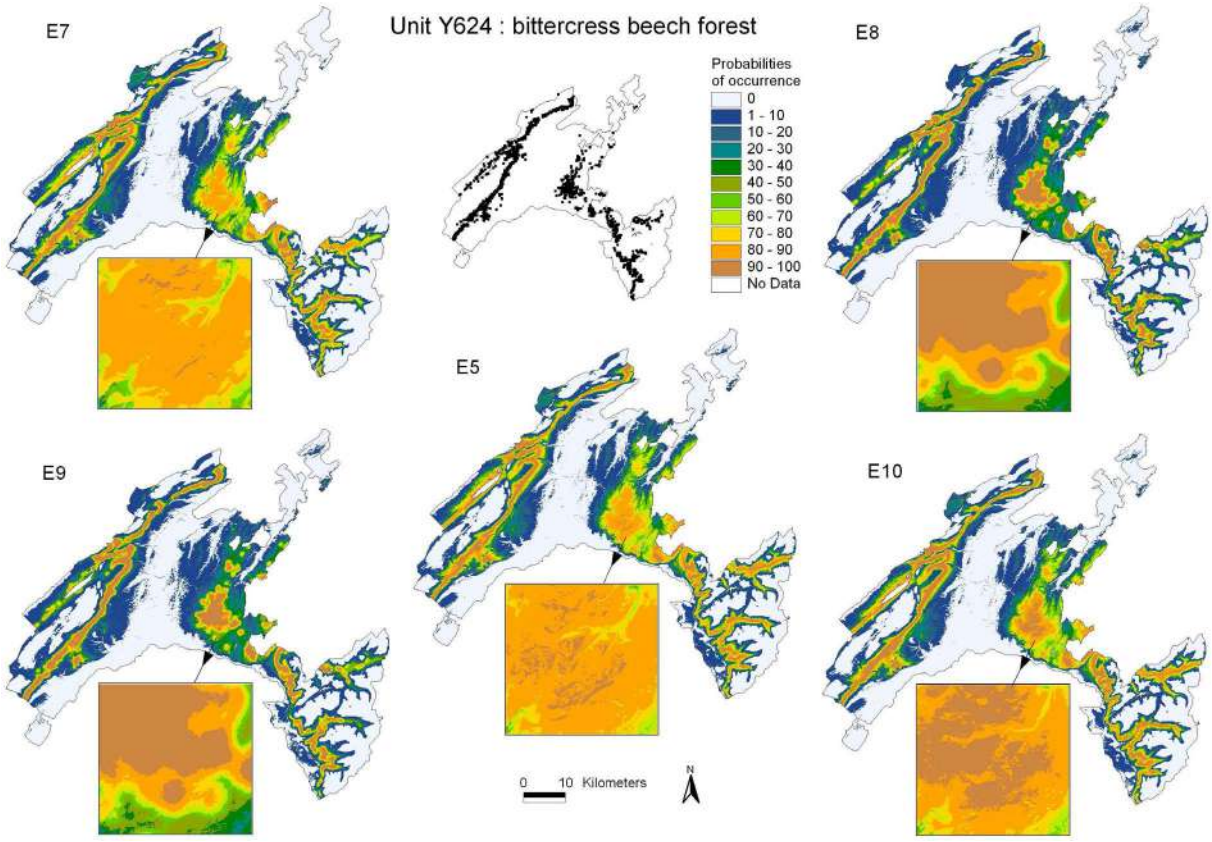

Figure 2.8 Spatial predictions for bittercress beech forest (unit Y624) obtained from the E5 baseline model, the E7 (trend), the E8 (AR tested), the E9 (AR forced) and the E10 (AR on residuals).

2.4.5 Interactions (E11)

An example of interactions defined by sequences of environmental predictors along branches of a regression tree is given for bittercress beech forest (unit Y624, Figure 2.9). Forcing the interaction term as a factor in the E5 baseline model significantly increased ROC and D^2 values ($p<0.01$), but not CVROC values.

Overall, spatial prediction maps from E11 models look similar to those obtained for E5 models. However, average predicted probabilities can be enhanced or lowered in particular areas according to the combined effect of some predictors.

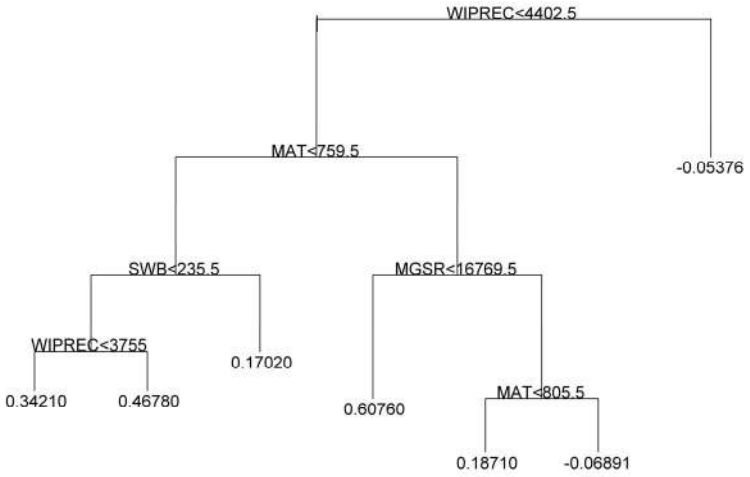

Figure 2.9 Regression tree obtained from residuals of the E5 baseline model and showing interactions between environmental predictors for unit Y624, bittercress beech forest.

2.4.6 Forest units and predictors

All forest units were successfully modelled (Figure 2.10). ROC values over all experiments ranged from 0.781 for unit Y642 (ignoring outliers) to 0.998 for unit Y665. According to the classification of Swets (1988; 0.5-0.7: poor discrimination ability; 0.7-0.9: reasonable discrimination; 0.9-1: very good discrimination), values obtained in the framework of this study therefore show reasonable to very good discrimination ability. This is also true for ROC values obtained by cross-validation (CVROC, Figure 2.10). The fact that ROC values remain high after cross-validation denotes high model stability. The number of degrees of freedom used varied greatly across the different experiments.

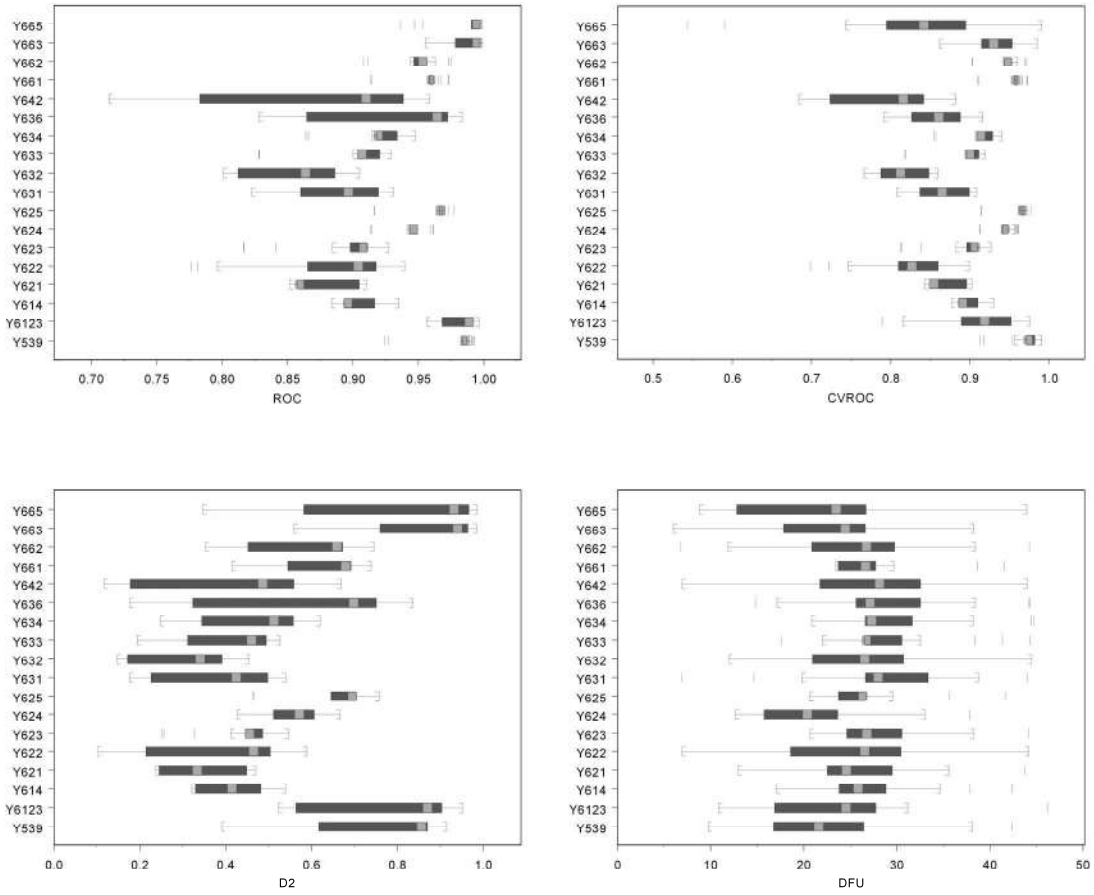

Figure 2.10 ROC, CVROC, explained deviance (D2) and degrees of freedom used (DFU) for each forest unit across all experiments.

The best ROC and D^2 values across all experiments were obtained for units Y539 (N=80), Y6123 (N=28), Y663 (N=24) and Y665 (N=10). A second group with reasonably good models includes units Y661, Y662, Y624 and Y625. These units were essentially modelled using two main predictors: mean annual temperature (*mat*) and site water balance (*swb*). Their cumulative contribution varies between 60 and 80 % (Table 2.5). Remaining units have ROC values that vary over a larger range depending on the type of experiment.

Table 2.5 Contribution in percentage of each predictor within the selected models (Model contribution in GRASP) in experiment E5 (baseline environmental models with weighted zeroes). * = 10%; + = contribution lower than 10%; - = predictor not proposed in the selection procedure; 0 = predictor proposed in the selection procedure but not retained in the model.

Unit	mat	wiprec	mgsr	slope	nness	distriv	swb	CaCO3	permea	aptsoil	alluv
Y539	******	**	**	+	+	+	0	-	0	0	-
Y6123	+	-	**	***	+	+	*	*	+	+	+
Y614	*	**	+	***	0	**	+	+	0	0	+
Y621	****	**	*	+	0	-	+	+	0	*	-
Y622	***	**	**	**	+	-	*	+	0	+	-
Y623	*****	**	+	+	0	-	+	0	+	+	-
Y624	****	*	+	0	+	-	****	0	0	0	-
Y625	***	+	+	+	0	-	*****	+	+	+	-
Y631	**	*	+	***	+	-	**	+	+	+	-
Y632	****	+	+	**	0	-	+	+	*	+	-
Y633	**	***	+	*	0	-	**	+	+	+	-
Y634	***	**	*	**	+	-	*	+	+	+	-
Y636	*	***	+	+	+	-	*	*	*	+	-
Y642	***	+	+	**	+	-	**	+	+	+	-
Y661	****	*	0	+	+	-	***	+	+	+	-
Y662	****	*	+	+	+	-	**	+	+	+	-
Y663	****	+	+	+	+	-	***	+	+	0	-
Y665	***	***	+	+	+	-	0	+	**	*	-

Table 2.5 shows the contribution of each predictor within the selected models (model contribution in GRASP) in baseline experiment E5. Mean annual temperature (*mat*) and site water balance (*swb*) have the highest contributions in models, followed by winter precipitation (*wiprec*), which is related to mean annual temperature. *Slope* and mean growing season solar radiation (*mgsr*) also play an important role, followed by calcareous content of parent material (*CaCO3*), permeability of parent material (*permea*) and soil potential for forestry (*aptsoil*). Contribution of South-North orientation (*nness*) is low and the predictor was not retained for about one third of the forest units. Distance to river (*distriv*) was always retained when proposed, but its contribution was noteworthy only for *ash-alder woods* (unit Y614). The contribution of predictor *alluv* was low overall.

2.5 DISCUSSION

We were able to model successfully the distribution of 18 forest communities in Western Switzerland, using climatic, topographic and geological predictors. As reported by many authors, temperature is a proximal predictor that has a direct impact on vegetation growth (e.g., Austin & Meyers, 1996) and plays an important role in the altitudinal distribution of forests (e.g. Brzeziecki *et al.*, 1995; Leathwick *et al.*, 1996). In the present study, mean annual temperature represented the main environmental gradient with a model contribution (as defined in GRASP) reaching 60%. Site water balance was also very important. Similar to the root zone water deficit variable used by Leathwick & Whitehead (2001), this predictor is a measure of water stress for trees and hence represents an important limiting factor for their distribution and survival. The statistically significant contribution of mean solar radiation on

forest distribution supports its use as surrogate for light (Austin & Meyers, 1996), a limiting factor of photosynthetic activity.

Slope is a frequently used predictor related to hydrology (and hence potential soil moisture) and solar radiations (Franklin, 1995). In our case, these parameters were expressed by *swb* and *mgsr*; *slope* mainly accounted for direct gravitational processes acting on tree distribution. Its contribution was particularly important (up to 30% of the sum of model contributions) for alluvial forests where it helped characterise flat areas.

Geology is often used as a surrogate for soil properties, as information on the latter are most often lacking. Geological predictors are generally defined as categories of geological substratum (e.g. Leathwick, 1998). In the present study, geology was translated into calcareous content of parent material and bedrock permeability. Their contribution was relatively low (generally inferior to 10% of the sum of model contributions) but still significant. Two reasons can explain such limited contribution: i) the coarse scale of the geotechnical map (1:200,000), as previously reported by Brzeziecki *et al.* (1993), or ii) the precision in estimating the calcareous content and permeability properties of the different bedrocks types. Geology is only an indirect parameter influencing the local distribution of vegetation; more direct predictors would have been soil pH, soil nutrients (e.g. Coudun *et al.*, 2006), soil depth or particle size. The only direct soil predictor we tested – the soil potential for forestry as extracted from the Swiss soil suitability map - was only marginally important and this most likely reflects the main focus of this information layer on open agricultural fields.

Overall, the best results were obtained for communities that were rare in the sample. This was previously reported by Franklin (1998) for shrub species and by Guisan & Hofer (2003) for reptile species. Reasons for this are probably related to their restricted niche breadth along particular environmental gradients, which are easier to capture in a model than the larger niche breadth of widespread species.

2.5.1 Selecting selection criteria

Variable cross-selection appears to be the best compromise between model stability and performance among the five tested methods. However, methods had only a very small impact on evaluation statistics, maybe because of the very large size of our dataset. With large datasets, Burnham and Anderson (2002) recognize that statistical tests become irrelevant and that other issues such as interpretability should be predominant. Indeed, other criteria can determine the choice of method. Our preferred selection methods within GRASP are from the most to the least recommended: (i) cross-selection, because it creates the most stable models; (ii) BRUTO, because it is fast and chooses smoothing degrees of freedom (e.g. Leathwick *et al.*, 2006); (iii) F-test because of its flexibility with p-values; (iv) BIC, because it is too selective; and lastly, (v) AIC, because it is too permissive (e.g. Hastie *et al.*, 2001; Kuha, 2004). Broadly speaking AIC and BIC provide respectively the lower and upper bounds for the set of adequate models (Kuha, 2004). More general statements are difficult to make as most methods used here can be modified from their original S-Plus settings, yielding different results; for instance to account for over- or under- dispersion by using scale parameters, or for overestimation by using penalty parameters. Our ranking of selection methods comes in contrast to the wide use of AIC (Manly *et al.*, 2002; Burnham & Anderson, 2004; Johnson & Omland, 2004).

For Burnham & Anderson (2002), model selection is best interpreted under the general framework of parsimony. These authors explore model selection under the assumption that no true model exist. The aim of model selection is parsimony, the tradeoff between bias (underfitting) and variance (overfitting) of the parameter estimators. In this context, these authors recommend the use of different AIC methods that are based on the information theory (Akaike, 1973). Bayesian methods such as BIC tend to be very complex and to underfit the data. Selection by cross-validation is recognized as a good option that remains, however, computer intensive. In the light of newly available methods, test of hypotheses (Chi, F) are not statistically adequate for model selection (Burnham & Anderson, 2002).

Alternatives to stepwise selection procedures have been developed in recent years based on: (i) *shrinkage rules* (Harrell, 2001), such as ridge regression or lasso; these are promising methods when using GLMs or GAMs because variables do not need to be properly selected but are given a decreasing weight according to their influence in the model (Tibshirani, 1996; Harrell, 2001; Hastie *et al.*, 2001); ii) *model averaging*, where several statistically significant models are averaged (Burnham & Anderson, 2004; Johnson & Omland, 2004). Model averaging approaches are robust and avoid the hard choice of selecting just one "best model", where several others might be similarly justified.

2.5.2 The weight of weighting

Setting weights on absences affects variable selection, model validation and spatial predictions. Weighting absences to bring the average prevalence to a value of 0.5 returned models that seemed to perform better (better fit and better cross-validation) than models fitted with the original sample prevalence. A more careful analysis showed that the ROC statistic is systematically lower at extreme prevalence values (prevalence <0.05 or >0.70). In our case, the majority of modelled units presented a very low prevalence and their ROC performances were therefore improved by weighting absences. The ROC statistic appears to be independent of prevalence only in its middle range. This is in agreement with the study of McPherson *et al*. (2004) in which different sample prevalence values were tested and the best compromise occurred at intermediate prevalence, where a balance exists between omission and commission errors. As mentioned by many authors, particular attention should thus be paid to the measure of model performance used (Fielding & Bell, 1997; Manel *et al.*, 1999a), especially at extreme prevalence values. McPherson *et al.* (2004) also showed that overfitting is minimized at intermediate prevalence when using ROC evaluation. These reasons supported our choice of weighting absences in our comparative experiments in order to avoid the potential effect of prevalence on the different statistics used.

The standardization of prevalence by weighting allows relative comparisons of predicted probabilities within a single forest unit, but precludes absolute comparisons between maps of different forest units. Using weights remains particularly justified when the true prevalence between presences and absences is lost, such as when using pseudo-absences (Zaniewski *et al.*, 2002).

The effect of weighting absences on spatial predictions was to inflate the overall probability of all forest units. In order to test whether these changes led only to a linear increase of all probabilities, we compared standardized predictions made on the linear predictor scale with and without weights. These additional analyses (not reported here) showed that there were differences between standardized

predictions, suggesting that weighting absences is also affecting the general equilibrium of model fit. Further investigations are needed on this particular aspect.

2.5.3 To the limits

Limiting zeroes changes the set of selected predictors and potentially the shape of their response curves. Unlike weights, limits can modify the relative proportion of presences and absences along gradients in the environmental space; therefore we expect more changes in the shape of response curves. In our case, we did not observe drastic changes, suggesting that the removal of some zeroes did not affect this relative proportion in environmental space. By reducing the range of data, colinearity between predictors can either increase or decrease (Austin & Barry, 1998). Since colinearity is known to influence stepwise selection (Guisan *et al.*, 2002), setting limits to the number of zeroes can thus affect final model composition.

Models fitted on limited datasets seem to perform worse, according to ROC and CVROC validation values, than those fitted on the entire dataset. A logical explanation could be that limiting zeroes cuts off absences that are relatively easy to predict. Moreover, discrimination is more difficult inside the range of presence of the community leading therefore to a lower evaluation statistic, but not necessarily to less interpretable response curves or lower model predictive power. A more realistic assessment was performed by comparing evaluation statistics calculated on the same dataset. Baseline models give slightly worse evaluation statistics than “limited” models when re-adjusted to the limited dataset. Conversely, “limited” models give better evaluation values when re-adjusted on the entire dataset. Thus, using limits gives more discriminating models that in turn can lead to better spatial predictions and reveal patterns that were otherwise hidden (e.g. Guisan *et al.*, 1998). Furthermore, setting limits can significantly reduce the size of the calibration dataset and therefore improve computation time through model selection and validation.

There is no established rule concerning the choice of which predictors to limit. One can put limits on all predictors (e.g. Lehmann *et al.*, 2002a) or just on some of them. A common practice is to choose the most influential predictors, e.g. temperature (Austin & Barry, 1998, Guisan *et al.*, 1998) or predictors defining the climatic range of the species (Thuiller *et al.*, 2004). In the present study, we decided to limit mean annual temperature and site water balance because of their evident direct influence on plant growth and survival. However, caution must be taken when using limits on factors (i.e. qualitative predictors) or on rapidly changing continuous variables such as *northness*. Limiting those types of predictors can lead to spatial predictions that become very discontinuous.

Finally, setting limits on some or all predictors prevents predicting outside of the species or community environmental envelope. Indeed, as previously reported by Austin & Meyers (1996), naughty noughts can distort the response curves yielding positive predictions where the species is known to be absent. Thuiller *et al.* (2004) insist, however, on the importance of capturing the full environmental range of the species, otherwise uncontrolled effects on the tails of the response curves can result in unreliable projections into the future when assessing climate change.

2.5.4 Spatial autocorrelation: opportunity or problem?

The presence of spatial autocorrelation in the response and/or in explanatory variables can represent a problem for modellers (Liebhold & Gurevitch, 2002; Hampe, 2004; Wagner & Fortin, 2005). The main issue is that spatial autocorrelation violates the assumption of data independence on which regression analyses are based. The choice for modellers is either to quantify, avoid or integrate spatial autocorrelation, but not anymore to ignore it. Wagner & Fortin (2005) describe three different approaches for dealing with spatial autocorrelation in models: i) regression models incorporating a spatial term (i.e. autoregressive models, Keitt *et al.* 2002); ii) partialling–out of the spatial component in the species-environment relationship (i.e. variance partitioning, Legendre, 1993); and iii) residuals analysis (i.e. multiscale ordination). In our study, we explored the use of autoregressive terms. As in Lichstein *et al.* (2002), we added a general spatial trend to an environmental model to assess broadscale spatial patterns, and we incorporated an autoregressive term to account for local autocorrelation. The general spatial trend significantly improved model performance and stability; even though better models were obtained by incorporating a predictor accounting for local spatial autocorrelation. While the former is an efficient way to account for historical patterns of distribution (like glaciations or volcanic activity, e.g. Leathwick, 1998; Svenning & Skov, 2005), the latter rather expresses biological properties of the species (or of many species in a community perspective; e.g. dispersal for plants, behaviour for animals) and human disturbances. Schwarz *et al.* (2003) provide empirical evidence that neighbouring factors like competition, vegetative reproduction or seed dispersal, play a significant role in determining spatial patterns of abundance of many tree species in forested landscapes. In Switzerland, forests are confined to limited patches and their composition is mostly controlled by human management. In this case, spatial autocorrelation reflects human activities more than natural interactions or dispersion.

Several authors have shown that the incorporation of autoregressive terms reduces the spatial autocorrelation in model residuals produced by ecological processes (e.g. Lichstein *et al.*, 2002). As stated by Wagner and Fortin (2005), spatial autocorrelation represents a problem mainly when it is still found in model residuals. Zhang *et al.* (2005) highlight the tendency of modern modelling techniques to produce residual clusters of similar values that traditional measure of spatial autocorrelation (Moran's I or Geary's c) might not be able to detect. They therefore recommend the use of local indicators of spatial association (i.e. LISA; Anselin *et al.*, 2005). When spatial autocorrelation is found in model residuals, statistics with exaggerated type I error are produced (detection of patterns that do not exist) as a result of pseudoreplication (Hurlbert, 1984; Legendre *et al.*, 2002, Hampe 2004). Cross-validation does not avoid the effect of spatial (and temporal) autocorrelation in the assessment of model predictive accuracy, resulting generally in overfitted models (Araújo, 2005a). Statistical solutions exist for correcting this bias (Dutilleul *et al.*, 1993; Keitt *et al.*, 2002; Legendre *et al.*, 2002; Perry *et al.*, 2002), but these are not yet commonly applied in species distribution modelling. Fielding & Bell (1997) suggest for instance correcting validation statistics based on the confusion matrix by weighting errors according to their distance to, or number of, positive observations in the neighbourhood.

In conclusion, spatial autocorrelation remains a very complex subject on which a general agreement has not been reached. For instance, in their comparison of different modelling techniques, Zhang *et al.*

(2005) conclude that modern regression analyses can improve model fitting, but they remain non-spatial in nature. They therefore recommend the use of geographically weighted regression (GWR), which estimates model coefficients at all locations in the study area. Our results, combined with a review of the literature, suggest that the best approach with GAMs is to include trend and autoregressive terms when ecological and/or statistical evidence of spatial autocorrelation is found. General trend should be removed first; then, an environmental model should be fitted on detrended residuals. Finally, local autocorrelation should be tested on the residuals of the environmental model. A final spatial prediction could be obtained by summing the contributions of the two or three levels of analysis.

2.5.5 Toward a simple integration of predictor interactions

Including an interaction factor built from a regression tree on the residuals of a first environmental model proved to be an efficient way to account for interactions between all predictors in a single step. However, our results suggest that forcing this interaction factor in a model can result in overfitting the data, with ROC statistics being significantly improved, but CVROC decreased. One way to avoid overfitting would be to build the model in two steps by adding the contributions of a first environmental model to the predictions of its residuals by a regression tree, as tested in the last experiment dealing with spatial autocorrelation (E10).

Alternative methods exist to describe and test interactions of different orders. Interaction terms are usually added as a multiplicative term between two or more variables, leading to a laborious series of tests to choose significant interactions and an expanding number of degrees of freedom used (e.g. Guisan *et al.*, 1999). Once an interaction between two terms has been identified, more flexible methods exist to fit it. An attractive but computer intensive solution is to add a bivariate local regression in a model. Another alternative in GLMs and GAMs is to create a coefficient of a variable which is a function of another variable (e.g. $Y \sim \beta_0 + \beta_1 X1 + f(X1)*X2$) (T.Hastie, pers. comm.). This latter solution has the advantage of simplicity and is easier to express as a mathematical function that is then portable into a GIS for making spatial predictions. Similarly, multivariate adaptive regression splines (MARS) have brought new perspectives to test and implement interactions between predictors (e.g. Moisen & Frescino, 2002; Leathwick *et al.*, 2006). These methods are currently being assessed and the interaction factor tested here remains an interesting option to treat most important interactions in a simple way within a GLM and GAM framework.

Furthermore, the interaction factor approach we proposed only represents a solution for statistical interactions between predictors, where the effect of one predictor is modified by the value of another one. The literature on interactions mostly concentrates on biological interactions such as competition, predation or mutualism occurring between several species (e.g. Dambacher *et al.*, 2002). The influence of one species on another species can be included in regression models as an additional predictor (Palomares *et al.*, 1998; Leathwick & Austin, 2001; Leathwick, 2002). Biological interactions with multiple responses can be fitted simultaneously with vgam (Yee & Mackenzie, 2002) and neural networks (e.g. Ozesmi & Ozesmi, 1999).

2.6 CONCLUSIONS

Models and spatial predictions made for 18 forest communities in a region of Switzerland could be significantly improved from current practice. Based on our methodological tests, our main conclusions are:

1. Predictor cross-selection appears to be the best compromise between model stability and performance (i.e. parsimony) among five tested methods.

2. Weighting absences returns models that perform better and are more stable than models fitted with the original sample prevalence due to the impact of low prevalence values on ROC statistics. Standardized prevalence is particularly interesting in comparative studies and when pseudo-absences are used.

3. Limiting zeroes within the range of presences on main predictor gradients changes the set of selected predictors and potentially the shape of their response curves. Limiting zeroes only slightly improves model performance and stability when compared with the baseline models on the same dataset. The advantage of setting limits is to prevent predicting outside the environmental envelope of a species or community. It also accelerates the whole modelling process.

4. Incorporating large spatial trends significantly improves model performance and stability, although better models are obtained by accounting for local spatial autocorrelation.

5. Interaction factors built from a regression tree on residuals of a first environmental model proved to be an efficient way to account for interactions between all predictors, but can lead to some overfitting.

The final choice of model strategy should depend on the nature of available data and on the specific study aims. Statistical evaluation is useful in searching for best modelling practice, however, one should not forget to consider response curve shapes and interpretability, as well as the resulting spatial predictions in the final assessment.

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3 REMOTE SENSING IN DISTRIBUTION MODELS

3.1 INTRODUCTION

Remotely sensed information is widely used in ecological studies. Supervised or unsupervised classification of satellite images using field training data and ancillary environmental variables are used for a variety of purposes including: the mapping of vegetation (e.g. Homer *et al.*, 1997; Tottrup, 2004); forest structure evaluation (e.g. Hudak *et al.*, 2002); forest fires mapping (e.g. Li *et al.*, 2000); the assessment of biodiversity (e.g. Nagendra, 2001); the classification of landuse/landcover (e.g. Hansen *et al.*, 2000) and its monitoring over time (Stehman *et al.*, 2003) or the delineation of animal habitats (Hepinstall & Sader, 1997; Hansen *et al.*, 2001; Osborne *et al.*, 2001; Luoto *et al.*, 2002). On the contrary, only few examples exist in the literature that use spectral data as ancillary predictors directly in spatial distribution models. Between them, Moisen & Frescino (2002) use spectral bands of an AVHRR composite image in order to predict forest characteristics; Parra *et al.* (2004) evaluate the contribution of remotely-sensed normalized difference vegetation index (NDVI) data for modelling the ecological niche of birds; and Zimmermann *et al.* (2007) test the contribution of a Landsat 7 ETM+ image for tree species habitat modelling. By using unclassified spectral information directly in models, one can take advantage of the modelling flexibility offered by GAMs (Hastie & Tibshirani, 1990) for example, where smooth functions with sufficient degrees of freedom can follow the data very closely. This study assesses the contribution of different sources and types of remotely sensed information in base environmental distribution models when added as supplementary predictors.

3.2 METHODS

3.2.1 Data

The study area corresponds to the surface of state of Vaud (Switzerland) covered by the Landsat scene positioned on track 195, frame 28 (see Figure 3.2, map E1). Data were obtained from the phytosociological atlas of State of Vaud (PhytoVD; © SFFN-Vaud) and are a subsample (N=8376) of the data used for modelling in Chapter 2. Only releves situated in the area covered by the Landsat scene positioned on track 195, frame 28 were kept for analysis. Original phytosociological units were recoded in the Swiss habitat classification system (Delarze *et al.*, 1998), leading to 18 forest communities for modelling (see Table 2.1 in Chapter 2 as a reminder).

3.2.2 Predictors

Models were calibrated using the same climatic, geological and topographic predictors already used in Chapter 2. As a reminder these are: mean annual temperature (*mat*); winter precipitations (*wiprec*); mean potential direct solar radiations of the growing season (*mgsr*); site water balance (*swb*); calcareous content of parent material (*CaCO3*); parent material permeability (*permea*); soil potential for forestry (*aptsoil*); slope angle (*slope*); northness (*nness*, cosine transformation of aspect) and distance to river (*distriv*). For a detailed description, please report to Chapter 2.

In addition to these, various remotely sensed predictors were prepared from: i) a single Landsat 7 ETM+ image (track 195, frame 28, date: 25.07.1999) covering almost completely the study area of state of Vaud; ii) the Swiss Landsat (RGB) mosaic created from Landsat scenes covering the entire Swiss territory; and finally iii) the Swiss forest mixture map describing the proportion of broadleaved and coniferous tree mixtures.

For the single Landsat 7 ETM+ image partially covering state of Vaud (source: NPOC- National Point of Contact for Satellite images), spectral values of band 1 to 5 plus band 7 (*b1-b5, b7*) were extracted. A transformation was applied because of the non-normal distribution of the spectral values. We applied a log transformation, multiplied by 100 and then kept the integer part of resulting values. The image was acquired as a 1G level product, i.e. a radiometrically and systematically corrected image. The image was subsequently georeferenced with 40 GCPs (ground control points), leading to a final total error of 0.3168 pixels. Normalized Difference Vegetation Index (NDVI) was also derived from this Landsat scene.

The Swiss Landsat mosaic image (source: NPOC) is composed of 3 georeferenced and radiometrically corrected bands only, i.e band TM03, TM02 and TM01 of original Landsat images, which allows an RGB display. Spectral values of the 3 bands (*mos1-mos3*) were transformed (square root) and multiplied by 100 prior to their use as predictors.

The forest mixture map (WMG25; source: OFS/Geostat) was derived from multitemporal Landsat 5 TM images of Switzerland recorded between 1990 and 1992 (period: mid July – mid September). The map distinguishes 6 categories defined as follows: category 1: non-forest; category 2: coniferous forest (90-100% coniferous trees); category 3: mixed forest dominated by coniferous (50-90% coniferous trees); category 4: mixed forest dominated by broadleaved trees (10-50% coniferous trees); category 5: broadleaved forest (0-10% coniferous trees); category 9: no classification. Category 9 was transformed into "no data" values for our analysis.

3.2.3 Statistical models

Models were fitted with generalized additive models (GAMs; Hastie & Tibshirani, 1990) using the GRASP v.3.1 package for S-Plus (Insightful Corp., Seattle, USA). Responses were forest communities defined as binary variables. Three degrees of freedom were given to each smoothed environmental predictors, and six to remote sensing bands. Absences were weighted in order to have the same total weight as presences (sum of 1s = sum of 0s). Selection was performed with the cross method presented in Chapter 2.

All models and predictions were evaluated: i) statistically, using the area under the curve of a ROC plot on the training dataset, a 5-fold cross-validated ROC (CVROC), the percentage of explained deviance (D^2) and the number of degrees of freedom used (DFU); and ii) visually, looking at response curves and spatial predictions. Wilcoxon-signed rank tests were used to compare validation statistics between pairs of experiments.

3.2.4 Modelling experiments

Several experiments were planned in order to assess the contribution of different remote sensing sources in distribution models (Table 3.1). A first set of experiments (E1-E4) was performed in order to evaluate the contribution of: E1) spectral bands of a single Landsat 7 ETM^+ image covering (partially) the study area; E2) spectral bands of the Swiss Landsat mosaic; E3) categories of a forest map (derived from Landsat images) representing the degree of mixture between coniferous and broadleaved trees; and E4) a normalized difference vegetation index (NDVI) calculated from band 3 and 4 of the single Landsat 7 ETM^+ image used in E1. In order to compare and assess the contribution of remote sensing, a base environmental model was also calibrated on the same dataset (E0). Since many spectral bands of the single Landsat 7 ETM^+ image were not independent, only bands 3 and 4 were used to conduct experiment E1.

A second set of experiments (E6-E9) was performed using the same remote sensing sources but with a modified calibration dataset, i.e. additional random absences were set outside forested areas. For comparison, a new base environmental model was also calibrated on the enlarged dataset (E5).

Table 3.1 Modelling experiments for testing the contribution of remotely sensed predictors.

EXPERIMENTS	
REMOTE SENSING	
E0	Base environmental model
E1	Remotely sensed model: habitat ~ environmental predictors + remote sensing (**single Landsat**)
E2	Remotely sensed model: habitat ~ environmental predictors + remote sensing (**Landsat mosaic**)
E3	Remotely sensed model: habitat ~ environmental predictors + remote sensing (**forest mixture map**)
E4	Remotely sensed model: habitat ~ environmental predictors + remote sensing (**NDVI** from single Landsat)
REMOTE SENSING & RANDOM ZEROES	
E5	Base environmental model calibrated with background zeroes in non forested areas
E6	Remotely sensed model: habitat ~ environmental predictors + remote sensing (**single Landsat**) calibrated with background zeroes in non forested areas
E7	Remotely sensed model: habitat ~ environmental predictors + remote sensing **(Landsat mosaic)** calibrated with background zeroes in non forested areas
E8	Remotely sensed model: habitat ~ environmental predictors + remote sensing (**forest mixture map**) calibrated with background zeroes in non forested areas
E9	Remotely sensed model: habitat ~ environmental predictors + remote sensing (**NDVI** from single Landsat) calibrated with background zeroes in non forested areas

3.3 RESULTS

Including remote sensing information significantly improves the predictive power of models as expressed by D^2 and ROC values (Figure 3.1, Table 3.2). Model fits are higher, but the models are not necessarily more stable as shown by CVROC values.

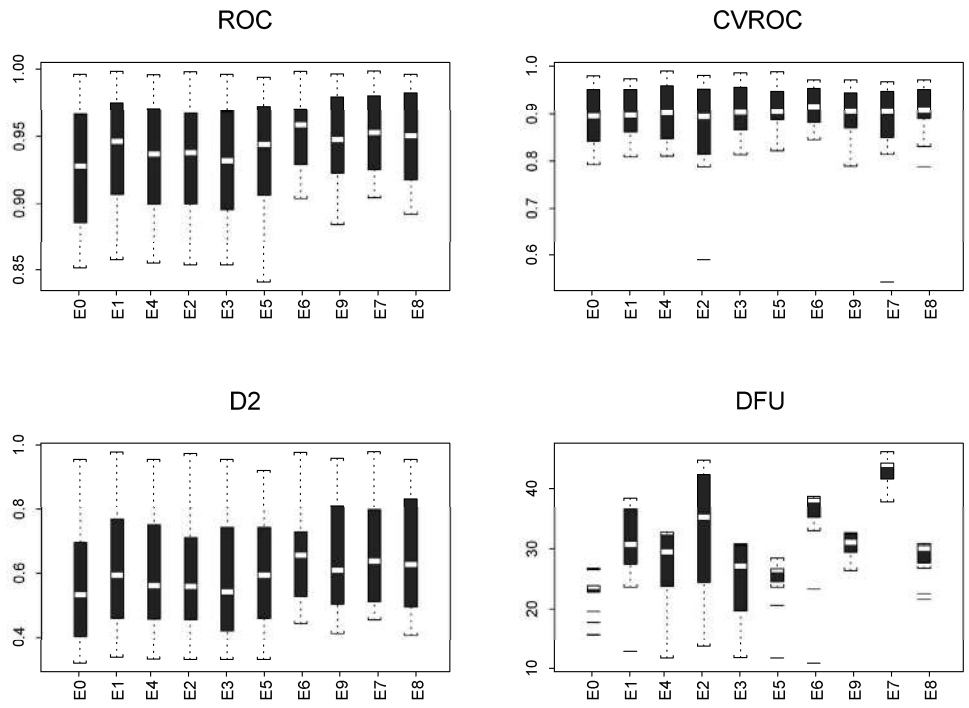

Figure 3.1 ROC, CVROC, explained deviance D2 and total number of degrees of freedom used for two groups of experiments: E1-E4 incorporating remote sensing predictors; E6-9 incorporating remote sensing predictors and using supplementary random absences. (E0, E5: reference experiment without remote sensing; E1, E6: band 3 and 4 of the single Landsat7 ETM+ image covering State of Vaud; E2, E7: bands TM03-TM01 of the Swiss Landsat mosaic image; E3, E8: categories of the Swiss forest mixture map; E4, E9: NDVI index).

Table 3.2 Significance of the Wilcoxon signed rank test based on D2, ROC, CVROC and DFU values of the 18 models of experiments E0-E4 (ns>0.1; *<0.1; **<0.05; ***<0.01).

	D^2				ROC				CVROC				DFU			
	E1	E4	E2	E3	E1	E4	E2	E3	E1	E4	E2	E3	E1	E4	E2	E3
E0	***	***	***	**	***	***	***	***	ns	***	ns	***	***	***	***	**
E1	-	**	ns	**	-	**	**	***	-	ns	**	ns	-	***	ns	***
E4	-	-	ns	ns	-	-	ns	ns	-	-	*	ns	-	-	***	***
E2	-	-	-	*	-	-	-	ns	-	-	-	**	-	-	-	***
E3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

The comparison of the contribution of Landsat 7 ETM^+ bands 3 and 4 (E1) with the contribution of the NDVI (E4), shows that model performance is significantly higher when using single bands, whereas model stability is not significantly different. Models including single bands use more degrees of freedom than models that include NDVI. In 13 out of 18 models, both bands 3 and 4 were retained, whereas in four models (units Y661, Y662, Y633 and Y634, respectively) only band 4 was retained. In one case (unit Y6123), neither band 3 nor band 4 was retained. Moreover, the final model for unit Y6123 did not retain any remotely sensed predictor.

Using bands from the single Landsat image (E1) provides models with significantly better performances and stability than models using bands from the mosaic image or the forest mixture map.

The performance of models integrating bands of the mosaic image (E2) is slightly higher than models based on the mixture map (E3), but models are less stable and use significantly more degrees of freedom (Table 3.2). For four forest units (Y621, Y631, Y634 and Y636) the environmental predictors (= climate, soil or miscellaneous) retained in models for experiments E1-E4 were exactly the same as those retained in the reference experiment E0. Overall, the introduction of remote sensing predictors in models only slightly changes the set of base environmental predictors retained.

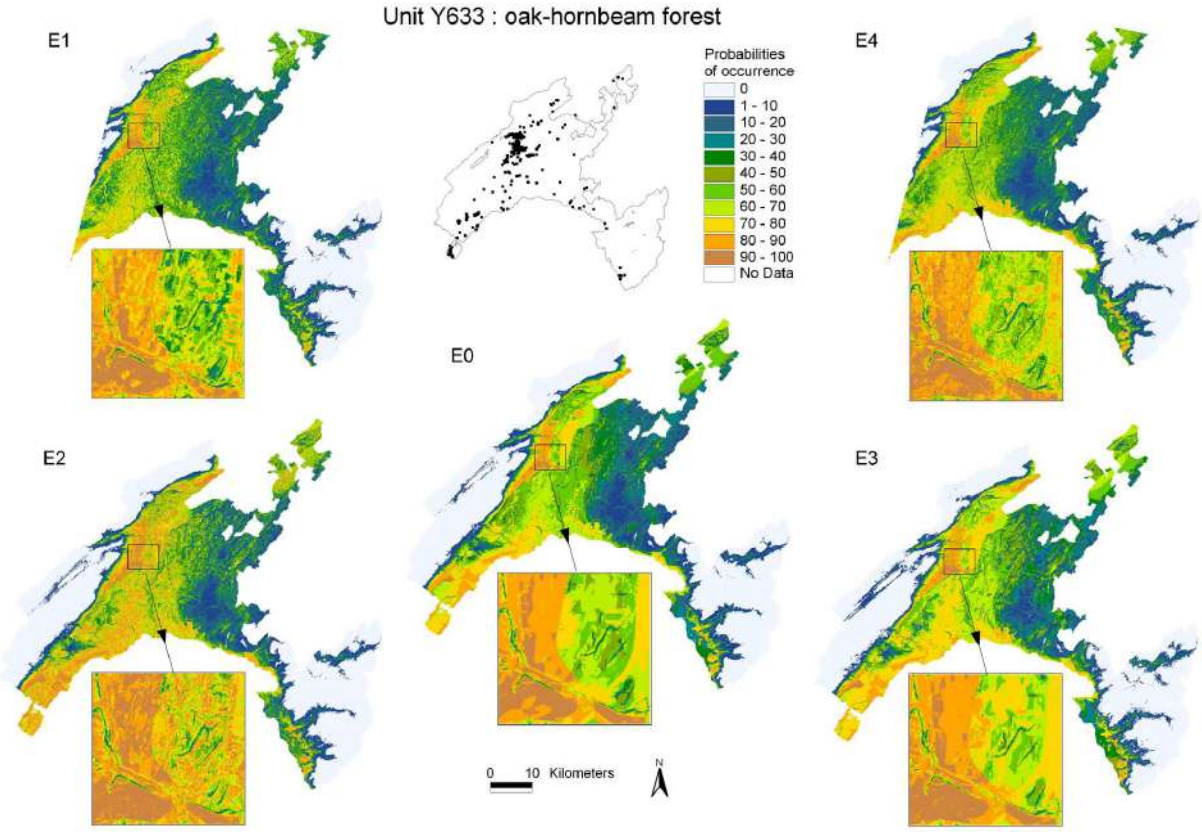

Figure 3.2 Spatial predictions obtained for forest unit Y633, oak-hornbeam forest, from models calibrated in experiment E0 (base environmental model), E1 (single Landsat image), E4 (NDVI), E2 (Landsat mosaic image) and E3 (forest mixture map).

The most important effect of remote sensing is apparent on predictions maps as shown by the simulated distribution of oak-hornbeam forests (unit Y633; Figure 3.2). Bands of both the single Landsat image and the mosaic image generate new spatial details on the distribution maps. On the other hand, the contribution of the forest mixture map generated relatively large uniform patterns that do not provide the same level of spatial details. Since experiment E1 was conducted using a single Landsat image that only covers a part of the study area, spatial predictions are restricted to this limited extent.

Performance of models is significantly improved ($p<0.01$) when complemented with additional absences outside of forested areas (Figure 3.1). This is also true, but to a lesser extent, when comparing the performance of the base environmental model: the addition of supplementary absences

increases performance of the model but the difference between ROC values is only slightly significant and difference between D^2 values is not significant. Models calibrated with background random zeroes are in general more stable and have significantly higher values of CVROC. The only exceptions are models that integrate NDVI. Comparisons between experiments with remote sensing predictors and background zeroes show the same relative behaviour observed without background zeroes.

The main effect of using additional randomly allocated zeroes is made visible on spatial predictions maps (Figure 3.3, unit Y633). Potentially suitable zones follow precisely the forest edges as identified from the satellite without additional landcover information.

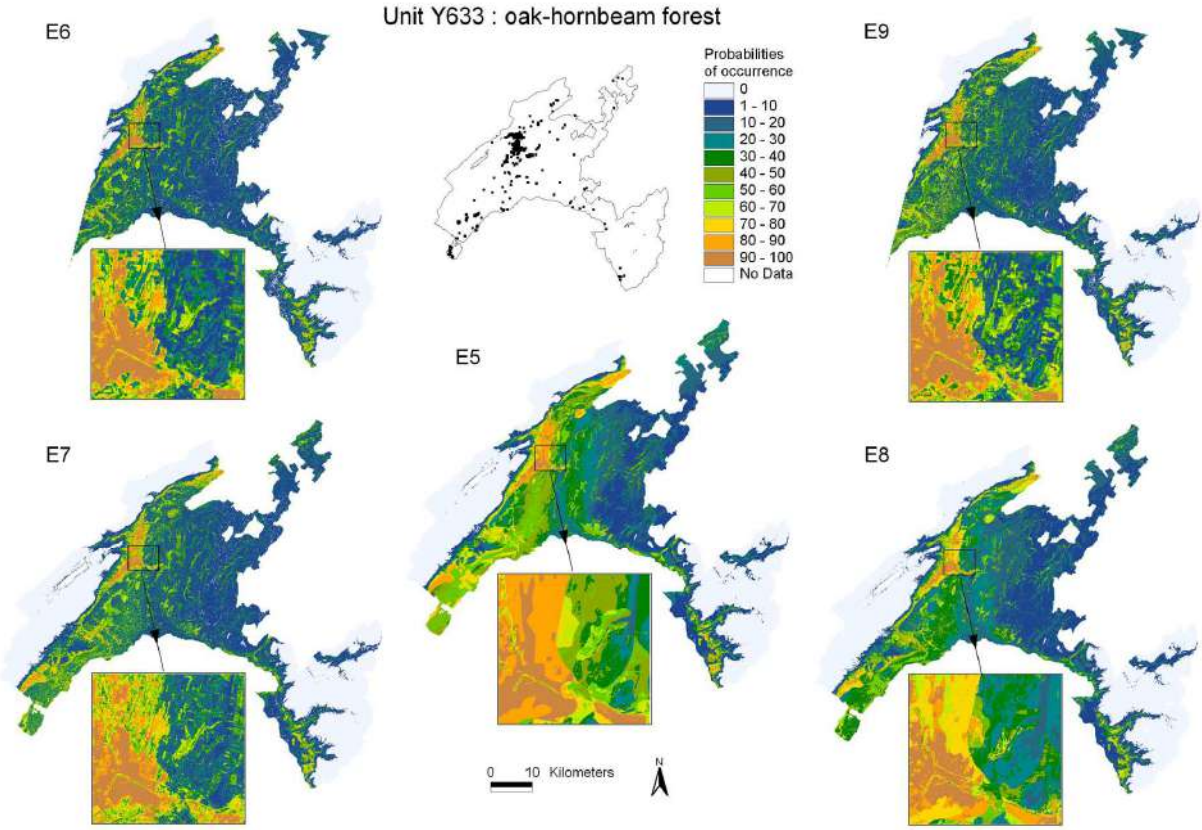

Figure 3.3 Spatial predictions obtained for forest unit Y633, oak-hornbeam forest, from models calibrated with remote sensing predictors and background zeroes: E5 (base environmental model), E6 (single Landsat image), E9 (NDVI), E7 (Landsat mosaic image) and E8 (forest mixture map).

3.4 DISCUSSION

Integrating remote sensing information as predictor allows moving from potential distribution that are independent of existing land cover to spatial predictions that are much closer to landscape reality. Ideally we would like to distinguish forest types but in practice this remains very difficult. This is due to intrinsic problems of remote sensing information (e.g. noise and shading) and small difference in

the reflectance of forest types. Much better results are usually obtained when remote sensing is used to segregate totally different types of land cover, as for instance forest and non-forest cover. Remote sensing can thus be considered as a potential surrogate for landuse or landcover predictors in models. Indeed, it is easier to get updated versions of remote sensing data from satellites than survey every region of the globe regularly.

Examples of studies using raw remote sensing data (i.e. spectral bands) directly as predictor in the model are rare. Raw remote sensing information has the advantage of carrying the full spectral information that flexible models such as GAMs are able to use to build predictions close to the data. This approach can avoid long and fastidious image analysis and the possible loss of information linked to classification prior to prediction. Another advantage of using unclassified spectral information in GAMs is that interactions between spectral bands, which are often necessary for better discriminations, could also potentially be included (e.g. using a ratio of two bands directly as predictor). However, as raw bands are often correlated, some authors suggested transforming this RGB (red-green-blue) information in hue, saturation and intensity scale (Chibani & Houacine, 2002), which corresponds to a change of reference system leading to uncorrelated variables.

Our approach here is based on the "predict first, classify later" paradigm that aims at classifying maps at the very end of the mapping process in order to keep as long as possible a maximum of information from all available predictors (Ferrier *et al.*, 2002; Overton *et al.*, 2002; Ferrier & Guisan,2006). This is why we try to predict each forest type independently with the full spectrum of remote sensing information. The two approaches can be compared with relative performances of experiments with Landsat bands, mosaic bands and NDVI on the one hand, and forest mixture on the other hand. The formers are statistically better and result in spatial predictions that incorporate much more details of true landcover, whereas the latter represents a classified remote sensing product.

The choice of one method is a trade-off between showing true details observed by satellites sensors and removing noises produced by heterogeneity in reflectance measures. In this sense, NDVI, as other vegetation indices (e.g. Enhanced Vegetation Index (EVI); Soil Adjusted Vegetation Index (SAVI)) can be considered as an interesting compromise, as it uses less degrees of freedom than raw bands, but can still encompass details from true landcover. As NDVI can be considered a non-linear interaction term based on the difference between two bands (TM3 and TM4), its results might hold better when predicted across the landscape, and when extrapolating to other regions or time windows.

3.5 REFERENCES

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4 PREDICTING THE DISTRIBUTION OF GRASSLAND COMMUNITIES ACROSS SWITZERLAND: HOW MUCH DATA IS ENOUGH DATA?

Ramona Maggini[1*,2], Anthony Lehmann[2,3], and Antoine Guisan[1]

[*] Address for correspondence: Ramona.Maggini@unil.ch

[1] Department of Ecology & Evolution (DEE), Biophore Building, University of Lausanne, CH-1015 Lausanne, Switzerland

[2] Research Group on Climatic Change and Climate Impacts, Institute for Environmental Sciences, University of Geneva, Battelle D, CH-1227 Carouge, Switzerland

[3] UNEP/DEWA/GRID-Europe, International Environment House, CH-1219 Châtelaine, Switzerland

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4.1 ABSTRACT

The importance of predictive distribution modelling has been largely recognized in recent years and is now current practice in different fields such as ecology, conservation biology, biogeography and many others. All distributional studies require data to feed the models and stratifying sampling can optimize sampling size. In the present study we use grassland data from Switzerland to assess the combined effects of sample size and data stratification on the accuracy of models, response curve shapes and spatial predictions. More specifically, we addressed the following questions: i) how many occurrences are necessary to perform accurate modelling; ii) what is the effect of geographical and environmental data stratification on resulting models; iii) how are response curve shapes and spatial predictions influenced by sampling size and stratification.

Ten grassland communities were selected from a newly compiled data set of 22,000 observations. A spatially uncorrelated data set was first extracted, and then split in a training (7,000 records) and test data set (3,811 records). Models were calibrated using data stratified by different stratification schemes (no stratification, geographic or environmental stratification) and with an increasing number of occurrences (from 25 to 250). Models were evaluated using resubstitution, cross-validation and independent validation methods and according to the area under the curves of the ROC statistics and a Spearman correlation coefficient. The outputs of the models were also evaluated by analysing the resulting response curves and spatial predictions.

The results show that an increasing number of presences (Np) in the training sample improves model accuracy with a threshold value around 75 presences when the data are highly stratified, 100 for broadly stratified data and 150 otherwise. The stratification (either geographic or environmental) only improves model accuracy at low sample sizes. Stratification has a greater effect on the standard deviation of the performance statistics (ROC and COR) than on their means. Environmental stratification performs better than the geographic one and both perform better than full random sampling.

In conclusion, as stratification and Np can significantly modify model selection, response curve shapes, resulting spatial predictions and their uncertainty, a new validation procedure should be developed that encompass not only statistical but also ecological significance and spatial accuracy of a model.

Keywords: species distribution modelling, number of occurrences, sample size, prevalence, geographical stratification, environmental stratification

4.2 INTRODUCTION

The importance of predictive distribution modelling has been largely recognized in recent years and is now current practice in different fields as ecology, conservation biology, biogeography and many others (e.g. Guisan & Zimmermann 2000, Guisan *et al.* 2006b, Ferrier 2002, Ferrier *et al.* 2002a, Ferrier *et al.* 2002b, Overton *et al.* 2002, Araújo & Guisan 2006). Models and the derived spatial predictions of species distribution are today used for a variety of applications: the assessment of rare (e.g. Guisan *et al.* 2006a) or invasive species (e.g. Thuiller *et al.* 2005b, Thuiller *et al.* 2006b, Broennimann *et al.* 2007, Richardson & Thuiller 2007), the prediction of range shift as a consequence of climate change (e.g. Thuiller 2004, Araújo *et al.* 2005, Thuiller *et al.* 2005a, Thuiller *et al.* 2006a), the optimized selection of reserve networks (e.g. Araújo & Williams 2000, Ferrier 2002, Araújo *et al.* 2004). Distribution modelling is applied in all sorts of ecosystems, from lake shores (e.g. Lehmann 1998) to ocean (e.g. Leathwick *et al.* 2006a), from river beds (e.g. Leathwick *et al.* 2005, Leathwick *et al.* 2006b) to wetlands (e.g. Bio *et al.* 1998), from grasslands (e.g. Zimmermann & Kienast 1999, Maggini *et al.* 2002, Dirnbock & Dullinger 2004) to forests (e.g. Edwards *et al.* 2006, Maggini *et al.* 2006, Zimmermann *et al.* 2007). While this discipline has clearly entered an application phase, efforts are still directed towards models improvement and the identification of the factors affecting model accuracy. Previous studies have highlighted the importance of data sample size (e.g. Stockwell & Peterson 2002), sample prevalence (e.g. Manel *et al.* 2001, McPherson *et al.* 2004), grain size (e.g. Guisan *et al.* 2007a), model selection algorithm (e.g. Burnham & Anderson 2004, Maggini *et al.* 2006) and the modelling techniques used (Elith *et al.* 2006, Leathwick *et al.* 2006b, Pearson *et al.* 2006, Guisan *et al.* 2007b). All these studies require data to feed the models. Such data can be costly to obtain from own sampling campaigns, thus existing data – such as found in natural history collections (NHC, Graham *et al.* 2004) - constitute a valuable source for fitting these models. However, these databases are often entailed with bias and errors, and one may want to resample subsets of the data to attempt removing or minimizing bias, using some sort of stratified resampling approaches.

In the present study we use observational data to assess the combined effects of sample size and data stratification on fitting predictive distribution models, using open habitats as a case study. In particular, the aim of the study is to model grassland communities across Switzerland and to test the effect of i) the number of presences in the sample (Np) and ii) different methods of data stratification, on the accuracy of models, response curve shapes and spatial predictions. More specifically, we addressed the following questions: i) how many occurrences are necessary to perform accurate modelling; ii) what is the effect of geographical and environmental data stratification on resulting models; iii) how are response curve shapes and spatial predictions influenced by sampling size and stratification.

4.3 MATERIALS AND METHODS

4.3.1 Data description

4.3.1.1 Study region

The study was conducted on the Swiss territory. Switzerland is situated in the centre of Western Europe, in Euro-Siberian phytobiogeographic region, medio-European domain (Takhtajan 1986 see Cox 2001). Its climate is mostly temperate, with Atlantic and continental influences and highly variable conditions across the country. The Swiss territory, which covers an area of 41,293 km^2, is classically subdivided in six biogeographic regions: the Jura Mountains, the flat area of the Plateau, and the Alps that are divided in the Northern Prealps, Western Valais, Eastern Grison and Southern Ticino regions (Gonseth *et al.*, 2001). Jura Mountains are a limestone range of mountains stretching from Lake Geneva to the Rhine. It occupies 12% of the surface and is characterized by an average altitude of 811m, a mean annual temperature of 7 °C, and a mean sum of annual precipitation of 1345 mm. The densely populated region of the Plateau covers about 30% of the country and is characterized by a mean altitude of 544 m, a mean annual precipitation of 1135 mm and a temperature of 8.4 °C. The Alps occupy nearly two thirds of the Swiss territory and have temperature and precipitation that average in the Prealps to 4.3°C and 1653 mm, in Valais to 1.1°C and 1518 mm, in Grison to 0.9°C and 1249 mm and in Ticino to 5°C and 1735 mm.

4.3.1.2 Grasslands

Data on grasslands distribution were obtained from our own sampling (Landspot project) complemented by data from other sources: Modiplant project (University of Lausanne); DGS project for the cartography and evaluation of dry grasslands of national importance (Swiss Federal Office for the Environment, FOEN); the grassland data base of Dr N.E. Zimmermann (Swiss Federal Institute for Forest, Snow and Landscape Research, WSL). The additional vegetation data sources were employing different classification systems. In order to homogenize them, they were thus all translated into the same classification system used for the Landspot project, i.e. the Swiss habitat typology (Delarze *et al.* 1998).

The Landspot project was the original source of data for this study. Data were collected according to a random stratified design across the entire Swiss territory. The potential distribution of the target grassland communities was first modelled with expert models based on the information provided by

the typology of the Swiss habitats (Delarze *et al.*, 1998) and subsequently translated within a GIS using the numeric layers corresponding to the main ecological drivers (R. Maggini, A. Lehmann, R. Delarze & Y. Gonseth, unpublished, Annex 1). Sampling units were then chosen: i) randomly within the population of sites that had at least a probability of 50% of hosting the target community; and ii) proportionally from the 50 environmental strata defined by the Swiss environmental domains (SED, Maggini *et al.* 2004). Sampled units in the field were plots of 30 x 30 m. For each plot a non-exhaustive relevé was performed and a phytosociological unit or mixture of units was assigned to the relevé using a decision-support system developed within the framework of the project and integrated in the Landspot database. The decision-support system is based on a histogram representing the total score obtained for each possible phytosociological unit for the site. Points are assigned to each unit according to the number of species that belong to it, weighted by the relative importance of the species in the unit (characteristic versus accompanying species). Phytosociological units were named according to the Swiss habitat typology (Delarze *et al.* 1998).

Modiplant project mainly focused on grasslands in the Prealps region of Canton Vaud (Guisan, 2005). Data were sampled according to a random stratified sampling based on the altitudinal gradient, terrain slope and aspect. Exhaustive vegetation relevés were performed according to the Braun-Blanquet approach (species are listed with the corresponding ordinal abundance; see Guisan & Harrell 2000). These relevés were manually classified into a main and supplementary vegetation units using the decision-support system integrated in the Landspot database.

The "Dry Grassland in Switzerland" (DGS) is a project of the Swiss Federal Office for the Environment that aims at inventorying and mapping the most valuable dry grasslands and pastures of the country. We used the database in its state at the beginning of 2005. Sites are first identified trough a differentiated mapping of the vegetation using aerial photographs. In the field, an exhaustive relevé was performed in a homogeneous area (circular plot of 3 m radius) of the grassland polygon of each site. Grasslands were then classified according to the DGS modular vegetation key (Eggenberg *et al.* 2001). The original DGS classification system could be translated into the Swiss typology system thanks to the correspondences established by Dr S. Eggenberg from the Atelier für Naturschutz und Umweltfragen (UNA, Bern).

The grassland database assembled by Dr N.E. Zimmermann at WSL originated from different sources and encompasses mainly alpine grasslands across the Alps (Zimmermann 1996). Original vegetation types were defined according to Theurillat (1995). A translation key was established between the original classification system and the Swiss typology.

Finally, the merging of the four data sets led to a unique data set of 22'720 records. In order to avoid spatial autocorrelation, plots separated by less than 200 m were not considered for modelling. The threshold was fixed according to a semi-variogram analysis (Figure 4.1) performed within S-Plus ver. 6.2 (Insightful Corp., Seattle, WA, USA). The resulting spatially-independent data set counted 10,811 records, from which 7,000 were used for training and 3,811 were kept apart for the independent model evaluation. Ten grassland communities having sufficient positive occurrences in the training dataset (minimum of 25 presences) were chosen for modelling (Table 4.1).

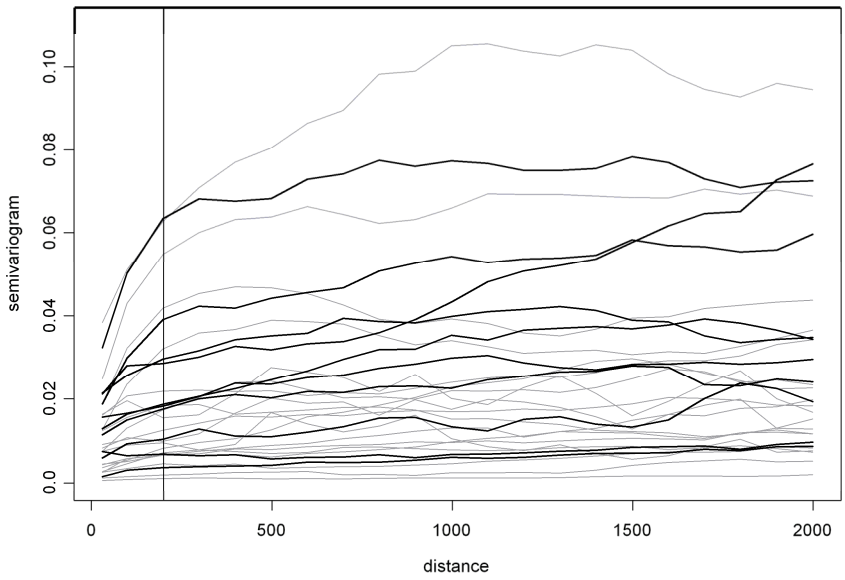

Figure 4.1 Semi-variogram performed on the merged data set of grasslands communities. The vertical line corresponds to a distance of 200 m. Dark lines represent the 10 grassland communities selected for modelling (list in Table 4.1).

Table 4.1 Communities selected for modelling, together with their code and phytosociological name as defined in Delarze et al. (1998) and the corresponding units in the classification of the European CORINE biotopes (Devillers et al., 1991). Np = number of presences in the training data set (7,000 records). Prev = prevalence in the training data set.

GRASSLAND TYPE	GRASSLAND UNIT	CODE	CORINE BIOTOPES	PHYTOSOCIOLOGICAL UNIT	Np	Prev
Steppic and dry thermophile grasslands	Steppic grassland	4.2.1.1	*34.313* *34.314*	*Stipo-Poion*	280	0.040
	Middle-European semi-dry grassland	4.2.4	*34.322*	*Mesobromion*	2555	0.365
Subalpine and alpine dry grasslands and pastures	Blue Moorgrass dry calcareous grassland	4.3.1	*36.431*	*Seslerion*	539	0.077
	Fresh calcareous grassland	4.3.3	*36.412*	*Caricion ferruginae*	361	0.052
	Dry acid pasture	4.3.5	*36.31*	*Nardion*	834	0.119
	Rocky acid grassland	4.3.6	*36.33*	*Festucion variae*	263	0.038
	Acid grassland of the higher alpine belt	4.3.7	*36.34*	*Caricion curvulae*	274	0.039
Fertilized grasslands	Lowland hay meadow	4.5.1	*38.22*	*Arrhenatherion*	1167	0.167
	Lowland and montane pasture	4.5.3	*38.1*	*Cynosurion*	456	0.065
	Subalpine and alpine rich pasture	4.5.4	*36.52*	*Poion alpinae*	388	0.055

4.3.2 Modelling

4.3.2.1 Models

Models were fitted with GAMs (Hastie & Tibshirani 1990) using the GRASP ver.3.2 package (Generalized Regression Analysis and Spatial Predictions; Lehmann *et al.* 2002) within S-Plus v.6.2 (Insightful Corp., Seattle, WA, USA). A binomial probability distribution and a logit link function were used for the response. Models were selected using BRUTO, a backfitting selection procedure that identifies significant predictors and the optimal degree of smoothing for each of them (Hastie & Tibshirani 1996, see also Maggini *et al.* 2006).

4.3.2.2 Experimental design

From the source training data set, several sub-samples were created using different stratification schemes (environmental, geographical, no stratification) and with an increasing number of presences.

The environmental stratification was performed using Swiss environmental domains (SED; Maggini *et al.*, 2004). SED results from an environmental classification of Switzerland that groups together areas characterized by the same climatic, topographic and geological characteristics. The classification is hierarchical and the 209 domains defined for the country can be aggregated and displayed at different levels. Stratification was performed with 10 and 26 domains (ED10, ED26; Figure 4.2) in order to be comparable with the 10 biogeographic regions and 26 cantons of the geographical stratification (description below). Points were chosen randomly within each domain.

Geographical stratification was performed using the 10 biogeographical regions (Gonseth *et al.* 2001) defined for Switzerland according to the global distribution of its flora and fauna (GEO10) and the 26 political states or cantons (GEO26; Figure 4.2). Points were also chosen randomly within each geographical unit.

In order to be able to asses the effect of stratification, reference sub-samples were created by choosing points completely randomly (NO, meaning “no stratification”).

According to the different types of stratification (NO, GEO10, GEO26, ED10, ED26), 8 sub-samples were generated with an increasing number of positive observations (Np): 25, 50, 75, 100, 125, 150, 200 and 250 occurrences respectively.

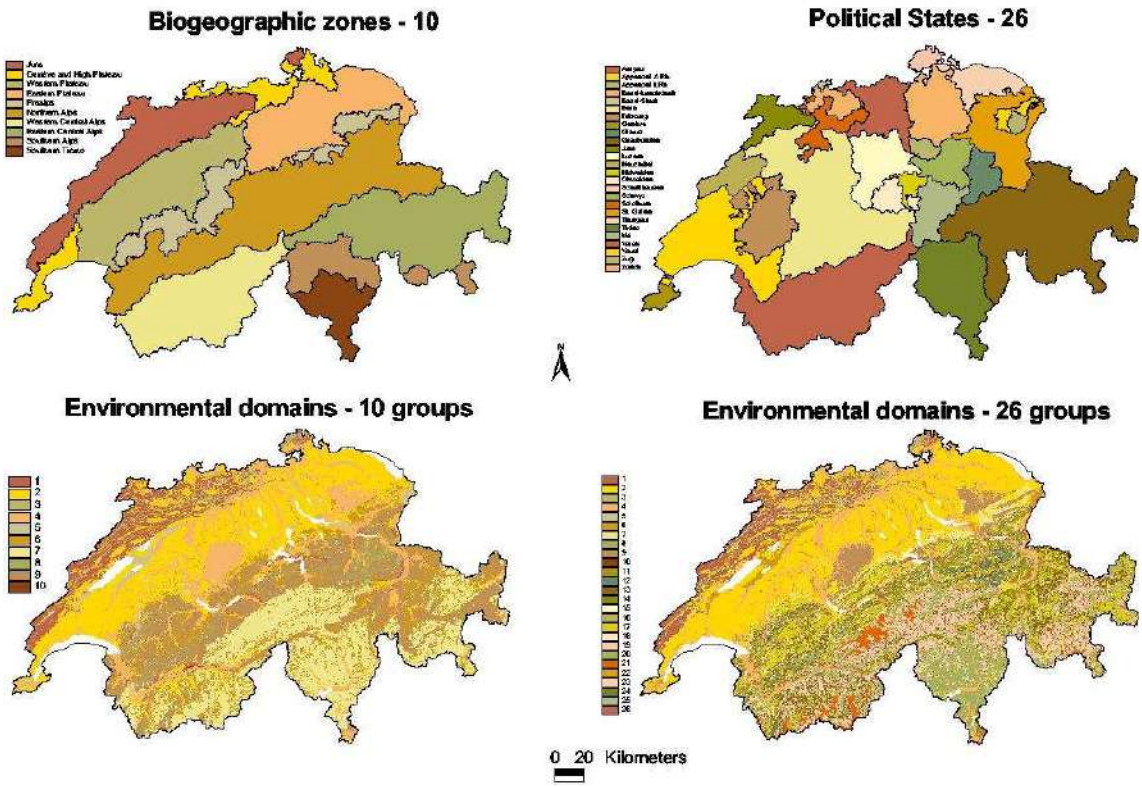

Figure 4.2 Swiss territory classified according to a) biogeographic regions; b) political states (cantons); c) environmental domains, 10 groups; d) environmental domains, 26 groups.

The selection (with replacement) of points in the strata was automated and performed by a script with a loop visiting subsequently each stratum and selecting randomly a point (presence or absence) in each stratum. The loop stops when the desired total number of presences is reached, which in turn results in a varying number of absences and therefore a varying prevalence for each training sub-sample. However, the number of absences increases as a function of the specialisation/localisation of the community in one or few strata and this somehow reflects its original prevalence. The selection script was run 10 times, thus generating 10 replicates for each combination of stratification x Np x community.

4.3.2.3 Predictors

We tested different categories of predictors, namely climatic, geological and topographic predictors. Climatic predictors were obtained from the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) and have already been extensively described in Maggini *et al.* (2006). They include mean annual temperature (*mat*); winter precipitation (*wiprec*), i.e. precipitation occurring during winter months (December to February); mean potential direct solar radiation (*mgsr*) during growing season (March to October); and site water balance (*swb*) integrating the difference between monthly precipitation and potential evapotranspiration over a soil bucket for a full water year.

The geological predictors used were: calcareous content of parent material (*CaCO3*); parent material permeability (*permea*), and soil potential for agriculture (*aptsoil*). Geological information is used in replacement of soil information. The digital layer for *CaCO3* and *permea* were derived from the

geotechnical map of Switzerland (OFS 2003) using an expert classification (J. Ayer, University of Neuchâtel). A semi-quantitative variable representing the proportion of calcareous content within each type of parent material (class 1 to 4 from low to high content) as well as its permeability (class 1 to 3 from low to high permeability) were created. The layer for soil potential for agriculture (class 1 = low production to class 6 = high production) was derived from the digital soil suitability map of Switzerland (OFS 2003).

As topographic predictors, we used slope angle and a topographic wetness index. Slope (*slope*) was derived from the digital elevation model at 25 m resolution. The topographic wetness index (*twi*), obtained from the Federal Institute WSL, is calculated as the natural logarithm of A/SLP, where A is the "upslope contributing area" for a given pixel, and SLP is the slope of the pixel (Beven *et al.* 1984). It is thus a measure of wetness that considers the area that drains into a pixel, weighted by its slope: the steeper the pixel is, the more the incoming water will run off. High values for the index will occur in relatively flat and wet areas, whereas low values will occur in dry and steep areas. A detailed list of all predictors used for modelling is provided in Table 4.2.

Table 4.2 Predictors used in the modelling experiments. WSL, Swiss Federal Institute for Forest, Snow and Landscape Research; OFS, Swiss Federal Statistical Office; CSCF, Swiss Center for Faunal Cartography; SWISSTOPO, Swiss Federal Office of Topography.

NAME	DEFINITION	RANGE within study area	SOURCE
CLIMATE			
MAT	Mean annual temperature: average of mean monthly temperatures	-1051 - 1222 (C°)*100	WSL
MGSR	Mean growing season solar radiation: average of mean monthly solar radiation over growing season (March-October)	2507 - 27394 (KJ/m2/day)	WSL
WIPREC	Mean winter precipitation: average of mean monthly rainfalls over winter time (December -February)	907 - 7255 (mm)*10	WSL
SWB	Site water balance: estimation of water amount available for plants during a year obtained by integrating monthly precipitation and potential evapotranspiration over time, and considering soil storage capacity	- 7514 - 1500 1/10(mm/year)	WSL
GEOLOGY			
CaCO3	Calcareous content of parent material derived by expert knowledge (J.Ayer, University of Neuchâtel) from the Swiss geotechnical map (OFS 2003)	4 classes	OFS transformed by CSCF
PERMEA	Rock permeability derived by expert knowledge (J.Ayer, University of Neuchâtel) from the Swiss geotechnical map (OFS 2003)	3 classes	OFS transformed by CSCF
APTSOIL	Soil potential for agriculture extracted from the Swiss soil suitability map (OFS 2003)	4 classes	OFS
TOPOGRAPHY			
SLOPE	Slope angle derived from the DEM at 25m resolution	0 to 8014 (°)*100	SWISSTOPO (DEM)
TWI	Topographic wetness index	- 817 to 1379 unit less	WSL

The numerical layers corresponding to each predictor were stored in a geographical information system (ArcView ver. 3.3; ESRI, Redlands, CA, USA) in order to build spatial predictions. All layers have a resolution of 25 m.

The contribution of each predictor in model was calculated as a percentage of the total model contributions as defined in GRASP. For each predictor, model contribution is defined by the possible range of variation on the linear predictor scale when the other ones are kept constant.

4.3.2.4 Validation

Models based on presence absence data were validated both on the *training* data set (resubstituition and cross-validation) and using an independent *test* data set (independent validation). As validation statistics we used the Area Under the Curve of a Receiver Operating Characteristic plot (ROC; Fielding & Bell 1997). The same statistics was also evaluated by cross-validation (5-fold) and named cvROC. Finally, the models were evaluated on the independent test data set (T.ROC). A supplementary validation was provided by the calculation of a coefficient of correlation between observed and predicted values for the training data set (COR; Elith *et al.*, 2006), the cross-validated training data set (cvCOR) and the independent test data set (T.COR).

The independent data set counted a total of 3,811 spatially uncorrelated points not used for calibrating the models. The points used for the validation were different for each community, but remained constant for a given community, throughout the different treatments. The prevalence for each community in the test data set was set to 0.5 by selecting a number of random absences equal to the number of presences found in the test data set.

For each grassland community, the validation statistics were summarized by calculating the mean and standard deviation ROC, cvROC and T.ROC over 10 replicates. Variations in the mean and standard deviation of T.ROC values were then analysed as a function of the stratifying method and the number of presences (Np) using generalized linear mixed models (GLMMs; Breslow & Clayton 1993). T.ROC was chosen as the most reliable evaluation method for the GLMM analyses as it presents the advantage of being calculated on a fixed selection of points with an equal number of presences and absences for each community (prevalence set to 0.5). Prior to that, evaluation statistics (spanning between 0.5 and 1) were stretched between 0 and 1 (as in e.g. Engler *et al.* 2004). The new values (T.ROC*) were then set as response variables and a quasi-binomial distribution was assumed for them. In order to linearize the relationship between the evaluation statistics and Np, a logarithmic transformation was applied to the latter. Log(Np) within stratifying methods was set as a fixed effect. The grassland communities within the logarithm of Np were set as random effects. The logarithm of Np was also added as random effect because the slope of the line from Np=25 to Np=250 could not be considered constant between communities.

Analyses were performed in S-Plus ver. 6.2 (Insightful Corp., Seattle, WA, USA) using the function *glmmPQL* of the MASS library (Venables & Ripley 2002). This function fit a GLMM using a penalized quasi-likelihood algorithm.

4.3.3 Spatial predictions

Spatial predictions were built in ArcView ver. 3.3 (ESRI, Redlands, CA, USA). Models were exported from S-Plus as lookup tables (Lehmann *et al.* 2002) and then interpreted in the geographic information system by an Avenue script available within the GRASP package. Maps of spatial predictions presented in the results section give the mean probability of occurrence calculated over ten replicates (Figure 4.9) and its standard deviation Figure 4.10).

4.4 RESULTS

Model discrimination ability can be assessed through its performance (ROC), stability (cvROC) and generality (T.ROC). Altogether (all stratification types, Np and communities confused) these validation statistics showed poor (0.5-0.7) to very good (0.9-1) discrimination according to the classification of Swets (1988). Nevertheless, up to 97% of ROC values and 90% of cvROC and T.ROC values were between 0.8 and 1, which is an indication of good to high discrimination ability. Concerning calibration ability, values for the correlation coefficients varied altogether between 0.09 and 1. Nonetheless, 67% of COR, 44% of cvCOR and 71% of T.COR values were higher than 0.5.

4.4.1 The effect of the number of positive observations (Np)

The number of positive observations (Np) in the data set used for calibration had an effect on the discrimination ability of the resulting models, as shown in the simple case of non-stratified data (NO; Figure 4.3). Indeed, values for cross-validation and in particular independent validation were increasing as a function of the number of presences (Np) in the calibration data set. However, for the majority of the modelled communities, there seemed to be a threshold around 100 occurrences above which the improvement was much less important and reached a plateau (Figure 4.3). Exceptions were observed for few grassland communities for which model stability (cvROC) was higher for models calibrated with a low Np value than for model calibrated with a high Np value. Resubstituition statistics failed to show the effect of increasing Np.

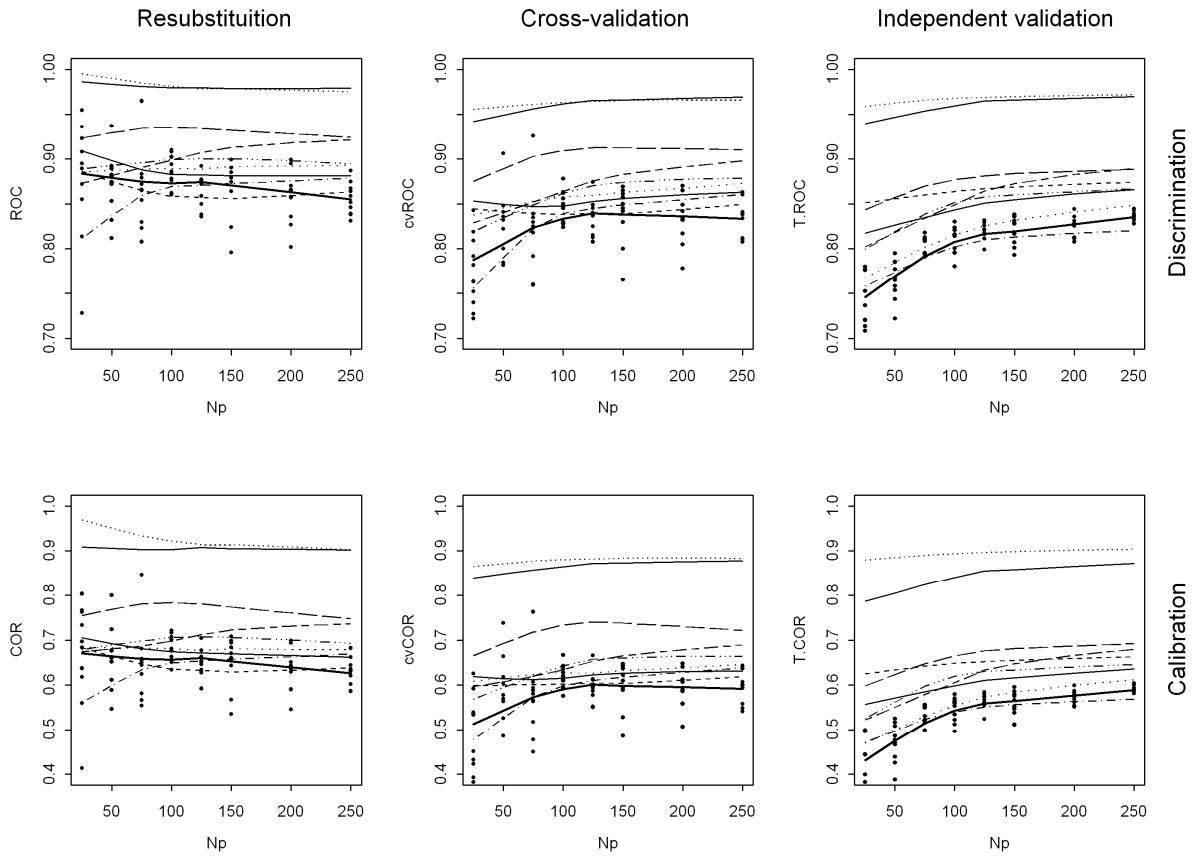

Figure 4.3 Discrimination ability of models assessed through their performance (ROC), stability (cvROC) and generality (T.ROC). Calibration of models assessed through the correlation coefficients calculated between the observed and the predicted values within the framework of direct, cross- and independent validation (COR, cvCOR, T.COR). Lines represent the mean values for the ten replicates for each grassland community. As an example, the ten replicates of the community Y 4.2.4 are shown for each Np value and are graphically represented by black dots. (mean represented by the black continuous line).

As expected, values decreased on average from resubstituition to cross-validation to independent validation. As an indication, Table 4.3 shows the mean values for the simple case of non-stratified data (NO) as a function of the number of presences in the training data set (Np). Values were averaged over the ten grassland communities and the ten replicates per community. Similar trends were also observed for models calibrated with the stratified datasets.

Table 4.3 Mean ROC, cvROC, T.ROC (averaged over the ten grassland communities and the ten replicates per community) as a function of the number of non stratified presences (Np) in the calibration data set.

	Np							
	25	**50**	**75**	**100**	**125**	**150**	**200**	**250**
ROC	0.900	0.903	0.900	0.908	0.906	0.907	0.907	0.906
cvROC	0.838	0.863	0.869	0.882	0.882	0.884	0.888	0.889
T.ROC	0.805	0.842	0.857	0.864	0.871	0.875	0.879	0.883

Correlation coefficients between observed and predicted values for points in the training, cross-validation and test data sets globally followed the same trend as the discrimination statistics. As shown by Table 4.4 for the simple case of non-stratified data (NO), values decreased from resubstituition to cross-validation to independent validation and increased as a function of Np. Values were averaged over the ten grassland communities and the ten replicates. The same trend was observed for models calibrated with the stratified datasets.

Table 4.4 Mean COR, cvCOR, T.COR (averaged over the ten grassland communities and the ten replicates per community) as a function of the number of non stratified presences in the calibration data set (Np).

	Np							
	25	**50**	**75**	**100**	**125**	**150**	**200**	**250**
COR	0.729	0.731	0.722	0.736	0.730	0.730	0.728	0.725
cvCOR	0.621	0.660	0.666	0.689	0.686	0.690	0.694	0.695
T.COR	0.549	0.610	0.636	0.652	0.664	0.672	0.678	0.685

4.4.2 The effect of data stratification

The evaluation of model discrimination on an independent dataset (T.ROC) was considered as most reliable and was therefore chosen to analyse the effect of stratification. .

Figure 4.4 shows the variation in mean T.ROC values (averaged over the 10 replicates) for each grassland community as a function of the number of presences (Np) in the training data set and according to the different stratification types: geographical (GEO10, GEO26), environmental (ED10, ED26), none (NO). Within the figure, graphical windows were sorted from left to right according to the increasing overall (over the 10 communities) mean T.ROC values, which resulted in the following order: GEO26, NO, GEO10, ED10 and ED26. Within each stratification type and for the majority of the communities, T.ROC values increased as a function of Np up to a plateau after which no further improvement was observed.

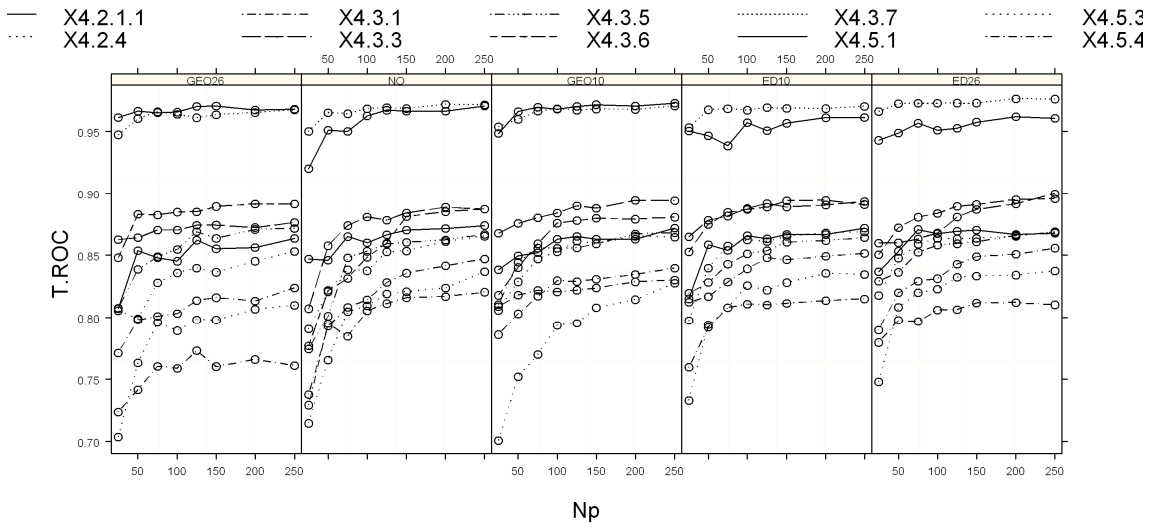

Figure 4.4 T.ROC validation statistic calculated by applying on an independent test data set the models calibrated with an increasing number of presences (Np) selected according to different types of stratification: geographical stratification (GEO10 and GEO26), environmental stratification (ED10 and ED26) and random choice (NO stratification)

Figure 4.5 shows how the error associated to the mean T.ROC values (standard deviation based on the 10 replicates) varied with Np and stratification type. Graphical windows were sorted from left (lower value) to right (higher value) according to the mean overall value of the standard deviations which leaded to the following order: ED26, GEO10, ED10, GEO26 and NO. Globally, standard deviations on T.ROC values were relatively higher at low Np values.

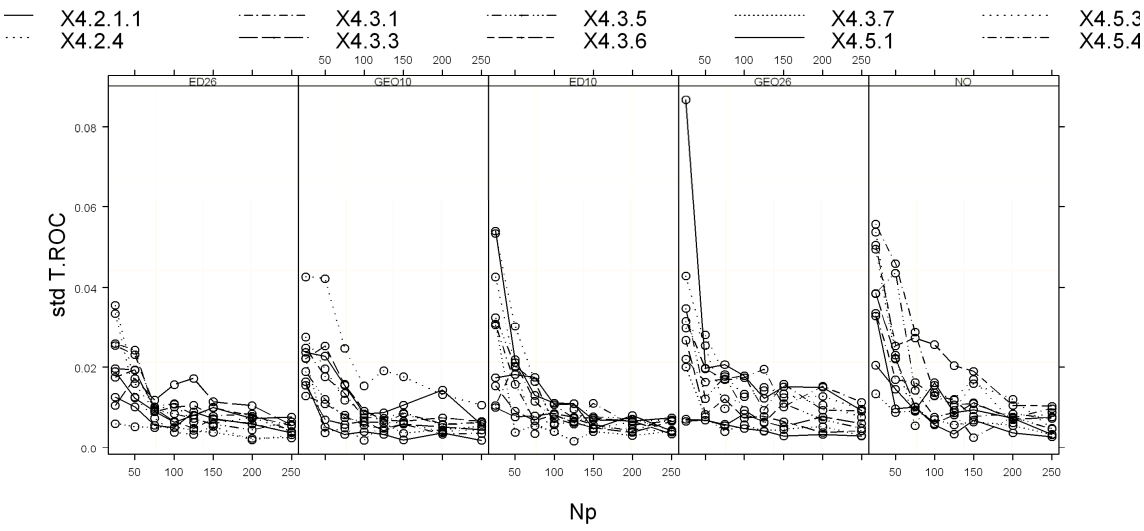

Figure 4.5 Standard deviations associated to the T.ROC mean values differ according to the type of stratification and the number of presences.

Differences in T.ROC values for the different stratification methods were confirmed by the results of the generalized linear mixed models (GLMM). Indeed, results identified a significant effect of the stratification type and of Np on T.ROC means and relative standard deviations (Table 4.5). More precisely, the effect of the stratification on means was always significant except between random (NO) and geographical stratification by the 26 political states (GEO26); between geographical and environmental stratification with 10 regions/domains respectively; and between the two environmental stratifications (ED10, ED26). The effect of the stratification on standard deviations was very similar. Inside the stratification method, the effect of Np was always highly significant ($p < 0.001$).

Table 4.5 Significance of stratification methods in generalized linear mixed models (GLMM) on T.ROC mean and standard deviations. Each cell gives the significance of the stratification method (symbol=*). ns, >0.05; *, < 0.05; **, < 0.01; ***, < 0.001. The effect of logNp inside the stratification method was systematically highly significant (<0.001).

	Mean T.ROC				T.ROC standard deviation			
	GEO10	GEO26	ED10	ED26	GEO10	GEO26	ED10	ED26
NO	***	ns	***	***	***	ns	***	***
GEO10	-	***	ns	**	-	**	ns	ns
GEO26	-	-	***	***	-	-	*	**
ED10	-	-	-	ns	-	-	-	ns

Figure 4.6 shows boxplots of T.ROC values per Np and per stratification type. Each boxplot give the values for the ten communities and the relative ten replicates. In order to determine the threshold above which T.ROC values stopped to increase and showed a plateau, a Wilcoxon rank sum test was performed. T.ROC values for models calibrated with 250 presences were set as the reference to which T.ROC values for models obtained at the other Np values were compared. The reference was set at Np=250 because 250 is the most distant value from the threshold we wanted to determine along the plateau representing the best T.ROC values. Threshold values differed according to the stratification type and the community as well (not presented here). The threshold for not stratified data is 150, 100 for GEO10 and ED10, and 75 for GEO26 and ED26.

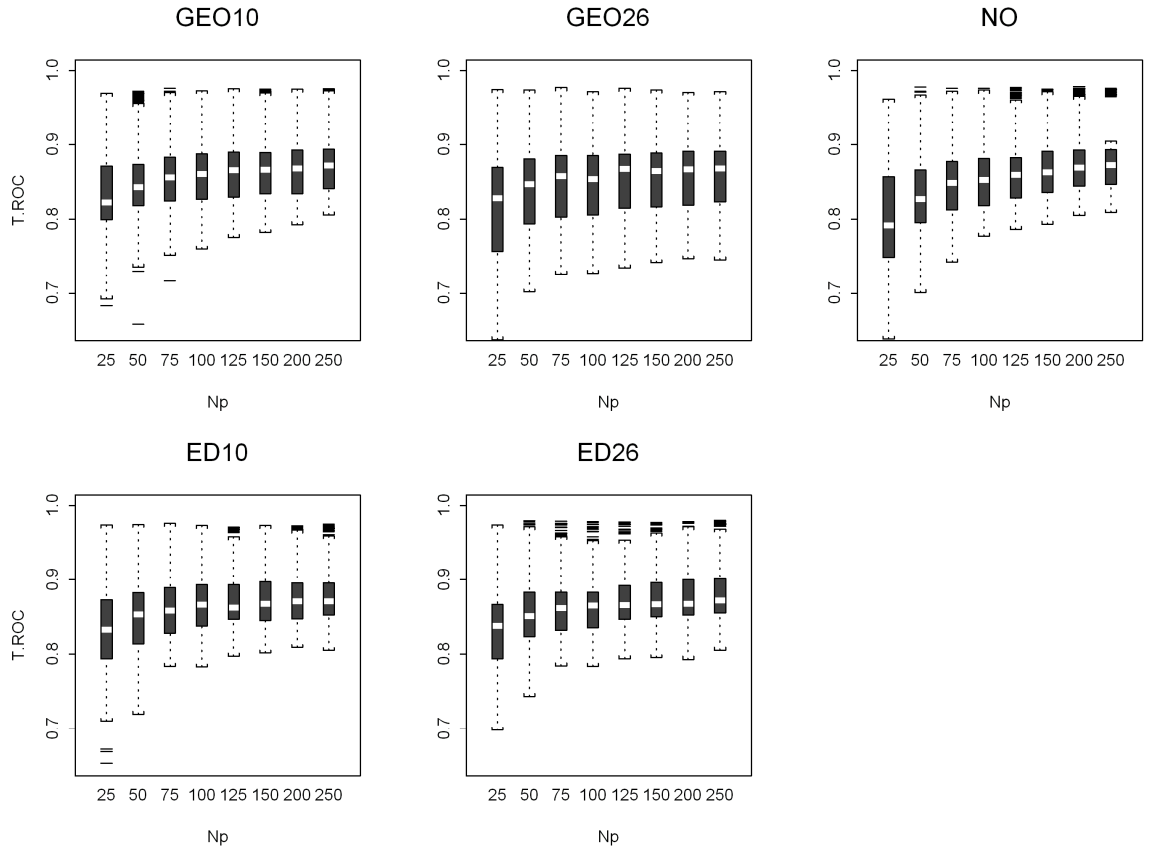

Figure 4.6 Boxplots of T.ROC values represented by stratification type and by Np. Each boxplot give the values for the ten grassland communities units and the 10 relative replicates.

The effect of the stratification was found to be mostly significant at low Np values. As shown by Figure 4.7, T.ROC values for models calibrated with 25 stratified presences were significantly different from values obtained for non stratified presences. This difference faded at large sample sizes (Np=250).

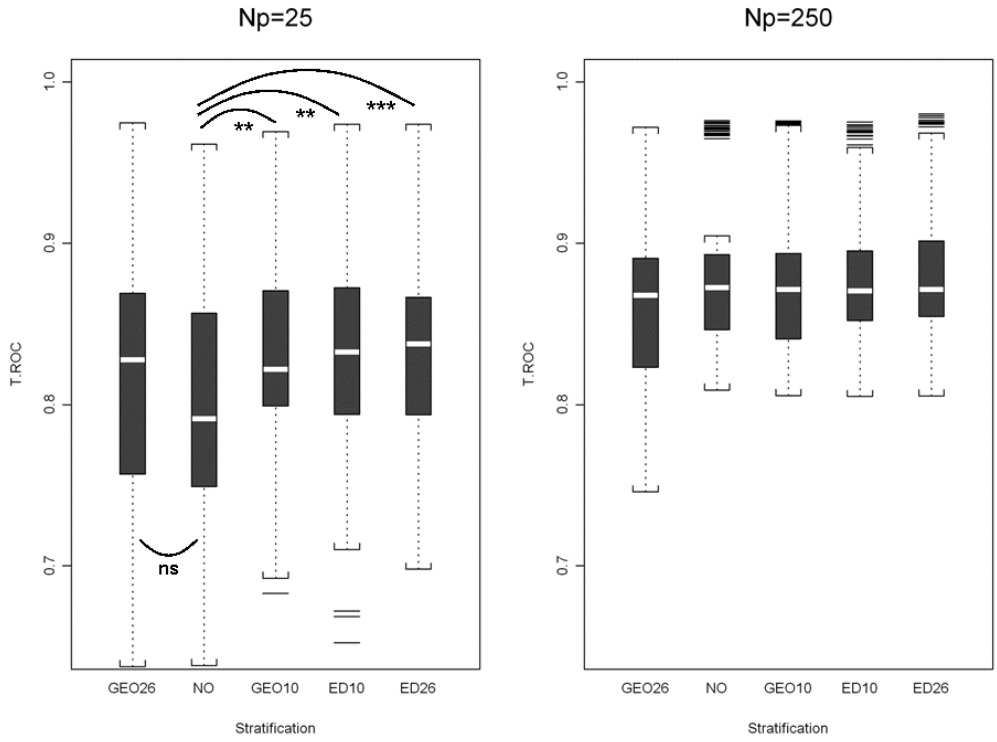

Figure 4.7 Boxplots of T.ROC values obtained at Np=25 and Np=250 for the different stratification types. Each boxplot give the values for the ten grassland communities and the 10 relative replicates. All differences between the boxplots of the right panel are non significant.

4.4.3 Model selection and shape of response curves

Figure 4.8 shows the predictors that were retained in the models calibrated with 25, 100 and 250 environmentally stratified (ED26) presences and the corresponding ten replicates response curves for the case of the community 4.2.4. Response curves for models calibrated with 25 presences were most often linear, whereas responses for Np=250 were more curvilinear and closely followed the distribution of the data (higher number of degrees of freedom allowed by the BRUTO selection procedure). Moreover, while particular predictors were not or not often retained in models calibrated with 25 presences (e.g. *wiprec*, *slope*, $CaCO_3$), their importance was highlighted by models calibrated with higher Np values. Variable selection and shape of response curves can therefore change considerably from one sample size to another.

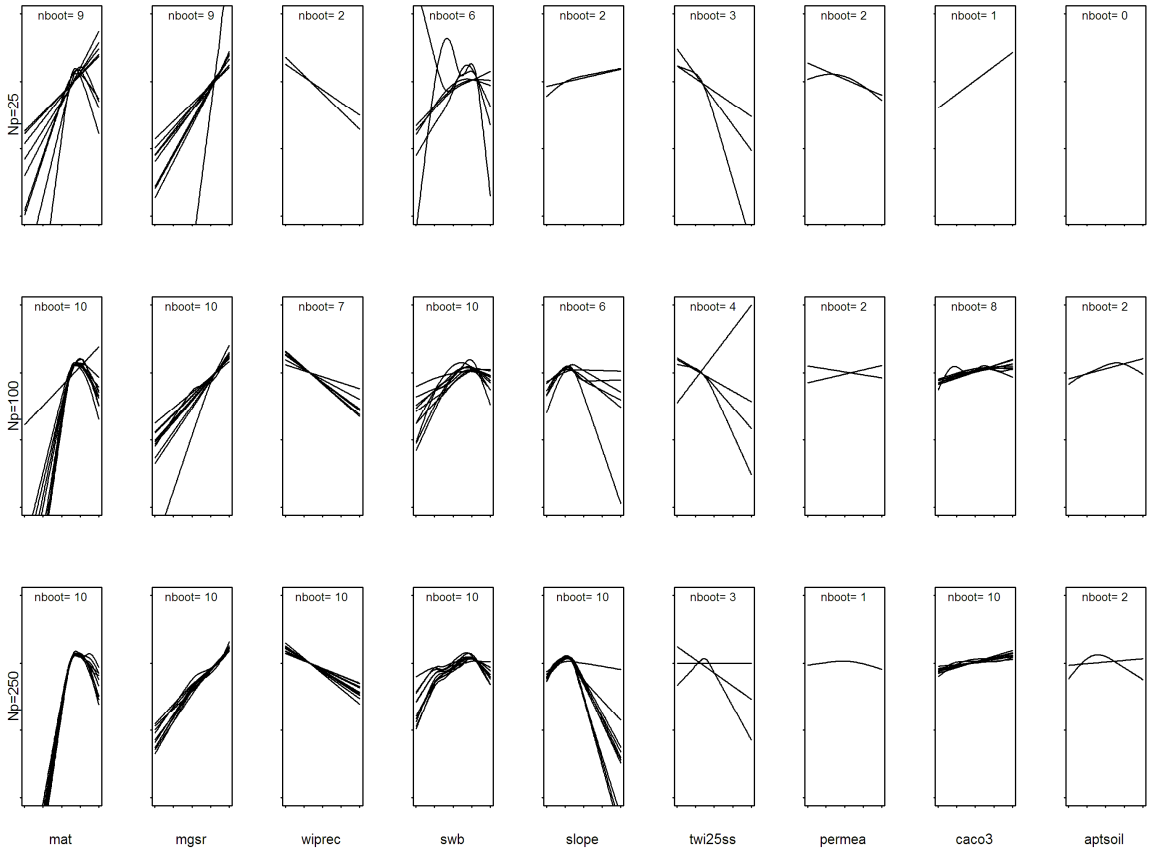

Figure 4.8 Predictors retained in models for the grassland community 4.2.4 (Mesobromion) calibrated with 25, 100 and 250 presences stratified by 26 environmental domains. nboot = number of models (replicates) incorporating the predictor.

4.4.4 Spatial predictions

As showed in the previous section, the predictors retained in models as well as the degree of freedom of their response curves could vary greatly according to Np values. As a consequence, one would expect a great variation in the corresponding spatial predictions as well. As shown by Figure 4.9 in the case of community 4.2.4 (*Mesobromion*), differences in spatial predictions of mean (over the 10 replicates) probabilities of distribution of a given community do not appear to be very important when compared across number of presences used or across stratification methods. The general distribution of the community is well captured by all predictions and differences can only be detected in the details where both stratification and number of positive observations seemed to improve the local accuracy of the predictions.

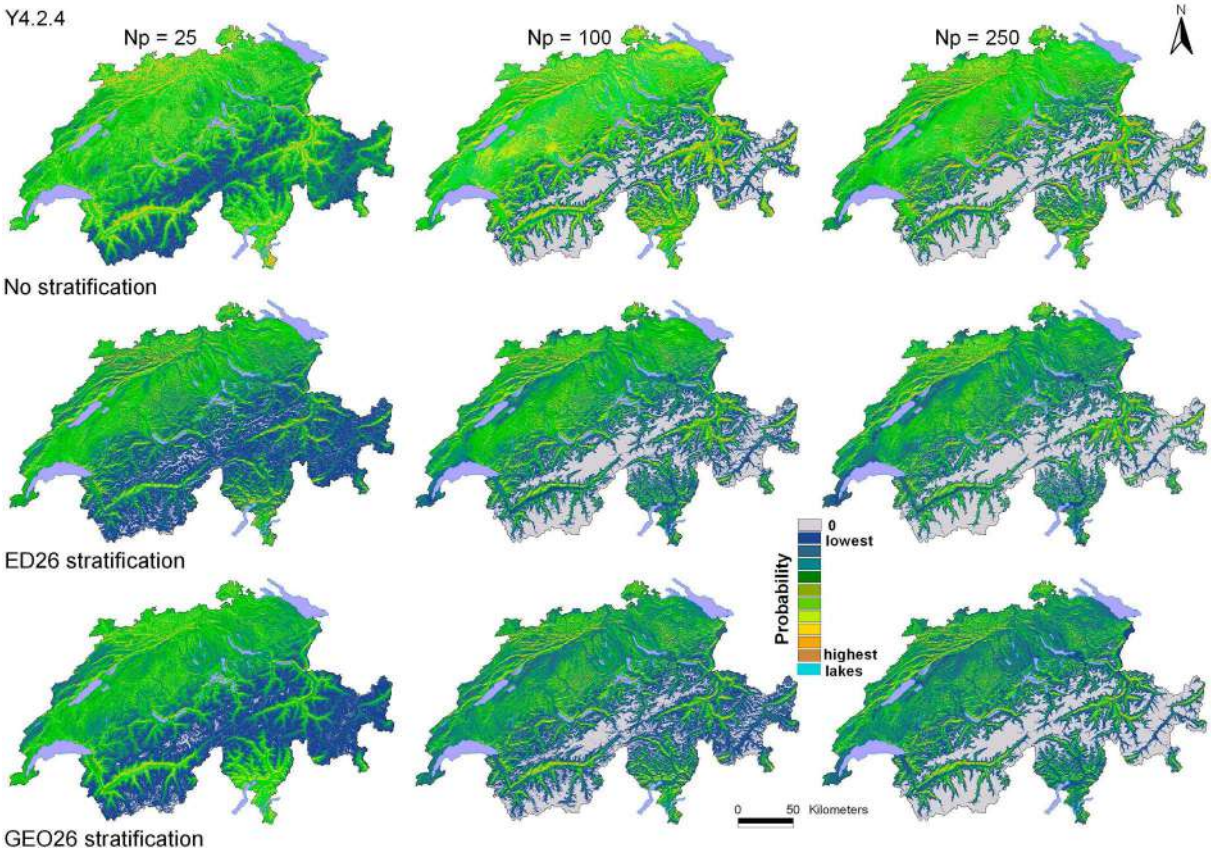

Figure 4.9 Mean of 10 spatial predictions for community 4.2.4 (*Mesobromion*) obtained from models calibrated with increasing Np of randomly chosen, environmentally or geographically stratified data.

In order to formalize these differences, correlations coefficients were calculated between the mean probabilities of occurrence of the community at 4000 locations randomly chosen across the Swiss territory. The calculated coefficients showed however that probabilities predicted by models calibrated with 100 and 250 presences were more similar than probabilities predicted by models calibrated with 25 and 100 presences, thus suggesting an influence of Np. The higher Np is, the higher is the coefficient of correlation between the predicted probabilities. The effect of data stratification was more evident at low Np values whereas at higher Np values this seemed to disappear (very similar correlation coefficients) as shown by the correlation coefficients in Table 4.6.

Table 4.6 Correlation coefficients between the predicted probabilities by models calibrated with 25, 100 and 250 presences stratified by 26 environmental domains, 26 political states or randomly chosen.

	NO			ED26			GEO26		
	Np25	Np100	Np250	Np25	Np100	Np250	Np25	Np100	Np250
NO : Np250	0.837	0.974	1	0.921	0.971	0.932	0.856	0.941	0.933
ED26 : Np250	0.796	0.881	0.932	0.867	0.972	1	0.799	0.917	0.925
GEO26 : Np250	0.845	0.897	0.933	0.913	0.958	0.925	0.885	0.980	1

These differences and trend could be verified by mapping the standard deviations calculated on the 10 replicates spatial predictions of community 4.2.4. As shown by. Figure 4.10, standard deviations were clearly smaller for high Np values and stratification (environmental or geographical) notably reduced standard deviation of spatial predictions especially at low Np values.

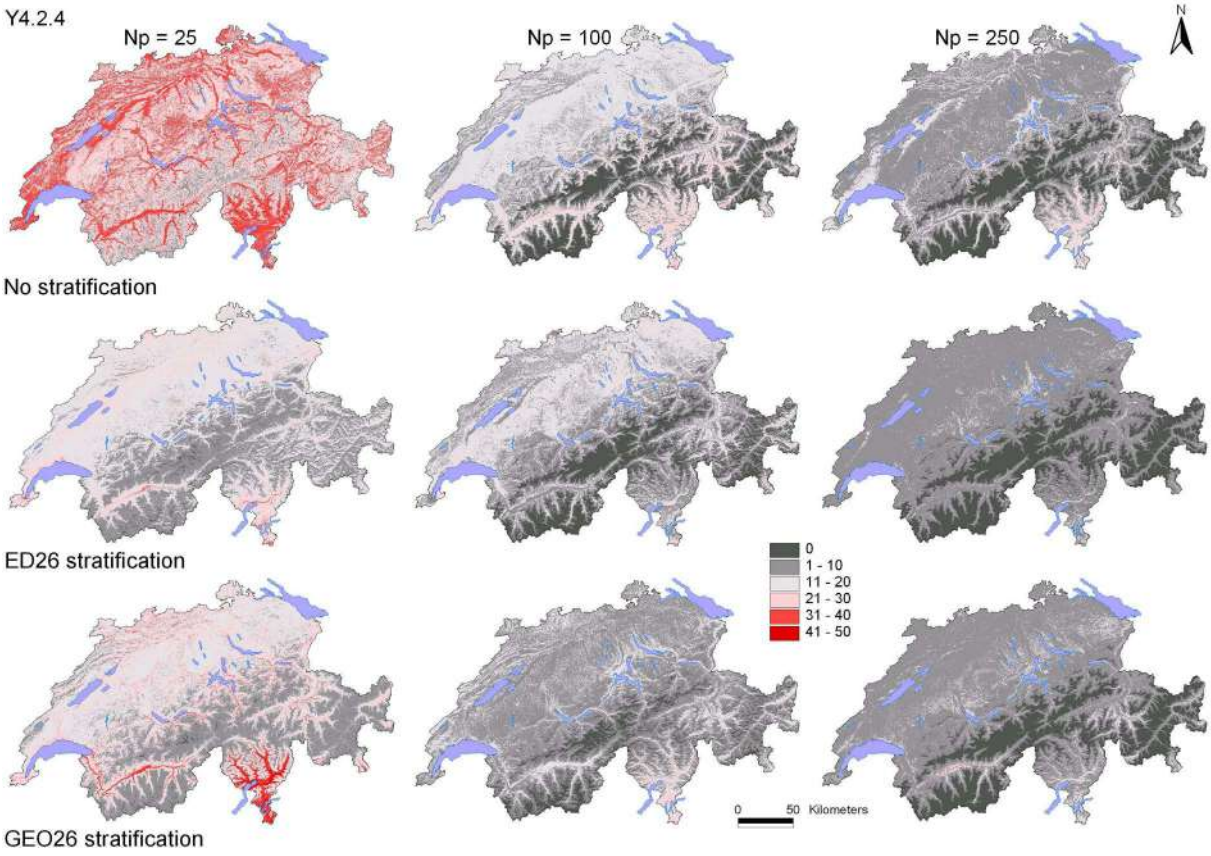

Figure 4.10 Standard deviations calculated on the 10 replicates of the spatial predictions of community 4.2.4 obtained from models calibrated with increasing Np of randomly chosen or environmentally stratified data.

4.4.5 Grassland communities and predictor contributions

All open habitats units were modelled successfully as reported at the beginning of the results section. Figure 4.11 highlights differences in the T.ROC values obtained for the different grassland communities. More accurate models were clearly obtained for the communities 4.2.1.1 (*Stipo-Poion*) and 4.3.7 (*Caricion curvulae*) whereas values obtained for the community 4.2.4 (*Mesobromion*), and to some extent for 4.3.1 (*Seslerion*), were significantly lower than the values obtained for the majority of the modelled grasslands which varied between 0.8 and 0.9.

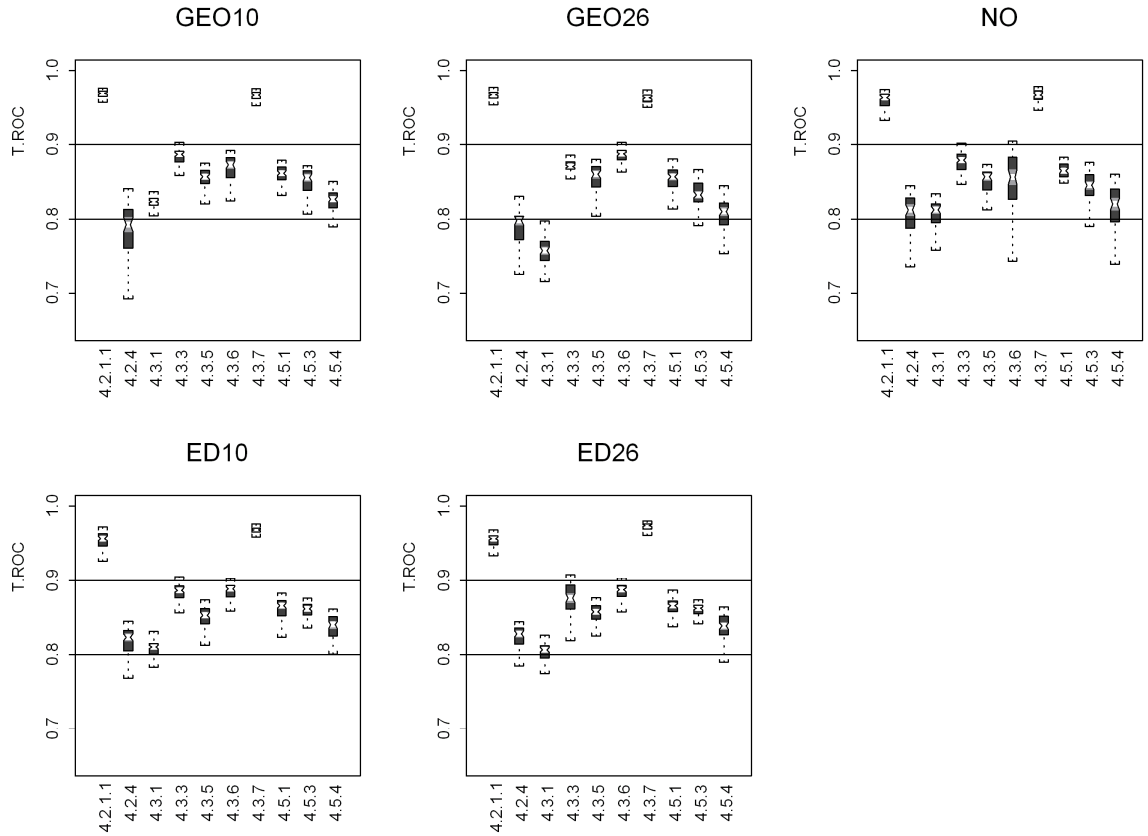

Figure 4.11 Boxplots of T.ROC values represented by stratification type and by grassland community. Each boxplot give the values for all the tested Np values and the 10 relative replicates.

Table 4.7 shows the mean contribution (over 10 replicates) of each predictor within the models (model contribution in GRASP) calibrated with 250 presences previously stratified by 26 environmental domains. Mean annual temperature (mat) and site water balance (swb) were the main contributors within models. Their cumulative contribution varied between 40 and 70 %. Slope and mean growing season solar radiation (*mgsr*) also played an important role, followed by the topographic wetness index (*twi*) and winter precipitations (wiprec). The contribution of the calcareous content of parent material (CaCO3), permeability of parent material (permea) and soil suitability (aptsoil) was low overall. Permeability was very often not retained in models.

Table 4.7 Mean contribution (over 10 replicates), in percentage, of each predictor within the models (model contribution in GRASP) calibrated with 250 points of occurrence previously stratified by 26 environmental domains.

Unit	*mat*	*swb*	*mgsr*	*wiprec*	*slope*	*twi*	*aptsoil*	*caco*	*permea*
Y 4211	*+	**+	*+	*+	+	*+	+	+	0
Y 424	****+	+	*+	+	*+	+	0	+	0
Y 431	***	***	+	+	*	+	+	+	+
Y 433	***+	**+	*+	+	*+	+	+	+	0
Y 435	**+	****+	*	+	+	0	+	+	+
Y 436	**	**+	*+	+	+	*+	+	+	+
Y 437	****	+	+	+	*+	*+	+	+	+
Y 451	*****+	+	+	+	+	+	+	+	0
Y 453	****	*+	+	*+	*+	+	+	+	+
Y 454	*+	****+	+	+	*+	*+	+	+	+

*, 10%; **, 20%; ***, 30%; ****, 40%; *****, 50%; +, contribution < 10%; 0, predictor not retained in the model or characterized by a contribution <1%.

4.5 DISCUSSION

4.5.1 Were grasslands communities modelled successfully?

All grassland communities could be successfully modelled, but with significant differences in model accuracy. Two communities obtained models with a very good discrimination ability, namely the *Stipo-Poion* (4.2.1.1.) and *Caricion curvulae* (4.3.7). These are highly localized and/or specialized communities. *Stipo-Poion* is a typical steppe lawn of the intra-alpine Swiss valleys characterized by a continental climate (Delarze *et al.* 1998). In Switzerland we can mainly find it on the sunny and rocky hillsides of the states of Valais and Graubünden. The *Caricion curvulae* is a typical acid lawn that is found at high elevation (alpine belt) on acidic soils throughout the crystalline Alps (Delarze *et al.* 1998). Both units are characterized by a very low prevalence in the training data. Very accurate modelling for rare units has already being reported in the literature (e.g. Franklin 1998, Guisan & Hofer 2003, Maggini *et al.* 2006) and is likely attributable to their narrow distribution and environmental specialization (Guisan *et al.* 2007b), both of which are easier to capture in a model than the larger niche breadth of widespread units.

Models for the two units *Mesobromion* (4.2.4) and *Seslerion* (4.3.1) obtained the smallest discriminating power. The former is a semi-dry grassland mainly found on sunny, calcareous and nitrogen-poor substrates. Although of wide environmental tolerance, its existence depends mostly on agricultural practices and their intensity: extensive pasture or extensive exploitation, mowed late in the season (Delarze *et al.* 1998). Various anthropogenic factors - intensification of agricultural practices, land use change in favour of vineyards and urban areas, abandon and return to forest - have reduced its distribution in the last fifty years, making it currently highly fragmented. Landuse was thus likely the missing predictor to accurately model this community. The only indirect landuse predictor - soil potential for agriculture (*aptsoil*) – did not show great explanatory power in our study. The same limitation was highlighted by Zimmermann & Kienast (1999), while modelling alpine grasslands in Switzerland.

Models for the Seslery (*Seslerion*) were poor. This unit occupies sunny and stony slopes on limestone or dolomite and has its optimum in the alpine belt between 2000 and 2500 m, but it can spread down to the montane belt (~900-1500 m) on shady slopes (Delarze *et al.* 1998). It is thus not very specialized and commonly found in the Alps and in the Jura Mountains, where it can mix up with other grasslands communities, particularly with the *Mesobromion* at low elevations (Eggenberg *et al.* 2001). This broad tolerance can explain the low discriminating power observed.

4.5.2 How powerful were the various predictors?

Predictors could be classified in three groups, depending on their influence in models. The first group is composed by mean annual temperature and site water balance, the two most important contributors in all models. Their combined contribution, as defined in GRASP, reached 70% in models stratified by 26 environmental domains. Mean annual temperature is a proximal predictor (Austin 2002) that has a direct impact on growth and distribution of plants. Site water balance, being a measure of soil water availability, helps discriminating communities along a gradient of soil moisture. The second group is composed by predictors of moderate importance. They are, by decreasing order of importance: mean solar radiation during growing season (*mgsr*); slope; topographic wetness index (*twi*) and winter precipitations (*wiprec*). Solar radiation is a proximal predictor representing light for photosynthetic activities. Slope is generally employed as a surrogate for hydrology or solar radiation. In our study, these factors were expressed by other more direct predictors, namely *swb* and *mgsr*. Slope therefore translated gravitational phenomenon and indirectly suggested the type of exploitation at the site: intensive and machine-driven exploitation for small slopes, extensive and manual exploitation for moderate slopes, natural habitats for important slopes. The topographic wetness index reflects soil wetness. High values indicate relatively flat and wet areas, whereas low values indicate dry and steep areas. It differs from site water balance in that *swb* integrates precipitation, evapotranspiration, soil properties and topography, but the latter only in a qualitative manner (ridge vs slope). *Twi* on the other hand, only account for topographical conditions (slope and upslope contributing area), but in a quantitative manner. It is thus best associated with a flow accumulation capacity index. Winter precipitations mainly refer to precipitation as snow, indirectly determining the length of the growing season and thus the main altitudinal distribution of the community. In this sense, it refers directly to *mat*, but additionally represents the available amount of water available in spring for the onset of the vegetation.

Finally, the less contributing predictors were related to geology that was used as surrogate for soil information. Since some communities are clearly linked to calcareous or crystalline substrates, we expected a more significant contribution at least for the calcareous content of parent material ($CaCO_3$). The weak explanatory power may be related to the coarse resolution of the geotechnical map (1:200,000) and to the expert estimation of the calcareous content of the different bedrock types.

4.5.3 What does the different validation methods mean?

Validation is a crucial part of any modelling activity. With presence-absence models in ecology, Fielding and Bell (1997) have clearly set the standard by presenting the ROC statistics as an appropriate measure of model accuracy that is independent of the choice of the threshold used in order to classify predicted value into positive and negative observations. An alternative, recently revisited by

Elith *et al.* (2006), is a simple correlation coefficient (COR) between observed and predicted values. This approach is similar to ROC, because it is threshold-independent but brings supplementary information concerning model calibration by taking into account how far predictions are from observations (Elith *et al.*, 2006).

When used between observed and predicted values on the training data set (resubstituition), validation statistics such as ROC and COR only provide an additional measure of model fit, and as such are of limited interest. Validating models on independent data remains the best option if a true evaluation of model accuracy and generality must be obtained. However, as observations are often scarce and costly to obtain, it is not always technically feasible nor defendable to set apart a significant number of observations. For this reason, cross-validation, can be used instead, as it allows validating a model in a reasonably robust manner without loosing informative observations for building the model. Despite the fact that partitioning of the training set results in overestimates of the actual error rates, it is still possible to average the results from several partitions and make the accuracy estimate less dependent on a single partition (Fielding & Bell 1997).

In this study, we decided to concentrate on independent ROC (T.ROC) for several reasons. First, we had enough data to set apart approximately 35% of our observations to build an independent evaluation data set. Second, this approach allowed us specifying a neutral prevalence of 0.5 when evaluating the models. Third, we eliminated observations that were too closely located within a distance of 200m. These three steps helped us avoiding some of the major pitfalls encountered when comparing models for many species or communities or modelling techniques.

4.5.4 How much data is enough?

Model predictive accuracy is clearly related to the number of occurrences (Np) and hence, in this study, to the size of the training data set. Accuracy increases relatively rapidly when adding data at low sample sizes, whereas increments are less important when adding data at large samples sizes. The threshold after which no significant increase in model accuracy is observable differs according to the species/community modelled (Pearce & Ferrier 2000), the characteristics of the particular data set used and the modelling technique adopted (Stockwell & Peterson 2002, Pearce & Ferrier 2000, Guisan *et al.* 2007b). In our case, the threshold was situated, on average, around 100 occurrences. Stratified data had, on average, a lower threshold (Np=100 for coarsely stratified data and 75 for finely stratified data) than non stratified data (150). Moreover, thresholds calculated for the single grassland communities (results not presented) were highly variables.

Several studies exist in the literature dealing with the issue of the optimal sample size. As an example, Stockwell & Peterson (2002) achieved the highest accuracy as well with 100 occurrence points when modelling birds in Mexico using generalized linear models. Their study was however differently designed and, more importantly, 100 was the last value tested. When modelling birds in South Africa with logistic regression, McPherson *et al.* (2004) obtained the best accuracy for models calibrated for a total (presences and absences) training sample size situated between 300-500. Between several factors affecting the predictive performance of models, Pearce & Ferrier (2000) identified sample size as being the factor having the strongest effect. Their multi-taxon study determined that at least 250 sites were needed in order to model the regional distribution of species in New South Wales using

GLMs and GAMs. In a multi-techniques comparison, Guisan *et al.* (2007b) found that techniques fitting simple response curves tended to be less affected by decreased sample sizes than more complex techniques (e.g. GAM) that fit more complex response curves of species along environmental gradients. Therefore, we can conclude that each particular study should look for its own threshold value. When collecting new data, this could be an iterative procedure alternating the collection of new data and the construction of new models in order to determine the threshold after which no more increase in model performance and stability is observed. This is especially useful when working with rare species that are by definition infrequently observed in the field. The iterative procedure allows stopping when a sufficient amount of data is reached. Moreover, at each step new distribution models can be used to stratify the subsequent field sampling and therefore increase sampling efficiency. An example of this procedure has been illustrated in Guisan *et al.* (2006a) for *Eryngium alpinum* L., a rare and endangered species of the Swiss flora.

A side effect of our selection algorithm is that the number of presences in the training sample is fixed but the number of absences varies as a function of the rarity of the community. The rarer the community, the greater the number of loops required to obtain the desired number of presences. This somehow preserves the original prevalence of the communities and reinforces their rarity/commonness when creating the different training samples.

4.5.5 What is the effect of stratification?

Globally, environmentally stratified data gave better models (higher ROC values) than pure random or geographically stratified data. Stratification by environmental domains also gave models with a better generality (higher T.ROC values) when applied to an independent data set, thus suggesting a higher transferability to other situations (see Randin *et al.* 2006). Concerning geographic stratification, the scheme using ten biogeographical zones yielded models with higher accuracy than the one using 26 political states. This is not surprising, as biogeographical zones are defined according to the main faunal and floristic patterns in Switzerland (Gonseth *et al.* 2001) and therefore correspond more closely to an indirect environmental stratification than to a purely geographical classification. Stratification using 26 political states yielded results very close to those obtained without stratification. This stratification is indeed artificial, no environmental signification, and has the only advantage of distributing the data across the whole territory and hopefully across different environmental gradients. However, results showed that stratification had mainly a significant impact at low sample sizes, as models become comparable at large sample sizes. Thus, environmental stratification is particularly worth for supporting field sampling designs when resources and time are limited, using the main environmental gradients that are known to affect the distribution of the species/community modelled. Our findings confirm those of Hirzel & Guisan (2002) while testing different types of data stratification and the effect of sample size with a virtual species, they found that increasing sample size increased model accuracy and that the best sampling strategy tended to be the one using environmental stratification balanced by strata rather than proportional to the size of the strata, geographic or random (i.e. no stratification).

A question that could arise with this type of study is whether post-stratification is useful to resample heterogeneous datasets, as obtained from natural history collections (Graham *et al.* 2004) or from the

merging of different projects' databases. The assumption is indeed that environmentally well distributed information should yield better models than non-stratified information. Our results showed that stratification has no significant impact at large sample sizes; therefore it seems to be no good reason to set apart a portion of the available data when dealing with large datasets. Moreover, heterogeneity in the distribution of observations in the environmental space (composed by the selected predictors) is only affecting the local accuracy of a model. Removing data can only diminish this accuracy in some parts of the environmental space, but we do not see how it could improve it.

This approach of post-stratification could however be very useful for preparing pseudo-absences to be used with museum or herbarium data (e.g. Zaniewski *et al.* 2002, Elith *et al.* 2006, Elith & Leathwick 2007). Pseudo-absences can be created by randomly sampling the geographical space as in Zaniewski *et al.* (2002), but possibly better results could be obtained by a stratified sample in the environmental space. This idea remains to be tested.

4.5.6 How are model selection and response curves influenced?

Austin (2002) advocated that statistical models used to predict species distribution should remain closely related to ecological theory. By using the continuum concept of species distribution along gradients, he encouraged very much the use of Generalized Additive Models to assess the shape of response curves (Austin 2007). GAMs fit smoothing splines very close to the data instead of assuming linear or quadratic functions, allowing shapes of response curves to be interpreted ecologically. However, the flexibility of GAMs is often attenuated by the fact that, due to limited sample size, modellers often specify a small number of degrees of freedom for fitting response curves (Austin 2007). This was circumvented in the present study by using the BRUTO algorithm for model selection. BRUTO fits a GAM by identifying significant predictors and the optimal degree of smoothing for each of them (Hastie & Tibshirani 1996). As a result, when testing the effect of sample size on model accuracy, shapes of response curve were mainly linear when modelling with 25 presences, and became more complex and followed data more closely when modelling with larger sample sizes. Hence, model validation must not only rely on good agreement statistics (such as ROC), but additionally – and as importantly - assess the shape and ecological interpretability of response curves. As yet, very few studies discussed the interpretability of the fitted models (Austin 2007) and more effort is still needed here.

4.5.7 Comparing spatial predictions

A third important aspect of model validation is the quality of spatial predictions. Our experiments showed that equally good model, as assessed statistically, can produce significantly different spatial patterns of predictions. This is particularly true at the level of the replicates for a given Np and stratification type. However, averaged maps looked relatively similar. All maps captured the coarse distribution of the community and the effect of Np and stratification was mainly perceptible in the details within the global distribution pattern. Visually, the increase of Np as well as the stratification seemed to better delineate the fine distribution of the community, with more details in the favourable zones and better discrimination of non favourable zones.

This appears as evidence when looking at maps of the standard deviation relative to the averaged maps. Variation was significantly higher at low Np and for non-stratified data. Np thus appears to have the greatest effect whereas stratification seems to be important especially at low Np values. At higher sample sizes the effect of stratification is less evident.

In addition to global evaluation statistics and the assessment of ecologically-interpretable response curves, model evaluation should thus additionally consider patterns of spatial predictions, especially when results are to be used within the framework of species and ecosystem conservation planning (e.g. Margules & Pressey 2000). Inaccurate predictions can potentially have very negative impacts on conservation actions, in particular when dealing with rare species management, reserve network selection or specific site protection. Decision makers involved in nature conservation should be informed of the many forms of uncertainty associated with the modelling process, from data deficiency to model specification (Barry & Elith 2006), through inappropriate (Austin 2007) or inaccurate predictors (e.g.Van Niel *et al.* 2004, Van Niel & Austin 2007). While modellers actively work in order to minimize all these forms of uncertainty, managers should take decisions that consider alternatives in order to maximize the chance of a tolerable outcome (Burgman *et al.* 2005).

In conclusion, it is very important to be able to better assess the quality of spatial predictions. We made a first step in this direction by using a simple index that is the correlation coefficient calculated between observed and predicted values on the training, cross-validated or test data set. A step further would consist in evaluating the predictions by expert knowledge and eventually cross-check the results in the field. These are however time and cost-consuming actions that are often undertaken only for very specific and particularly delicate purposes.

4.6 MAJOR FINDINGS AND CONCLUSIONS

1. Overall, models could successfully predict the distribution of grassland communities. The best predictors were mean annual temperature and site water balance.
2. Cross and independent validation only should be considered for evaluation: cross-validation allows keeping all the available data while assessing the model performance; independent validation enlightens model generality.
3. The generally used ROC statistic only informs on how well the model discriminates the presences and absences (discrimination); COR additionally inform on how well the model fits the data (calibration) and should be used in complement.
4. Increasing number of presences (Np) in the training sample improves model accuracy with a threshold value around 75 presences for data highly stratified, 100 for broadly stratified data and and 150 otherwise.
5. Stratification (either geographic or environmental) only improves model accuracy at low sample sizes.
6. Stratification has more effect on the standard deviation of performance statistics (ROC and COR) than on their means.
7. Environmental stratifications perform better than geographic ones; both perform better than full random sampling.

8. In conclusion, as stratification and Np can significantly modify model selection, response curve shapes, resulting spatial predictions and their uncertainty, a new validation procedure should be developed that encompass not only statistical but also ecological significance of a model.

4.7 ACKNOWLEDGMENTS

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5 LAND USE VERSUS VEGETATION COMMUNITIES IN DISTRIBUTION MODELS FOR ANIMALS: A CASE STUDY WITH GRASSLANDS AND BUTTERFLIES IN SWITZERLAND

Ramona Maggini[1,2 *], Anthony Lehmann[2], Yves Gonseth[3], Daniel Cherix[1,4] and Antoine Guisan[1]

[*] Address for correspondence: Ramona.Maggini@unil.ch

[1] Department of Ecology & Evolution (DEE), Biophore Building, University of Lausanne, CH-1015 Lausanne, Switzerland

[2] Research Group on Climatic Change and Climate Impacts, Institute for Environmental Sciences, University of Geneva, Battelle D, CH-1227 Carouge, Switzerland

[3] Swiss biological record center (CSCF), Passage Max-Meuron 6, CH-2000 Neuchâtel, Switzerland

[4] Museum of Zoology, Palais de Rumine, Place de la Riponne 6 CP, CH-1014 Lausanne, Switzerland

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5.1 ABSTRACT

The term 'habitat' has been used confusingly and inconsistently in the literature either referring to populations of different species co-occurring at a specified point in space and time - the habitat concept of community ecology – or to environmental conditions (abiotic and biotic) determining the presence of a particular species at a given location - the niche concept adopted in species distribution modelling. In this article we present an original approach that combines these two concepts: first are modelled 'habitat' units, i.e. vegetation communities, per se, and then these units are used to model the habitat of an animal species. Vegetation communities are defined at the phytosociological level of the alliance, it is therefore very likely that the habitat of a given species will encompass several of them. We illustrate the approach using butterflies and pre-modelled grassland communities across Switzerland. While doing so we also addressed two main questions. The first one aimed at assessing

the relative performance in faunal SDMs of pre-modelled vegetation communities and of land use categories. Results clearly showed that vegetation communities better predict butterfly distribution than simple land use/land cover information. The second question aimed at determining the best way to combine climatic and vegetation information. Best results were obtained by assembling climatic and vegetation predictors in a same model. However, the Bayesian combination of the probabilities of occurrence of the vegetation communities and suitable climatic conditions gave very similar results. With the Bayesian combination approach, highly appealing is the possibility to update the information concerning vegetation with the real distribution captured by remote sensing or vegetation mapping. In this case, probabilistic maps are replaced by actual vegetation maps with probability 0/1 for a given vegetation type. The Bayesian combination approach will in this case lead to a filtered environmental prediction.

Keywords : habitat; vegetation community; land use; butterfly; species distribution modeling (SDM); generalized additive models (GAMs); Bayes; Switzerland

5.2 INTRODUCTION

The term “habitat” has been used confusingly and inconsistently in the literature (Whittaker et al., 1973) and this has slightly changed trough time (Mitchell, 2005; Kearney, 2006). Habitat either refers to populations of different species co-occurring at a specified point in space and time - the community concept – or to environmental conditions (abiotic and biotic) determining the presence of a particular species at a given location - the niche concept adopted in species distribution modeling (SDM). The difference between the realization of these two concepts is merely a question of scale and perspective (Ricklefs, 2008). The local community that is recognized as a unit from the discipline of community ecology, can be seen as “a single point shared by many species” “with partially overlapping distributions” (Ricklefs, 2008) at a regional scale. At this scale the spatial distributions of populations replace the community concept.

Commonly accepted is the idea that the area of distribution of a species is related to its environmental niche. Niche is a central concept in ecology. Hutchinson (1957) defined the fundamental niche as a hypervolume in a multi-dimensional environmental space the axes of which correspond to available conditions and resources. The hypervolume represents the different states of the environment that would allow a species to survive and reproduce. Conceptually, the potential area of distribution of a species corresponds to the translation of this environmental envelope into the geographic space. In reality, the distribution we observe is re-shaped by other factors like competition with other species having the same environmental requirements. We therefore deal with the realized niche of the species, which is a portion of the fundamental one where the species is competitively dominant. Some authors have hypothesized that the measured realized niche could possibly be larger than the fundamental niche in a metapopulation perspective if sink habitats, where individuals may occur due to dispersal and immigration from source areas, are accounted for (Pulliam, 1988; Pulliam, 2000).

In SDM the area of distribution of a species is estimated by modelling its realized niche. This implies to find multiple correlations between the observed presence or abundance of the species and the

different environmental predictors. In recent years, the scientific community in the discipline of SDM has grown significantly and a great step forward has been made in the development of working theories (Guisan and Zimmermann, 2000; Austin, 2002; Guisan and Thuiller, 2005; Araújo and Guisan, 2006; Guisan et al., 2006b; Moisen et al., 2006; Austin, 2007), methods and tools (Busby, 1991; Ozesmi and Ozesmi, 1999; Boyce et al., 2002; Ferrier et al., 2002a; Ferrier et al., 2002b; Guisan et al., 2002; Hirzel et al., 2002; Lehmann et al., 2002b; Thuiller, 2003; Leathwick et al., 2005; Maggini et al., 2006; Prasad et al., 2006; Elith et al., 2008; Olden et al., 2008) that have now being compared (Manel et al., 1999; Cairns, 2001; Moisen and Frescino, 2002; Segurado and Araújo, 2004; Elith et al., 2006; Leathwick et al., 2006b; Marmion et al., 2009) and applied in a variety of fields (Lehmann, 1998; Zimmermann and Kienast, 1999; Ferrier, 2002; Lehmann et al., 2002a; Thuiller et al., 2005; Araújo et al., 2006; Guisan et al., 2006a; Leathwick et al., 2006a; Maggini et al., 2006; Thuiller et al., 2008). In this paper we will present a new and original approach in order to model faunal distribution. This two-steps approach integrates the two previously discussed concepts of "habitat" by combining community ecology with spatial ecology. First vegetation communities are modelled per se. These units are then used in order to model animal species habitat. Vegetation communities are defined very finely (alliance level) and it is therefore very likely that the habitat of a given animal species will encompass several of them. We are here positioned at the landscape level or ecoscape as recently defined by Lidicker (2008). We will illustrate the approach with a case study which aims at modelling the distribution of ten butterfly species across Switzerland using pre-modelled grassland communities. By doing so, this paper will also address two main questions: i) are vegetation communities better predictors than simple land use information in distribution models for fauna?; ii) if yes, how can best predictions be obtained: by integrating vegetation communities directly into the model as predictors or by combining the vegetal and climatic spatial predictions? Our hypothesis is that vegetation communities have a much stronger biological content than simple land use information and should therefore better predict the distribution of animal species and in particular of phytophagous groups such as butterflies. Concerning the way to integrate them, we assess two main approaches: a modelling approach and an approach based on map combination. From a practitioner perspective, it is probably easier to combine a map giving the potential climatic distribution of a species with a map presenting information about the distribution of target vegetation units within a geographic information system than to go through a whole modelling process. On the other hand, we expect the modelling approach to be more effective and to combine these two sources of information in a more balanced way. Our analysis will thus assess if there is a significant advantage to combine climate and vegetation information in a model instead of simply combine the resulting maps.

5.3 MATERIALS AND METHODS

5.3.1 Study region

Data were collected and models calibrated for the entire Swiss territory, located in the centre of Western Europe. Its climate is mostly temperate, with atlantic and continental influences and highly variable conditions across the country. The Swiss territory is classically subdivided in three main regions: the Jura Mountains, the lowland area of the Plateau and the Alps. According to the land use survey of 1992/97 (OFS, 2003), the Swiss territory is composed for 6.8% of settlements and urban

areas, 36.9% of agricultural areas, 30.8% of wooded areas and 25.5% of unproductive areas (lakes, rivers, unproductive vegetation, rock, sand, scree, glaciers, perennial snow).

Jura Mountains are a limestone range of mountains stretching from Lake Geneva to the Rhine near Basel. It occupies 12% of the Swiss territory and is characterized by an average altitude of 700 m a.s.l. Part of the beech forest domain was cleared in the Jura Mountains in order to increase the surface available for pasture. This practice has created the so called "wooded pastures", which are mosaics of woods and grasslands very typical of this region. At high altitude xerophile and oligotrophic grasslands non- or extensively exploited are characterized by *Sesleria caerulea* (*Seslerion, Seslerio-Bromion*), whereas oligotrophic pastures on acid substrate are characterized by *Nardus stricta* (*Nardion*). On deeper and richer soils grasslands are dominated by *Poa alpina* (*Poion alpinae*). At lower elevation, the *Mesobromion* semi-dry grasslands replace the *Seslerion* in the extensively exploited grasslands. Pastures belong mainly to the *Cynosurion* and the majority of meadows to the *Arrhenatherion* (lowland) or the *Polygono-Trisetion* (mountain) (Hegg et al., 1993, Küpfer, 2010).

The densely populated and intensively cultivated region of the Plateau covers about 30% of the country and is characterized by mean annual precipitation of 1000 mm and mean temperature of 9 °C (OFS, 2007). Besides arable land, the Plateau is characterized by lowland and montane rich hay meadows (*Arrhenatherion, Polygono-Trisetion*) that are mown but also grazed in autumn. At higher elevation, they are replaced by pastures characterized by *Cynosurus cristatus* or *Bromus erectus* (*Cynosurion, Mesobromion*) (Hegg et al., 1993).

The Alps span over 200 km at an average altitude of 1700 m (the highest point being the Dufourspitze in the State of Valais, at 4634 m a.s.l.). Alps occupy nearly two thirds of the Swiss territory and have precipitation that can exceed 2500 mm. The lowest valleys of the alpine region are still characterized by agricultural activities. Large areas are covered by hay meadows (*Arrhenatherion, Polygono-Trisetion*) that are gradually replaced by pastures with altitude. The montane and subalpine belts are characterized by pastures dominated by *Cynosurus cristatus*, *Poa alpina* and *Nardus stricta* respectively. In the central Alps, steppic grasslands are also to be found (*Stipo-Poion*). The type of alpine lawn is dictated by the nature of the bedrock. The northern Alps, where bedrocks are carbonated, are dominated by cliff and limestone screes vegetation communities as well as *Sesleria caerulea*, *Carex ferruginea* and *Elyna myosuroides* grasslands (*Potentillion caulescentis*, *Thlaspion rotundifolii*, *Seslerion*, *Caricion ferrugineae*, *Elynion*). South of the Alps, on the steep sides of the mountains we can often find large tufts of *Festuca varia* and siliceous cliff vegetation (*Androsacion vandelii*) can cover relatively large areas. Siliceous lawns (*Caricion curvulae*, *Nardion*, *Caricetum sempervirentis*, *Festucetum variae*) cover the majority of the insubrian domain where soils are very poor (Hegg et al., 1993).

5.3.2 Data

5.3.2.1 Vegetation communities

The modeled vegetation units are grassland communities of natural and anthropogenic origin. Table 5.1 gives a detailed list of the communities that were modeled and subsequently integrated in models of butterfly species. Modeled communities are mainly defined at the phytosociological level of the alliance. For their description and environmental determinants please refer to Delarze et al. (1998).

Data on grasslands distribution were obtained from in-house research projects - Landspot and Modiplant project, University of Lausanne – and from external sources - "Dry Grassland in Switzerland" (DGS project), Swiss Federal Office for the Environment (FOEN); grassland database of Dr N.E. Zimmermann (Swiss federal Institute for forest, snow and landscape research, WSL). A detailed description of these projects is given in Maggini et al. (in prep.). The distribution of marshes and peats was not modelled but directly extracted from the Swiss federal Inventory of peat bogs and transitional marshes (source: FOEN, Bern; description: OFS, 2003).

Table 5.1 List of the modeled vegetation communities. Communities marked with the symbol # were subsequently used in order to model the distribution of butterfly species. Communities are defined according to the classification of natural vegetation communities in Switzerland (Delarze et al., 1998). The table also gives the correspondence with CORINE, the classification of European biotopes (Devillers et al., 1991). * The distribution of peat bogs and marshes were not modeled but extracted from the Swiss federal Inventory of peat bogs and transitional marshes (FOEN, Bern).

VEGETATION TYPE	VEGETATION UNIT	CODE	PHYTOSOCIOLOGICAL UNIT	CORINE CODE
HUMID GRASSLANDS	Purple Moorgrass meadow	2.3.1 #	*Molinion*	37.31
	Marsh Marigold meadow	2.3.2 #	*Calthion*	37.21
	Marshy tall herb community	2.3.3 #	*Filipendulion*	37.1
STEPPIC GRASSLANDS	Steppic grassland	4.2.1.1 #	*Stipo-Poion*	34.313 & 34.314
	Continental semi-dry grassland	4.2.1.2	*Cirsio-Brachypodion*	34.3122
DRY THERMOPHILE GRASSLANDS	Middle-European dry grassland	4.2.2 #	*Xerobromion*	34.332
	Middle-European semi-dry grassland	4.2.4 #	*Mesobromion*	34.322
SUBALPINE AND ALPINE DRY GRASSLAND AND PASTURES	Blue Moorgrass dry calcareous grassland	4.3.1 #	*Seslerion*	36.431
	Cushion sedge dry calcareous carpet	4.3.2	*Caricion firmae*	36.433
	Fresh calcareous grassland	4.3.3 #	*Caricion ferruginae*	36.412
	Wind edge naked-rush swards	4.3.4	*Elynion*	36.42
	Dry acid pasture	4.3.5 #	*Nardion*	36.31
	Rocky acid grassland	4.3.6 #	*Festucion variae*	36.33
	Acid grassland of the higher alpine belt	4.3.7	*Caricion curvulae*	36.34
SNOW-PATCH COMMUNITIES	Snow-patch communities of calcareous soils	4.4.1	*Arabidion caerulae*	36.12
	Snow-patch communities of acid soils	4.4.2	*Salicion herbaceae*	36.11
FERTILIZED GRASSLANDS	Lowland hay meadow	4.5.1#	*Arrhenatherion*	38.22
	Mountain hay meadow	4.5.2 #	*Polygono-Trisetion*	38.3 & 36.51
	Lowland and montane pasture	4.5.3 #	*Cynosurion*	38.1
	Subalpine and alpine rich pasture	4.5.4 #	*Poion alpinae*	36.52

VEGETATION TYPE	VEGETATION UNIT	CODE	PHYTOSOCIOLOGICAL UNIT	CORINE CODE
HEATHS	Sub-atlantic acidophilous heath	5.4.1	*Calluno-Genistion*	31.21 & 31.22
	Subalpine xerophilous heath	5.4.4	*Juniperion nanae*	31.431 & 31.47
	Subalpine meso-hygrophilous heath on acid soil	5.4.5	*Rhododendro-Vaccinion*	31.42
	Wind-exposed alpine heath	5.4.6	*Loiseleurio-Vaccinion*	31.41
PEAT BOGS AND MARSHES	marsh *	#		54
	peat *	#		51

5.3.2.2 Butterfly species

Data on the distribution of butterflies were obtained from the Swiss biological record center (CSCF). CSCF is responsible for gathering, storing and analyzing faunal observations in Switzerland except birds that are managed by the Swiss Ornithological Institute. Butterfly species listed in Table 5.2 were selected because they are commonly found in specific vegetation communities or linked to particular plant species, and because they are representative of different status in the Swiss Red list (Gonseth, 1994). Data for modeling were point observations with a spatial accuracy higher or equal to 25 m (level 5 and 6 of the CSCF code; CSCF, 2003), which is the resolution of the predictor maps, and sampled between 1980 and 2006.

Table 5.2 List of the modelled butterfly species with their Swiss Red list status and the main vegetation communities in which they can be observed according to expert knowledge (Delarze et al., 1998) and according to the observations in the CSCF database. N*=number of observations with geographical precision of category 5 (10-25 m) or category 6 (<=10 m) and sampled between 1980 and 2006. Swiss Red list status # (Gonseth, 1994): 2 = very threatened (corresponds to category "Vulnerable" of the IUCN Red list); 3 = threatened (corresponds partially to category "Vulnerable" of the IUCN Red list); - = not threatened.

SCIENTIFIC NAME	DESCRIPTOR	FAMILY	CSCF CODE	N*	SWISS RED LIST STATUS[#]	ASSOCIATED VEGETATION COMMUNITY expert knowledge (Delarze et al., 1998)	ASSOCIATED VEGETATION COMMUNITY according to data (CSCF database)
Maculinea teleius	Bergstraesser 1779	Lycaenidae	MATE	391	2	2.3.1	2.2, 2.31
Brenthis ino	Rottemburg 1775	Nymphalidae	BRIN	1074	3	2.3.3	2.2, 2.3.1, 2.3.3, 4.2.4, 4.5.1, 4.5.3
Polyommatus thersites	Cantener 1834	Lycaenidae	PTHE	90	3	4.2.4	4.2.2, 4.2.4, 4.5.1
Polyommatus (Agrodiaetus) damon	Denis & Schiffermüller, 1775	Lycaenidae	PDAM	51	3	4.2.4	4.2, 4.2.4, 4.3.1, 4.5.2, 4.5.4
Erebia cassioides	Hochenwarth 1793	Nymphalidae	ERCA	22	-	4.3.1	4.3.1, 4.3.3, 4.5.4

SCIENTIFIC NAME	DESCRIPTOR	FAMILY	CSCF CODE	N*	SWISS RED LIST STATUS[#]	ASSOCIATED VEGETATION COMMUNITY expert knowledge (Delarze et al., 1998)	ASSOCIATED VEGETATION COMMUNITY according to data (CSCF database)
Erebia pronoe	Esper 1780	Nymphalidae	ERPR	493	3		4.3.1
Boloria (Clossiana) titania	Esper 1793	Nymphalidae	BTIT	454	3	4.5.2	2.2, 4.2, 4.3
Coenonympha pamphilius	Linnaeus 1758	Nymphalidae	CPAM	2713	-	4.5.3	4.2.4, 4.5.1, 4.5.3
Polyommatus icarus	Rottemburg 1775	Lycaenidae	PCRS	2004	-	4.5.1, 4.2.4	4.2.4, 4.5.1, 4.5.3
Erebia parthe	Huebner 1804	Nymphalidae	ERPH	73	-	4.3	2.2, 4.3

5.3.3 A two steps modeling approach

5.3.3.1 Selected modeling tool

Generalized additive models (GAMs; Hastie and Tibshirani, 1990) were fitted using the GRASP ver.3.2 package (Generalized Regression Analysis and Spatial Predictions; Lehmann et al., 2002b; Maggini et al., 2006) within S-Plus v.6.2 (Insightful Corp., Seattle, WA, USA). A binomial probability distribution was used to fit presence/absence of vegetation communities or presence/absence of butterfly species according to the modeling design described in Table 5.4. An overall prevalence of 0.5 was artificially obtained for each butterfly species by weighting the observations (Lehmann, 2005): a weight of 1 was attributed to each presence while the weight for the absences was defined by the ratio [number of presences/number of absences]. Three degrees of freedom were allowed to fit smoothed response curves for the predictors listed in Table 5.3. Models were selected using the CROSS procedure, a selection method available in GRASP which is based on cross-validation (Maggini et al., 2006). At each step of the selection procedure, a cross-validation (5 groups) is performed and a cross-validated area under the curve of a ROC plot calculated (cvROC). The procedure stops when no supplementary predictors can be added or removed according to a Bayesian information criterion (BIC; Schwarz, 1978) and the model reaching the best cvROC value is finally retained. The direction of the procedure was set to backward, therefore starting with a full model and subsequentially testing for the less contributing predictor that is removed. The contribution of each predictor in the selected model was calculated as a percentage of the sum of model contributions as defined by GRASP. For each predictor, model contribution was defined by the possible range of variation on the linear predictor scale.

5.3.3.2 Predictors

Different categories of predictors were tested and Table 5.3 shows the full list of predictors that were finally retained for modeling the distribution of the vegetation communities and butterfly species. These are climatic, geological, topographic and landuse-related predictors. The majority of these

predictors was previously employed and extensively described in Maggini et al. (2006); only additional predictors will be described in details here.

A continentality index (*gams*), defined on the basis of annual precipitation and mean annual temperature (Zimmermann and Kienast, 1999), was added to the climatic predictors. In particular, this index helps differentiating the southern part of the study area (South of the Alps) that is characterized by milder temperatures and higher precipitation when compared to the northern part.

The soil potential for grasslands (*grass*) was derived from the digital soil suitability map of Switzerland (OFS, 2003) and gives the soil potential for grassland production (class 1 = low production to class 4 = high production).

Landform classes were defined using the free extension Topographic position index (TPI) v. 1.3.a (Jenness, 2005) for ArcView ver. 3.x (ESRI, Redlands, CA, USA). This extension calculates topographic position index grids from elevation grids and classifies the landscape into landform categories. The radius for the calculation of the small- and large-area TPI grid was set to 500 and 2000 m respectively. Two of the original 10 landform classes were significantly under-represented and therefore aggregated with one of the most similar main categories. The landform predictor (*lf5002000*) was thus finally composed of 8 classes defined as follows: class 1 = canyons, deeply incised streams; class 2 = mid slope drainage; class 3 = U-shaped valleys; class 4 = plains; class 5 = open slopes; class 6 = upper slopes, mesas; class 7 = mid slope ridges; class 8 = mountain tops, high ridges.

Finally, land use / land cover information was added trough the predictor *lu* that was derived from the Swiss land use statistics 1992/97 (OFS, 2003). The information of the Swiss land use statistic (original resolution: 100 m) was downscaled to a resolution of 25 m (Lehmann et al., in prep.) and non relevant classes filtered out (e.g. lakes, glaciers, forested areas, urban areas). Classes retained were grouped as follows: class 1 = favorable arable land and meadows (81); class 2 = other arable land and meadows (82); class 3 = farm pastures (83); class 4 = scrub vegetation (16, 84, 86); class 5 = mountain meadows (85); class 6 = alpine pastures (88, 89); class 7 = remote and steep alpine meadows and pastures (87) & unproductive grass (97); class 8 = wetlands (95); class 9 = bare land (99). The original code of the classes used in the Swiss land use statistics is given in brackets as reference.

Table 5.3 Predictors employed for modeling the distribution of vegetation units and butterfly species. * Employed for the modeling of vegetation communities; # Employed for the modeling of butterfly species.

PREDICTORS	DEFINITION	RANGE within the study area	SOURCE
CLIMATE			
MAT * #	Mean annual temperature: average of mean monthly temperatures	- 1051 - 1222 (°C)*100	WSL
MGSR * #	Mean growing season solar radiation: average of mean monthly solar radiation over growing season (March-October)	2507 - 27394 (KJ m^{-2} day^{-1})	WSL
MGMI #	Mean growing season moisture index: average of mean monthly moisture index over growing season (March-October)	-949 – 2530 (mm)	WSL
WIPREC * #	Mean winter precipitation: average of mean monthly rainfalls over winter time (December -February)	907 - 7255 (mm)*10	WSL
PREC7 #	Mean July precipitation	310 - 2807 (mm)*10	WSL
SWB*	Site water balance: estimation of water amount available for plants during a year obtained by integrating monthly precipitation and potential evapotranspiration over time, and considering soil storage capacity	- 7514 - 1500 1/10 (mm $year^{-1}$)	WSL
GAMS* #	Continentality index	50 – 731 (°C/mm)	WSL
GEOLOGY			
CaCO3*	Calcareous content of parent material derived by expert knowledge (Jacques Ayer, University of Neuchâtel) from the Swiss geotechnical map (OFS, 2003)	6 classes	OFS transformed by J.Ayer
PERMEA*	Rock permeability derived by expert knowledge (Jacques Ayer, University of Neuchâtel) from the Swiss geotechnical map (OFS, 2003)	4 classes	OFS transformed by J.Ayer
GRASS*	Soil potential for agriculture (grasslands) derived from the Swiss soil suitability map (OFS, 2003)	5 classes	OFS transformed by R.Maggini
LANDUSE			
LU*#	Land use/ land cover information derived from the Swiss land use statistics 1992/97 (OFS, 2003) downscaled to a resolution of 25 m by expert rules and focal analyses (Lehmann et al., in prep.) and reclassed into 9 main classes.	9 classes	OFS/Geostat transformed by A.Lehmann, R.Maggini et al.
TOPOGRAPHY			
SLOPE*	Slope angle derived from the DEM at 25m resolution	0 to 88 (°)	SWISSTOPO (DEM)
Lf5002000*	Landform classes defined according to (Jenness, 2005) and using 2 radii (500m, 2000m). The original 10 classes have been regrouped into 8 main classes.	8 classes	SWISSTOPO (DEM) transformed

For each predictor a corresponding layer was prepared and stored in the geographic information system ArcView ver. 3.3 (ESRI, Redlands, CA, USA) in order to build spatial predictions. All layers were prepared at a resolution of 25 m.

5.3.3.3 Experimental design

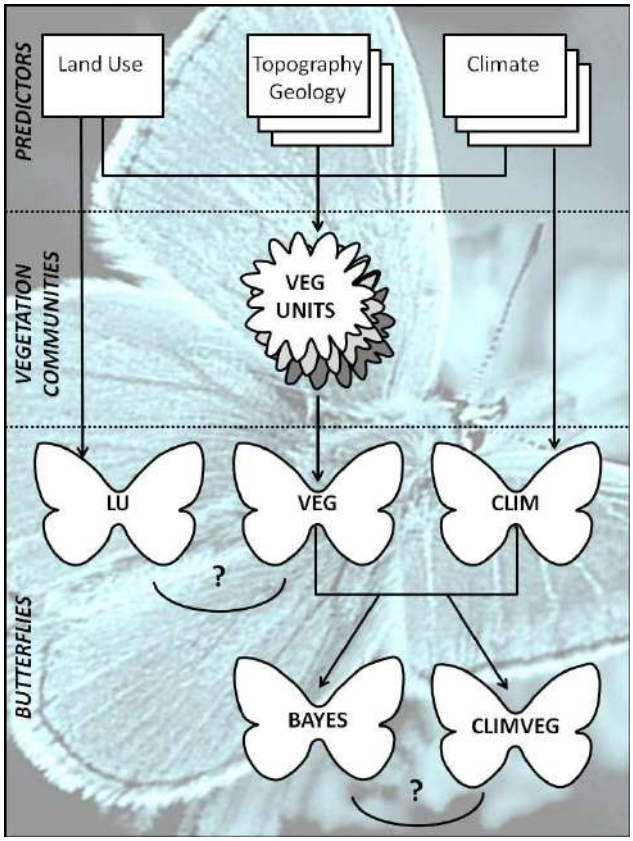

Figure 5.1 Experimental design. At the top are listed the different categories of predictors ▭ used for the modeling of the vegetation communities and the butterfly species . The flow of analysis is described in the text and Table 5.4 describes the content of the different models. Photo ©CSCF website.

The distribution of different grassland, pasture and mowing meadow communities were modeled as a first step (VEG UNITS) using environmental predictors (climate, geology, topography) and land use information. The distribution of butterfly species was then modeled using three separate types of predictors: land use information (LU), the pre-modeled vegetation communities (VEG) and climatic predictors (CLIM). This preliminary step in the modeling of the butterfly distribution aims at assessing which source of information between land use and vegetation communities is contributing the most. Our hypothesis is that information on the distribution of vegetation communities has a sounder biological content than pure land use information and will therefore contribute more significantly. The rest of the experimental design is therefore illustrated using this source of information. The distribution of the butterfly species was then determined using information related to climate and vegetation communities that were integrated: i) in a same model as predictors (CLIMVEG); ii) by combining the occurrence probabilities issued from the corresponding single models (CLIM; VEG) using the formula of Bayes (BAYES). The predictors used to calibrate the CLIMVEG model were the predictors that were finally retained in the preliminary models CLIM and VEG. These predictors

define the starting model that undergoes a new selection procedure and can therefore differ from one butterfly species to another. Within the BAYES experiment the spatial predictions issued from the climatic model (CLIM) and the predictions issued from the vegetation model (VEG) were combined using the formula of Bayes. The detailed experiments are described in Table 5.4 and the experimental design presented graphically in Figure 5.1.

Table 5.4 Description of the modeling experiments presented in Figure 5.1.

EXPERIMENTS	
VEGETATION COMMUNITIES	
VEG UNITS	Vegetation communities model: veg. unit (p/a) ~ climate + geology + topography + land use
BUTTERFLY SPECIES	
CLIM	Climatic model: butterfly (p/a) ~ climate
VEG	Vegetation model: butterfly (p/a) ~ veg. units (modeled in VEG UNITS)
LU	Land use model: butterfly (p/a) ~ land use (same classes used to model VEG UNITS)
CLIMVEG	Climatic and vegetation model: butterfly (p/a) ~ climate (predictors retained in CLIM) + veg. units (predictors retained in VEG)
BAYES	Combination of CLIM and VEG predicted probabilities of occurrence (spatial predictions) according to the formula of Bayes (Pereira and Itami, 1991)

5.3.3.4 Spatial predictions

Spatial predictions were obtained in ArcView ver. 3.3 (ESRI, Redlands, CA, USA). Models were exported from S-Plus as lookup tables (Lehmann et al., 2002b) and then interpreted in the geographic information system by an Avenue script available within the GRASP package. Spatial predictions for the LU, CLIM, VEG, and CLIMVEG experiments were built directly from the corresponding lookup tables. Maps of spatial predictions presented in the results section give the probability of occurrence of the different butterfly species across Switzerland.

Integrated spatial predictions (BAYES) were obtained by the combination of the probabilities obtained from CLIM and VEG spatial predictions. Probabilities were combined according to the Bayes formula as previously performed by Pereira and Itami (1991) while defining the habitat for the Mt Graham Red Squirrel by combining satellite imagery and land use information. The formula allows to revise a prior probability (here the CLIM probability) by an additional information (the VEG probability).

For comparison purposes, predictions for CLIMVEG and BAYES were also translated into presence/absence maps. Predicted probabilities were transformed into presences/absences according to the currently most recommended thresholds (Jimenez-Valverde and Lobo, 2007; Freeman and Moisen, 2008). These were defined according to the following criteria: a) predicted prevalence = observed prevalence (PrevPred=PrevObsT); b) maximum Kappa value (maxKappaT); c) sensitivity-specificity difference minimizer (MDT); d) sensitivity-specificity sum maximizer (MST); and finally e) a user defined sensitivity threshold of 95%, i.e. 95% of the observed occurrences are in fact reclassified as presences (95%T; Lehmann, 2005). The resulting surfaces, which should correspond to the areas of occupancy (AO) used in conservation biology, were then compared by a Wilcoxon signed-rank test.

5.3.3.5 Validation/Evaluation

All models were validated using the Area Under the Curve of a Receiver Operating Characteristic plot (ROC; Fielding & Bell, 1997) and a fivefold cross-validated ROC (cvROC) on the calibration data set. Model accuracy was classified according to the scale of Swets (1988): 0.5–0.7, poor discrimination ability; 0.7–0.9, reasonable discrimination; 0.9–1, very good discrimination. A supplementary validation statistic was provided by the calculation of the correlation coefficient between observed and predicted values (COR; Elith et al., 2006) and the corresponding cross-validated value (cvCOR).

ROC, cvROC, COR and cvCOR were only available for the modeling experiments (i.e., VEG UNITS, CLIM, VEG, LU, CLIMVEG) as a GRASP output. In order to validate and compare with the experiment BAYES - which is mainly a combination of spatial predictions taking place within the GIS - ROC* and COR* values were calculated directly on the spatial predictions for all the experiments. Plots in the Results section present the average median value as well as the confidence interval obtained by bootstrapping the ten ROC* and COR* values of each experiment a 1000 times. An independent evaluation was performed on an independent dataset counting 2906 more recent observations (2006-2007) for the ten target species. Spatial predictions corresponding to the observational points were sampled and ROC* and COR* statistics calculated for the different experiments. There are thus two levels of validation: cross-validation of the training data and fully independent evaluation.

5.4 RESULTS

5.4.1 Vegetation communities

All vegetation communities were modeled successfully: the ensemble of the ROC values was higher than 0.8 (Figure 5.2) and 75% of the values were higher or equal to 0.9, which corresponds to a very good discrimination ability according to Swets (1988). After cross-validation, 96% of the ROC values were still higher than 0.8 and 46% higher than 0.9, indicating a fairly good model stability. COR values ranged between 0.23 for unit 5.4.1 and 0.702 for unit 4.2.1.1 (Figure 5.2), these are the same communities found for ROC extremes values. The majority (79%) of COR values ranged between 0.3 and 0.6. After cross-validation, 54% of the values were still between 0.3 and 0.6.

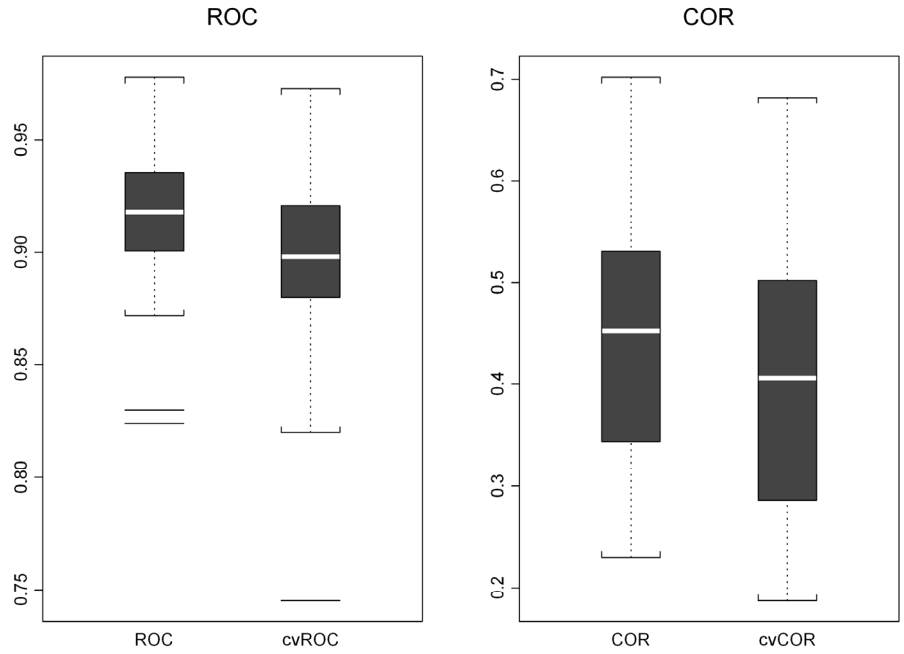

Figure 5.2 ROC and cvROC statistics obtained for the models of the vegetation communities. Coefficient of correlation (COR) and cross-validated coefficient of correlation (cvCOR) calculated between observed and predicted values.

The contribution (in percentage) of each predictor within the model (model contribution in GRASP) calibrated for each vegetation community is shown in Table 5.5. Mean annual temperature (mat), land use/cover (lu) and site water balance (swb) were the main contributors within models. Their mean contribution (averaged over the 24 vegetation communities) was 23.15, 21.93 and 18.43 % respectively. The continentality index (gams) and slope played a relative important role, followed by the mean growing season solar radiation (mgsr) and winter precipitations (wiprec). The contribution of the calcareous content (CaCO3) and permeability (permea) of parent material, as well as the soil potential for agriculture (grass) and landform (lf5002000, shortened to LF in Table 5.5) was low overall. Interestingly, *grass* was mainly retained in models for nutrient-poor grasslands, the only exception being the lowland hay meadow (4.5.1). Landform was mainly retained by two vegetation communities: the fresh calcareous lawn (4.3.3) and the acid rocky lawn (4.3.6). The predictor for calcareous content was relatively important only for unit 4.3.7, which is a grassland that grows on acid soils.

Table 5.5 Contribution in percentage of each predictor within the selected model for each vegetation community (VEG UNITS). Predictors are here listed with their abbreviation described in Table 5.3; the only exception is Lf5002000 that has been shortened to LF.

UNIT	MAT	SWB	MGSR	WIPREC	GAMS	CaCO3	PERMEA	LU	GRASS	SLOPE	LF
Y2.3.1	9	0	13	9	11	0	2	50	0	6	0
Y2.3.2	18	11	4	6	16	4	1	20	0	20	0
Y2.3.3	5	10	6	6	21	0	2	29	0	20	0
Y4.2.1.1	19	15	4	6	16	3	3	25	0	9	0
Y4.2.1.2	16	5	6	4	15	0	1	24	23	6	0
Y4.2.2	37	6	0	3	13	0	0	36	0	5	0
Y4.2.4	40	15	8	5	22	2	0	4	1	3	0
Y4.3.1	13	32	2	4	8	5	2	28	0	5	0
Y4.3.2	9	54	2	2	7	3	1	22	0	0	0
Y4.3.3	11	30	1	3	7	2	1	15	12	5	13
Y4.3.4	28	8	3	3	6	6	3	36	0	7	0
Y4.3.5	29	18	0	8	24	4	2	4	3	5	2
Y4.3.6	14	11	4	3	11	4	1	22	2	5	23
Y4.3.7	29	16	0	1	12	17	0	11	10	2	0
Y4.4.1	10	51	4	2	5	3	0	14	10	2	0
Y4.4.2	31	5	5	3	7	3	3	21	14	6	3
Y4.5.1	49	12	1	4	9	3	2	11	2	3	4
Y4.5.2	38	0	13	16	0	0	0	18	0	15	0
Y4.5.3	41	16	2	9	22	0	0	7	0	3	0
Y4.5.4	27	0	2	2	26	2	1	31	0	7	2
Y5.4.1	17	33	20	0	0	0	0	27	0	3	0
Y5.4.4	9	46	4	5	12	3	0	21	0	0	0
Y5.4.5	12	46	3	4	8	0	2	25	0	0	0
Y5.4.6	46	0	8	3	0	0	0	27	0	16	0

5.4.2 Butterflies

5.4.2.1 Are vegetation communities better predictors than land use in distribution models for fauna?

Altogether all butterfly species could be modeled successfully. For the main modeling experiments (CLIM, VEG, CLIMVEG), 90% of ROC values ranged between 0.7 and 1, the only exception was the species *Coenonympha pamphilius* (CPAM) for which we obtained low ROC values (0.632-0.694). For the CLIM experiment, 60% of ROC values were higher than 0.9, whereas the proportion for VEG was of only 30 % and for CLIMVEG 70%. As shown by Figure 5.3 and according to a Wilcoxon signed-rank test, the validation statistics obtained for the pure vegetation model (VEG) were significantly lower ($p \leq 0.01$) than the statistics obtained for the climatic model (CLIM). However, ROC values for the full model (CLIMVEG) were significantly higher ($p<0.01$) than ROC values for the pure climatic model, thus revealing a significant contribution of pre-modeled vegetation communities.

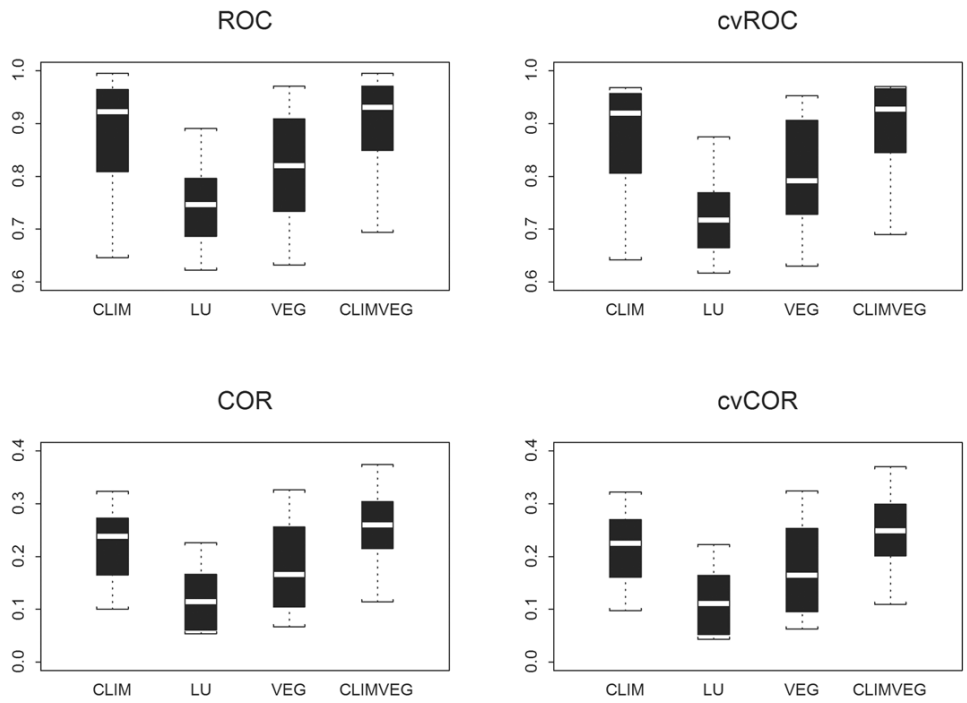

Figure 5.3 Area under the curve (ROC) of a ROC plot, cross-validated ROC (cvROC), coefficient of correlation (COR) and cross-validated COR (cvCOR) for the climatic (CLIM), the land use (LU), the vegetation (VEG) and the full butterfly model (CLIMVEG). Boxplots represent validation statistics for the 10 modeled butterflies.

The same pattern could be identified for COR values. According to the Wilcoxon signed-rank test the coefficients of correlation (COR) calculated between observed values and predicted values for VEG were significantly lower ($p<0.05$) than the coefficients calculated for CLIM. However, the correlation coefficients for experiment CLIMVEG were significantly higher ($p<0.001$) than the coefficients for the pure climatic or pure vegetation model.

Moreover, altogether validation statistics obtained for VEG were significantly higher ($p<0.01$) than validation statistics obtained for LU, thus indicating that the significant contribution of VEG is not merely related to the land use information incorporated in it.

Table 5.6 Contribution in percentage of each predictor within the selected full model CLIMVEG for each butterfly species. Underlined null contributions belong to predictors that were retained in the base pure environmental or pure habitat model, but that were not retained in the full model.

	BRIN	BTIT	CPAM	ERCA	ERPH	ERPR	MATE	PCRS	PDAM	PTHE
MAT	12	25	26	41	49	16	13	25	26	31
MGMI	12	22	22	0	0	7	35	25	0	44
MGSR	20	4	0	0	0	0	6	0	25	0
WIPREC	8	4	3	8	4	20	12	13	7	9
PREC7	5	4	8	25	0	12	14	2	6	11
GAMS	22	34	36	23	0	45	15	30	31	0
MARSH	6	1	0	0	4	0	1	0	0	0
PEAT	1	1	0	0	0	0	0	0	0	0
X2.3.3	9	0	0	0	0	0	0	0	0	0
X4.5.2	5	1	0	0	7	0	3	0	0	0
X2.3.1	0	0	0	0	0	0	2	0	0	0
X4.5.1	0	0	3	0	0	0	0	2	0	2
X4.2.4	0	0	0	0	0	0	0	2	1	4
X4.3.1	0	0	0	4	5	0	0	0	4	0
X2.3.2	0	0	0	0	0	0	0	0	0	0
X4.3.3	0	1	0	0	0	0	0	0	0	0
X4.5.3	0	2	2	0	0	0	0	1	0	0
X4.5.4	0	1	0	0	10	0	0	0	0	0
X4.3.5	0	0	0	0	10	0	0	0	0	0
X4.3.6	0	0	0	0	12	0	0	0	0	0

The contribution of each predictor within the CLIMVEG butterfly models is shown in Table 5.6. Climatic predictors and in particular the mean annual temperature (mat), the continentality index (gams) and the mean growing season moisture index (mgmi) were the major contributors. The cumulated contribution of vegetation communities was generally lower than 10 %. Exceptions were detected for *Brenthis ino* (BRIN) and *Erebia parthe* (ERPH) for which this contribution reached 21 % and 47 % respectively. For the species *Erebia pronoe* (ERPR) no vegetation-related predictor was retained in the full model.

As an example, response curves of the predictors retained in the CLIMVEG model of the BRIN species are presented in Figure 5.4. Its habitat is characterized by sunny areas with a high continentality index and a certain amount of humidity at different period of the year: during the growing season (mgmi), winter time (wiprec) and in particular during the emergence (prec7) which takes place during summer (Ligue suisse pour la protection de la nature, 1987). *Brenthis ino* is linked to humid types of vegetation. Main predictors retained in the model are indeed marshes, marshy tall herb communities (2.3.3) and humid mowing meadows (4.5.2).

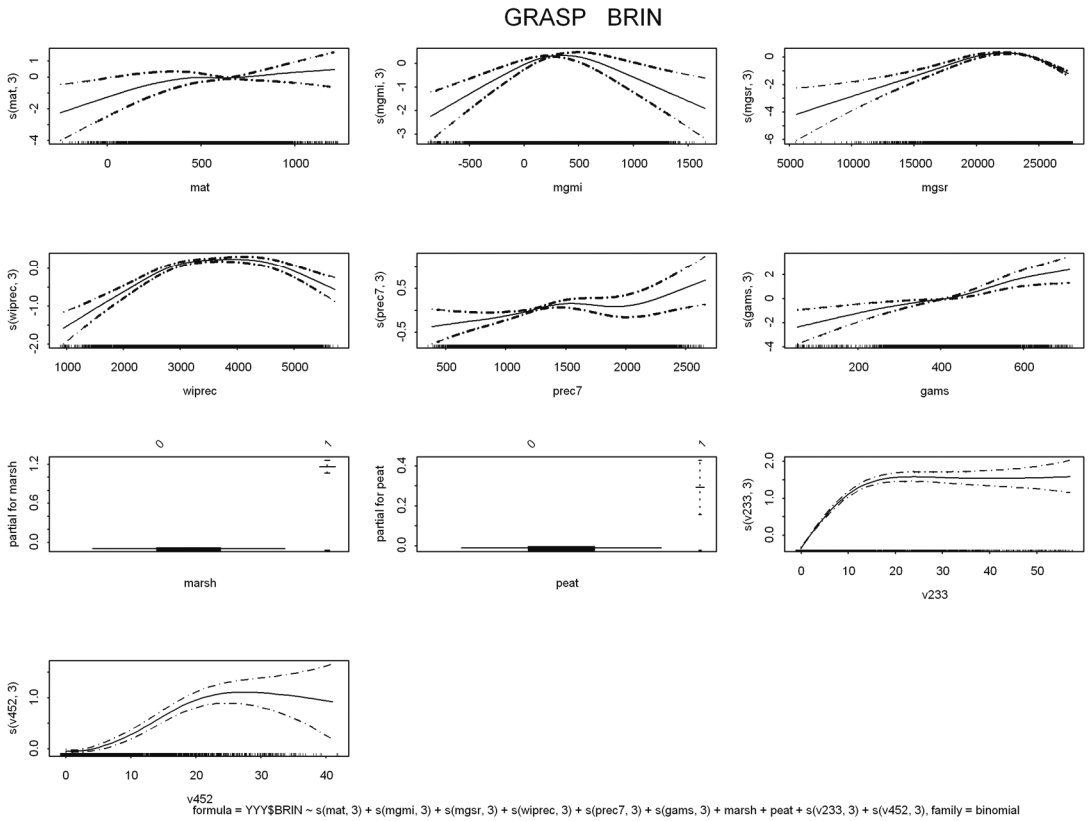

Figure 5.4 Response curves for predictors retained in the full model (CLIMVEG) for *Brenthis ino* (BRIN).

The vegetation communities retained in the model for the different butterfly species were mainly those indicated in the Swiss habitat typology (Delarze et al., 1998) on the basis of expert knowledge or those observed in the field by volunteers and reported in the CSCF databank. Few exceptions are represented by the humid mowing meadow *Polygono-Trisetion* (4.5.2), which was often retained in models in association with other humid environments and the subalpine-alpine fertilized pasture *Poion alpinae* (4.5.4) that is not a main habitat for butterflies but is often mixed with either dry or wet grasslands, which are important elements of butterflies habitats.

5.4.2.2 What is the best way to integrate vegetation information?

In order to be able to perform a comparison with results of experiment BAYES, which were here obtained by the combination of spatial predictions and not directly by modeling, validation statistics (ROC* and COR*) were recalculated for each experiment on the probabilities given by the spatial predictions within the regions shaped by VEG and the land use information incorporated in it that filters out non relevant land use classes.

The best validation statistics were obtained by the CLIMVEG model. Putting climatic and vegetation predictors inside the model therefore gave better predictions than the Bayesian combination of the corresponding predictions (BAYES) or the base climatic (CLIM) or vegetation (VEG) predictions ($p<0.001$ for ROC* and $p<0.01$ for COR* according to a Wilcoxon signed-rank test). ROC* values for the CLIMVEG predictions ranged between 0.670 and 0.995 (all butterfly species confounded),

whereas COR* values ranged between 0.128 and 0.379. Figure 5.5 shows the bootstrapped ROC* and COR* medians and relative confidence interval for the different experiments.

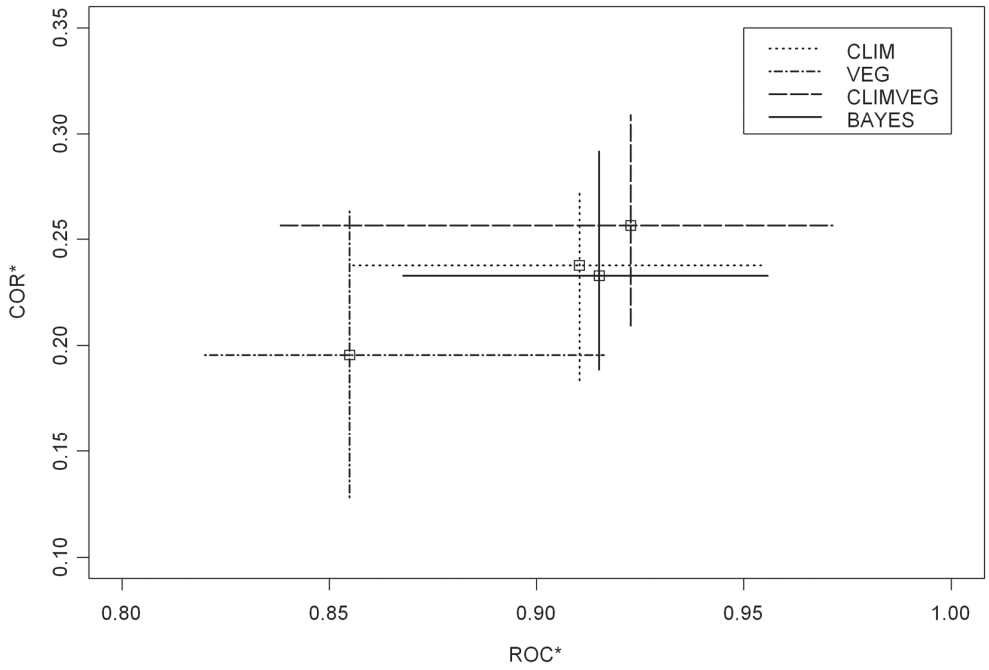

Figure 5.5 Average median value and confidence interval obtained by bootstrapping a 1000 times the ROC* and COR* calculated on the climatic predictions (CLIM), the vegetation-related predictions (VEG), the predictions derived from the full model (CLIMVEG) and the Bayesian combination of the climatic and vegetation predictions (BAYES) for the 10 butterfly species.

How these translate spatially? Figure 5.6 shows the spatial predictions for *Brenthis ino* (BRIN) across the entire Swiss territory and within one particular area for each experiment. As shown by the figure, the climatic predictions (CLIM) define the relatively large pattern of potential distribution within which vegetation (VEG) delineates more precisely the patches that are/could be occupied in reality. Spatial predictions obtained from the full model (CLIMVEG) or by the combination of the climatic and vegetation-related predictions (BAYES) are very similar at least in the configuration and emplacement of favourable zones. However, the probabilities of occurrence of the species within these zones differ: CLIMVEG incorporates the climatic and the vegetation information in a balanced way, whereas the Bayesian combination of predictions seems to favour the climatic information, which has clearly the major contribution. This first appreciation is confirmed by the assessment of the predicted probabilities. The mean probability of occurrence predicted for pixels where the species was actually observed is on average significantly higher ($p<0.01$) for BAYES than for CLIMVEG. The median of the average probabilities for the ten butterfly species is 0.89 for BAYES and 0.81 for CLIMVEG.

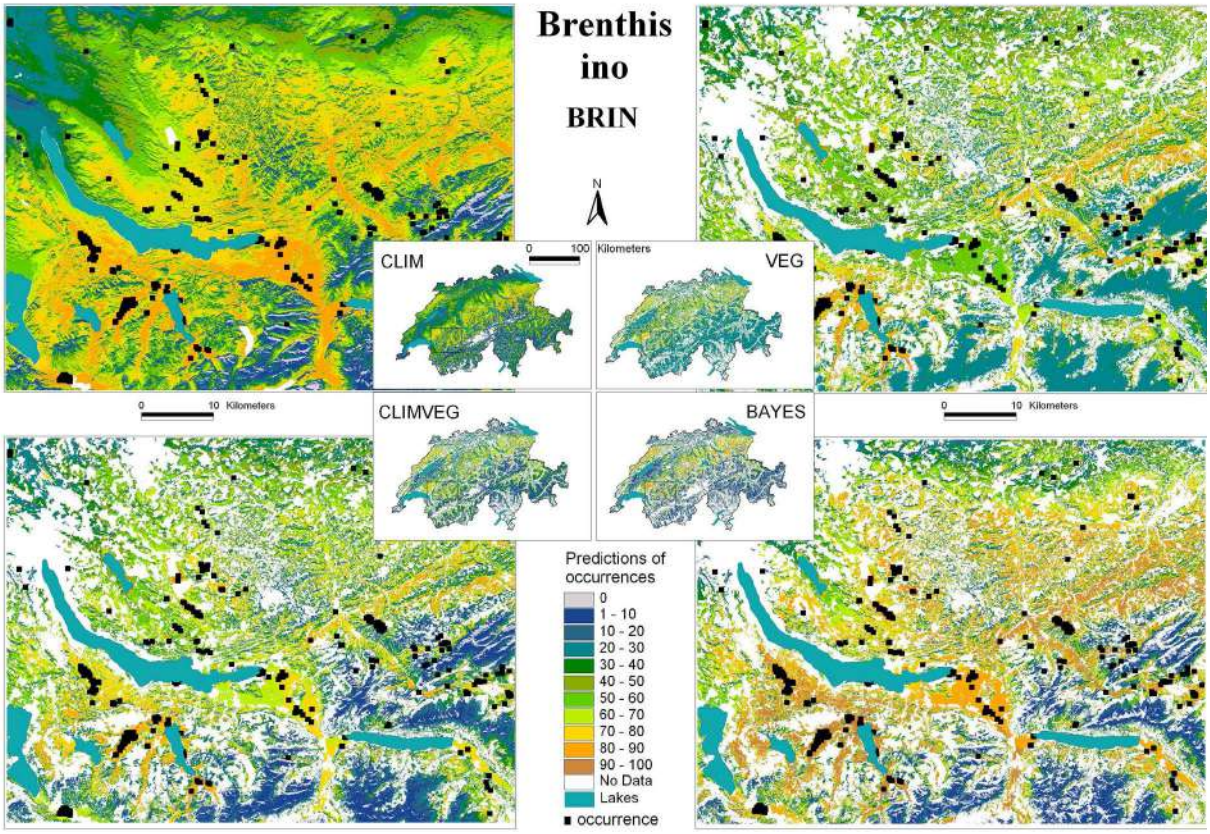

Figure 5.6 Spatial predictions for *Brenthis ino* (BRIN) obtained from the climatic model (CLIM), the vegetation model (VEG), the full model (CLIMVEG) and the Bayesian combination of climatic and vegetation-related predictions (BAYES) within the zone defined by the habitat filter.

When transforming the predicted probabilities into presences/absences, thresholds determined for BAYES were systematically higher than for CLIMVEG according to all criteria, except for the 95%T and the MST.

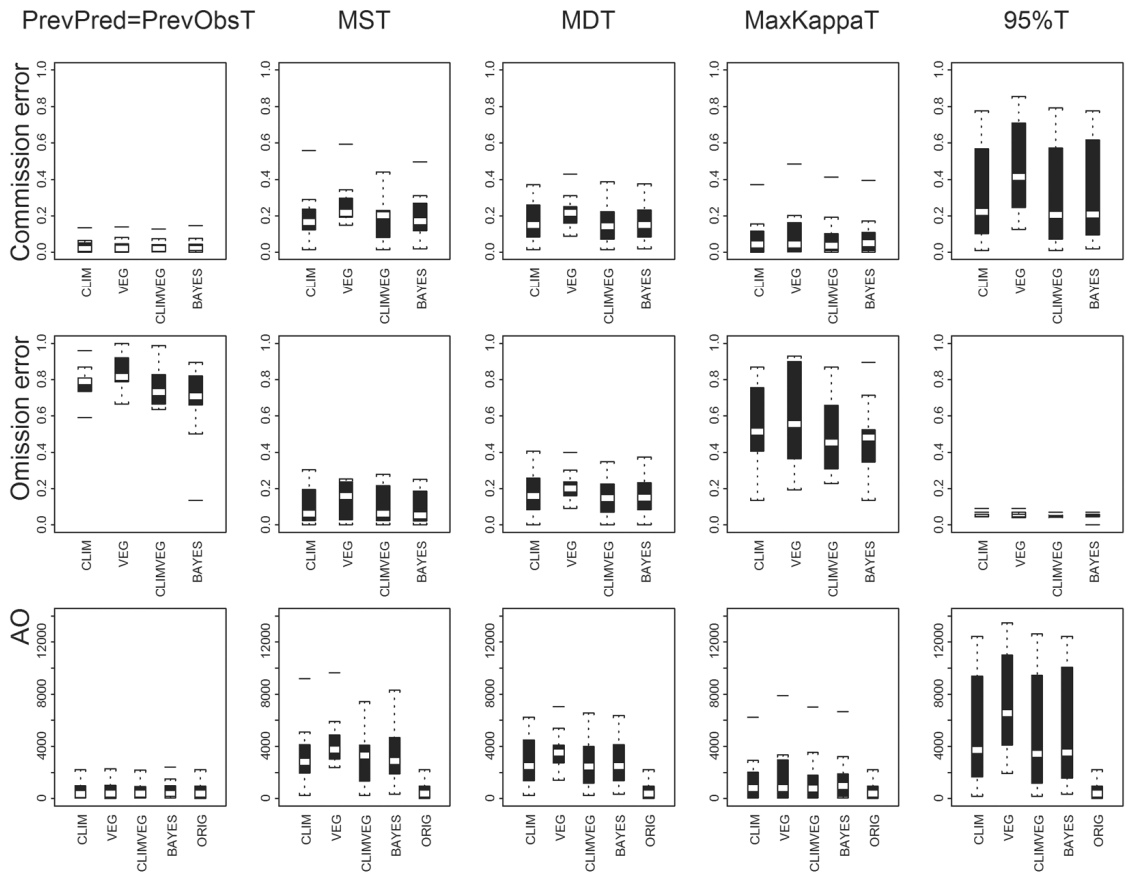

Figure 5.7 Commission, omission errors and areas of occupancy (AO) resulting from the transformation of the predicted probabilities into presences/absences according to different thresholds: PrevPred=PrevObsT, MST, MDT, MaxKappaT and 95%T. Boxplots represent values for the 10 modeled butterfly species in the different experiments: CLIM, VEG, CLIMVEG and BAYES. To the plots representing AO we also added the original AOs (ORIG) for comparison**.**

In Figure 5.7 are represented the commission and omission errors as well as the areas of occupancy obtained when transforming the predicted probabilities into presences/absences according to the different thresholds. Results obtained for CLIMVEG and BAYES are not significantly different except for the threshold 95%T. When using this threshold, commission errors and AOs are higher for BAYES ($p<0.05$) according to a Wilcoxon signed rank test. More globally, commission, omission errors and the extent of predicted AOs vary greatly according to the chosen type of threshold. With threshold PrevPred=PrevObsT the commission error is very low and predicted AOs are very close to the observed ones, but omission errors are the largest. The omission error obtained with threshold 95%T is the smallest in absolute, but on counterpart commission error is the highest, leading to the largest AOs. As for PrevPred=PrevObsT, predicted AOs obtained with the threshold maxKappaT are very close to the observed ones and commission error is low, but omission error is very high. Commission and omission errors obtained with MST and MDT are low and balanced between the two types of error. The correct classification rate is however higher for MDT in all experiments except for CLIM (results not presented here). With threshold MDT, CLIMVEG results in a higher correct classification rate than BAYES.

Evaluation statistics calculated on the independent dataset are summarized by Figure 5.8. Best values were again obtained by CLIMVEG and in this case BAYES values were closer to CLIMVEG than to CLIM values. However, altogether ROC* values were not significantly different according to a Wilcoxon signed-rank test. COR* values of CLIMVEG were significantly different from those of CLIM ($p<0.01$); this was not true for BAYES in respect to CLIM.

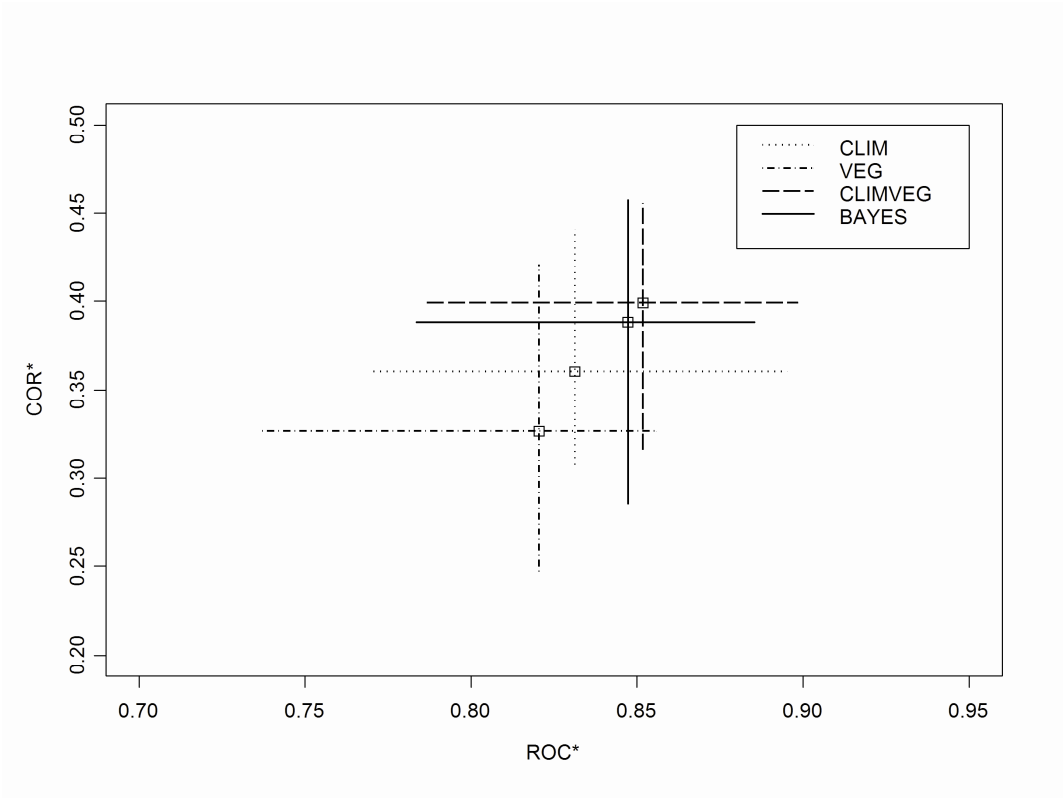

Figure 5.8 Average median value and confidence interval obtained by bootstrapping a 1000 times the ROC* and COR* calculated on the climatic predictions (CLIM), the vegetation-related predictions (VEG), the predictions derived from the full model (CLIMVEG) and the Bayesian combination of the climatic and vegetation predictions (BAYES) for the 10 butterfly species of the independent evaluation data set.

5.5 DISCUSSION

5.5.1 Modelling vegetation communities

As a first step of the proposed approach, the distribution of natural and anthropogenic grassland communities was modeled successfully. The main predictors were the mean annual temperature, land use/cover and site water balance. The continentality index and slope played a relative important role, followed by the mean growing season solar radiation and winter precipitation. The contribution of the calcareous content and permeability of parent material, as well as the soil potential for agriculture and

landform was surprisingly low. Main retained predictors were similar to those found in Zimmermann and Kienast (1999). Indeed, in their study the four main bioclimatic parameters for modeling alpine grasslands were degree-days of growing season, July moisture index, March potential direct solar radiation and the continentality index. While not used for their modeling, land use was however detected by the authors as a major factor that could improve models for both, single species and communities. Similarly, Pearson et al. (2004), found that the incorporation of land-cover data significantly improved purely climatic predictions when modeling plant species, but land-cover was fitted locally whereas the European scale was necessary to capture the whole climatic niche of the species. This confirms the general hypothesis that factors affect the distribution of species at different scales and in a hierarchical manner, climate being the major factor at the global scale while land cover and topography becoming more important at local scale (Pearson and Dawson, 2003; Pearson et al., 2004).

While predicting species composition of *Nardus stricta* plant communities, Peppler-Lisbach and Schroder (2004) used a set of predictors reflecting soil properties, human management and climatic conditions. The variables most frequently retained in models were climatic predictors (annual precipitation and mean temperature in January) as well as variables related to soil acidity and moisture. Soil pH was in their case a good predictor to account for soil acidity. In our study, acidity was indirectly represented by the calcareous content of parent material, which contribution was low. This predictor is very likely too distal to reflect soil pH. Indeed, even if parent material is at the origin, other important phenomena contribute to soil development and to its final acidity.

In our modeling we integrated information concerning soil potential for agriculture, which aimed at differentiating soil supporting grasslands with low production from enriched soils supporting high productive grasslands. This predictor was mainly retained in a negative way for vegetation communities that are not linked to agricultural exploitation (acid lawn of the higher alpine belt, communities associated with localized snow accumulation, semi-dry continental grasslands). It was therefore useless to differentiate the different degrees of exploitation of “agricultural grasslands”, but helpful in discriminating natural from anthropogenic grasslands.

Land form was retained only for few communities and importantly only for two of them, which are the fresh and the acid rocky lawns. These are characterized by relatively large depressions in the mountain side where water or rocks can accumulate. The combination of radii that were chosen (i.e. 500 and 2000 m) allows discriminating these kinds of soil depressions, but not smaller depressions where snow accumulates. For the latter smaller radii are needed (Guisan and Theurillat, 2000).

5.5.2 Community vs single species modelling

This paper focuses on modelling and predicting vegetation communities directly as entities. Is this a reasonable approach? The alternative approach is the so-called “predict first, classify later” (Overton et al., 2000), where the distribution of individual species are first predicted and then communities are reassembled from independent species predictions. This approach mainly results in assemblages of species co-occuring in space from which biotic domains can be defined (Leathwick, 2001; Overton et al., 2002) or “site-groups” species mapped by “modelling-then-classification” according to Ferrier et al. (2002a). Our approach corresponds rather to the “classify first, predict later” approach also known

as “assemble first, classify later” (Ferrier and Guisan, 2006). Releves performed in the field were first classified according to the Swiss typology of natural vegetation communities (Delarze et al., 1998) and then communities (alliance level) were modelled as a function of environmental variables. In order to classify releves we used a decision support system created within the framework of the Landspot project. Each species was weighted according to its importance (characteristic versus accompanying species) within the different typological units and the unit(s) accumulating the highest score was assigned to the releve. A similar system or a system based on expert knowledge could be applied in order to guide the classification *a posteriori* of the single species predictions in order to obtain the desired level of classification (ex. alliance). The weighting system would in this case be complemented by the occurrence probabilities of the single species in order to define the communities at a given site. In principle we therefore agree that communities should be derived *a posteriori* from individual species predictions. However, the direct approach was adopted here to improve land cover/use maps with a sound biological content and then use them to predict animal species distribution. Indeed, for conservation purposes, “*Mesobromion*” is more useful information than the general class “meadow” found in land cover classification. Also, when modelling communities directly one intrinsically captures biotic interactions among species, the lack of which is often criticized in species distribution modelling. In contrast, the “predict first, classify later” approach is a relatively complex, data hungry and time consuming approach.

A compromise would have been to directly model the host species for the target butterflies. Several examples exist in the literature of this kind of direct approach (e.g. Luoto et al., 2001; Krauss et al., 2004; Araújo and Luoto, 2007). Even though this is certainly an elegant and powerful approach, it also suffers from several limitations. It relies on knowledge of the host species, which is far from being complete and that is often site-specific (Hardy et al., 2007). Moreover, butterflies have a complex lifecycle. Their habitat is thus not simply defined by the species on which caterpillars develop, but also by the species providing nectar to the adults which are often different species. According to a recent review Dover and Settele (2009) factors determining habitat for butterflies act at different scales with the size and arrangement of patches being important at the landscape level in determining the presence of the butterfly and the percentage of cover of host/nectar plant influencing the abundance of the butterfly at the level of the patch itself (Heikkinen et al., 2005). The host species approach would nonetheless be indicated in the case of studies dealing with climate change. In order to predict the distribution change for the butterfly it would be necessary to predict the vegetation shift as a first step. Indeed, as supported by Schweiger et al. (2008) while modelling and projecting the distribution for the butterfly *Boloria titania* and its larval host plant *Polygonum bistorta*, all warming scenarios resulted in a pronounced spatial mismatch of the future distributions of the two species with a consequent disruption of the trophic interactions. As several studies suggest that vegetation will not shift as a whole but that species will migrate independently (Rehfeldt et al., 2006), projecting the distribution of an entire community would therefore results in misleading approximations. Future distributions of butterflies should therefore be best predicted using individual host plant species as predictors.

Vegetation communities are assemblages of species co-occurring at a particular place as a result of their overlapping resources requirements and ecological tolerances, biotic interactions, historical dispersal and perturbation events (Zimmermann and Kienast, 1999). One can therefore ask the question, how does the “realized niche” of a community compare to those of its composing species?

According to several authors, communities have narrower “realized niches” than the single species composing them and are therefore easier to model because more uniform and limited in the environmental space (hypervolume according to Hutchinson, 1957). As an example, Zimmermann and Kienast (1999) found that the current patterns for alpine grasslands were better predicted from communities than from dominant species. Modern techniques now exist that simulate a community approach by using information relative to the presence/absence from other co-occuring species in order to model single species. These belong to the so-called “assemble and predict together” approach (Ferrier and Guisan, 2006). Multivariate adaptive regression splines (MARS) are an example of these modern techniques and comparison of individual vs community models accuracy reveal that community models perform better than single species models (Elith et al., 2006), even though this is not consistent across the application studies (Leathwick et al., 2005). While this may be, the motivation for using this kind of technique is inherent to the fact that important environmental trends may only be apparent when considering multiple species at once (Elith et al., 2006) and this would also indirectly plead in favour of the “assemble first, predict later” approach we adopted.

5.5.3 Integrating vegetation information into animal species distribution models

For species that exhibit a metapopulation dynamic, the assessment of the factors determining their distribution at the landscape level is essential. Patch area, number and connectivity have indeed proved to explain patch occupancy patterns in a satisfactory manner for butterflies (Luoto et al., 2001; Heikkinen et al., 2007). Habitat quality on the other hand seems to act at more local scale determining the abundance of the species within patches. For butterflies, habitat quality has proven to be related to the local availability of larval host plant and adult nectar sources (Luoto et al., 2001; Heikkinen et al., 2005). Without direct field work this information is only seldom available, reason why land use/cover information is often used in replacement. Land use/cover represents a first approximation of this focal information and allows narrowing the climatically favourable area for the species to something more realistic in consideration of the human activities exerted in the region. It normally allows discriminating forests from grasslands or agricultural land, but generally does not allow discriminating between different types of a same cover category, e.g. different types of grasslands. This is the improved information we could bring in with our approach. Vegetation communities are indeed a sounder predictor of animal species distribution because they indirectly inform about the presence of their resources. In particular for butterflies, vegetation communities inform about the presence of the larval host or the nectar plant, which is essential information especially when dealing with specialists. This was supported by our results, which showed that the contribution of vegetation communities to the models was significantly higher than the contribution of pure land use information. However, results also showed that the average contribution of vegetation communities in butterfly models was low overall compared to other environmental variables. Is it therefore worth the effort? The answer is clearly affirmative. As we could observe in the corresponding spatial predictions, the climatic prediction define the relatively large area that species can climatically tolerate, in this area the distribution of the vegetation communities then acts as a filter and delineates more precisely the favorable patches that are or could be occupied. Once again it appears very important to look at the spatial predictions derived from SDM since small differences in the statistical assessment can often correspond to very different spatial predictions (Maggini et al., 2006).

In consideration of the points exposed above, one could ask if the information about the distribution of vegetation communities could be used interchangeably for the distribution of animal species. This approach was often used in the past, especially prior to the development of the species distribution modeling discipline. A “cover-type model” is actually the simplest model that can be used in order to describe animal habitats (Schlossberg and King, 2009). In this kind of simplistic model, the species is assumed to be present in certain vegetation types and absent in others. Yet, this kind of models make mistakes in more than 20% of the cases and these are for the majority commission errors (up to 20%), but omission error can reach 10% (Schlossberg and King, 2009). This can finally lead to poor management decisions. Reasons for the high level of inaccuracy are to be found in the fallibility and subjectivity of expert opinion, the oversimplification of the pattern of habitat use by the animal species and neglect of important factors within cover type that determine occupancy (Schlossberg and King, 2009). This is the reason why in our modeling approach we have integrated the information relative to vegetation communities with other environmental predictors: more general predictors like climatic variables, but also more local predictors like landforms. Moreover, our approach allows different vegetation types to be integrated in the model in a probabilistic manner. The defined habitat can therefore encompass several vegetation communities and the more favourable ones will contribute more strongly to the final probability of occurrence of the species. This is a significant advantage compared to the binary information brought by simple “cover-type models”.

Once established that information about vegetation communities significantly improve models for fauna, the open question is how to integrate this information in SDMs. Two approaches were tested in this paper. Incorporating climatic and vegetation units as predictors directly in the model gave better results, according to ROC and COR values, than combining the corresponding spatial predictions with the formula of Bayes. This is probably due to the fact that the predictors that were selected in CLIM and VEG experiments undergo a new selection procedure within the experiment CLIMVEG. The selection procedure therefore allows finding the best combination of and a new equilibrium between climatic and vegetation-related predictors, avoiding redundant information. This is not possible in the BAYES experiment where base probabilities are simply combined. Corresponding spatial predictions were very similar and showed similar patterns of suitable habitat. Differences were found in the range of predicted probabilities, BAYES yielding slightly higher probabilities than CLIMVEG. When transformed into presences/absences according to different thresholds, the commission and omission errors and the predicted area of occupancy were however not significantly different between BAYES and CLIMVEG except when using the threshold 95%T (at least 95% of the observed occurrences are effectively reclassified as presences). In this case BAYES gave higher commission errors and larger AOs. Also, with threshold MDT (sensitivity-specificity difference minimizer), BAYES gave a lower correct classification rate than CLIMVEG. As a conclusion, our results did not show a clear advantage or a great difference between the CLIMVEG and the BAYES approach. However, from a practical point of view, the BAYES approach is maybe preferable because it allows better separating the role of the environment, defining the potential of distribution of the species, from the role of the vegetation communities combined with land use that reshape the potential to something closer to the actual area of occupancy of the species, i.e. its realized niche. Note also that if the probabilistic vegetation maps are replaced by actual vegetation maps, with probability 0/1 for a given vegetation type, then the BAYES approach will lead to a filtered environmental prediction.

5.5.4 Implications for conservation planning

Introducing vegetation or at least land cover information allow moving away from the spatial representation of the species fundamental niche and get closer to its realized niche, which is essential when working for conservation purposes. “Extent of occurrence” and ”area of occupancy” are concepts employed by the International Union for the Conservation of Nature in order de define the level of threat of species (IUCN, 2001). The extent of occurrence (EO) is generally estimated by a minimum convex polygon encompassing all the sites of occurrence of a given species, while the area of occupancy (AO) is defined as the area within the extent of occurrence which is actually occupied by the species. Now, these are parameters that can easily be estimated through modeling: EO being the zone of possible distribution of a species mainly defined by a climatic model and AO being the favorable climatic zone refined by favorable land use or vegetation. As an example, this kind of modeling approach was adopted in order to establish the Swiss Red list for Orthoptera (Monnerat et al., 2007).

The modeling approach has several advantages. Indeed, with the standard IUCN approach we expect EOs to be most of the time overestimated - the convex polygon encompassing non favorable environmental zones - and AOs to be most likely underestimated - favorable zones within the polygon being currently unoccupied. This expectation has been verified for example for plant by Solano and Feria (2007) when assessing the geographic distribution of the genus *Polianthes* (Agavaceae) in Mexico. Now, underestimating the potential area of occupancy of a species can be very damageable for efficient conservation planning based on a spatially explicit approach. On the other hand, AOs estimated by statistical modeling may indicate the potential rather than the actual area of occupancy of a species (Gaston and Fuller, 2009). We believe this is quite an advantage in conservation planning because it allows to assess the habitat availability in the surrounding of the currently occupied patches and thus the possibilities of survival of species with metapopulation dynamics. AOs *sensu* IUCN can always be calculated from the source occurrence data employed to calibrate the model - this measure is important because a decline in area of occupancy indirectly informs on a reduction in population size according to IUCN criteria – but potential AOs could suggest effective measures of conservation for the species. To some extent we agree with Gaston and Fuller (2009) when asserting that modeling estimates can be highly variables depending on the environmental variables retained in the model. In this respect, we can only reiterate the recommendation of Araújo and New (2007) to work within an ensemble forecasting framework, where instead of relying on only one model that we assume to be the best one, we synthesize the information brought by several similarly good models. Whatever the method, attention has to be paid to the fact that estimations are highly dependent on the spatial resolution at which base data were sampled and in particular on the spatial resolution at which distribution maps are created (Shriner et al., 2006; Gaston and Fuller, 2009; Meynard et al., 2009). At coarse resolution AOs are indeed largely over-estimated and, as stated by Gaston and Fuller (2009), a cell resolution of 3.2 x 3.2 km prevent the categorization of a species as critically endangered on the basis of the AO because resulting estimates will always be greater than the IUCN criteria of 10 km^2. We therefore agree with Shriner et al. (2006) and Gaston and Fuller (2009) that producing distribution maps at fine resolution should be a priority for conservation practitioners. And in this sense we think we performed our duty by producing distribution maps at a resolution of 25 m. A supplementary positive point of modeling is that it can be performed from data already existing, if representative, thus

avoiding long and expensive field campaigns covering the entire territory. Field work could then concentrate on the prospection of the new favorable areas designated by the model instead of surveying systematically (e.g. Boitani et al., 2008). Furthermore, modeling approaches have now been developed for presence-only data which would significantly improve the estimation of the area of occupancy of species presenting problems of detection such as rare, cryptic or nocturnal species (Thorn et al., 2009).

As mentioned earlier, the approach described in this study is probably not ideal to predict species distribution in a climate change framework; climate change being one of the recent main concern in spatial ecology. This is mainly due to the fact that vegetation communities are not expected to shift as a whole, but rather that species will shift their ranges independently. We therefore do not recommend using vegetation communities as units for studies dealing with climate change. Nonetheless, integrating information about vegetation, even only in the form of the distribution of key plant species, allows improving landscape description by adding sound biological content to basic land cover categories, which, in turn, allows improving animal species distribution modeling. Improved distribution maps are essential for a spatially explicit management of metapopulations and thus an effective conservation planning. Indeed they allow identifying new favorable areas to put under protection, to plan corridors or stepping stones in order to connect them and ultimately to design reserve networks.

Particular care has to be employed when transforming probabilities of occurrence into presence/absence. As showed in Figure 5.7, commission and omission errors as well as the derived AOs vary greatly according to the threshold employed. Lately, numerous studies have been published comparing different thresholds either on real or simulated data. Somehow, all came to the same conclusion: the threshold should be chosen in respect to the intended use of the resulting map. In order to estimate the range of a threatened species for example, it is important to avoid overestimating its AO and thus commission error. In this case it would be recommended to use a user-defined threshold of required specificity (Freeman and Moisen, 2008). The false positive error should also be minimized when the purpose is to identify experimental sites in the field where a particular species is to be found (Liu et al., 2005). Conversely, for conservation purposes it could be tolerated to have a high commission error and to put some less suitable area under protection for a particularly endangered species (Liu et al., 2005). A user-defined threshold of required sensitivity like our 95%T would thus ensure that the majority of the favorable habitat for the species will be protected, included patches that are not yet occupied but that could be crucial for the survival of the species with a meta-population dynamic in the future, especially under climate change. To a certain extent, this would meet the idea of Early et al. (2008) who suggest to translate model predictions into connectivity maps that allow conservation planning to take into account long-term spatial population dynamics. Note however that the overestimation of the area of occupancy could also lead in the short-term to the selection of reserves that do not contain the target species (Loiselle et al., 2003) with a consequent waste of resources. As a general rule of thumb, when the cost associated to false positive is greater than the cost for false negative then the threshold should favor specificity. Conversely, when the cost of false negative is greater, the threshold should favor sensitivity (Liu et al., 2005). When specificity and sensitivity are equally important, the recommended thresholds are the sensitivity-specificity sum maximiser and the sensitivity-specificity difference minimizer, the latter being the one of more general

use (Jimenez-Valverde and Lobo, 2007). Finally, when it is important to preserve observed prevalence, it is recommended to use threshold for which the predicted prevalence is equal to the observed prevalence or the threshold that maximize the kappa value (Freeman and Moisen, 2008). As a general conclusion, providing end users with probability maps instead of reclassified maps is maybe the only objective way of communicating modeling results in ecology. Reclassification can then be performed with the appropriate threshold according to the final intended use of the map.

5.6 MAJOR FINDINGS AND CONCLUSIONS

- The distribution of vegetation communities across Switzerland could be successfully modeled trough climatic, geological, topographic and land use related predictors. The most contributing predictors were mean annual temperature, land use and site water balance.
- Vegetation communities better predict butterfly distribution than simple land use/land cover information.
- Pre-modeled vegetation communities significantly improved distribution models for butterflies. Best results were obtained by incorporating them directly in the model together with the climatic predictors. However, Bayesian combination of the probabilities of occurrence of the vegetation communities and suitable climatic conditions gave very similar results. Moreover, with this latter approach the probabilistic vegetation maps can easily be replaced with a cartographic vegetation map when available to obtain a filtered environmental prediction.
- High quality habitat maps with sound biological content and high resolution are essential for effective conservation planning. Maps produced within the framework of this study meet these requirements.
- Particular care has to be employed when transforming probabilities of occurrence into presence/absence. Derived AOs can vary greatly according to the type of threshold employed. This should be chosen according to the intended use of the resulting map.

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6 ARE SWISS BIRDS TRACKING CLIMATE CHANGE? DETECTING ELEVATIONAL SHIFTS USING RESPONSE CURVE SHAPES

Ramona Maggini[1*2], Anthony Lehmann[2], Marc Kéry[1], Hans Schmid[1], Martin Beniston[2], Lukas Jenni[1], Niklaus Zbinden[1]

[*] Address for correspondence: Ramona.Maggini@vogelwarte.ch

[1] Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[2] Research Group on Climatic Change and Climate Impacts, Institute of Environmental Sciences, University of Geneva, Battelle D, CH-1227 Carouge, Switzerland

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6.1 ABSTRACT

Climate change is affecting biodiversity worldwide inducing species to either “move, adapt or die”. In this paper we propose a conceptual framework for analysing range shifts, namely a catalogue of the possible patterns of change in the distribution of a species along elevational or other environmental gradients and an improved quantitative methodology to identify and objectively describe these patterns. Patterns are defined in terms of changes occurring at the leading, trailing or both edges of the distribution: a) leading edge expansion, b) trailing edge retraction, c) range expansion, d) optimum shift, e) expansion, f) retraction, and g) shift. The methodology is based on the modelling of species distributions along a gradient using generalized additive models (GAMs). Separate models are calibrated for two distinct periods of assessment and response curves are compared over five reference points. Changes occurred at these points are formalized into a code that ultimately designates the corresponding change pattern. We tested the proposed methodology using data from the Swiss national common breeding bird survey. The elevational distributions of 95 bird species were modelled for the periods 1999-2002 and 2004-2007 and significant upward shifts (all patterns confounded) were identified for 35% of the species. Over the same period, an increase in mean temperature was registered for Switzerland. In consideration of the short period covered by the case study, assessed change patterns are considered to correspond to intermediate patterns in an ongoing shifting process.

However, similar patterns can be determined by habitat barriers, land use/ land cover changes, competition with concurrent or invasive species or different warming rates at different elevations.

Keywords: climate change; elevational shift; environmental gradient; leading edge; trailing edge; patterns; generalized additive models (GAMs); response curve; breeding birds; Switzerland

6.2 INTRODUCTION

Climate change is affecting biodiversity worldwide (Kappelle et al., 1999; Heller and Zavaleta, 2009). In recent years, evidence has mounted about its impacts on different groups of species and stages of a species lifecycle (Hughes, 2000; Parmesan, 2006). Especially for birds (Crick, 2004; Chambers et al., 2005; Leech and Crick, 2007; Wormworth and Mallon, 2007), climate change has been shown to induce poleward (Hitch and Leberg, 2007) and upward shifts of the distributional ranges (Pounds et al., 1999), to alter the timing of major seasonal events such as migration (Jenni and Kéry, 2003; Jonzen et al., 2006; Gordo, 2007) or egg laying (Crick and Sparks, 1999; Torti and Dunn, 2005; Both and te Marvelde, 2007) and to influence survival and productivity and hence, population dynamics (Sanz et al., 2003).

Organisms can adapt to climate change either via phenotypic plasticity (physiological, behavioural plasticity) and/or evolutionary changes (microevolution or evolutionary genetic changes involving multiple generations) (Visser, 2008; Williams et al., 2008). Adaptation can take place in different dimensions: in geographic space, individuals can adapt by modifying their distribution in order to follow favourable climatic conditions and habitats; in environmental space, individuals can shift their phenotypes according to the new environmental conditions, which can possibly lead to the inheritance of new traits through selection; finally, in the temporal dimension, seasonal events such as reproduction or migration may ultimately occur earlier or be delayed (Figure 6.1). Adaptation can occur predominantly in one particular dimension, but generally involves all of them. When populations cannot adapt in one of these dimensions or cannot adapt fast enough (Devictor et al., 2008; Visser, 2008), a species may be driven to extinction, even though today's projections are probably overestimated (Botkin et al., 2007) due to assumptions and limitations of current forecasting methods (refer to Thuiller, 2004, and Thuiller et al., 2008, for the spatial dimension).

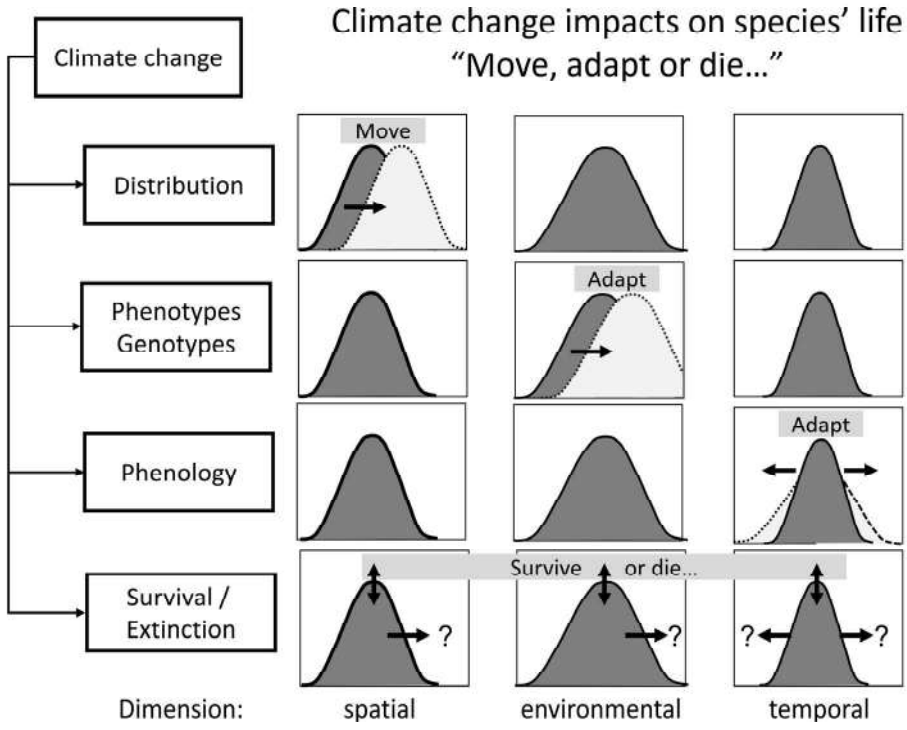

Figure 6.1 «Move, adapt or die». Individuals can adapt to climate change by either shifting their distribution in the geographic space or adapting in the environmental or temporal space. Populations that are not able to adapt in one of these dimensions or adapt fast enough can drive their species to extinction.

As stressed by Parmesan (2006), in spite of numerous studies indicating local adaptation to climate change, Pleistocene fossil records reveal little evidence for the evolution of new phenotypes despite temperature shifts of a greater magnitude than currently observed. It can therefore be assumed that species are more prone to shift their ranges to track favorable climatic conditions, rather than to remain in place and evolve new forms, especially in view of the speed of projected climatic change. The large majority of recent studies on climate change impacts have therefore focused on the estimation of the shifts in species ranges that are expected according to different climatic and land use scenarios. These studies are mainly based on species distribution modelling and are employed in order to forecast changes in the distribution of single species (Pearson and Dawson, 2003; Araújo et al., 2006; Beaumont et al., 2007; Huntley et al., 2007; McKenney et al., 2007; Lawler et al., 2009), ecosystems (Berry et al., 2003; Thuiller et al., 2006) or biodiversity (Bakkenes et al., 2002; Thuiller et al., 2005; Dormann et al., 2008). These techniques allow forecasting changes and are therefore important tools for current conservation planning in order to mitigate the impacts of climate and land use change on biodiversity (Hannah et al., 2007). However, the question can be posed as to the evidence for the influence of recent climate change on species distribution. Monitoring programs are essential in order to observe biodiversity and detect shifts in species ranges. In recent decades, many

schemes have been established, especially after the adoption by many countries of the UN Convention on Biological Diversity at the UNCED summit in Rio de Janeiro in 1992 (Schmeller et al., 2008). Data gathered in these schemes now begin to provide evidence for changes in species' distributions even though the cause-effect relationship with climate change is not always obvious (Thuiller, 2007).

The Swiss national breeding bird survey (MHB; Schmid et al., 2004) was launched in 1999 and is conducted on an annual basis. Although a priori a decade appears a rather short period to relate climate change to possible changes in bird distributions, the highly variable Swiss topography may let one expect distributional changes at least in the third dimension, i.e. along the elevational gradient. Here, we propose a conceptual framework with a catalogue describing the possible patterns of change of a distribution along a gradient such as elevation and a quantitative methodology to identify and objectively describe these patterns. Theoretical expectations are verified using MHB data. Previous similar studies have expressed elevational changes in terms of changes that have occurred at the optimum of the species distribution (Wilson et al., 2005; Lenoir et al., 2008). This is based on the assumption that the entire distribution shifts as a whole, whereas in reality, and especially over short periods, different patterns in the elevational shift may be expected. Indeed, different processes may be responsible for the changes occurring at the "leading" and "trailing edges" of a distribution when range shifts occur: colonization and migration mostly happening at the leading edge, and speciation, persistence or extinction at the trailing edge (Hampe and Petit, 2005; Thuiller et al., 2008). Our description of range shifts also considers changes that have occurred at the borders of the distribution and is based on the outer and central border defined by Heegaard (2002). These measures allow describing the non-parametric response curve of a species-environmental relationship estimated by generalized additive models (GAMs). While Heegaard used them in order to define the range and tolerance of a species along an environmental gradient, we used these measures in order to position the response curve along the environmental gradient using five reference points and to evaluate the changes that have taken place between two distinct periods of assessment. Changes that occurred at the five reference points are formalized into a code that allows the identification of the corresponding change pattern described in the catalogue.

The main aims of this study are first, to conceptually define the possible patterns of change in the distribution of a species along an elevational or other environmental gradient and to propose a methodology in order to identify them. Second, to apply this methodology to the data of the Swiss national breeding bird survey to investigate whether elevational shifts occurred during the period 1999-2007 and, finally, to evaluate if temperatures significantly changed in Switzerland during the same period.

6.3 THEORETICAL PATTERNS OF SHIFT

6.3.1 A catalogue of shift patterns along a gradient

Especially when considering short periods, upward shifts observed along an elevational gradient - or shifts along any other gradient - are rarely complete shifts. Instead, intermediate patterns are observable. Figure 6.2 illustrates conceptually what are the possible patterns in an upward-shifting process. Curves represent the distribution of the abundance or the occurrence probability of a given

species along an elevational gradient at two different periods. Solid lines represent the initial distribution (time t_0) whereas dotted lines represent the distribution at the second period of assessment (time t_1). When capturing the entire distribution, this is represented by a bell-shaped curve (central column). However, when considering geographically limited areas, it is possible that only part of the entire elevational distribution of the species is captured and the curve is therefore truncated either at its lower (left column) or at its upper end (right column). Working at a regional scale can therefore prevent the detection of changes occurring at the truncated end of the distribution or prevent the unequivocal identification of the pattern of change (cases 1 to 5, which show similar truncated curves).

Changes can either occur at the leading or the trailing edge of the distribution with expansion towards higher elevations or retraction from lower elevations. Also, expansions of the leading edge and retractions of the trailing edge can occur with (types E-F) or without (types A-B) a follow up of the core of the distribution. Special cases are represented by pattern D, where only the optimum moves upward, the remainder remaining constant, or pattern C that corresponds to a range expansion in both directions, i.e. up- and downwards. Patterns A-F may be considered as intermediate steps towards a final pattern, pattern G, which is a complete shift of the distribution. Patterns A, B and D would correspond to early stages, whereas patterns E and F to more advanced stages in such a process. The patterns for a downward shift would simply be symmetrical to those described here for the upward shift. All these patterns are most of the time combined with pattern H that represents a change in the abundance or occurrence probability for an identical range of elevations.

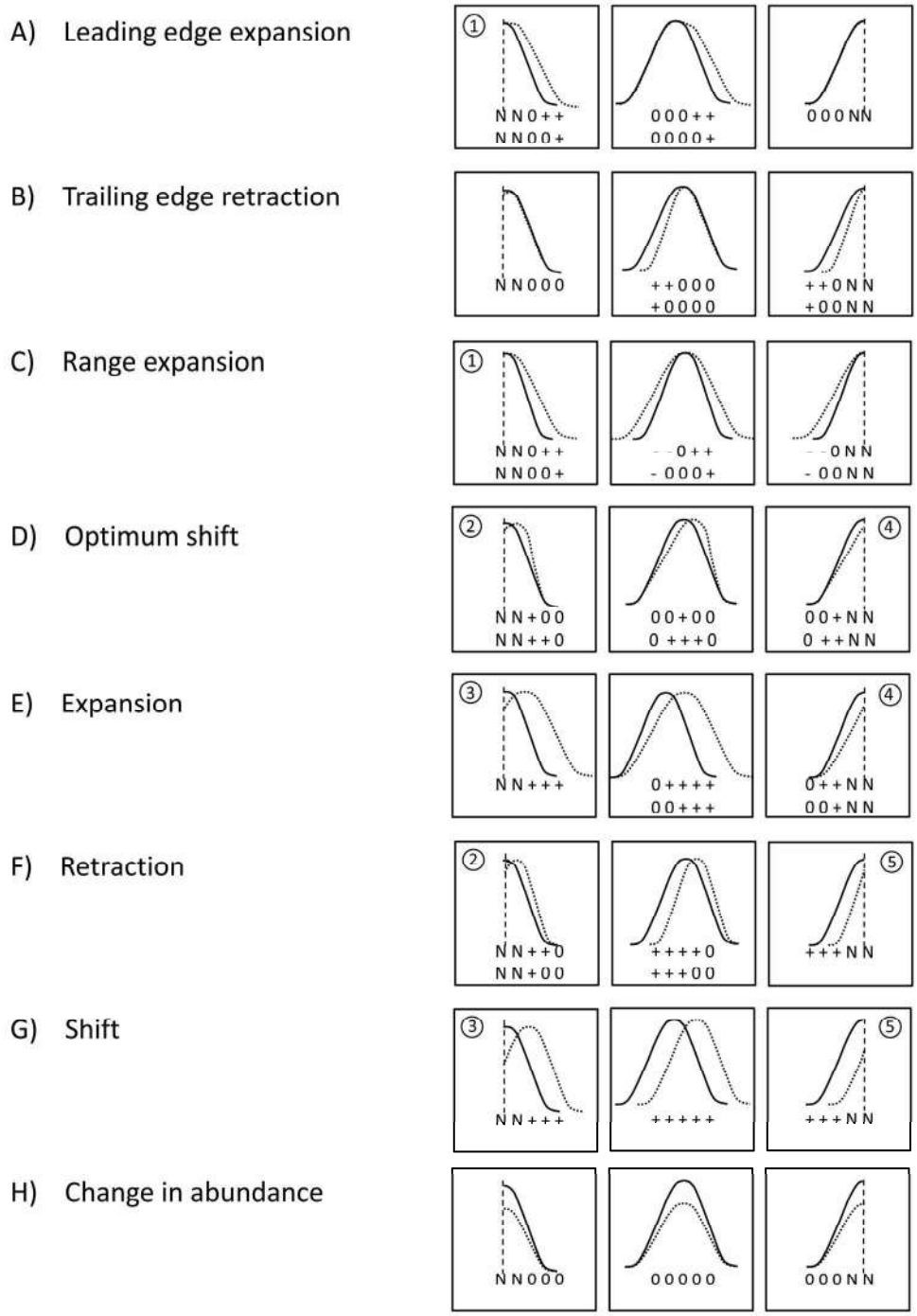

Figure 6.2 A catalogue of the possible shift patterns along a gradient. Solid lines represent the initial distribution (time t0) and dotted lines represent the distribution at the second period of assessment (time t1). The code under each curve expresses the significance and direction of the change that occurred at each of the five reference points (OBL, CBL, OPT, CBR, OBR, defined in section 2.2) with the following symbols: +, significant upward shift; -, significant downward shift; 0, non-significant shift; N, truncated curve with no information for the point. Response curves in the central column represent main shapes. Response curves in the left and right columns are curves that are truncated at the OPT point. Patterns with the same number are patterns corresponding to truncated curves that cannot be distinguished unequivocally from one another.

Patterns presented in Figure 6.2 can either correspond to intermediate steps in a process of upward shifting or be determined by other factors acting either at the leading or trailing edge of the distribution. These could be for example the encountering of barriers or unsuitable habitats along the gradient, biotic interactions or different warming rates at different elevations. In these cases, theoretically intermediate patterns could also become permanent. Patterns B or F, as an example, are characterized by an upper limit that remains constant and by a retraction of the lower limit towards higher elevations. An upward shift is probably initiated but some kind of barrier is preventing the shift at the leading edge of the distribution. This could be a physical barrier, especially in the case of animal species with reduced dispersal ability, or a change in habitat type or quality. The barrier could in this case correspond to the transition from open land to forest, to the treeline, to the transition from alpine grasslands to bare rocks, or ultimately to the top of the mountain. The movement could also be prevented by competition with a species persisting and dominating the upper elevations or by a symbiotic species that moves at a different rate. However, the same patterns could also be determined by factors acting at the trailing edge. The upward shift is possibly determined by a change in land use, with consequent habitat degradation or loss occurring at the lower elevations. As an example, this was observed for farmland specialist birds in the French Alps. Archaux (2007) found that farmland specialists decreased from the late 1970s onwards and that the decline was much more important below 1000 m (−70%) than above (−20%). This pattern was not found in farmland generalists or woodland species and may thus be more likely linked to changes in agricultural practices or type of land use than to climate change. This raises the problem of disentangling the effects of climate and land use (Lemoine et al., 2007). Indeed, especially at lower elevations, the effects of these two phenomena can hardly be distinguished because they are often acting in a synergistic manner. Another explanation for the upward shift of the trailing edge could be the competition and unseat by an invading species coming from lower latitudes/elevations. With climate warming, conditions will indeed become more similar to those of the native range of many invasive species and thus facilitate colonization. Moreover, climate change is expected to displace native species out of the conditions to which they are adapted and competitive resistance from native species may therefore become weaker (Hellmann et al., 2008). Shifts in suitable climatic zones will thus tend to benefit invasive species that have traits that favour them in a changing environment, like broad environmental tolerances, short juvenile periods, and long-distance dispersal (Hellmann et al., 2008). In particular for birds, favourable traits for invasive species would include good dispersal ability, high rate of population increase resulting from large clutch size and several clutches per season, ability to compete for resources and habitat with native species (O'Connor, 1986; Sakai et al., 2001).

Patterns A or E are characterized by an expanding leading edge and a persistent trailing edge. This could result from temperature warming at different rates at different elevations. This phenomenon has been reported by Pepin and Lundquist (2008) in their global assessment of extra-tropical regions that shows that 20th century temperatures increased more rapidly near the annual 0°C isotherm due to snow-ice feedbacks. Milder conditions at higher elevations allow the species to expand upwards, while conditions at lower elevations are still favourable and do not prompt the species to retract. Alternatively, populations at the trailing edge may have adapted to the new conditions and maintained their ability to compete with invading species.

Range expansion (pattern C) is a particular case. Dispersal-driven expansion that is normally contained by exogenous factors is here released. New favourable conditions created at higher elevations as a consequence of climate warming prompt the species to move upwards. Competition release or habitat restoration allows the species to reappropriate the lower fringe of its niche.

6.3.2 Assessing elevational shifts

In the previous section we proposed a catalogue of the possible steps in a process leading to a complete upward shift of the distribution. But, how can we detect these patterns in real data? The proposed flow of analysis is illustrated in Figure 6.3. As a first step, the presence or the abundance of a species is modelled as a function of elevation using generalized additive models (GAMs; Hastie and Tibshirani, 1990). GAMs are a generalization of GLMs (generalized linear models; McCullagh and Nelder, 1989) that estimate response curves with local smoothing functions. GAMs are therefore data-driven and flexibly explore the shape of complex relationships with much fewer restrictions and assumptions than GLMs (Yee and Mitchell, 1991). This is especially useful to fit response curves that are asymmetrical or that present a plateau or a multimodal distribution.

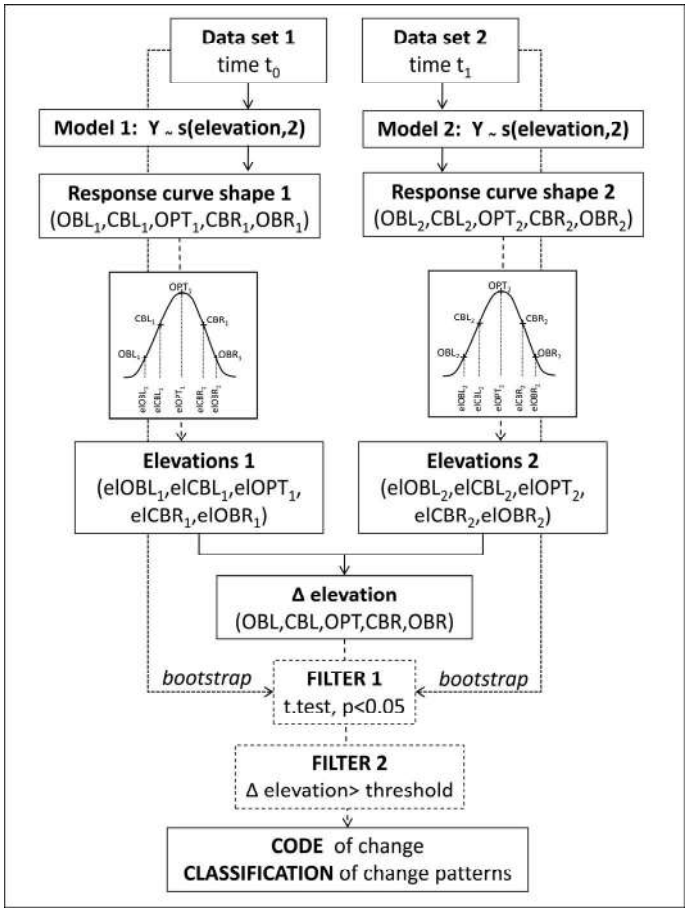

Figure 6.3 Analysis flow chart. Data are separated in two datasets relative to a first and a second period of assessment (t0 and t1, respectively). For each dataset the presence or the abundance of the species is modelled as a function of elevation using GAMs. The resulting response curve shape is described by five fixed points along the curve: OBL = outer border left; CBL = central border left; OPT = optimum; CBR = central border right;

OBR = outer border right. The significance of the shift at each point between the two periods is tested by a t-test on bootstrapped values (100 times). The shift is considered significant if the t-test between the bootstrapped values is significant at the threshold $p<0.05$. A supplementary filter can be applied in order to avoid dealing with shifts inferior to a certain threshold. According to the change occurred at the 5 reference points a code of change is defined and the different patterns grouped in main types.

Separate models are calibrated for two distinct periods of assessment (t_0 and t_1). The position of the response curve along the elevational gradient is described using five reference points (see Figure 6.4a). Three main measures determine their position along the response axis: a) the optimum (OPT), which represents the maximum modelled abundance or maximum occurrence probability; b) the central border (CB) and c) the outer border (OB). The central and the outer borders are defined according to Heegaard (2002), i.e. as the response value that is equal to a specified fraction of the maximum response: *maximum response x exp(-2)* for the outer border and *maximum response x exp(-0.5)* for the central border. On a bell-shaped distribution there are two points on the curve that correspond to each response value, one on the left and the other on the right of the optimum. Along the elevational gradient, the position of the response curve is thus described by the outer border left (OBL), central border left (CBL), optimum (OPT), central border right (CBR) and outer border right (OBR). The response curves corresponding to the two periods of assessment are compared on the basis of the elevation corresponding to these 5 reference points. The methodology is also applicable when a response curve is truncated, in this case the shift can only be assessed on a subsample of reference points. As an example, Figure 6.4b represents a bell-shaped distribution truncated on the right - this is the typical distribution for alpine species – for which only the position of the OBL, CBL and OPT can be assessed. Similarly, for the truncated distribution in Figure 6.4c – which mainly represents the distribution of lowland species – only the OPT, CBR, OBR can be assessed. The methodology has the advantage of being sensitive also to changes in the response curve shape. As an example, the response curve at time t_1 represented in Figure 6.4a is skewed on the right. This will be recognized when determining the elevations corresponding to the CBR and the OBR.

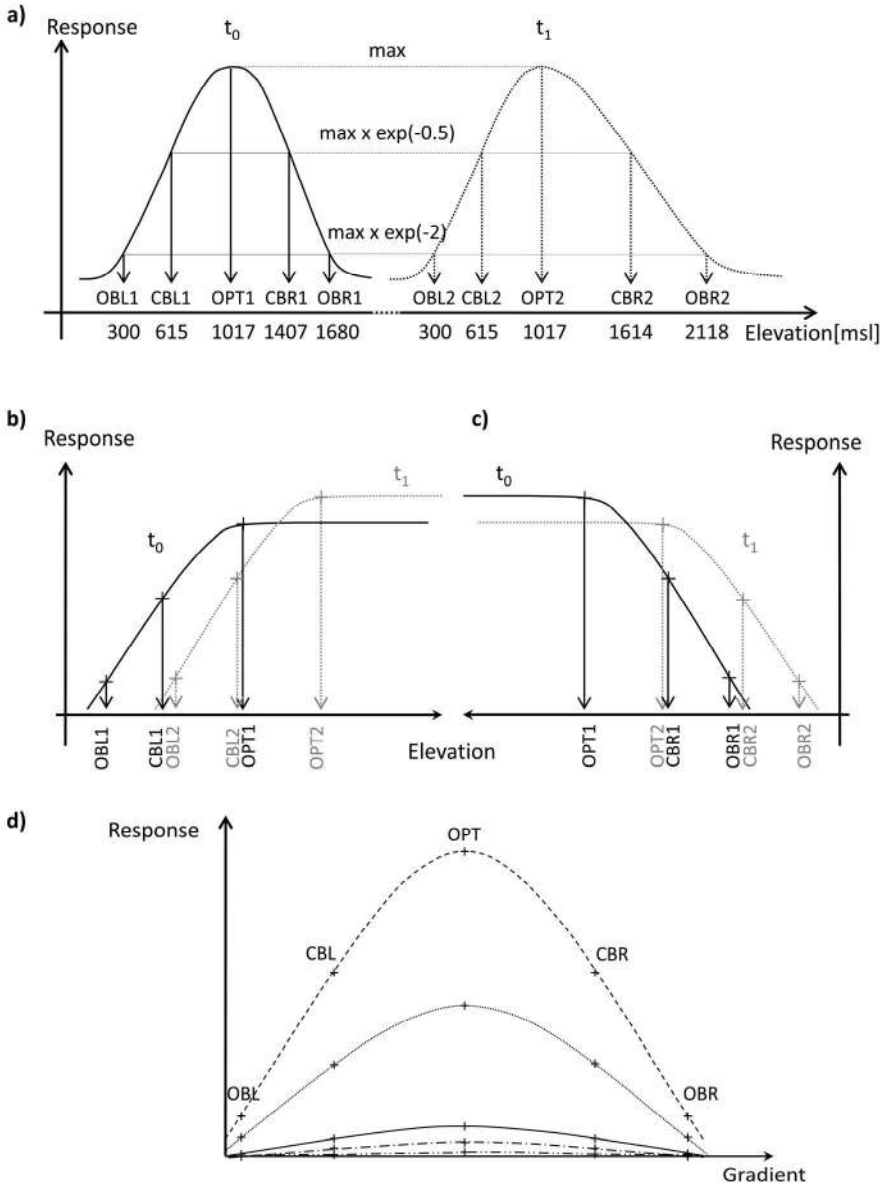

Figure 6.4 a) Response curves at time t0 (solid line) and time t1 (dotted line). The position of each curve along the elevation gradient is described using five reference points: OBL, CBL, OPT, CBR, OBR (see the text for detailed description). Response curve for time t1 is skewed, as a consequence CBR2 and OBR2 are more distant from the optimum than at t0. This is automatically taken into account when searching for the corresponding altitude using the relationship established by the model; b) example of a response curve truncated on the right. As a consequence shifts can only be assessed on a subsample of reference points, i.e. OBL, CBL and OPT. This is a typical distribution of an alpine species; c) example of a response curve truncated on the left. As a consequence shifts can only be assessed at OPT, CBR, OBR. This distribution is typical of a lowland species; d) an initial dataset is randomly generated according to a normal distribution. Supplementary datasets are obtained by multiplying the initial values by 10, 50, 100, 500 and 1000. These values are modelled as a function of the gradient and the responses curves shown in the figure. Crosses indicate the position of the reference points (OBL, CBL, OPT, CBR, OBR). This figure shows that a simple change in abundance does not induce a shift at the reference points.

To test whether the difference in elevation between the two periods is significant at each reference point, a bootstrapped t-test is performed with 100 replications per period. A supplementary filter may be applied to avoid dealing with shifts inferior to a certain threshold that may not be considered as ecologically significant. The changes at the five reference points are coded as follows: +, for a significant upward shift; -, for a significant downward shift; 0, for a non-significant shift; N, meaning "no data", for truncated curves at the lower or upper end of the elevational gradient. The resulting code allows identifying the pattern of change as defined in the catalogue of Figure 6.2. Note that a simple change in abundance (pattern H) does not induce a shift at any reference point (see Figure 6.4d); any detected change will therefore directly indicate a shift along the gradient.

6.4 CASE STUDY

6.4.1 Materials and methods

6.4.1.1 Study region

Switzerland is situated at the boundary between Central and Western Europe and is influenced by contrasting Atlantic, Mediterranean and continental regimes that result in highly variable conditions across the country. The Swiss territory is classically subdivided into six main biogeographical regions (Gonseth et al., 2001): the Jura Mountains, the flat and intensively cultivated area of the Plateau and four regions in the Alps, respectively the Western and Eastern Alps and the Northern and Southern slopes. The Jura Mountains are a limestone range of mountains characterized by an average elevation of 810 m above sea level (asl). The Plateau covers about 30% of the Swiss territory and is characterized by an average elevation of 540 m asl. The Alps, mainly crystalline rocks, occupy nearly two thirds of the Swiss territory. The mean range of elevations for the Alps is 3800 m and the highest point is the Dufourspitze in Canton Valais at 4634 m asl.

6.4.1.2 Data

We assessed our methodology and the relevance of the theoretical change patterns using the data from the Swiss national common breeding bird survey (MHB, Schmid et al., 2004). This monitoring program has been conducted on an annual basis by the Swiss Ornithological Institute since 1999. For the present study we used data sampled until 2007. The survey encompasses 267 squares of 1 km^2 that are distributed across Switzerland as a grid and thus are representative of different biogeographical zones, elevation bands and habitats. The elevation (median over the 1-km^2 square) of sampling units ranges from 210 to 2710 m asl. Each square is surveyed three times - twice for squares above the treeline - per breeding season (15 April-15 July) by skilled volunteers who map all birds seen or heard along a square-specific route. At the end of the season, territories are identified from the mapped points (see Schmid et al., 2004, for a detailed description of the survey protocol).

Data used for the analysis consist in the observed number of territories per km^2. These are an index of the true population size related to the latter quantity by detection probability. As is customary in many ecological studies, by drawing our inferences about abundance based on this index, we make the assumption that detection probability is not related to any of the factors studied (Kéry and Schmidt, 2008).

6.4.1.3 Application of the general methodology in order to detect elevational shifts

The observed number of territories per km^2 was modelled as a function of the median elevation of each sampling square according to the analysis flow chart presented in Figure 6.3. Separate models were calibrated for the periods 1999-2002 and 2004-2007. Using data sampled over several years avoid the comparison of the first and last year that might be exceptional and not representative for the particular period. In particular, the chosen design avoids the year 2003, which was characterized by an exceptionally hot summer in Switzerland (Beniston and Diaz, 2004). Assessing elevational shifts from data sampled in 1-km^2 squares is not ideal because the elevation range within a square in mountainous areas may be fairly important and could therefore hide an elevational shift that may have occurred due to climate change. For this purpose, data sampled on transect or point counts would be more appropriate, as suggested by Archaux (2004), especially for detecting early stages of distributional shifts. However, the fact that changes can be identified in spite of the coarse resolution of sampling units indicates that the distributional shift is sufficiently important to pass from one sampling square to a square with a higher median elevation. Only species observed in at least 10 squares were considered for analysis. This is the minimum number of data to be used when calibrating a model with one predictor. A second filter was applied to these data to avoid dealing with shifts of less than 50 m, which were not considered as significant. Despite a few exceptions, the difference between the median altitudes of the sampling squares was, respectively, less than 50 m and 14.55 m on average. A filter of 50 m therefore ensured that a species had shifted at least from one square to a higher one. All the analyses were performed with S-Plus ver. 8.0 (Insightful Corp. 2007, Seattle, WA, USA).

6.4.1.4 Spatial predictions

For each assessment period, the potential distribution of species abundance (i.e. expected number of detected territories per km^2) across the Swiss territory was calculated directly within SPlus and the predictions exported as ASCII grids to be displayed in a geographic information system (GIS; ArcMap ver. 9.2, ESRI 2006). In order to perform the predictions directly within S-Plus, a dataset was prepared by sampling within the GIS the mean elevation of the 41,300 1-km^2 squares that compose the Swiss territory. The abundance of each species was then predicted for each square as a function of elevation.

6.4.1.5 Population trends

Population trends were calculated using a GLM with a Poisson distribution within the program TRIM (Pannekoek and van Strien, 1998). Trends were calculated for populations at the trailing and leading edge of the elevational distribution. These populations were arbitrarily defined as the ensemble of individuals having defined their territory below the elevation corresponding to the central border left (CBL) and above the central border right (CBR) respectively.

6.4.1.6 Temperature trends

Temperatures for the period 1999-2007 were obtained from the weather stations of the automatic meteorological network of Switzerland (SwissMetNet). Daily minimum, mean and maximum temperatures were considered for 67 weather stations distributed throughout Switzerland that were selected for the completeness of their series. The weather stations are distributed between 203 and 3,315 m asl. In order to identify trends, temperatures were analysed as a function of elevation and time

using generalized linear mixed models (GLMMs; Breslow and Clayton, 1993). Within S-Plus, GLMMs were calibrated by penalized quasi-likelihood using the function *glmmPQL* contained in library MASS. Fixed effects were the elevational bands (lowland: < 700 m ; montane: 700-1500 m ; subalpine 1500-2300 m ; alpine-nival: >2300 m asl) and years (1999-2007) whereas weather stations were set as a random effect. Mean changes in minimum, mean and maximum daily temperatures between the beginning (1999) and the end (2007) of the study period are given for the elevational bands presenting a significant increase over the period. Mean daily temperature averaged over a year was also modelled as a function of elevation with a linear regression model using the ensemble of the 67 weather stations and the 9 years of the study period. This allowed defining a general rate of change in mean temperature with elevation for Switzerland. A similar model was also calibrated for the beginning of the study period (year 1999) and the end (year 2007); the difference in the intercept of the 2 linear regressions providing information on the general increase in mean temperature between the two years at a given elevation.

6.4.2 Results of the case study

6.4.2.1 Shifting patterns identified for breeding birds in Switzerland

The analysis was performed for 95 species that were observed in at least 10 out of the 267 squares covered by the monitoring program. For 33 species out of the 95 (i.e. for 35%), a significant upward shift was identified in at least one of the reference points along the response curve. That proportion increases when considering only sedentary species, 12 out of 27 species (44%). For the remaining species, 28 presented a significant downward shift and 34 species no significant change. Significant shifts, either upward or downward, were not linked to a particular habitat. According to the changes that occurred at the five reference points, different patterns could be identified and attributed to the theoretical patterns described in Figure 6.2. Concerning the change patterns of the 33 species presenting a significant upward shift, 3 were leading edge expansions (pattern A), 2 trailing edge retractions (pattern B), 6 range expansions (pattern C), 1 optimum shift (pattern D), 2 expansions (pattern E), 5 retractions (pattern F), 5 complete upward shifts (pattern G) and in 9 cases the curve was truncated and contained only two reference points (either OBL-CBL or CBR-OBR). The latter are curves belonging to lowland species, whose abundance decreases with elevation (left column of Figure 6.2), or alpine species, whose abundance increases with elevation (right column of Figure 6.2). Range expansions were mainly linked to rare species with very low abundances throughout the elevational gradient. Upward retractions in their broad sense (i.e. patterns B and F confounded) were mainly linked to species nesting in the forest (6 species over 7). Forest birds were also the most represented (4 cases over 5) among species having completely shifted upwards (pattern G). The mean shift at the five reference points for the 33 species presenting a significant upward shift was of 82 m for the OBL, of 52 m for the CBL, of 40 m for the optimum, of 91 m for the CBR and of 94 m for the OBR.

As an illustration, the response curves of three species with a significant change between the two periods are shown in Figure 6.5. The Marsh Tit (*Parus palustris*), a common lowland passerine, has started to move upwards with a significant shift of the optimum (OPT) and the central border right (CBR). However, the shift at the outer border right (OBR) is not significant. Thus, the change mainly consists in a retraction (type F) from low elevations with so far no significant upward shift at the

leading edge of the distribution. The change for the Ring Ouzel (*Turdus torquatus*) is quite similar but occurs at higher elevations. The change is significant for the OBL, CBL and OPT points, but not for the CBR. As the curve is truncated on the right, the situation for the OBR can thus not be assessed. This species is therefore mainly retracting from the lower elevations of its elevational range. For the Eurasian Bullfinch (*Pyrrhula pyrrhula*) the changes are significant and positive for all five reference points and thus represent a case of complete upward shift (type G). In Figure 6.5, the potential distribution of the abundance is also shown for the three species during the first (1999-2002) and the second period of assessment (2004-2007). The potential distribution is here determined solely as a function of elevation and does not include any other predictor.

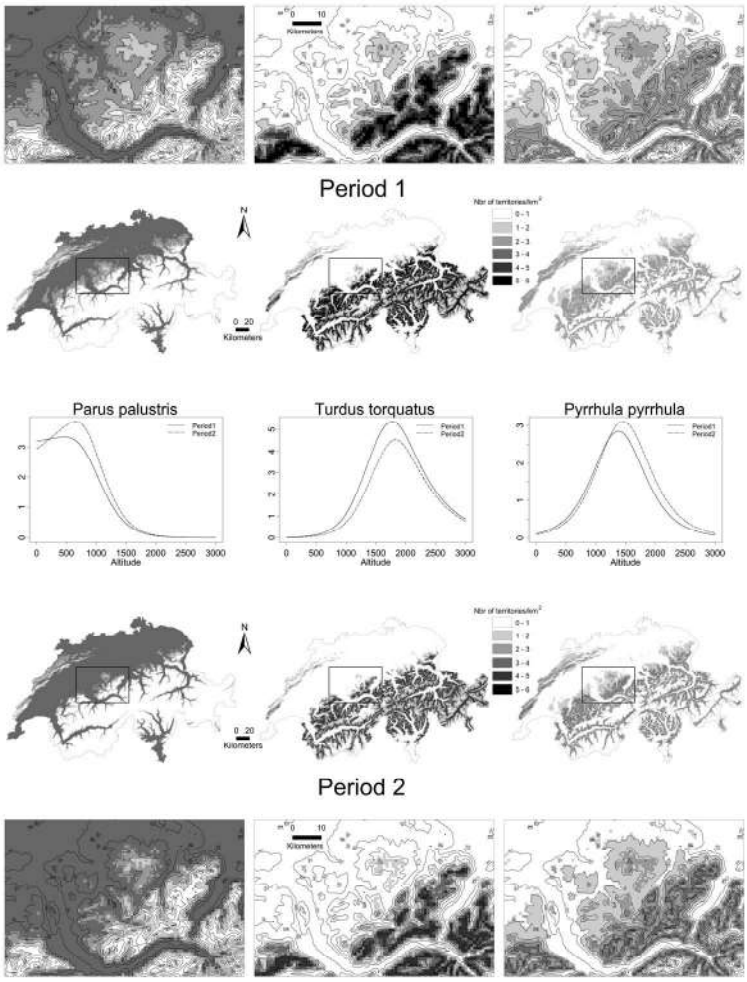

Figure 6.5 Response curve shapes of the modelled abundance as a function of elevation for the period 1999-2002 (solid line) and 2004-2007 (dashed line) for three species presenting different patterns in the upward-shifting process. The potential abundance-based distribution across Switzerland is determined for each species and for the two periods as a function of elevation solely (spatial prediction for period 1 on the top, spatial prediction for period 2 below). The change of the elevational distribution toward higher elevations can be appreciated in the zoomed areas.

6.4.2.2 Population trends at the leading and trailing edge

The change in the shape of the response curve at the trailing and leading edges of the same three focus species between the two periods with their population trends below the CBL and above the CBR respectively is presented in Figure 6.6. For the species characterized by a complete shift - the Eurasian Bullfinch (*Pyrrhula pyrrhula*) – the population trend significantly decreased at the trailing edge ($p<0.01$) and it significantly increased at the leading edge ($p<0.01$). The Ring Ouzel (*Turdus torquatus*) retracted from the lower elevations of its range with no significant change in the upper limit. This pattern is combined with an overall decrease in abundance. The population trend at the leading edge is therefore negative ($p<0.01$) as it is at the trailing edge ($p<0.01$). The curve for the Marsh Tit (*Parus palustris*) is truncated, therefore population trends were calculated above and below the same point, i.e., the CBR. Like the Ring ouzel, the Marsh Tit is retracting from the lower elevations, but this pattern is combined with an overall increase in the modelled abundance. The two trends are therefore positive ($p<0.01$).

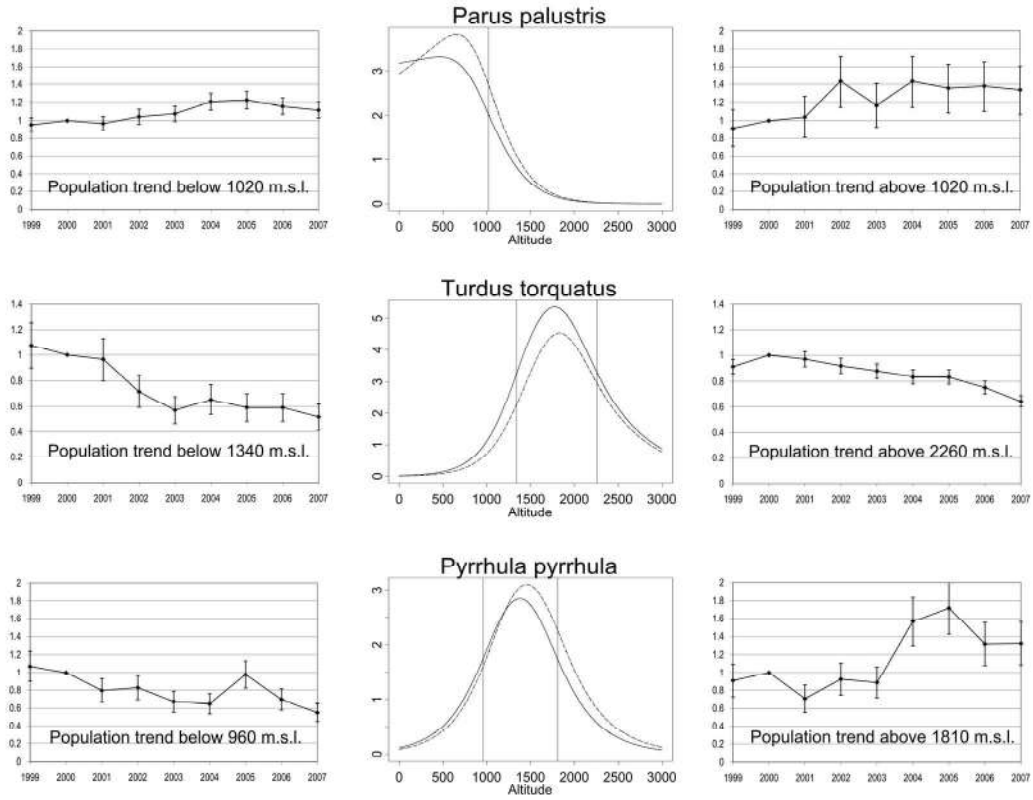

Figure 6.6 Response curve shapes of the modelled abundance as a function of elevation for the period 1999-2002 (solid line) and 2004-2007 (dashed line) for three species presenting different patterns in the upward shifting process. Graphics on the left and on the right represent population trends in the elevational bands below the CBL and above the CBR of each species respectively (vertical solid lines). On these graphics, populations in 2000 are set as reference (value 1) and populations for other years are expressed proportionally to this reference value.

6.4.2.3 Temperatures trends over the study period

Trends for the daily mean temperature in Switzerland for the period 1999-2007 and per elevational band are presented in Figure 6.7. The lowland band (< 700 m asl) includes 34 weather stations of the automatic meteorological network of Switzerland (SwissMetNet). The montane (700-1500 m asl), subalpine (1500-2300 m asl) and alpine-nival (> 2300 m asl) bands includes 14, 15 and 4 stations respectively. Altogether mean daily temperature tends to increase over the considered period. Results of the GLMM are significant for the montane ($p<0.05$) and subalpine ($p<0.01$) elevational belts. For the montane belt, mean daily temperature averaged over a year and over the 14 weather stations increased from 6.46 °C in 1999 to 7.25 °C in 2007, thus a mean increase of 0.79 °C. For the subalpine belt the mean increase was of 0.84 °C. The general shape of each trend remains however similar at each elevational band with synchronized yearly ups and downs. Similar trends were also observed for the maximum daily temperature and partly for the minimum daily temperature (graphs not shown). The maximum daily temperature trends were significant and positive for the montane ($p<0.001$) and the subalpine ($p<0.001$) belt. Maximum daily temperature increased on average by 1.03 °C between 1999 and 2007 for the montane belt and by 1.12 °C for the subalpine belt. Results of the GLMM for the minimum daily temperature were significant and negative for the lowland belt ($p<0.01$) and positive for the subalpine belt ($p<0.05$). Although exhibiting a negative trend, the averaged minimum daily temperature increased by 0.3 °C for the lowland belt between the beginning (1999) and the end (2007) of the study period. The increase for the subalpine belt was 0.68 °C.

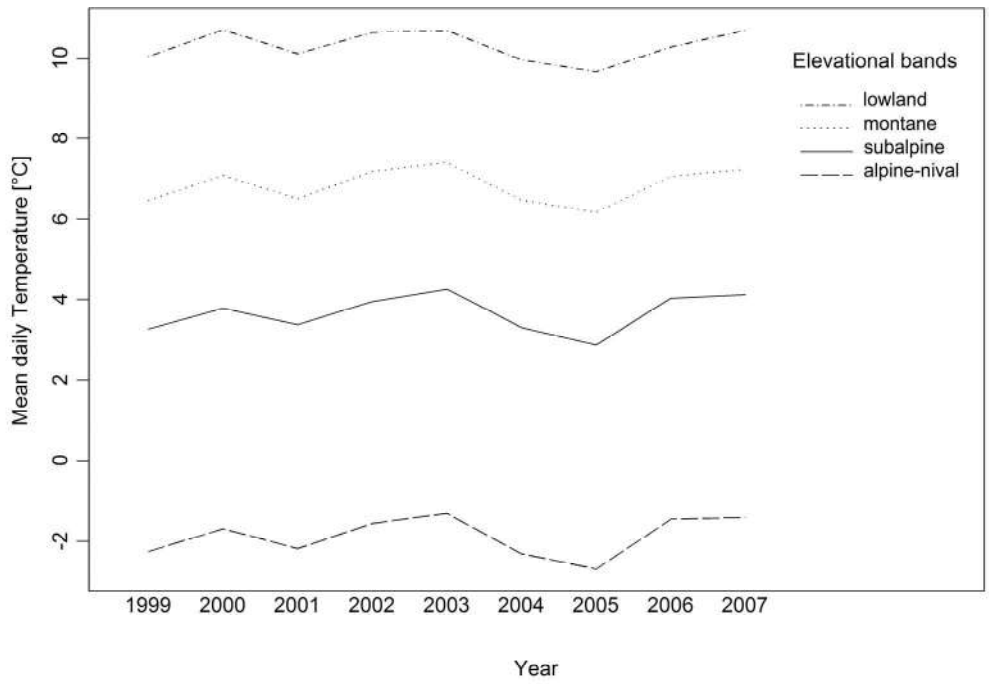

Figure 6.7 Trends for the mean daily temperature in Switzerland between 1999 and 2007 within the elevational bands. The figure is based on the measurements of 67 fixed weather stations of the automatic meteorological network of Switzerland (SwissMetNet).

The general model linking mean temperature (calculated from daily mean temperature averaged over a year) to elevation allowed defining a general rate of change in mean temperature with elevation for Switzerland of -0.52 °C/ 100 m. The general model was calibrated using the data of the 9 years and the ensemble of the 67 weather stations selected for the study. A similar model was calibrated considering only data for the year 1999 and a second considering only data for the year 2007; the difference in the intercept of the 2 models informing about the increase in mean temperature between the beginning and the end of the study period. The difference between the two intercepts was 0.60, which corresponds to a global increase of 0.6 °C. The slope of the two regression lines was very similar but not identical (-0.0053 vs. -0.0052 for 1999 and 2007, respectively). This indicates that the increase in mean temperature was not the same throughout the elevational gradient, but that it was more important at higher elevations, which confirms the results obtained by the analysis per elevational band. A t-test performed over bootstrapped model indices (1000 times) confirmed that slope and intercept were significantly different between 1999 and 2007.

6.5 DISCUSSION

6.5.1 Proposed methodology

The general methodology we have proposed here could be efficiently applied to the data of the Swiss breeding bird survey and proved to be effective in assessing in a quantitative manner the extent of the shifts that have occurred at five reference points defined along the response curve of the modelled distribution. Furthermore, the change at these five reference points and the resulting code allowed the identification of the type of shift pattern. All the shift patterns defined in our conceptual catalogue were found in real data either in their full or in their truncated form. The short time period covered by the data indirectly supports the hypothesis that the theoretically-defined patterns correspond in this case to transitional patterns in an ongoing upward-shifting process, but as mentioned in section 2.1 similar patterns can be determined by factors other than climate change, e.g. barriers, land use change, competition or different warming rates at different elevations.

Studies assessing climate change impacts generally compare distinct periods separated by several decades (Thomas and Lennon, 1999; Wilson et al., 2005; Lemoine et al., 2007; Lenoir et al., 2008). Such studies are even more likely to benefit from the proposed methodology to assess changes over these long periods. Furthermore, the proposed methodology can be applied to gradients other than elevation. The simplest example would be the latitudinal gradient to assess poleward shifts. Our approach can be compared to the methodologies of Thomas and Lennon (1999), Hitch and Leberg (2007) or Hill et al. (2002), which are essentially based on the average of the 10 northernmost/southermost latitudes. Assessing shifts directly at range margins is always risky because occurrence in this part of the distribution is often the result of isolated dispersal events which may result in non-lasting populations (Shoo et al., 2006). Moreover, an improvement in the detection probability between the two periods of assessment can lead to a spurious conclusion of a range expansion and this is particularly true when only range margins are assessed (Hitch and Leberg, 2007). It is therefore recommended to assess changes at margins in a substantial range. In order to use an established definition, for our methodology we adopted the outer border and central border

characteristics described in Heegaard (2002), which are defined with respect to the centre and not to the margin of the distribution. Our methodology could also be used to explore the time dimension in order to assess phenological shifts. It can then be compared to trends in the first arrival date (Donnelly et al., 2009), the quantile approach (Van Buskirk et al., 2009) or the first-versus-mean arrival date (Miller-Rushing et al., 2008). For the same reasons pointed out for range margins in the spatial dimension, range margins in the temporal dimension could also be misleading. The methodology we propose would therefore clearly perform better than the use of the first arrival date and would be more accurate than the single point of reference represented by the mean arrival date. On the other hand, the quantile approach would give very similar results. We believe also that our approach could be useful to explore other environmental gradients composing the environmental niche of a species such as water, energy or other resources. In the context of the study of resource sharing of competing plant species, a similar approach was used by Heikkinen and Mäkipää (2009) in order to assess plant response curves along a C/N gradient. Curves were described by three measures: the optimum, the niche width and the curve skewness. Similarly to our approach, the latter two measures were determined according to Heegards' central border but were used in order to define the ecological amplitude of the species and the degree of overlap with competing species while we used them in order to position the curves along the gradient.

Species are generally distributed within their range according to a central-margin (C-M) gradient, with the centre supporting the highest population density (Guo et al., 2005). This pattern can well be modelled by a bell-shaped distribution. Previous studies have employed generalized linear models (GLMs) with a quadratic term in order to model the elevational distribution of species (Wilson et al., 2007; Lenoir et al., 2008). This parametric method forces however the response to fit the predefined quadratic shape. Generalized additive models (GAMs) are more flexible, follow the data more closely and are therefore particularly suited for skewed or multimodal response curves or those characterized by a plateau (e.g. Yee and Mitchell, 1991). In our case, we limited the number of degrees of freedom of the smoothing functions to two. The resulting simplification of response curves was necessary in order to be able to compare the curves for the two periods.

6.5.2 Shifts in the elevational distribution of breeding birds in Switzerland

Estimates of elevation shifts in animal distribution due to recent climate change are still rare in the literature to allow direct comparison, particularly for birds (Parmesan, 2006; Shoo et al., 2006; Sekercioglu et al., 2008). As a first indication, the meta-analysis performed by Parmesan and Yohe (2003) over more than 1700 species of different (plant and animal) taxa documented significant upward range shifts averaging 6.1 m per decade. In the French Alps, Archaux (2004) recorded the greatest shift for the European Robin (*Erithacus rubecula*) with an upward shift of 114 m over a 30-years period. In Switzerland this species does not seem to have significantly changed its distribution, either up- or downwards, during the 9 years considered. Shifts of similar importance in the optimum of the distribution have however been modelled in Switzerland for the Marsh Tit (*Parus palustris*) (Figure 6.5), the Song Thrush (*Turdus philomelos*) and the Garden Warbler (*Sylvia borin*) (results not shown). The shift pattern for these species is of type F according to our catalogue, i.e., mainly a retraction from low elevations. In their assessment in an alpine valley in Italy, Popy et al. (2009) found that the mean elevations increased for the majority of species over the considered period of 11 years,

but that the average change was not significantly different from zero. However, a significant upward shift of 29 m of the bird zonation could be identified. Over the same period, mean temperature in the area (mean values over 4 nearby stations) increased by 1 °C and maximum temperature by 1.4 °C. The increase for the minima was of 0.5 °C although not significant. For Switzerland we were able to assess temperature increases of the same order of magnitude for the subalpine belt (+0.84 °C for mean, + 1.12 °C for the maximum and + 0.68 °C for the minimum daily temperature), but in our case elevational shifts were significant. For the 33 species presenting a significant upward shift, the mean upward shift at the five reference points was of 82, 52, 40, 91 and 94 m from left (OBL) - trailing edge - to right (OBR) - leading edge. The general model linking mean daily temperature to elevation allowed defining an approximate rate of change in mean temperature with elevation for Switzerland of -0.52 °C/ 100 m (rate calculated with the data of 67 weather stations of SwissMetNet over the study period). According to this rate, the overall increase of 0.6 °C that we assessed for the mean temperature between 1999 and 2007 would correspond to an upward shift of 115 m. The mean upward shifts we assessed for the CBR and OBR, 91 and 94 m respectively, are quite consistent with this expectation. However, we are aware that the temperature increase occurred over the study period is probably not the one that caused the observed elevational shift in bird distributions (assuming there is a causal relationship). Indeed, there is a certain inertia in population dynamics related to the lag over which effects on survival or reproduction become noticeable in population totals. So it may well be that the observed changes in the bird distributions are the effects of a warming process that started before the study period.

If we consider the analogy between latitudinal and elevational shifts, we can transpose some assumptions concerning the mechanisms occurring at the edges of the distribution. According to Hampe and Petit (2005) the main processes at the leading and trailing edges of the distribution in response to a given environmental change are migration, persistence or extinction. Within the context of climate change, migration depends mostly on populations at the colonization front. Indeed, it is at the leading edge that isolated long-dispersal events occur and potentially lead to exponential population growth (Thuiller et al., 2008). As a consequence, the population trends at the leading edge of a shifting distribution are in principle positive. In our study, this was confirmed in the case of the Eurasian Bullfinch. Its elevational change being a complete shift, the population trend was positive at the leading edge and negative at the trailing edge. This seems to be consistent with findings of Foden et al. (2007) who suggest that population trends calculated for the range boundaries are a sensitive and relevant indicator of incipient range changes. However, general population trends normally observable during a shifting process can be modulated by an overall increase or decrease in abundance due to other confounding factors. According to our conceptual framework, this would correspond to an interaction between the main types of shift patterns (A-G) and pattern H (change in abundance). The pattern displayed by the Ring Ouzel is an example of such an interaction. As suggested by Thuiller et al. (2008), one of the future challenges in species distribution modelling will be the incorporation of demographic parameters that provide information about the probability of local extinction or population increase. This remains a difficult exercise since it requires quantitative information about the relationship between demography and environment. Range limits, by latitude or with elevation, have received increasing interest lately (e.g. Gaston, 2009), particularly with the increasing research

on the impacts of climate change. Also, population trends are today combined with projections of future distribution ranges in order to define vulnerability indexes for species (Gregory et al., 2009).

6.5.3 Conservation implications

Opinions differ as to whether conservation actions should focus on the centre or on the edges of species distributions. Dispersal is often risky for the individuals and the long-term survival of newly implanted populations depends on having a critical number of individuals that move and assemble together in suitable breeding habitats (Kokko and Lopez-Sepulcre, 2006). From this point of view, conservation efforts should therefore be concentrated at the leading edge of the distribution in order to create suitable habitats along the expansion route. These are not necessarily to be envisaged as corridors, but more likely as 'stepping stones' sufficiently close to each other to lie within the species' dispersal capability (Huntley et al., 2006). Environmental conditions at the centre of the range are the most favourable and therefore support populations with the highest densities according to the centre-periphery hypothesis. Being less susceptible to environmental and demographic stochasticity, core populations are likely to be more persistent than marginal ones. Conservation should thus focus on core populations if the aim is to ensure the long-term persistence of the species (Thomas et al., 2008). Trailing edges have been largely underestimated in the past, but recent findings in phylogeography suggests that populations at trailing edges play an essential role in maintaining long term stores of genetic diversity and in promoting speciation (Hampe and Petit, 2005). Even though relict populations may show reduced intra-population diversity because of their small size and isolation, high levels of genetic diversity are observable between populations thus leading to high levels of regional diversity (Hampe and Petit, 2005). These are elements that should be considered for an evolutionarily-enlightened management strategy (Ashley et al., 2003). Finally, according to Araújo and Williams (2001), complementary hotspots for conservation are to be found within the margins of species' ranges. Conservation areas at the intersection of several species range margins allow protecting several species at a time. This is especially favourable for species with narrow ranges, i.e. endemic and rare species.

6.6 CONCLUSIONS

The proposed methodology was efficiently applied to the data of the Swiss breeding bird survey and proved to be effective in assessing in a quantitative manner the extent and the type of elevational shift. All seven theoretical patterns described in our catalogue were found in real data either in their full or truncated form. A significant upward shift was identified between the two periods of assessment for 33 breeding bird species out of 95. Changes in mean temperature were observed over the same period even if the cause and effect relationship was not directly established. Further investigations are needed to disentangle the effect of other potential confounding factors that could lead to similar patterns. These factors are for instance habitat barriers, land use/land cover change, species competition or different warming rates along the elevational gradient. Next steps will consider repeating this assessment in a few years' time in order to see whether change patterns have evolved towards their theoretical final pattern (type G - complete shift). This will probably be the case within homogeneous habitats, but intermediate patterns are likely to persist in situations influenced by other factors. Finally,

it would be interesting to apply and validate our approach for other gradients, taxa and regions of the world.

6.7 ACKNOWLEDGMENTS

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7 GENERAL DISCUSSION

The research activity in the field of species distribution modelling (SDM) in relation to ecology has significantly increased in the last 15 years as demonstrated by the number of citations reported by Web of Science (Figure 7.1 a). This increase was followed very closely by an increase in the number of applications of SDM in biodiversity conservation (Figure 7.1 b).

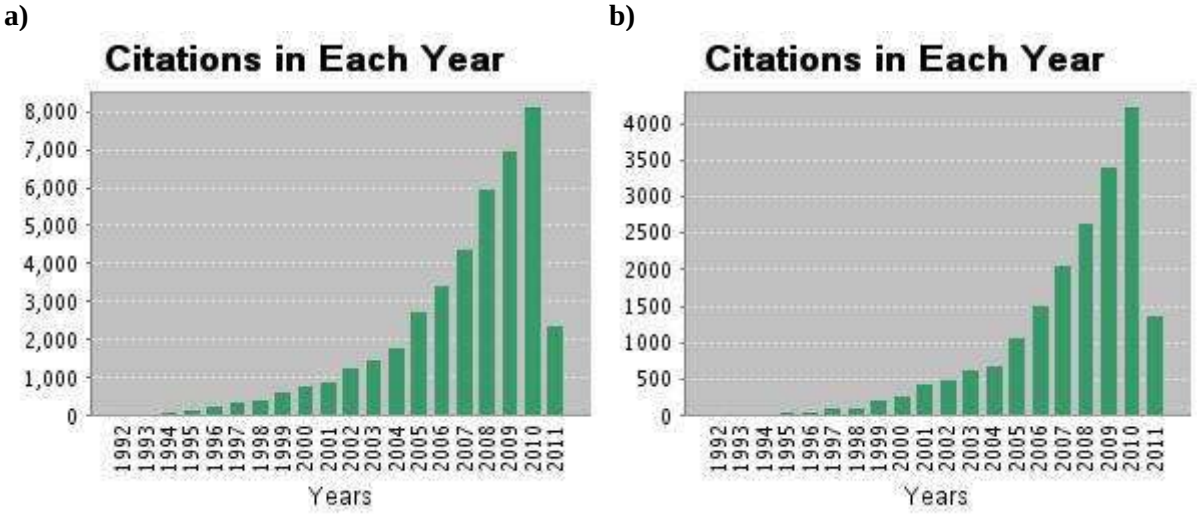

Figure 7.1 a) Number of citations per year related to the topic "Ecology" and "Species distribution model*" according to Web of Science (time span = all years; databases= SCI-Expanded, CPCI-S; search performed the 18/03/2011); b) Number of citations per year related to the topic "Species distribution model*" refined by the subject area "Biodiversity conservation" according to Web of Science (time span = all years; databases= SCI-Expanded, CPCI-S; search performed the 18/03/2011).

At the beginning, research related to SDM was mainly oriented towards methodological issues as attested by the first reviews (Franklin, 1995; Guisan and Zimmermann, 2000), but very rapidly these new methodologies were applied to address a variety of conservation issues as demonstrated by the topic of the three specialized SDM workshop that were held here in Switzerland in 2001, 2004 and 2008 at the Centre Pro Natura of Riederalp (Guisan and Thuiller, 2005). The topic of the first workshop (Riederalp 2001) was "Advances in GLM/GAM Modeling: from species' distribution to environmental management" and gave rise to two special issues published in Ecological Modelling (Vol. 157, Issues 2-3, p. 89-341; Guisan et al., 2002) and in Biodiversity and Conservation (Vol. 11, Issue 12, p. 2085-2338; Lehmann et al., 2002a). The second workshop (Riederalp 2004) focused on "Generalized Regression Analyses and Spatial Predictions: grasping ecological patterns from species to landscape" and produced three special issues, the first published in Ecological Modelling (Moisen et al., 2006), one in the Journal of Biogeography (Araújo and Guisan, 2006) and one in the Journal of Applied Ecology (Guisan et al., 2006b). More recently SDM started to be used in order to assess issues related to climate change and its impacts, the third workshop (Riederalp 2008) thus focused on the "Utility of Species Distribution Models as Tools for Assessing Impacts of Global Change" and gave rise to a special issue in Ecology (Vol. 33, Issue 6, p. 985-1081; Zimmermann et al., 2010).

Table 7.1 Main scientific contributions of this PhD thesis.

DATA AND SAMPLING DESIGN	
Improvement of sampling design	
Expert systems to target field survey	Annex 1,3
Stratification by Environmental domains	Annex 2,3
Assistance for releve classification	
Landspot database and decision-support system assisting classification	Annex 4
Improvement of predictors	
Downscaled land use information	Annex 5
SPECIES DISTRIBUTION MODELING	
Improvement of the modeling phase	
Selection methods	Chap.2
Weighted absences	Chap.2
Limited absences	Chap.2
Spatial autocorrelation	Chap.2
Predictor interactions	Chap.2
Remote sensing	Chap.3
Sample size and prevalence	Chap.4
Data post-stratification	Chap.4
Improvement for distribution models for fauna	
Pre-modelled vegetation communities to improve the modelling of fauna	Chap.5
Fine resolution maps that allows defining accurate AOs for conservation purposes	Chap.5
Improvement in the assessment of distributional changes	
Methodology in order to assess shifts along altitudinal or other environmental gradients	Chap.6

Along the numerous progresses made in species distribution modelling in recent years, this thesis aspired to contribute to the different steps of a modelling procedure, from optimizing the data survey to obtain the best spatial predictions for assessing the distribution of animal species in Switzerland. The concrete contributions are listed in Table 7.1 and their interconnections are presented in Figure 7.2. The most significant contributions are discussed in details hereafter.

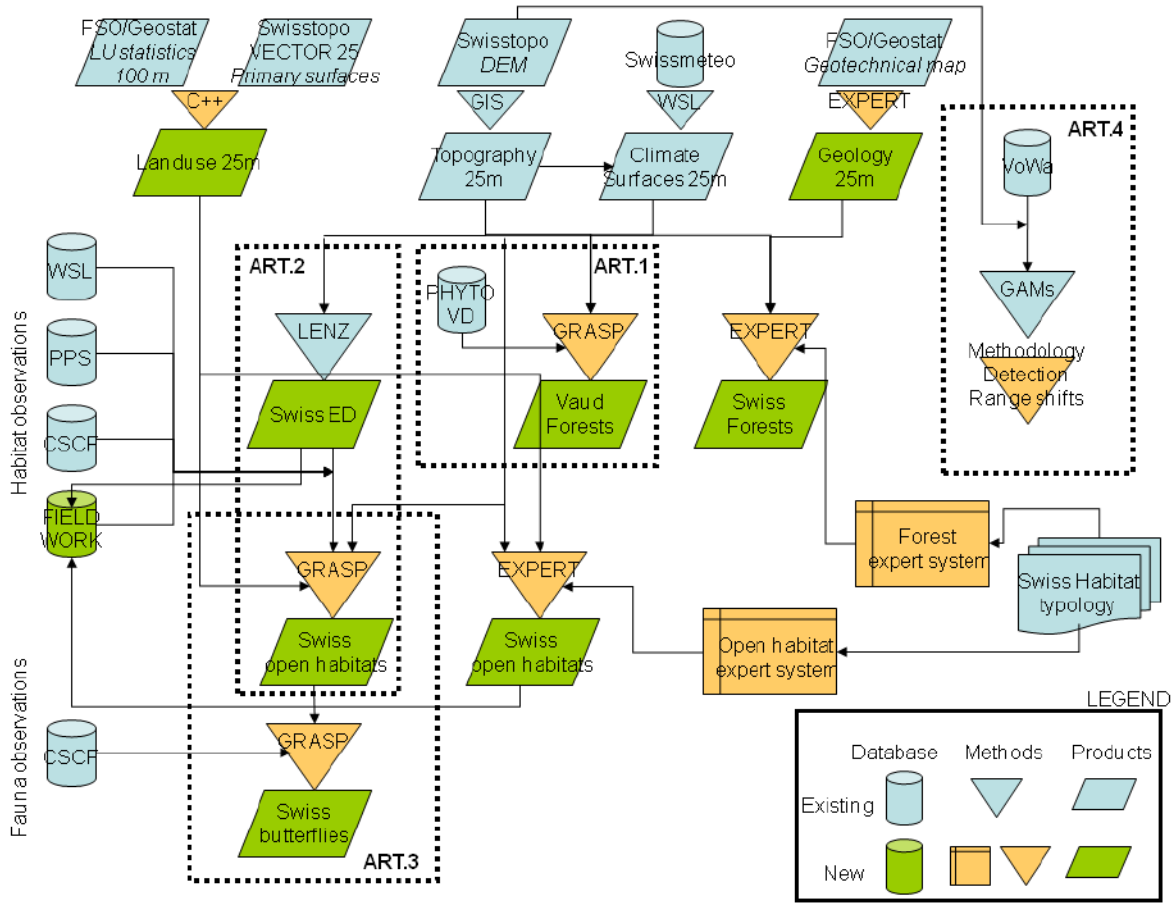

Figure 7.2 Main achievements of this thesis. Elements in blue are pre-existing elements that helped in developing new methods and generating new products (in orange and green, respectively).

7.1 DATA AND SAMPLING DESIGN

7.1.1 Improvement of sampling design

As mentioned in the introduction, this PhD thesis was started within the framework of the Landspot project (Swiss National Science Foundation, grant no. 3100-063147 obtained by Prof. A. Guisan). The main goal of the project was to assess the possible contribution of pre-modelled 'habitat' units (*sensu* biota) in order to model the distribution of animal species. This problem was mainly addressed in this thesis trough a case study aiming at modelling the distribution of a set of butterfly species across Switzerland. The 'habitat' units considered in this project were the natural and anthropogenic habitats (i.e. vegetation communities) of Switzerland as defined in the typology of Delarze et al. (1998). Since no comprehensive map of such habitats is so far available at the national scale, as a first step it was therefore necessary to create this information and thus to start by sampling the necessary data. First were considered forest communities that were sampled according to a) a first exploratory survey, in order to get familiarized with the typology and to learn to recognize the different units in the field, and

b) a subsequent survey stratified by altitudinal belts and land use categories (Annex 3.1). Indeed, an implicit question posed by the Landspot project was to elucidate the relative contribution of pre-modelled "habitat" units compared to land use categories that were generally used in replacement in SDMs. This random-stratified sampling helped in establishing a first correspondence with the categories of the Swiss land use/cover statistics (OFS, 2003) and lead to the conclusion that the land use/cover categories related to forest were mainly defined according to the structure (e.g. dense vs scattered trees, tall vs small stand) and not according to a biological content (e.g. *Fagus* vs *Pinus* forests). Structural categories have been showed to be useful in modelling some faunistic groups such as birds (Heikkinen et al., 2004; Manton et al., 2005; Luoto et al., 2007) or butterflies (Luoto et al., 2006; Kivinen et al., 2008). In these cases, the predictor is often defined as the percentage of cover of a given land use category in a given neighbourhood or within the sample unit and aims at assessing the habitat suitability at the landscape level. In some cases, the number, size or distance between the patches of a given land use category are also used in order to account for the habitat connectivity for the modelled species (e.g. for butterflies, Luoto et al., 2001; Heikkinen et al., 2007). However, there is a hierarchical effect of predictors in determining the distribution of the species, and while climatic variables are large scale determinants, land cover variables and topography mainly act at the regional (landscape) level and other important predictors act locally such as the presence of the larval host plant or the nectar/seed plant for the adults (Luoto et al., 2001; Luoto et al., 2006). The land use/cover category is therefore a first important approximation of the habitat (e.g. dense forest, scattered forest, natural grasslands, marshes, ...) but the nature and the main species characterizing these units are an essential information to finally determine the presence and abundance of the animal species. But, how to improve the biological content of coarse classes such as "dense forest" ? Either trough an extensive survey, or through modelling. We somehow combined the two by modelling the data of the forest inventory of State of Vaud presented in chapter 2.

The survey of "open habitats" was performed over two field seasons. As for forest communities and for the sake of comparison with land use, sampling units were centred on the same points evaluated by the Swiss Federal Statistical Office while producing the land use statistics. The first year, the sampling was centred on the points characterized by a category related to open habitats (pastures, grasslands, unproductive vegetation, etc.) and stratified by the six main biogeographical regions of Switzerland (Gonseth et al., 2001), by five classes of altitude and by the North/South aspect (Annex 3.2). This design allowed to survey 173 field units hosting different grassland, pasture and bushy communities. Although quite representative, the sample was not exhaustive of all communities present in Switzerland, also due to the fact that the survey was geographically limited. For the second field season, it was therefore decided to improve and specifically target the sampling (Annex 3.2). The main challenge was to determine where to go in the field in order to find the target, and in particular the still unsurveyed, vegetation communities, and to have a sample representative of all the environmental conditions characterizing the Swiss territory. In order to achieve this goal, two side products were developed, namely, expert models predicting the potential distribution of the target vegetation communities within Switzerland and environmental domains to be used to stratify the sampling so as to ensure that all environmental combinations are effectively surveyed. The incorporation of expert knowledge/opinion directly within statistical models has been showed to bring small but globally not significant gains in model predictive accuracy, reason why it is generally limited to the modelling of

species represented by insufficient data (Pearce et al., 2001). However, expert knowledge and any general information about the ecology are essential when sampling species or units in the field which distribution is mostly unknown. In order to target the sampling, expert models were therefore created on the basis of the information provided by the typology of Swiss habitats (Delarze et al., 1998) and other ancillary information, that was translated spatially within a GIS using the numeric layers corresponding to or approximating the main ecological drivers. This approach allows creating a map with all the vegetation communities that can potentially be found at a given location and thus to significantly increase the chance to finally find the target vegetation unit in the field. In order to ensure the collection of a sample representative of all the environmental conditions, the field sampling was further improved by stratifying it by environmental domains. Instead of simply stratifying this particular sampling with a series of selected environmental variables, we wanted to propose a new and general framework to be used for different studies and purposes at the national level.

Environmental domains results from an environmental classification of the Swiss territory based on key environmental drivers represented by climatic, geologic and topographic variables influencing both natural and anthropogenic processes at various scales (FOEN, GRID-Europe 2010). These selected variables delineate an environmental space in which domains are defined by grouping together territory units (i.e. grid pixels) that share similar environmental characteristics and that are therefore situated close to each other in this multidimensional space. In contrast to other existing frameworks in Switzerland such as the biogeographical zones of Gonseth et al. (2001), the floristic regions of Welten and Sutter (1982) or even the administrative regions (i.e. cantons), which are all defined as contiguous entities in the geographic space, Swiss environmental domains are directly defined in the environmental space, thus resulting in disjointed entities when projected into the geographic space. This is both the strength and the weakness of SwissED. It is clearly a strength to be defined in the environmental space since the resulting domains are much more likely to be representative of any phenomenon driven by environmental conditions, but at the same time it is also a weakness to be represented by disjointed entities in geographic space, because these are more difficult to apprehend by practitioners in charge of monitoring the environment and of making decisions about its protection (FOEN, GRID-Europe 2010). Environmental domains - also called ecoregions, ecological regions or land types - are entities that have been defined in many ways and for different purposes (Pressey, 2004), often in relation to biodiversity conservation and reserve planning. Examples of classification exists at different scales - regional (e.g. Host et al., 1996), national (e.g. Dufrene and Legendre, 1991; Belbin, 1993; Leathwick et al., 2003; Hargrove and Hoffman, 2004), continental (e.g. Metzger et al., 2005) and even global (e.g. Olson et al., 2001) - for terrestrial but also marine and river environments (e.g. Snelder et al., 2005; Snelder et al., 2007; Leathwick et al., 2011). Classifications can differ in respect to the employed methodologies (e.g. PCA, cluster analysis, cluster analysis supported by generalised dissimilarity modelling, hierarchical clustering, partitioning, etc.) the spatial resolution of the data (from several kilometres down to 25 m for the Swiss case) or the variables used to perform the classification (mainly climatic, topographic and geologic variables, but also vegetation and land use related information, plus specific variables for river and marine environments), but all share the same goal, which is to use modern data-driven and quantitative approaches to build objective, reproducible and hierarchical classifications of the environment that are to be used as analytical, reporting and management frameworks (Hargrove and Hoffman, 2004;

Loveland and Merchant, 2004; Omernik, 2004). Although classifications are generally designed for specific purposes and are thus performed using relevant variables (Loveland and Merchant, 2004), with SwissED we aimed at producing a general, multi-purpose and multi-scale framework defined by a set of base environmental variables influencing both natural and anthropogenic processes at various scales. In order to avoid encouraging any particular interpretation, variable selection was thus untargeted and avoided incorporating land use or any biotic information related to species or vegetation distribution, and each variable had the same weight for the classification. The classification is however flexible, in the sense that it can always be targeted for a specific purpose by applying different weights to the base environmental variables as it was tested by Snelder et al. (2009; 2010) with the target pattern of land cover categories within Switzerland.

Expert models and stratification by environmental domains finally allowed to efficiently target and optimize the field sampling in space. A further improvement was brought by the optimization of the time needed to go from one site to another. This was achieved by retaining only the sites that are located in a buffer of 200 m around the roads of category 1 (primary road) down to 4 (small rural or forest road) of the road network. In Switzerland the road network is very well developed also in the mountainous regions, the high density of roads and the large buffer defined around them thus allowed reaching either by car or by foot all the different vegetation communities that were to be prospected. Many studies have stressed the fact that samples taken along the roads are generally biased toward a reduced number of environmental combinations, but in our case this was avoided by stratifying the sampling by the environmental domains so as to ensure an environmentally representative sample. As a result of the improved sampling strategy the second season of survey for “open habitats” was much more efficient than the first one and allowed to survey 464 supplementary field units scattered across all the Swiss territory.

7.2 SPECIES DISTRIBUTION MODELING

7.2.1 Post-stratification, sample size and prevalence

Environmental domains can be used to stratify and thus to optimize the survey in the field, but can also be very useful for data post-stratification. Sampling campaigns can be very costly both in terms of resources and in terms of time, existing databases such as museum collections represents thus a valuable source of data that it is worth to use for modelling. However, these databases are often entailed with bias and errors that one would avoid for modelling purposes, resampling subsets of the data according to a stratified framework is thus a valuable strategy in order to remove or at least minimize those bias. Stratified resampling can also be an appropriate approach to apply when combining data issued from different databases and thus collected according to different sampling designs. In chapter 4, we assessed the effect of data stratification as well as the effect of the number of occurrences present in the sample used for modelling on the final model accuracy. In particular, we compared purely geographical to environmental stratification and assessed the impact of the increasing number of occurrences in the sample. Results showed that increasing the number of presences (Np) in the training sample improves model accuracy, but only until a given value after which an increase in Np does not further improve model accuracy (reach of a plateau). The threshold value differs

according to the stratification type of the data. With no stratification the threshold was reached only after 150 occurrences, whereas for stratified data this threshold was reached at 100 occurrences for coarsely stratified data (10 strata) and at 75 with a relatively finely stratification (26 strata). It is difficult to give general recommendations concerning the minimum sample size to use in order to obtain high accuracy models since values reported in the literature are highly variable and seem to depend on a variety of factors such as the modelling technique, the sample prevalence, the absolute sample size of each event (i.e. presences and absences), the method employed to select pseudo-absences (random vs further away from environmental regions established by presence data), the characteristics of the species (widespread vs rare) and its range size (Pearce and Ferrier, 2000; Stockwell and Peterson, 2002; Kadmon et al., 2003; McPherson et al., 2004; Guisan et al., 2007b; Chefaoui and Lobo, 2008; Wisz et al., 2008; Jimenez-Valverde et al., 2009). According to Jimenez-Valverde et al. (2009), it is possible to obtain reasonably accurate models even with very small sample sizes provided that the absolute number of presences and number of absences is large enough to represent all the environmental gradient. This seems to meet our conclusions related to the effect of data stratification. Indeed, our results showed that stratification has a significant impact especially when dealing with a low number of occurrences, suggesting that these really need to be representative of the different conditions favourable to the object being modelled. When preparing a survey, this also suggests that less data are needed to obtain accurate models when data are stratified with a relatively large number of strata. In particular, analyses showed that environmental stratification allowed obtaining more accurate models than purely geographical stratification at a comparable number of strata. Reasons for this are straightforward, but what is worth emphasizing is that environmentally stratified data not only gave models with higher validation statistics on the training data set, but they also gave better validation statistics on the independent data set thus suggesting a higher generality and transferability. Environmental stratification is thus worth for supporting field sampling designs when resources and time are limited since accurate models can be obtained with relatively less data. This finding is particularly interesting for the sampling and modelling of rare species. These are by definition difficult to observe in the field. Stratifying the survey by environmental domains would on the one hand improve the chance to find them by the survey of all possible environmental combinations and on the other hand would reduce the number of data and thus the total prospection time needed to obtain accurate models. The process could be iterative by alternating the collection of supplementary environmentally stratified data with the calibration of new more accurate models until no increase in performance can be obtained (Guisan et al., 2006a). Le Lay et al. (2010) used a very similar approach (model-based sampling, MBS) in which field sampling is guided by a first rough environmental model of the potential distribution of the species of interest that can then be improved with the newly collected data and in turn designate more accurate areas for prospection. Alternatively, our results showed that stratification has no significant impact at large sample sizes, in this case there is thus no justified reason to set apart a portion of the data by performing a post-stratification. This approach could however be very useful for preparing pseudo-absences to be used with museum or herbarium data. Indeed, it has been showed that the method used for preparing pseudo-absences can have an impact on model accuracy. Pseudo-absences chosen beyond the environmental envelope defined by presence data give models with higher explained deviance and accuracy than pseudo-absences chosen completely at random across the whole study area (Chefaoui and Lobo, 2008; Lobo

and Tognelli, 2011). This type of environmentally based choice of pseudo-absences can however lead to some over-prediction and thus result in predicted distribution areas that are larger than the areas obtained with random pseudo-absences (Chefaoui and Lobo, 2008). According to Chefaoui and Lobo (2008), random pseudo-absences rather model the realized distribution of the species whereas the environmentally selected pseudo-absences give predictions that are nearer to the potential distribution of the species. The explanation of this resides in the fact that by selecting random pseudo-absences we include in the model many absences near the environmental envelope of the presences, whereas with the environmental based selection outside the envelope defined by presences, pseudo-absences are selected from environments different from those of species presence (Chefaoui and Lobo, 2008).

7.2.2 Limited absences

In chapter 2, we also assessed the effect of the number of zero values considered beyond the environmental range of a species along an environmental gradient ('naughty noughts' sensu Austin and Meyers, 1996). Our results are in agreement with the findings of Chefaoui and Lobo (2008) just exposed in the previous section since models fitted with limited zeros (50 on each side of the presence range along two main environmental drivers, i.e. mean annual temperature and soil water budget) seem to have lower validation statistics than those fitted with the ensemble of zeros (i.e. including zeros far apart from the environmental optimum of presences). However, in this case lower validation statistics do not necessarily mean less accurate models or spatial predictions, since discrimination is more difficult within the range of presences than across the whole study area. This was confirmed by the cross-application of the models. Models fitted with limited zeros gave indeed better evaluations statistics than models fitted with the ensemble of zeros when re-adjusted on the entire dataset, while models fitted with the ensemble of zeros gave slightly worse evaluation statistics when re-adjusted to the restricted dataset. Thus, using limited zeros gives more discriminating models that in turn can lead to spatial predictions that are closer to the realized niche of the species and reveal patterns that were otherwise hidden (e.g. Guisan et al., 1998). This is also confirmed by the fact that predictors retained in the model are most of the time different.

7.2.3 Weighting absences

In chapter 2 again, we tested the effect of weighting zeros in order to artificially obtain a prevalence of 0.5 prior to modeling. Early studies have indeed showed that prevalence can have a significant impact on model performance (Fielding and Bell, 1997; Manel et al., 1999; Manel et al., 2001) and that a prevalence of 0.5 can be the best compromise in order to balance omission and commission errors (McPherson et al., 2004). According to Jimenez-Valverde et al. (2009), however, the effect of prevalence is significant only for extremely unbalanced samples, i.e. characterized by a prevalence lower than 0.01 or higher than 0.99, affecting sensitivity and specificity respectively, but still providing models with AUC scores higher than 0.90. Jimenez-Valverde et al. (2009) obtained these thresholds by working with a virtual species and simulated data. By using real data and artificially changing prevalence values by applying weights on the absences, we came to the same conclusions concerning the effect of extreme values of prevalence on model accuracy, but found that the effect started with less extreme thresholds already (prevalence < 0.05 or > 0.70). In particular, we found that the effect was more important for high prevalence values, which determined AUC values that could

drop much lower than 0.9. Explanations for this may be found in the absolute sample size of each event, i.e. presences and absences, as suggested by Jimenez-Valverde et al. (2009). What is important is indeed the absolute number of presences and absences in order to effectively represent the environmental gradient and not their relative size. At very high prevalence values, we can thus suppose that the number of zeros is insufficient.

7.2.4 Selection methods

Model selection is an extremely important phase in ecological modeling because different selection criteria can lead to different selected predictors and thus to different conclusions about the causal drivers of the distribution of the species. Predictors can be selected a priori, manually or trough automated selection procedures (Heikkinen et al., 2006). Several different criteria exist in order to decide for the inclusion/exclusion of a predictor in a model. Burnham and Anderson (2002) classified selection procedures in three main types: procedures based on the optimization of a given criteria (e.g. AIC, BIC), procedures based on test of hypotheses and p-values (e.g. χ^2, F), and finally ad hoc methods (e.g. cross-selection). Akaike's information criterion (AIC: Akaike, 1973) is based on an empirical log-likelihood function that estimates the relative distance between the fitted model and the observed data (Burnham and Anderson, 2002). The log-likelihood value is penalized by the number of parameters in the fitted model, following the principle of parsimony. The Bayesian information criterion (BIC: Schwarz, 1978) is similar to AIC, but is additionally penalized by the number of observations. χ^2 and F statistics test the significance of change in explained deviance when adding or dropping a term from the model. A valuable alternative method implemented in GRASP (Lehmann et al., 2002b) is CROSS, a method that couple a stepwise approach with cross-validation. With CROSS a cross-validated AUC statistic (named cvROC in GRASP) is calculated at each step of the selection procedure (Lehmann, 2005). The selection stops when no more predictors can be added or removed according to a BIC information criterion. CROSS then selects the model showing the highest value of cvROC. Models selected by CROSS are therefore parsimonious because based on the BIC criteria and highly stable since the final selection is based on the highest cross-validated AUC value. However, despite all these advantages, there is an important inconvenience which is the time needed to perform the selection. Since a cross-validation is necessary at each step of the procedure, CROSS is significantly more time consuming than the other methods. A much faster alternative method is BRUTO (Hastie and Tibshirani, 1990) which identifies significant predictors and the optimal degree of smoothing for each of them using a backfitting procedure. All these "old-generation but evergreen" selection criteria were tested within this thesis and main conclusions are that AIC appears to be too permissive, BIC too selective, cross-selection the best compromise between model stability and performance and Bruto has the advantage of providing automatic selection of smoothing degrees of freedom and to be computationally faster. A number of alternatives methods have been developed in recent years: hierarchical partitioning coupled with randomization, shrinkage methods such as ridge regression or lasso, model averaging, boosting, regularization in machine learning context (Araújo and Luoto, 2007; Elith and Leathwick, 2009). The use of these alternative model selection methods in ecology are still relatively rare in comparison to traditional stepwise methods, but very likely to increase in the future (Elith and Leathwick, 2009). The multitude of newly developed approaches suggests that model selection is still an open issue. Indeed, as pointed out by Araújo and Guisan

(2006), one can erroneously conclude that a modeling technique is inferior to another simply because the latter is more powerfully implemented. Model selection is thus an important step that surely deserves more attention than normally granted. It is thus advisable that future research continues to invest some prospecting efforts on this topic as well.

7.2.5 Spatial autocorrelation

The presence of spatial autocorrelation in model residuals represents both a challenge and an opportunity for modellers (Guisan et al., 2006b). The main issue is that spatial autocorrelation violates the assumption of data independence on which regression analyses are based and can lead to biased estimates of model parameters and to an increase of type I error (Dormann, 2007). In the past, the majority of the studies in SDM simply ignored spatial dependence or just tried to manipulate data in order to avoid autocorrelated observations (Miller et al., 2007). Today, techniques exist that allow taking advantage of this aspect to improve species distribution models. Indeed, as it has been showed by Segurado et al. (2006), data subsampling is partially effective in avoiding the inflation effect caused by spatial autocorrelation, but the inclusion of a contagion term fully eliminates this effect. In chapter 2, we tested different ways of dealing with spatial autocorrelation while modelling the distribution of forest communities. The data employed for the modelling were obtained from the forest inventory of State of Vaud which is based on a regular grid sampling of one plot every 400 m inside forested areas. In order to address the possible spatial correlation in the data, we prepared two specific predictors to be incorporated in the models: a general spatial trend (spatial interpolation of presences for a given forest community) to assess spatial patterns at the landscape level, and an autoregressive term to account for local autocorrelation that was defined as the kernel density of each forest unit in a circle of 1-km radius. Results showed that the general spatial trend significantly improved model performance and stability and that even better models were obtained by incorporating the autoregressive term. The inclusion of these predictors actually allows reshaping the potential distribution defined by environmental predictors to something closer to the actual distribution. While the general trend is an efficient way to account for historical patterns of distribution (e.g. glaciations or volcanic activity: Leathwick, 1998; Svenning and Skov, 2005), the autoregressive term expresses the local effect of biotic factor such as dispersal, competition and human disturbance (Miller et al., 2007). Several authors have shown that the incorporation of autoregressive terms reduces the spatial autocorrelation in model residuals produced by ecological processes (Lichstein et al., 2002). Segurado and Araújo (2004) modelled the distribution of 44 species of amphibians and reptiles in Portugal using different modelling techniques. The performance of generalized linear and additive models was assessed with and without a term accounting for spatial autocorrelation. Best results were obtained by the models including a covariate term for spatial autocorrelation. Modelling the distribution of butterfly species in France, Dennis et al. (2002) found that neighbourhood models were more successful than models based on the geographic position (latitude, longitude and altitude). They also found that a simple measure counting the proportion of occupied departments in the neighbourhood was more effective than a more complex distance-weighted neighbourhood measure. More generally, autoregressive methods can be more appropriate when the spatial dependence is intrinsic and causes local clusters in the data (Miller et al., 2007). Spatial autocorrelation have received particular attention

lately as testified by the two recent reviews of Miller et al. (2007) and Dormann et al. (2007) and an increasing number of methods have been developed to acknowledge it.

7.2.6 Remote sensing

Biodiversity monitoring requires frequent and spatially detailed assessments of species abundances and distributions. This information is generally very expensive to collect in the field, measuring it remotely is therefore an attractive alternative (Turner et al., 2003). Remote sensing has a considerable potential as a source of information on biodiversity at different scales (Gillespie et al., 2008). Approaches considering remotely sensed information are generally divided into two types (Turner et al., 2003; Aplin, 2005; Gillespie et al., 2008). Direct approaches use remotely sensed images to directly identify species (e.g. tree species), land cover types or species assemblages. Indirect approaches involve the derivation from remotely sensed images of environmental and biophysical parameters that are to be used for the modelling of species distributions and the distribution of diversity (Gillespie et al., 2008). Remotely sensed information is generally derived either by supervised or unsupervised image classification. In supervised classification, spectral signatures are developed using training sites of known land use class or vegetation type that are subsequently used in order to classify all the pixels in the image. Unsupervised classification first groups pixels according to their spectral properties into clusters and then try to assign them to land use or vegetation classes either by making a direct correspondence with ground control points, or by a modelling procedure using other supplementary variables. Within this thesis we tried an alternative approach that consists in using directly the rough spectral information as predictor within the model in order to model the distribution of different forest communities. This type of approach is not very common in the literature. Moreover, the contribution of the totality of the spectral information (band 1-5 and 7 of a Landsat 7 ETM^+ image) was compared to the contribution of the visible bands (bands 1-3: visible red, green and blue), the contribution of a derived index - the normalized difference vegetation index (NDVI), obtained by the combination of spectral band 3 and 4 – and finally, the contribution of pre-classified spectral information into classes of forest mixity (different percentages of broadleaved or coniferous trees). Results showed that the inclusion of remote sensing information significantly improves the predictive power but not necessarily the stability of the models. Model performance was significantly higher when using single bands when compared to the other raw or transformed spectral data. Similar results were obtained by Zimmermann et al. (2007) when assessing the contribution of topo-climatic and remotely sensed predictors to model the distribution of 19 tree species in Utah. Remotely sensed predictors also consisted in the reflectance of individual bands (bands 1–5 and 7 of a Landsat ETM^+ image) as well as derived indices such as NDVI. Their results showed that remotely sensed variables were useful predictors for the spatial distribution of trees. On average, 20% of the overall deviance was explained by the topo-climatic predictors, 10% by remote sensing predictors and a further 20% was explained jointly by both predictor sets. However, when evaluating the models, only a weak and non-significant increase was obtained in predictive cross-validated accuracy. Although model stability, i.e. applicability to other situations, is apparently not increased by the inclusion of remote sensing predictors, this information increases model accuracy by reshaping the potential distribution predicted by environmental and climatic predictors to something closer to the actual distribution, probably resulting from competition, perturbation or recolonisation events

(Dirnbock et al., 2003). This is clearly apparent in the resulting distribution maps. It has been shown that NDVI can differentiate very different land cover types such as savannah, dense forest, non-forest and agricultural fields, the index can also differentiate trees from shrubs, or evergreen from broadleaved forests using temporal trends (Pettorelli et al., 2005). However, differentiating different communities with different dominant species within forested areas is not possible using this kind of remote-sensing information, because several assemblages of plant species can produce a similar NDVI value or a similar NDVI temporal trend (Pettorelli et al., 2005). This explains why in our experience NDVI models were not more accurate than the models integrating the single bands: on the one hand NDVI is not effective in discriminating tree species and on the other hand we only used one NDVI, whereas it would have been necessary to consider several temporally distinct NDVI during the growing season for at least discriminating coniferous from broadleaved forest communities. However, pre-classified classes of forest mixity did not show significant higher model accuracy. More recent hyperspectral imagery has more discrete spectral bands now enabling the detection of spectral signatures that are characteristic of certain plant species or communities (Turner et al., 2003; Aplin, 2005; Pu, 2009). Another emerging technology, lidar (light detection and ranging) is particularly useful for measuring height and in particular tree height (Aplin, 2005).

7.2.7 Pre-modelled vegetation communities to improve the modelling of fauna

The term “habitat” has been used confusingly and inconsistently in the literature either referring to populations of different species co-occurring at a specified point in space and time - the habitat concept of community ecology – or to environmental conditions (abiotic and biotic) determining the presence of a particular species at a given location - the niche concept adopted in species distribution modeling. The difference between the materializations of this two concepts is merely a question of scale and perspective (Ricklefs, 2008). The local community that is recognized as a unit from the discipline of community ecology, can be seen as “a single point shared by many species” “with partially overlapping distributions” (Ricklefs, 2008) at a landscape level. At this scale the spatial distributions of populations replace the community concept. In chapter 5 was presented an original approach that combines these two concepts: first are modelled vegetation communities per se, and then these units are used to model the habitat of an animal species. Vegetation communities are defined very finely (alliance level) and it is therefore very likely that the habitat of a given species will encompass several of them. The approach is conceptually similar to the Gap analysis of Scott et al. (1993), but the implementation is much improved compared to a simple map overlay in a GIS. We illustrated the approach using butterflies and pre-modelled grassland communities across Switzerland and by doing so we addressed two more general methodological questions. The first one aimed at assessing the relative performance in faunal SDMs of pre-modelled vegetation communities and of land use categories. Results showed that models integrating vegetation communities as predictors were more accurate and stable than models integrating pure land use information. Predictors such as *Mesobromion* or *Seslerion* are indeed much more informative than the simple “grassland” information because they provide information about the presence of the host/nectar plant on which butterflies relies on. In the past the information about the distribution of vegetation communities was often used interchangeably for the distribution of animal species. This is actually the simplest model that can be used in order to describe animal habitats (‘cover-type model’; Schlossberg and King, 2009), but

present a certain number of problems. This kind of simplistic model make mistakes in more than 20% of the cases and these are for the majority commission errors (up to 20%), but omission error can reach 10% (Schlossberg and King, 2009). This is mainly due the imperfection and subjectivity of expert opinion and to the oversimplification of the pattern of habitat use by the animal species (Schlossberg and King, 2009).

The second question aimed at determining the best way to combine climatic and vegetation information between a modelling approach and an approach based on map combination. Assembling climatic and vegetation related predictors in a model gave slightly better results (higher AUC and correlation values), than the Bayesian combination of the corresponding spatial predictions. This is probably due to the fact that the predictors undergo a new selection procedure within the modeling approach that allows finding the best combination of and a new equilibrium between climatic and vegetation-related predictors, whereas in the Bayesian combination the base probabilities are simply combined. However, from the more applied perspective of a conservation manager, the Bayesian combination is maybe preferable because it allows better separating the role of the environment, defining the potential distribution of the species, from the role of the vegetation that reshape the potential to something closer to the actual distribution, i.e. the realized niche. Highly appealing is the possibility to easily update the information concerning vegetation with the "real distribution" captured by remote sensing or vegetation mapping. Note that in the latter case, probabilistic maps are replaced by actual vegetation maps with probability 0/1 for a given vegetation type. The Bayesian combination approach will in this case lead to a filtered environmental prediction. Although we do not recommend using vegetation communities as predictors for SDMs in the context of climate change – plant species are indeed expected to migrate independently and not as a whole - integrating information about vegetation, even only in the form of the distribution of key plant species, allows improving landscape description by adding sound biological content to basic land cover categories and thus improving model for fauna.

7.2.8 Improvement in the assessment of distributional changes

Climate change is affecting biodiversity worldwide and represents a supplemetary challenge for biodiversity conservation (Heller and Zavaleta, 2009). Climate change has been shown to perturb population dynamics by affecting the physiology, survival and productivity of individuals, to alter the phenology of major seasonal events such as migration and reproduction, and to induce shifts in species ranges (Hughes, 2000; Walther et al., 2002; Parmesan and Yohe, 2003; Parmesan, 2006). Species distribution models (SDMs) are an essential tool in this context since they allow making predictions about the future distribution of species, they suggest new areas to put under protection in order to assist the migration of the species, they predict the pathway of spread of invasive species and finally they can make estimations about the extinction risk (Thomas et al., 2004; Thuiller et al., 2005; Broennimann et al., 2006; Elith et al., 2010; Engler et al., 2011). SDMs can also be useful in assessing the extent of already occurred distributional shifts. In chapter 6 was presented a conceptual framework for analysing species range shift composed by a catalogue of the possible patterns of change in the distribution of a species along elevational or other environmental gradients and an improved quantitative methodology to identify and objectively describe these patterns (Maggini et al., 2011). Switzerland is a small country characterized by an important elevational gradient; with climate change

main distributional changes are therefore expected in the vertical dimension. As a case study, we thus applied the proposed methodology in order to assess changes in the elevational distribution of breeding birds in Switzerland. For this application we could benefit of a high quality data set issued from the Swiss national common breeding bird survey. This monitoring program is run on an annual basis by the Swiss Ornithological Institute since 1999; a substantial amount of data on species distribution and abundance has thus been accumulated. The survey encompasses 267 squares of 1km^2 that are distributed across the Swiss territory as a grid and are thus representative of different biogeographical zones, elevation bands and ecosystems. The methodology is based on the shapes of the response curves of GAMs. The presence or the abundance of a species is modeled as a function of elevation and the shape of the resulting curve is compared to the shape modeled for a different period using five reference points. This reference points are defined according to the "outer border" and "central border" previously defined by Heegaard (2002) for non-parametric functions (GAMs) and used to define species tolerance and range along environmental gradients. In our case, these reference points allowed to precisely describe the position of the curve along the elevational gradient and therefore to assess range shifts by the comparison of the two curves. Moreover, distributions are rarely shifting compactly, especially when considering short time periods, the displacement generally start at one end of the distribution, either the leading or trailing edge, with a subsequent follow up of the core of the distribution. The assessment of the change occurred at the five reference points thus also allow to determine the type of shift pattern. The proposed methodology has a high degree of generality since it can be applied to a variety of gradients: elevation to assess elevational shifts, latitude to assess polewards shifts, time to assess phenological shifts, or the different gradients composing the environmental niche of a species (humidity, temperature, energy sources or other environmental gradients) in order to assess species plasticity and adaptive capacity in respect to climate change. Previous methodologies in order to assess range shifts have employed techniques such as the 10 northernmost/southernmost latitudes (Hill et al., 2002; Hitch and Leberg, 2007) or the mean weighted elevation of a species (Popy et al., 2010), thus concentrating either on the margin or the center of the distribution but not the two. In this respect we believe that our methodology has a significant advantage.

7.3 POTENTIAL FOR CONSERVATION

The first approaches to reserve selection mainly used presence–absence data that were aggregated into species-richness maps on which the selection was to be based. Information about species distribution is however often incomplete or even completely lacking especially for species that are of particular interest for conservation, i.e. rare species. Selection algorithms were thus adapted in order to deal with probabilities of occurrence issued of distribution models rather than presence/absence data (Polasky et al., 2000). This was an enormous step forward, since it allowed apprehending a greater number of species. Compared with p/a data, reserve selection based on probabilistic occurrence data results in the selection of different sites and the difference is more pronounced when the occurrence probabilities are far away from 0 or 1 (Polasky et al., 2000; Loiselle et al., 2003). This is mainly related to the issue of transforming probabilities into presence/absence data, the choice of the threshold is indeed full of consequences because it changes the set of sites chosen and the expected number of species in the reserves (Polasky et al., 2000). While reserve selection algorithms continue to improve, the data used

for applying these methods is often inadequate. Data quality, quantity and distribution are critical in order to obtain valuable reserve networks. According to Cabeza and Moilanen (2001), algorithms are relatively robust to randomly distributed reductions of records, but significant less when the missing data are concentrated in particular sites or for given taxa, inventory efforts should thus be distributed as broadly as possible among sites and taxa. The use of species distribution modelling can help in filling the spatial gaps for insufficiently surveyed species, but has the drawback to show the potential rather than the real distribution of the species which can have been limited by historical factors, competition or human disturbance. Moreover, as shown in this thesis and by other authors, the size of the sample used for modelling and the spatial distribution of the data (environmentally representative vs biased towards a reduced number of environmental combinations) greatly affects the resulting model accuracy. This uncertainty about species distribution can lead to the selection of different reserve networks. It is thus very important to evaluate the conservation implications of model accuracy and in particular of false-positive and false-negative errors (Carvalho et al., 2010). Commission errors (false positive) generated by uncertainty in species distribution models can have important consequences since they can misdirect conservation actions towards reserves where species do not actually occur and this is particularly negative for rare species (Carvalho et al., 2010). A Type I error does not necessarily mean that the reserve is unsuitable, rather that the areas is favourable but presently unoccupied. In contrast, a Type II error can potentially result in sites not being selected even though target species are present (Loiselle et al., 2003). In general, reserve networks selected on the outputs of models minimizing false-positive errors correspond more closely to priority areas identified by specialists (Loiselle et al., 2003). Several studies have compared the final reserve network selected on the basis of occurrence data, predicted probabilities or hybrid data sets. Despite the fact that hybrid data sets can combine observed occurrences and predicted probabilities in different ways, results agree in saying that selected site locations and sizes is highly sensitive to the type of the data used and that the hybrid approach usually provides the most suitable compromise (Carvalho et al., 2010; Underwood et al., 2010). When selecting reserve sites simply according to the criteria of complementarity, the algorithm does not differentiate presences issued from the core of the distribution of the species and presences issued from the edge. This problem can be reduced by directly considering the predicted probabilities instead of the transformed p/a data (Loiselle et al., 2003) since probabilities can differentiate habitat suitability and therefore allow making assumptions about the core/edge of the distribution. An alternative solution would be the integration of the probability of persistence of the species, information that is supposed to exclude or at least decrease marginal habitats (Loiselle et al., 2003). Persistence depends on meta-population dynamic, demographic processes, local sources of threats and species' vulnerabilities. First approaches in this direction simply estimated the probability of persistence by integrating information on local threats and species vulnerability (Araújo and Williams, 2000; Williams and Araújo, 2000). More modern approaches are turned towards dynamic models and now start to integrate spatial population modelling (e.g. Haight and Travis, 2008).

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8 PERSPECTIVES

8.1 DATA AND SAMPLING DESIGN

8.1.1 Environmental Domains

In this study Swiss Environmental Domains were used in order to stratify the sampling in the field so as to obtain a sample representative of all the combinations of environmental conditions of the territory, but there are many other possible applications especially in relation to environmental research and management. SwissED can for instance identify the geographical range over which results from site-specific studies can be reliably extended or identify sites where analogous problems are likely to arise in response to human activities. Within the framework of conservation planning, SwissED can assist in identifying biodiversity hotspots in the country and suggest new areas to put under protection, thus supporting the most efficient use of limited financial resources for biodiversity conservation. More generally, SwissED are thought to represent a new effective framework for the analysis of data related to and the reporting of the state of our environment. Three concrete examples have been presented in FOEN, GRID-Europe (2010) already, but a more representative set of applications will be presented in a report currently under preparation with examples related to the assessment of biodiversity, land cover, demography, agriculture or economic activities within the environmental domains (Lehmann et al., in prep.). A highly interesting application would also be the use of SwissED for reporting on environmental sustainability (e.g. for Canada, Marshall et al., 1996). SwissED are still very young - the official version was made available and the related publication published end of 2010 - it is therefore too early to draw conclusions about their adoption by the concerned public (scientific and administrative communities) and the advantages vs disadvantages compared to existing frameworks. The future will tell us about their success and their dissemination, an important point to remind, however, is that SwissED are not though to replace existing analysis and reporting frameworks, rather to complement them especially when the accent has to be put on the link between a variable/statistic of interest and its relationships with key environmental drivers.

8.1.2 Downscaling

Downscaling of important environmental information such as those necessary for species distribution models is essential. Many downscaling approaches have been developed in different fields such as climatology, demography and land cover. In this study, we showed how land use data could be downscaled by combining different sources of information. The obtained downscaled information was essential to allow species distribution models at the finest possible resolution of 25m. As data quality and availability is improving for conservation purposes, it becomes more and more important to guarantee that the outputs of the analyses are brought at the scale at which conservation decisions are to be made. Species predictions at 1 km resolution in a country like Switzerland would be of very little interest, as everything can be found in such a kilometre, from the bottom of a dry and warm valley until a cold alpine summit.

8.2 SPECIES DISTRIBUTION MODELING

Species distribution modeling is a discipline in constant expansion as shown by the increasing number of papers published and the variety of topics addressed in the literature. In the last decade SDM has benefited from important methodological developments. New modeling approaches are now available that can for instance automatically integrate predictor interactions, an example are Boosted Regression Trees (BRT; Elith et al., 2008). BRT can be seen as additive regression models in which individual terms are simple trees that are combined in order to improve predictive performance (Elith et al., 2008). In this respect they differ significantly from conventional techniques in which model selection is mainly based on the criteria of parsimony. Other approaches such as multivariate adaptive regression splines (MARS; Elith and Leathwick, 2007) can now accommodate several responses at once and mimic communities. In this case information relative to the presence/absence from other co-occuring species can be used to determine the dominant environmental drivers of variation in species composition (Elith and Leathwick, 2007). MARS are closely related to GAMs but have the advantage of not being computer intensive and that results can be written as a mathematical equation easily exportable to a GIS. Additional techniques are represented by artificial neural-networks, genetic algorithms, generalized dissimilarity models and maximum entropy models (Elith et al., 2006; Elith and Leathwick, 2009). Performance of all these techniques have been compared in several studies in the context of different applications or with simulated data; the most comprehensive of these comparisons is certainly (Elith et al., 2006). The implementation of these new techniques was accompanied by the assessment of other important aspects of a modeling procedure such as the effect of the type of sampling stratification (Hirzel and Guisan, 2002), the effect of sample size and prevalence on model performance (Pearce and Ferrier, 2000; Manel et al., 2001; Stockwell and Peterson, 2002; Wisz et al., 2008; Jimenez-Valverde et al., 2009), criteria for model selection (Burnham and Anderson, 2004; Johnson and Omland, 2004; Kuha, 2004), evaluation statistics (Allouche et al., 2006), the effect of spatial correlation (Dormann et al., 2007; Miller et al., 2007), the effect of resolution (Araújo et al., 2005; Guisan et al., 2007; Pearman et al., 2008) and different threshold criteria for binary classification (Liu et al., 2005; Jimenez-Valverde and Lobo, 2007; Freeman and Moisen, 2008). New publications continue to regularly appear on these topics which means that original questions are at least in part still open and unresolved. The majority of the subjects addressed by this thesis are to be placed within this context and have or will hopefully contribute to make some significant advances in these areas of research (Araújo and Guisan, 2006). An update on the unresolved issues in the discipline of species distribution modelling has regularly appeared in the literature with the positive consequence of guiding new developments and assessments (Austin, 2002; Pearson and Dawson, 2003; Guisan et al., 2005; Araújo and Guisan, 2006; Guisan et al., 2006; Elith and Graham, 2009; Elith and Leathwick, 2009; Zimmermann et al., 2010). Very important conceptual points that are still open concern the foundation of species distribution modeling which is the concept of niche itself: operational definition of niche in SDM, niche conservatism, niche evolution (Araújo and Guisan, 2006; Zimmermann et al., 2010). Foundations of SDM are deeply embedded in Hutchinson fundamental and realized niche concepts, but there are still conflicting opinions on what models represent, i.e. species fundamental or realized niche (Araújo and Guisan, 2006). Moreover, niche conservatism is the strict assumption that SDM make when projecting species distributions into the future in a context of climate change (Pearman et al., 2008), but this assumption do not account for

adaptive capacity (physiological plasticity, genetic diversity) that could for example allow a species to maintain itself in a modified climatic environment. A possibility for evaluating niche stability is to analyse the environmental constraints over a phylogenetic tree and to explore to which extent particular environmental combinations can be considered as local adaptations (Zimmermann et al., 2010). The topic of niche evolution and the challenge of integrating evolutionary and ecological responses of species to climate change have recently being addressed within a special issue (Wake et al., 2009) and by the review of Lavergne et al. (2010).

8.3 SDM FOR CONSERVATION

Forecasting into the future actually violates several statistical and ecological assumptions of species distribution modelling (Elith and Leathwick, 2009). Indeed, one of the fundamental assumptions in SDM is that species are in equilibrium with their environment. The projection of species distributions into the future in a context of climate change or invasion is a delicate exercise since it requires to apply the model to a non-equilibrium situation and to extrapolate the distribution to new unsurveyed environmental conditions. There are several issues related to this: on one hand, the new environments and the altered biotic interactions may limit the distribution of the species, while species phenotypic plasticity and genetic variability could allow them to adapt at least in part to the new climatic conditions (Elith and Leathwick, 2009). The final distribution is therefore modulated by many factors that SDM cannot handle for the time being. Despite these approximations, SDM remain however one of the few available approaches in order to forecast species distributions and several new developments could improve their effectiveness in extrapolation and increase their reliability for conservation purposes. Elith and Leathwick (2009) suggest a list of these possible improvements that researchers now start to address: differences between the sampled and the new prediction environment can at least be quantified; species data could be weighted to represent the invasion process or the sample bias; dispersal can be integrated using estimates of dispersal rate, models of dispersal or by linking SDMs to cellular automata; evolutionary change might be estimated and included in models. Moreover, since projections from alternative models can be highly variable according to the input data sets, the modelling technique and the climate-change scenario considered, Araújo and New (2007) recommend to work within an “ensemble forecasting” framework. Differences between models can be reduced by either consensus or probabilistic approaches in order to summarize results (Araújo and New, 2007), but can also be used to discover the reason why predictions are different or be quantified to inform risk analyses (Elith and Leathwick, 2009). The vulnerability of a species facing climate change is not only defined as a function of exposure, other aspects such as the sensitivity and adaptive capacity of the species should be taken into account to obtain more reliable predictions (Williams et al., 2008; Dawson et al., 2011). As summarized by Dawson et al. (2011), several critiques have been expressed towards the use of species distribution modelling for making predictions for the future, between them the correlative nature of the models, their scale dependency, the extrapolation to new environmental conditions and in particular the failure to incorporate key ecological and evolutionary processes that at the end could allow the species to persist even in a highly modified landscape. The incorporation of ecophysiological and population models can deliver more precise estimations of diversity losses and hopefully lead to different conclusions about the future of our biodiversity. Some recent studies have indeed demonstrated that the combination of population models with SDMs can

offer a powerful mechanistic approach for assessing the extinction risks posed by climate change (Keith et al., 2008). Since species response to climate change may be influenced by changes in habitat availabilities but also in demographic processes, population and habitat models coupled together are likely to produce projections that are more robust to uncertainty (Keith et al., 2008). Similarly, mechanistic physiologically-based SDMs have the potential to deliver more robust predictions in new or non-equilibrium contexts such as invasion, translocation, climate change or evolutionary shift (Kearney and Porter, 2009). Moreover, leaving static models and moving towards dynamic models would certainly produce more realistic predictions. According to Franklin (2010) assessments of climate change impacts on the distribution of species should at least account for species dispersal ability, which will refine predictions normally made for the two extreme cases of full- and none-dispersal scenarios (as in Engler et al., 2009). On a higher level of analysis, linking models of habitat suitability, habitat dynamics and spatially explicit population dynamics would provide an effective framework for understanding the potential interactions between the factors affecting species distributions and population persistence such as climate and land use change (Franklin, 2010). Analyses performed within such a framework would allow designating more effective reserve networks for the future that compensate for climate-induced species range shifts and account for species persistence and land cover dynamic.

A supplementary element of improvement could come from considering more systematically biotic interactions (Guisan et al., 2006). Only few SDM studies have explicitly included predictors describing biological interactions until now but all agree in saying that the incorporation of biotic interactions into SDMs allow to better model species distributions and are thus important for more valuable projections in response to climate change (Araújo and Luoto, 2007; Heikkinen et al., 2007; Preston et al., 2008; Meier et al., 2010; Pellissier et al., 2010; Van der Putten et al., 2010). SDMs accounting for biotic interactions are particularly important for the reserve design of species that are highly habitat specialists or have strong dependency on other species (Preston et al., 2008). The remaining challenge is to know how these biotic interactions will change - as a general rule species will indeed migrate independently (e.g. Rehfeldt et al., 2006; Baselga and Araújo, 2009) - and how to model them (Elith and Leathwick, 2009). Finally, biotic interactions are also important in the context of species invasion. SDMs have often been used to assess the potential of invasion of species into new habitats. One of the major issues is the assessment of the invasive potential in different continents. Sampling the current invaded range may underestimate the niche response, because the species has not reached an equilibrium yet and may not realize its full niche potential (Broennimann and Guisan, 2008; Zimmermann et al., 2010). On the other hand, fitting a model with data of the original range may not give the full niche, as the original range may not include all the possible environmental combinations that can be occupied by the species (Broennimann and Guisan, 2008; Zimmermann et al., 2010). Moreover, new continents also imply new biotic interactions that will alter the realized niche of the species. Recently, a great step forward in modelling range-shifting species was made by Elith et al. (2010) while trying to model the distribution of the cane toad, an invasive species spreading across Australia. Results confirmed the already suspected problems of SDMs for extrapolation but also showed that the integration of information from mechanistic models, ecophysiological models in the particular case, could enhance the reliability of the predictions (Elith et al., 2010). While the superiority of SDMs coupled with mechanistic models starts now to be confirmed by several

prospective studies, a still open question is how to effectively couple them (Guisan and Thuiller, 2005; Gallien et al., 2010). In conclusion, several highly challenging issues are still open and will attract the attention of the species distribution modelling community in the next years with the primary aim of providing increasingly accurate information for conservation planning. This will however not be sufficient for stopping our biodiversity loss: scientific innovations need to be supported by a strong political willingness in order to achieve this vital objective.

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ANNEXES

ANNEX 1: EXPERT MODELS

When data available for modelling the distribution of a species are insufficient to perform statistical modelling, expert knowledge can be used in replacement. The distribution of the species can then be modeled according to the main environmental factors known to influence the distribution of the species according to the literature or to the personal expertise. Expert knowledge can also be very useful in targeting field campaigns, especially when dealing with rare species or species which environmental requirements are only partially known. Within the framework of this thesis, expert models were primarily used to predict the potential distribution of grassland communities so as to better target the sampling in the field. The expert system for grassland communities is presented in Annex A1.1 and the corresponding field work in Annex A3.2. An expert system was subsequently developed for forest communities and is presented in Annex A1.2.

A1.1 GRASSLANDS

The expert models were created on the basis of the information provided by the typology of Swiss habitats (Delarze et al., 1998). The environmental requirements of the units described in the typology as well as other ancillary information were translated into an expert system (table) that was subsequently implemented in a GIS using spatial information relative to the main environmental drivers. This approach allowed creating a map with all the vegetation communities that can potentially be found at a given location and thus significantly increased the chance to finally find the target vegetation unit in the field during the survey.

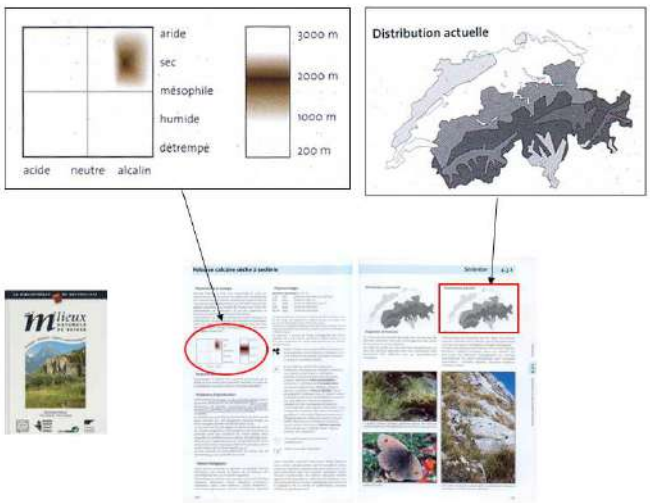
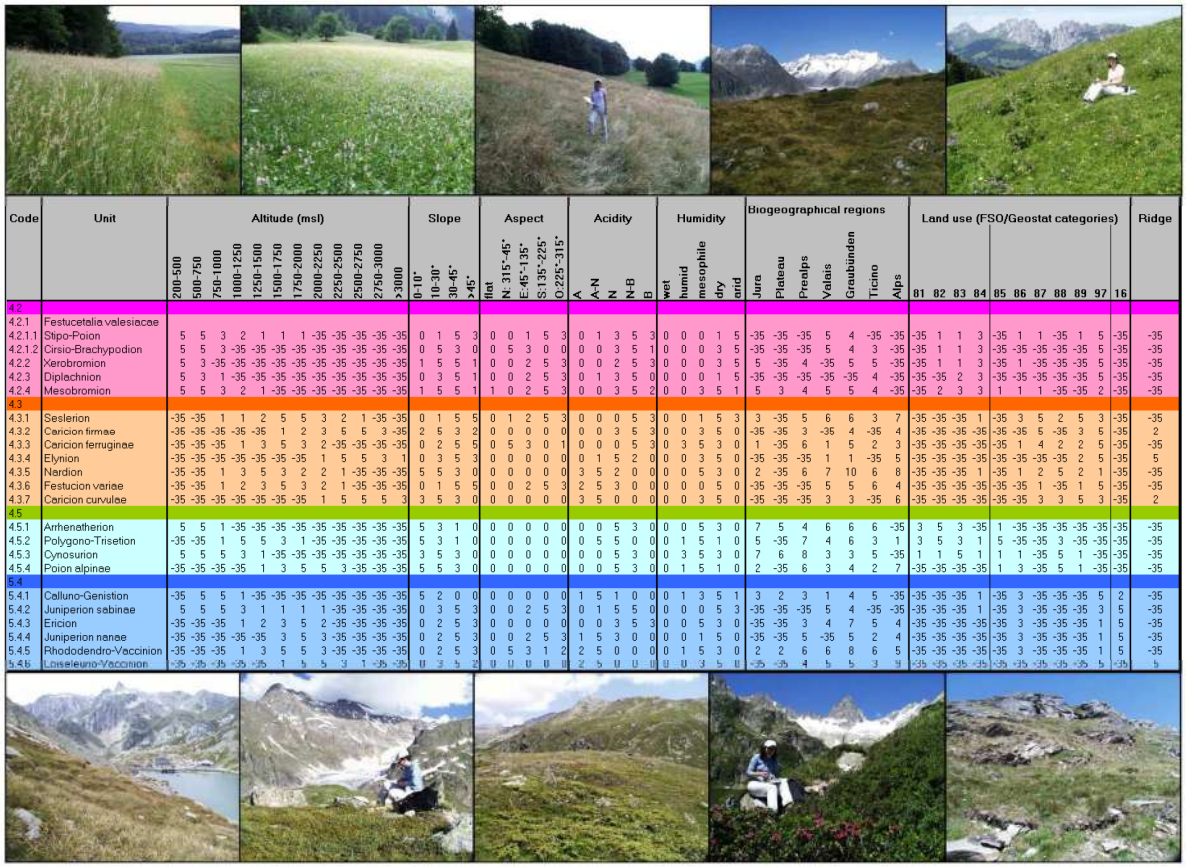


Figure A1. 1 Exemple of the description of one phytosociological unit within the typology of the Swiss habitats (Delarze et al., 1998). The expert system is based on information relative to the distribution of the unit along the humidity, acidity and altitudinal gradient as well as its distribution across Switzerland.

Figure A1. 1 shows an example of the description of the phytosociological units within the typology. The expert models are mainly based on variables describing the distribution of the unit along the humidity, acidity and altitudinal gradient as well as its distribution across Switzerland (graphical information shown in Figure A1. 1). This information was supplemented with information concerning the terrain slope and aspect, the potentially favourable land use categories and presence in mountain summit. Each variable was subdivided in different classes. For each vegetation unit a probability of occurrence (values between 1 and 5) was assigned to each class. Where no information was available a value of 0 was assigned and where a negative effect was suspected a negative value of -35 was attributed. In Figure A1. 2 is presented the final expert system for 'open habitats' revised by Dr Yves Gonseth (CSCF) and Dr Raymond Delarze (Bureau Delarze) both co-authors of the Swiss typology.



Code	Unit	Altitude (msl)										Slope			Aspect				Acidity				Humidity			Biogeographical regions						Land use (FSO/Geostat categories)										Ridge
		200-500	500-750	750-1000	1000-1250	1250-1500	1500-1750	1750-2000	2000-2250	2250-2500	2500-2750	2750-3000	>3000	0-10°	10-30°	30-45°	>45°	flat	N: 315°-45°	E:45°-135°	S:135°-225°	O:225°-315°	A	A-N	N	N-B	B	wet	humid	mesophile	dry	arid	Jura	Plateau	Prealps	Valais	Graubünden	Ticino	Alps	81	82	83	84	85	86	87	88	89	97	16	
4.2																																													
4.2.1	Festucetalia valesiacae																																												
4.2.1.1	Stipo-Poion	5	5	3	2	1	1	1	-35	-35	-35	-35	-35	0	1	5	3	0	0	1	5	3	0	1	3	5	3	0	0	0	1	5	-35	-35	-35	5	4	-35	-35	-35	1	1	3	-35	1	1	-35	1	5	-35	-35
4.2.1.2	Cirsio-Brachypodion	5	5	3	-35	-35	-35	-35	-35	-35	-35	-35	-35	0	5	3	0	0	5	3	0	0	0	0	3	5	1	0	0	0	0	3	5	-35	-35	-35	5	4	3	-35	-35	1	1	3	-35	-35	-35	-35	-35	5	-35	-35
4.2.2	Xerobromion	5	3	-35	-35	-35	-35	-35	-35	-35	-35	-35	-35	1	5	5	1	0	0	2	5	3	0	0	2	5	3	0	0	0	0	3	5	5	-35	4	-35	5	5	-35	-35	1	1	3	-35	1	-35	-35	-35	5	-35	-35
4.2.3	Diplachnion	5	3	1	-35	-35	-35	-35	-35	-35	-35	-35	-35	0	3	5	1	0	0	2	5	3	0	1	3	5	0	0	0	0	1	5	-35	-35	-35	-35	-35	4	-35	-35	-35	2	3	-35	-35	-35	-35	-35	5	-35	-35
4.2.4	Mesobromion	5	5	3	2	1	-35	-35	-35	-35	-35	-35	-35	1	5	5	1	1	0	2	5	3	0	0	3	5	2	0	0	3	5	1	5	3	4	5	5	4	-35	-35	2	3	3	1	1	1	-35	-35	2	-35	-35
4.3																																													
4.3.1	Seslerion	-35	-35	1	1	2	5	5	3	2	1	-35	-35	0	1	5	5	0	1	2	5	3	0	0	0	5	3	0	0	1	5	3	3	-35	5	6	6	3	7	-35	-35	-35	1	-35	3	5	2	5	3	-35	-35
4.3.2	Caricion firmae	-35	-35	-35	-35	-35	1	2	3	5	5	3	-35	2	5	3	2	0	0	0	0	0	0	0	3	5	3	0	0	3	5	0	-35	-35	3	-35	4	-35	4	-35	-35	-35	-35	-35	-35	5	-35	3	5	-35	2
4.3.3	Caricion ferruginae	-35	-35	-35	1	3	5	3	2	-35	-35	-35	-35	0	2	5	5	0	5	3	0	1	0	0	0	5	3	0	3	5	3	0	1	-35	6	1	5	2	3	-35	-35	-35	-35	-35	1	4	2	2	5	-35	-35
4.3.4	Elynion	-35	-35	-35	-35	-35	-35	-35	1	5	5	3	1	0	3	5	3	0	0	0	0	0	0	1	5	2	0	0	0	3	5	0	-35	-35	-35	1	1	-35	5	-35	-35	-35	-35	-35	-35	-35	2	5	-35	5
4.3.5	Nardion	-35	-35	1	3	5	3	2	2	1	-35	-35	-35	5	5	3	0	0	0	0	0	0	3	5	2	0	0	0	0	5	3	0	2	-35	6	7	10	6	8	-35	-35	-35	1	-35	1	2	5	2	1	-35	-35
4.3.6	Festucion variae	-35	-35	1	2	3	5	3	2	1	-35	-35	-35	0	1	5	5	0	0	2	5	3	2	5	3	0	0	0	0	0	5	0	-35	-35	-35	5	5	6	4	-35	-35	-35	-35	-35	-35	1	-35	1	5	-35	-35
4.3.7	Caricion curvulae	-35	-35	-35	-35	-35	-35	-35	1	5	5	5	3	3	5	3	0	0	0	0	0	0	3	5	0	0	0	0	0	3	5	0	-35	-35	-35	3	3	-35	6	-35	-35	-35	-35	-35	-35	3	3	5	3	-35	2
4.5																																													
4.5.1	Arrhenatherion	5	5	1	-35	-35	-35	-35	-35	-35	-35	-35	-35	5	3	1	0	0	0	0	0	0	0	0	5	3	0	0	0	5	3	0	7	5	4	6	6	6	-35	3	5	3	-35	1	-35	-35	-35	-35	-35	-35	-35
4.5.2	Polygono-Trisetion	-35	-35	1	5	5	3	1	-35	-35	-35	-35	-35	5	3	1	0	0	0	0	0	0	0	5	5	0	0	0	1	5	1	0	5	-35	7	4	6	3	1	3	5	3	1	5	-35	-35	3	-35	-35	-35	-35
4.5.3	Cynosurion	5	5	5	3	1	-35	-35	-35	-35	-35	-35	-35	3	5	3	0	0	0	0	0	0	0	0	5	3	0	0	3	5	3	0	7	6	8	3	3	5	-35	1	1	5	1	1	1	-35	5	1	-35	-35	-35
4.5.4	Poion alpinae	-35	-35	-35	-35	1	3	5	5	3	-35	-35	-35	5	5	3	0	0	0	0	0	0	0	0	5	3	0	0	1	5	1	0	2	-35	6	3	4	2	7	-35	-35	-35	-35	1	3	-35	5	1	-35	-35	-35
5.4																																													
5.4.1	Calluno-Genistion	-35	5	5	1	-35	-35	-35	-35	-35	-35	-35	-35	5	2	0	0	0	0	0	0	0	1	5	1	0	0	0	1	3	5	1	3	2	3	1	4	5	-35	-35	-35	-35	1	-35	3	-35	-35	-35	5	2	-35
5.4.2	Juniperion sabinae	5	5	5	3	1	1	1	1	-35	-35	-35	-35	0	3	5	3	0	0	2	5	3	0	1	5	5	0	0	0	0	5	3	-35	-35	-35	5	4	-35	-35	-35	-35	-35	1	-35	3	-35	-35	-35	3	5	-35
5.4.3	Ericion	-35	-35	-35	1	2	3	5	2	-35	-35	-35	-35	0	2	5	3	0	0	0	0	0	0	0	3	5	3	0	0	0	5	3	0	-35	-35	3	4	7	5	4	-35	-35	-35	-35	-35	3	-35	-35	-35	1	5	-35
5.4.4	Juniperion nanae	-35	-35	-35	-35	-35	3	5	3	-35	-35	-35	-35	0	2	5	3	0	0	2	5	3	1	5	3	0	0	0	0	1	5	0	-35	-35	5	-35	5	2	4	-35	-35	-35	-35	-35	-35	3	-35	-35	-35	1	5	-35
5.4.5	Rhododendro-Vaccinion	-35	-35	-35	1	3	5	5	3	-35	-35	-35	-35	0	2	5	3	0	5	3	1	2	2	5	0	0	0	0	1	5	3	0	2	2	6	6	8	6	5	-35	-35	-35	-35	-35	3	-35	-35	-35	1	5	-35
5.4.6	Loiseleurio-Vaccinion	-35	-35	-35	-35	-35	1	5	5	3	1	-35	-35	U	U	5	2	U	U	U	U	U	2	5	U	U	U	U	U	3	5	U	-35	-35	4	5	5	3	3	-35	-35	-35	-35	-35	-35	-35	-35	-35	5	-35	5

Figure A1. 2 Expert system describing the distribution of the different vegetation units across Switzerland.

The implementation in the GIS (ArcView ver. 3.3, ESRI, Redlands, CA, USA) was performed using lookup tables similar to those used within GRASP (Lehmann et al., 2002) in order to describe step by step the response curves of the different predictors retained in the model. Similarly, lookup tables were here used in order to describe the probability of occurrence in the different classes of variables. Maps corresponding to the distribution of each variable (subdivided in classes) across Switzerland were prepared within the GIS (Figure A1. 3): altitude, slope, aspect and ridge were derived from the Swiss

DEM (Swisstopo); soil acidity was approximated by parent material acidity and derived from the Swiss geotechnical map (OFS, 2003); humidity was derived from the site water balance layer (swb, produced by Dr Niklaus Zimmermann at WSL); biogeographical regions were defined using assemblages of Welten and Sutter (1982) floristic domains and do not correspond here to the standard biogeographical regions of Gonseth et al. (2001); land use was derived from the map of Swiss land use statistics 1992/1997 (OFS, 2003). The probabilities of occurrences within the different land use categories were determined by expert knowledge mainly acquired directly in the field during the first field season.

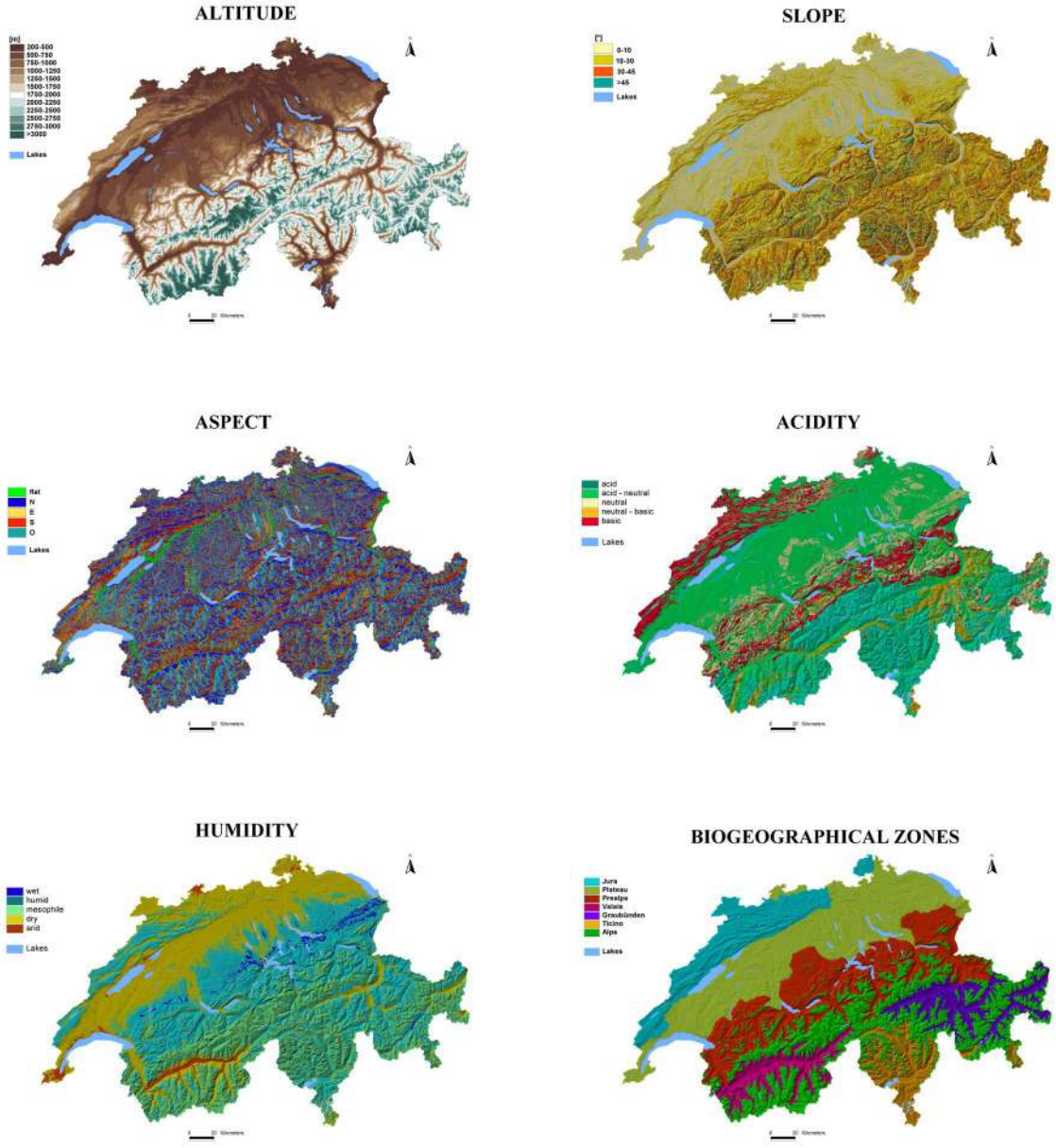


Figure A1. 3 Maps corresponding to the variables used in the expert system.

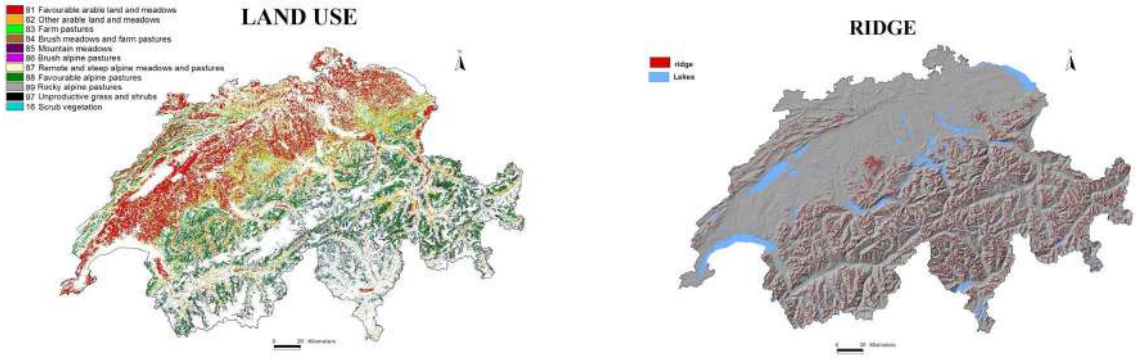


Figure A1. 3 continued: Maps corresponding to the variables used in the expert system.

Spatial predictions for the different target vegetation communities were obtained by translating the lookup tables within the GIS with the assistance of an Avenue script as normally done for statistical models and lookup tables issued from GRASP. Figure A1. 4 shows few examples of the spatial predictions obtained with expert models.

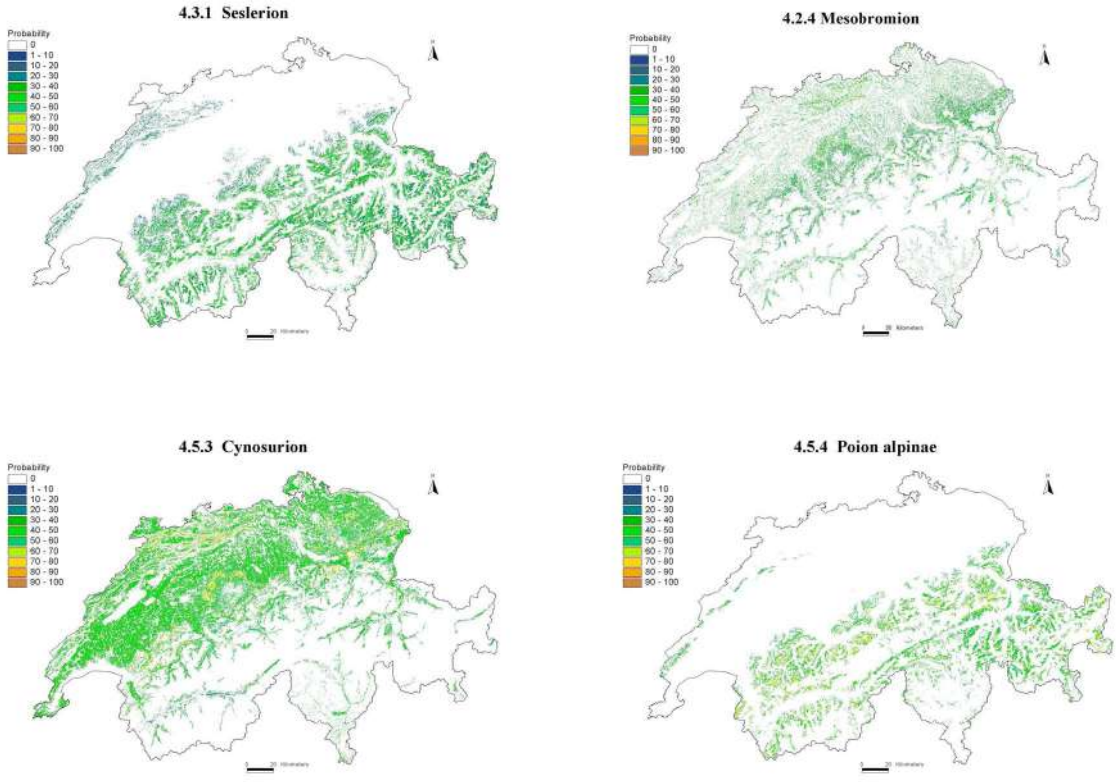


Figure A1. 4 Examples of spatial predictions obtained from experts models for the phytosociological units of Seslerion, Mesobromion, Cynosurion and Poion alpinae.

A1.2 FORESTS

An expert system similar to the one previously developed for grasslands was also developed for forest units. The expert system for forest was based on the same information as the system for grasslands and was thus mainly derived from the Swiss typology (Delarze et al. 1998)**.** However, land use and ridge information were not considered for the forest expert models, instead another type of information was integrated, namely the Swiss forest mixture map (WMG25; OFS, 2003). The map distinguishes 5 categories of forest mixture: non-forest, pure coniferous forest, mixed forest dominated by coniferous, mixed forest dominated by broadleaved trees and pure broadleaved forest. The expert system for forest is presented in Figure A1. 5.

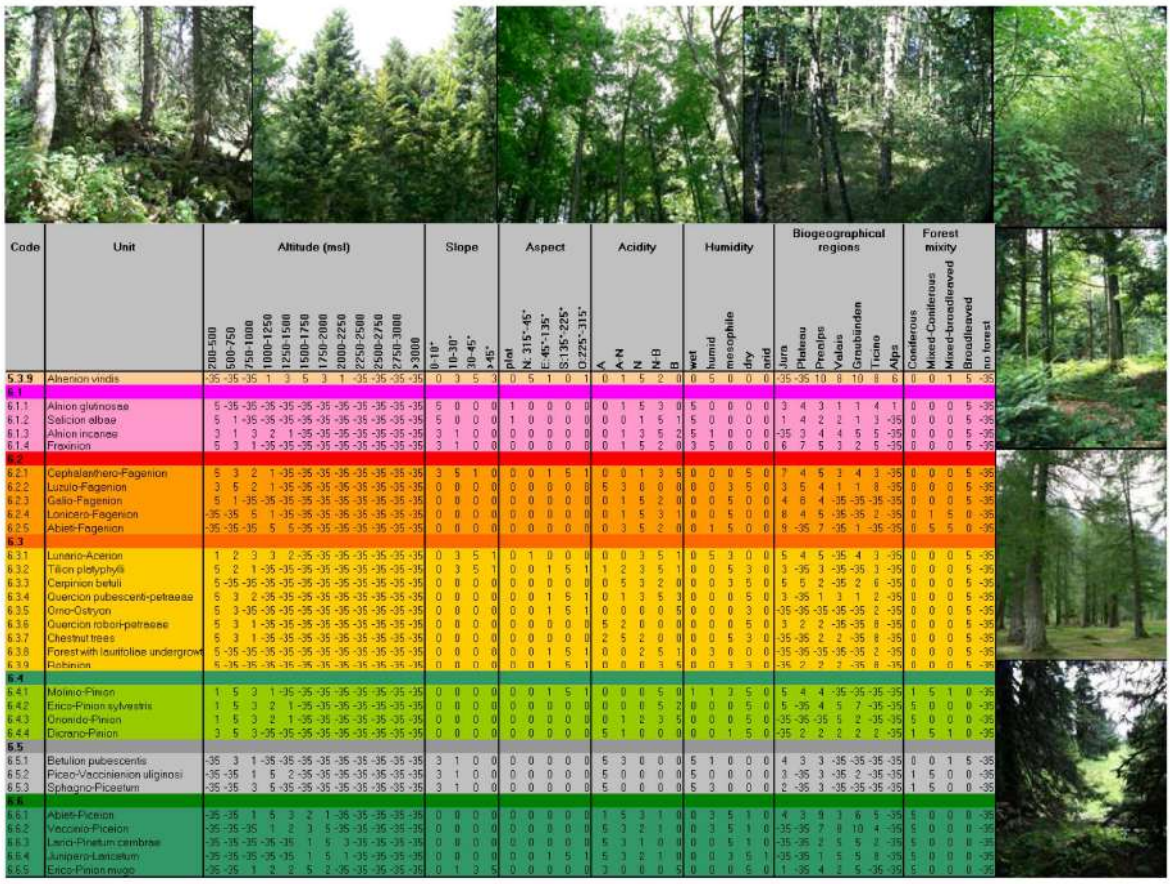


Figure A1. 5 Expert system describing the distribution of the different forest units across Switzerland.

Each line of the table was then formatted as a lookup table normally used by GRASP in order to enter the GIS environment and translate models into spatial predictions. The map corresponding to the variable forest mixture is shown in Figure A1. 6.

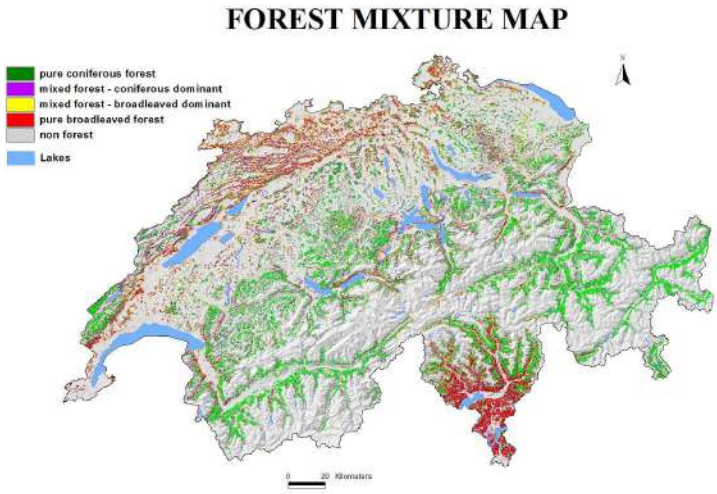


Figure A1. 6 Map showing the different categories of forest mixture (coniferous vs broadleaved) within Switzerland (source: FSO/Geostat; OFS, 2003).

Two sets of spatial predictions were created within the GIS environment. The first set does not consider the forest mixture map whereas the second incorporates this additional information. Few examples of the predictions obtained with and without the forest mixture information are shown in Figure A1. 7. The first set of maps (left column) gives an idea of the potential of these forest units across the Swiss territory, whereas the second set (right column) draws a more realistic picture of their actual distribution, result of human management. *Galio-Fagenion* (6.2.3), *Lonicero-Fagenion* (6.2.4) and *Abieti-Fagenion* (6.2.5) are forest communities that are naturally distributed along an altitudinal gradient, from low to high elevation respectively, and that present an increasing percentage of coniferous trees.

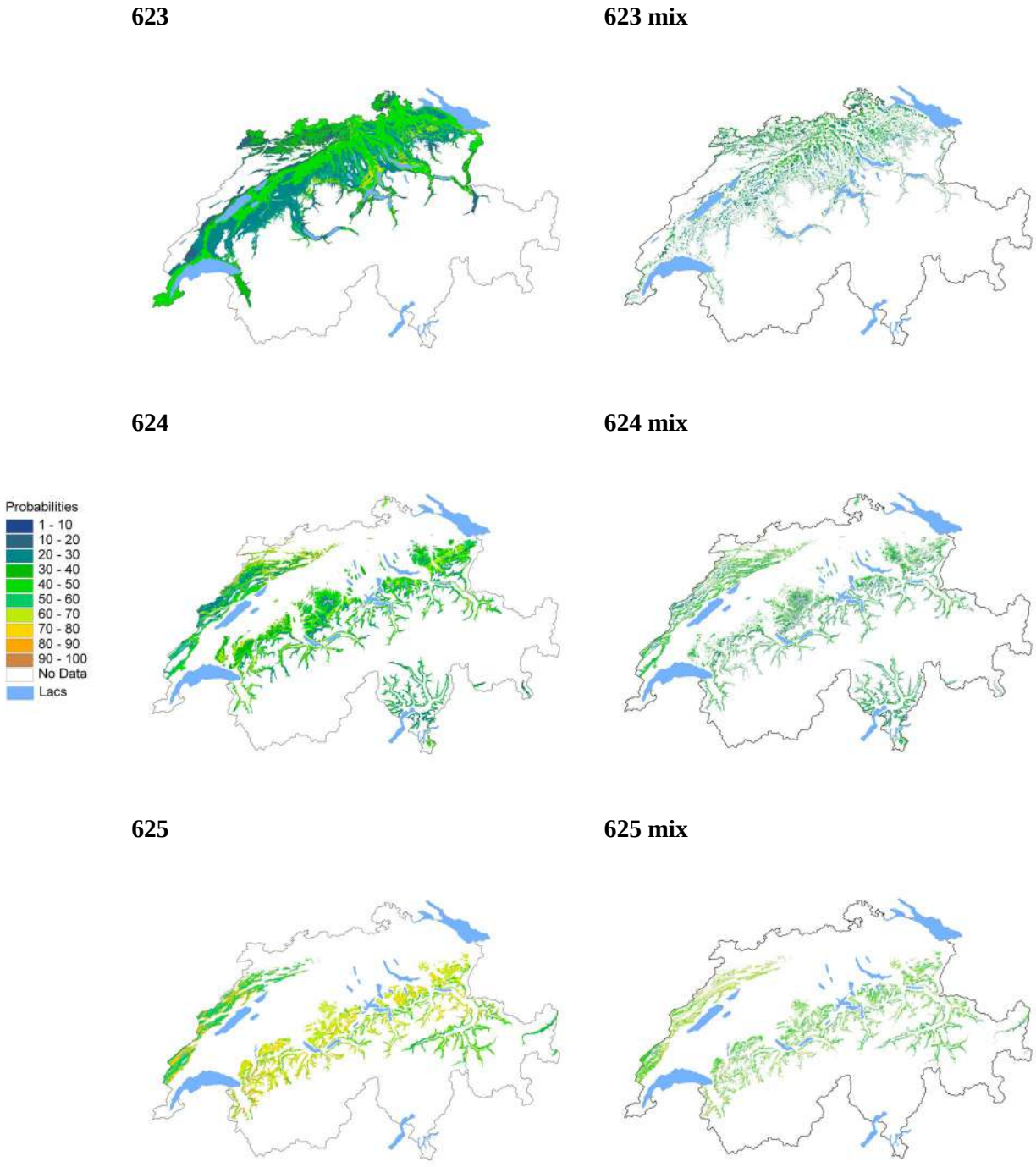


Figure A1. 7 Examples of spatial predictions obtained from experts models for the phytosociological units of Galio-Fagenion (6.2.3), Lonicero-Fagenion (6.2.4) and Abieti-Fagenion (6.2.5).

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ANNEX 2: SWISS ENVIRONMENTAL DOMAINS

Several versions and outputs:

- First version (SED) produced during a 1-month stay at Landcare Research, New Zealand, in collaboration with Dr Anthony Lehmann (at that time at the Swiss Center for Faunal Cartography) and Dr John Leathwick (at that time at Landcare Research) who previously developed domains for New Zealand. This first trial was supported by the Swiss National Science Foundation (SNSF project N° PIOIA-100962 obtained by Dr. Anthony Lehmann). This first version was described in a scientific report for the SNSF:

  Lehmann, A., Leathwick, J. and Maggini, R., 2003. Swiss Environmental Domains. Scientific report.

- First version used in order to design the field sampling 2003 of the Landspot project (this thesis).

- Poster with the first version of Swiss Environmetal Domains (SED) presented at Biology04, the Swiss annual meeting of the Zoological, Botanical and Mycological Societies:

  Maggini, R., Lehmann, A. and Leathwick, J., 2004. Swiss Environmental Domains (SED). Biology04, University of Fribourg, Switzerland, 12-13 February 2004. Poster.

- The first version of Swiss Environmental Domains was compared to other traditional spatial frameworks (biogeographical regions, administrative boundaries) in order to produce statistics concerning species richness in Switzerland:

  Lehmann, A., Maggini, R., Leathwick, J. and Gonseth, Y., 2004. Domaines environnementaux et richesse faunistique de Suisse (Swiss environmental domains and faunal richness of Switzerland). SIG 2004, ESRI Conference, Paris, France.

- Development of a second version in collaboration with Karin Allenbach (UNEP/DEWA/GRID-Europe) and Dr Anthony Lehmann (UNEP/DEWA/GRID-Europe & University of Geneva) under mandate of the Swiss Federal Office for the Environment (FOEN). This second and official version of the Swiss Environmental Domains (SwissED) was described in a technical report and is the object of a FOEN publication:

  Allenbach, K., Maggini, R. and Lehmann, A., 2008. SwissED : Swiss Environmental Domains. Technical report. FOEN Report.
  http://www.grid.unep.ch/product/publication/download/SwissED_FOEN_report.pdf

  FOEN, GRID-Europe (Lehmann, A., Allenbach, K., Maggini, R., Richard, J.-P., Jaquet, J.-M. and Dao, H.), 2010. Swiss Environmental Domains. A new spatial framework for reporting on the environment. Swiss Federal Office for the Environment (FOEN), Bern, Switzerland. Environmental studies no. 1024: 71 pp.
  http://www.bafu.admin.ch/publikationen/publikation/01564/index.html?lang=en&show_kat=/publikationen

- Examples of applications using SwissED for producing statistics on different topics such as land use evolution, population growth or biodiversity will be assembled in a supplementary report that is currently under preparation:

  Lehmann, A., Allenbach, K., Maggini, R., Richard, J.-P., Jaquet, J.-M. and Dao, H., in prep. SwissED II: Swiss Environmental Domains – Applications. FOEN Report, Bern.

A2.1 WHAT ARE SWISS ENVIRONMENTAL DOMAINS (SED) ?

Swiss Environmental Domains (SED) are the result of an environmental classification of the Swiss territory according to key climatic, topographic and geologic variables influencing both natural and anthropogenic processes at various scales. Sites that have similar environmental characteristics are grouped together in the environmental space defined by the selected key variables. The resulting domains are defined regardless of their geographic location and possibly results in entities that are scattered across the landscape. Frameworks currently in use (e.g. biogeographical regions, administrative boundaries) rather define entities by grouping sites that are close together in the geographic space. Swiss Environmental Domains represent a new spatial framework for analyzing data related to our environment - e.g. biodiversity, land cover, demography, agriculture - that is not replacing existing frameworks but simply complementing them. Main advantages of such a classification when compared with traditional ones are: the process is objective, empirical and reproducible; domains are not geographically constrained; result is hierarchical and scalable (national, regional, local scale).

A2.2 HOW ARE SED DEFINED?

SED were realized applying the methodology developed for the environmental domains of New Zealand (LENZ; Leathwick et al., 2002; Leathwick et al., 2003). Environmental variables selected for building the first version of Swiss Environmental Domains were: mean annual temperature, mean solar radiation over growing season, mean moisture index over growing season (calculated as the difference between precipitation and evapotranspiration), site water balance (water availability in the soil), slope, permeability and CaCO3 content of parent material. All the climatic layers were obtained from Dr Niklaus Zimmermann (Swiss Federal Institute for Forest, Snow and Landscape Research, WSL), whereas permeability and CaCO3 were derived from the geotechnical map of Switzerland (OFS, 2003) using an expert classification (J. Ayer, University of Neuchâtel).

Main analytical steps include : a) sub-sampling of pixels: 25m grids of environmental variables retained for the analysis were sampled at a 100 m resolution (i.e. 1 out of 4 pixels); b) non-hierarchical classification of sub-sampled pixels: pixels were assembled in different groups, i.e. domains, according to their environmental distance to group centroids; c) hierarchical classification: group centroids were subsequently hierarchically classified in order to define relationships (dendrogram) between domains; d) reallocation of each 25 m pixel of the Swiss territory to a domain by comparison of pixel attributes to the group centroids in environmental space. Classifications (hierarchical and non) were performed within PATN (Belbin, 2001). The C++ code developed at Landcare Research for LENZ was adapted to the Swiss case study and used to assign each of the original 64 million pixels of

the Swiss territory to the closest domain defined in the environmental space. As an output, different maps of Swiss Environmental Domains can be created at the desired scale and level of hierarchy (national, regional, local).

Figure A2. 1 shows the distribution of the 209 domains (SED) defined at the national scale. Color scheme are defined performing a principal component analysis (PCA) on the average environmental attributes of the domains (i.e attributes of groups centroids). Scores for the domains on each of the three first axes are rescaled in a range from 0 to 255 and used to define their color in a red-green-blue (RGB) color scheme. In the present case red-cyan gradient represents a temperature-humidity gradient, the green-magenta gradient represents a geology-permeability gradient and the blue-yellow gradient represents a slope-solar radiation gradient.

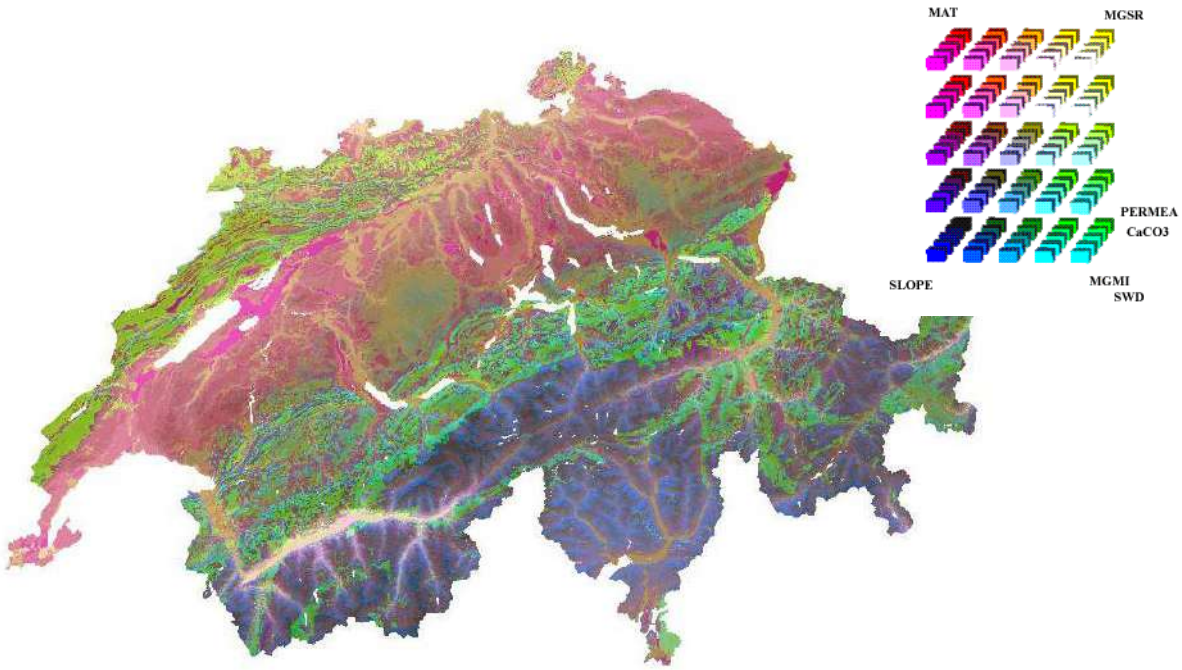

Figure A2. 1 Swiss Environmental Domains (SED) on a national scale. 209 different domains are represented and colored according to a RGB color scheme. Values on the three first axes of a PCA on the average environmental attributes of the domains define the corresponding values for the red, green, blue bands in the resulting image. Red-cyan gradient represents here a temperature-humidity gradient, the green-magenta gradient represents a geologic gradient and the blue-yellow gradient represents a topographic gradient.

All the different steps that lead to the creation of the first version of Swiss Environmental Domains are illustrated in Figure A2. 2. This poster was presented at Biology04, the Swiss annual meeting of the Zoological, Botanical and Mycological Societies:
Maggini R., Lehmann A. and Leathwick J., Swiss Environmental Domains (SED). Poster. Biology04, University of Fribourg, Switzerland, 12-13 February 2004.

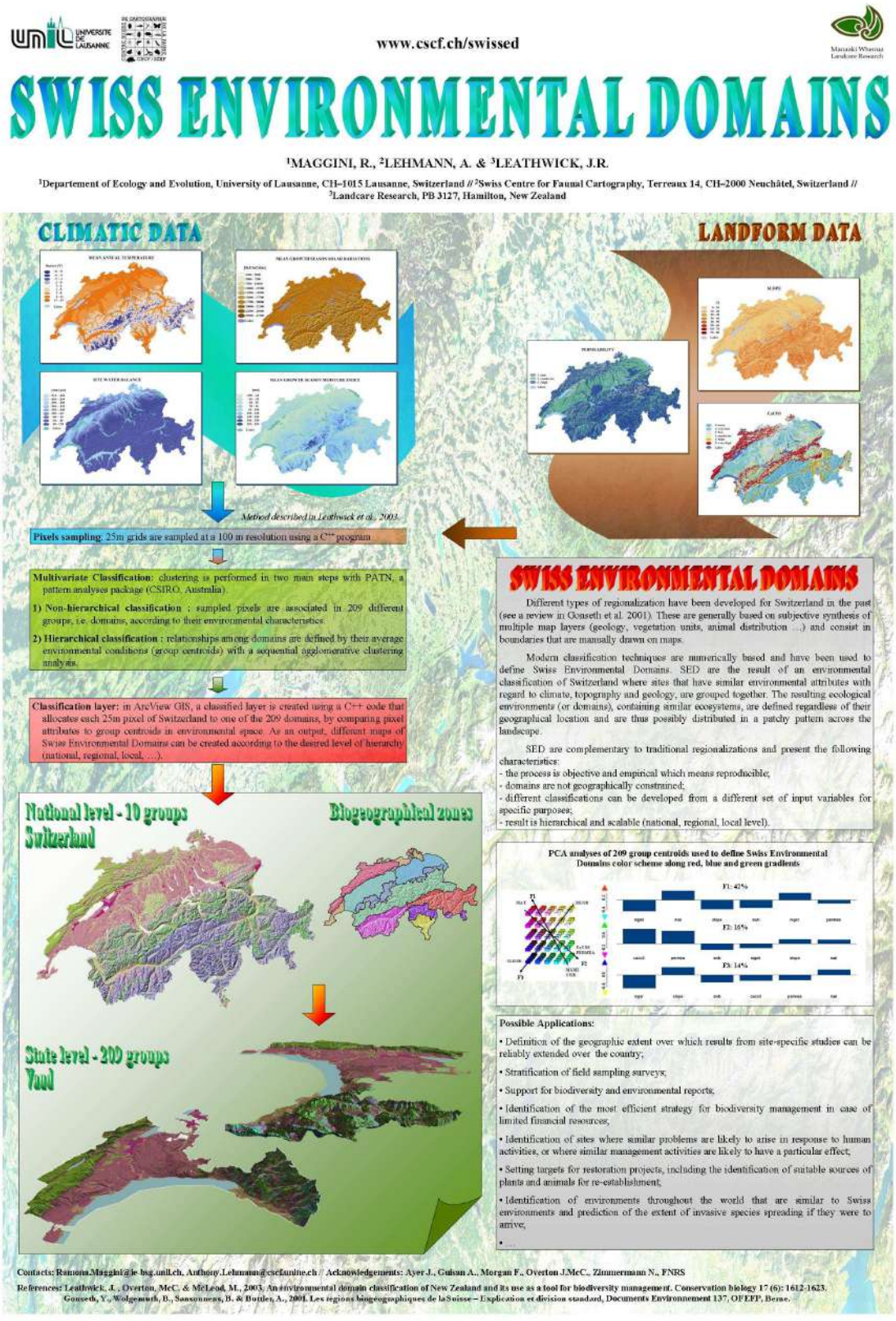

Figure A2. 2 Poster presented at Biology04 (12-13 February 2004, Fribourg, Switzerland) and summarizing all the steps necessary to the definition of the Swiss Environmental Domains.

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Leathwick, J.R., Wilson, G., Rutledge, D., Wardle, P., Morgan, F., Johnston, K., McLeod, M. and Kirkpatrick, R., 2003. Land Environments of New Zealand, Landcare Research & MFE, David Batterman.

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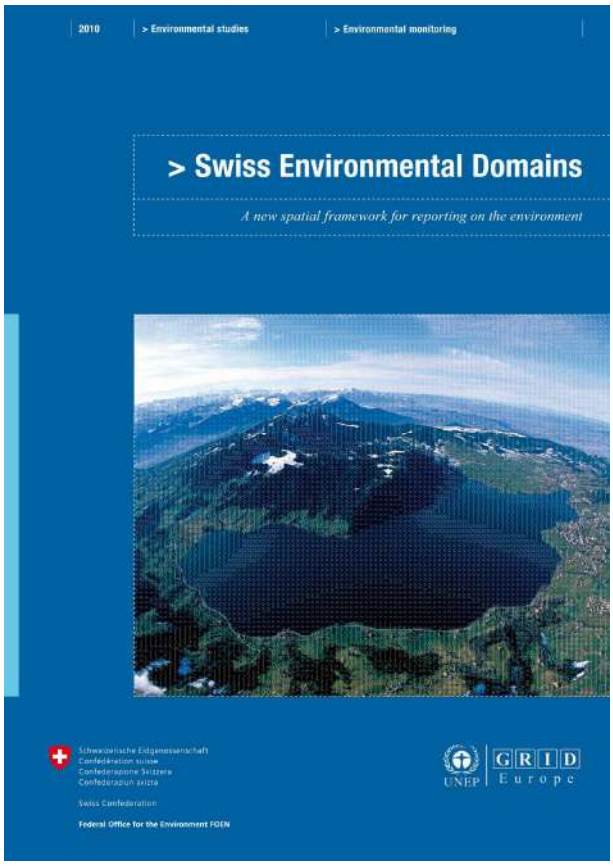
A2.3 SWISSED: OFFICIAL VERSION

The last and official version of the Swiss Environmental Domains is described in a publication of the Swiss Federal Office of the Environment (FOEN) that can be downloaded at the following address (last access: 19.04.2011):

http://www.bafu.admin.ch/publikationen/publikation/01564/index.html?lang=en&show_kat=/publikationen



Reference

FOEN, GRID-Europe (Lehmann, A., Allenbach, K., Maggini, R., Richard, J.-P., Jaquet, J.-M. and H., Dao), 2010. Swiss Environmental Domains. A new spatial framework for reporting on the environment. Swiss Federal Office for the Environment (FOEN), Bern, Switzerland. Environmental studies no. 1024: 71 pp.

ANNEX 3: FIELD SURVEY

The following descriptions of the field surveys performed within this thesis (Landspot project) are mainly extracted from the yearly scientific reports that were prepared for the Swiss National Science Foundation.

A3.1 FOREST COMMUNITIES

A first exploratory field survey focusing of forest communities was conducted during the period 26 July – 2 August 2001. This field work was thought to give a first field feeling of the units described in the Swiss habitat typology (Delarze et al., 1998) and to allow establishing a first link between the typology units and the categories of the Swiss land use/cover statistics (OFS, 2003). A linear transect was sampled on Mount Suchet (Jura Mountains, Canton of Vaud), along an altitudinal gradient ranging from 670 to 1490 m. The central position of the sampling plots corresponded to the points evaluated by the Swiss Federal Statistical Office while producing the land use statistics (intersection points of a 100 m grid laid over the Swiss territory). The position was determined using a differential GPS. For each sampling plot dominated by forest, the canopy density was determined with a spherical densiometer and four pictures were taken from the center towards the four cardinal points. Sampled plots belonged mainly to four land cover categories, namely: normal dense forest (11); open forest on agricultural areas (13); clusters of trees on agricultural areas (18) and favorable alpine pastures (88). The main typological units determined for *normal dense forest* were beech forest units as well as spruce forests and coniferous plantations. For *open forest on agricultural areas* the main typological unit was composed of a subalpine rich pasture mixed with a beech-coniferous forest. The *cluster of trees on agricultural areas* corresponded to a group of beech trees in a pasture, and finally *favorable alpine pastures* corresponded to alpine rich pastures. More generally, category 11 seems to apply to natural dense forest which tree composition depends upon altitude. Category 13, *open forest on agricultural areas*, generally consists in trees scattered over pasture areas. In the Jura Mountains, this category often corresponds to the 'paturage boisé', which consists in an open pasture scattered of single or little groups of trees, mainly spruce (*Picea abies*). The density and the disposition of trees on the surface will determine the assignment to category 13 (*open forest on agricultural areas*), to category 18 (*cluster of trees on agricultural areas)* or 88 (*favorable alpine pastures)*. These findings confirm that land use/cover categories are mainly structural and that forest types can potentially be derived using variables such as elevation, tree density and proportion of coniferous vs broadleaved trees as measured from remote sources.

The second exploratory field survey was conducted within the same study region (Jura Mountains) over the period 8 August - 15 September 2001. The survey was based on a random-stratified sampling design stratified according to land use/cover categories and altitude. Land use categories were *normal dense forest* (11), and *open forest on unproductive areas* (12) and *open forest on agricultural areas* (13) considered together. Three main altitudinal belts were considered for stratification: the lowland, montane and subalpine belts. Stratification leaded to the definition of 6 strata to be sampled proportionally to their representativity in the Canton de Vaud. Sampling plots (centered on the same points as the land use statistics) were then chosen randomly within each stratum. For each randomly

chosen point, two additional and consecutive (i.e. spaced of 100 m) points were sampled in a random direction (out of 8 possible neighbors), thus defining a mini-transect at each sampling site. Such mini-transect allows a sound representation of the site and mitigates the difficulty of the definition of transitional situations. At each sampling site were performed the same measures as during the first field survey. One supplementary measure was taken, namely the number of standing trees in a 10-m^2 surface. This additional measure can be compared to the densiometer measures for estimating tree density and potentially be combined to remote sensing data in order to extrapolate tree density over the entire study region. 76 plots were finally surveyed and Table A3. 1 lists the forest units found in the different sampling strata.

Table A3. 1 Results of the second exploratory field survey for forest communities. The table list the forest communities sampled within each stratum of the random-stratified filed sampling.

Strata		**Typological units** (Delarze et al., 1998)
Land cover category	**Altitudinal belt**	
11	Lowland	6.2.1, 6.2.3, 6.2.4 [beech forests]
	Montane	6.2.2, 6.2.3, 6.2.4, 6.2.5 [beech forests]; 5.2.1 [forest clearing]; 6.6.1[spruce-fir forest]; 6.0.2 [tree plantation]; 5.1.3, 5.3.3 [forest edges]
	Subalpine	6.6.2 [spruce forest]
12 + 13	Lowland	6.3.4 [oak bushy grove]; 2.1.2.1/2.2.1.1/6.1.1 [reedbed/alder wood]
	Montane	4.5.3/6.6.2 [pasture/spruce forest]; 2.2.1.1 [marsh]
	Subalpine	4.5.4/6.6.2 [rich pasture/spruce forest], 6.6.2 [spruce forest]

A3.2 GRASSLAND COMMUNITIES

FIELD WORK 2002

The first field campaign in order to survey 'open habitats' was conducted over the period 12 July – 8 September 2002. The sampling mainly focused on vegetation communities found in meadows, grasslands, pastures, and heaths, i.e. non-forested habitats others than marsh, bog, peat or riverbank habitats. In order to be able to make a link between the vegetation units and the land use/cover categories, the sampling units were centred on the same points evaluated by the Federal Statistical Office while producing the Swiss land use statistics (OFS, 2003). Sampling plots (30 x 30 m) were thus centered at the intersection points of a 100 m grid laid over the Swiss territory. Sampling was targeted on land use categories thought to shelter an 'open habitat' community: mountain meadows (85); brush alpine pastures (86); remote and steep alpine meadows and pastures (87); favorable alpine pastures (88); rocky alpine pastures (89); unproductive grass and shrubs (97); bare land (99) and scrub vegetation (16). Sampling survey was planned on the Swiss territory as a whole and sampling was stratified by: biogeographical regions (6 classes: Jura, Plateau, Northern Alps, Western Alps, Eastern Alps, Southern Alps; Gonseth et al. 2001); altitude (5 classes); North/South aspect (2 classes) and land

use (6 classes; categories 86, 87 and 88 were indeed considered together). Two points were randomly chosen in each strata, although when visiting a point in the field, all interesting neighboring points were also checked (for example same topography but different land use category). The exact geographic position of the sampling units was reached using a GPS. For each sampled plot a form was filled with main site characteristics and with a non-exhaustive but representative list of plant species. Whenever possible, a phytosociological unit (as defined in the habitat typology system of Delarze et al., 1998) or a mixture of several units was already attributed in the field; otherwise it was attributed a posteriori with the help of the picture taken in the field and expert knowledge.

The 173 sampling units visited were mainly distributed in the states of Vaud, Neuchâtel, Jura, Valais, Bern, Uri and Ticino (red dots in Figure A3. 1). Main phytosociological units represented in the sampling squares were: *Arrhenaterion*, *Polygono-Trisetion*, *Cynosurion* and *Poion alpinae* for eutrophic meadows; *Seslerion*, *Nardion*, *Caricion curvulae* for dry and alpine grasslands; *Rhododendro-Vaccinion*, *Loiseleurio-Vaccinion* for heaths; *Alnenion viridis* and *Sambuco-Salicion* for bushy formations; *Mesobromion* for dry grasslands; *Petasition paradoxi* and *Androsacion alpinae* for screes. An Access database was created in order to store field data and is presented in Annex 4.

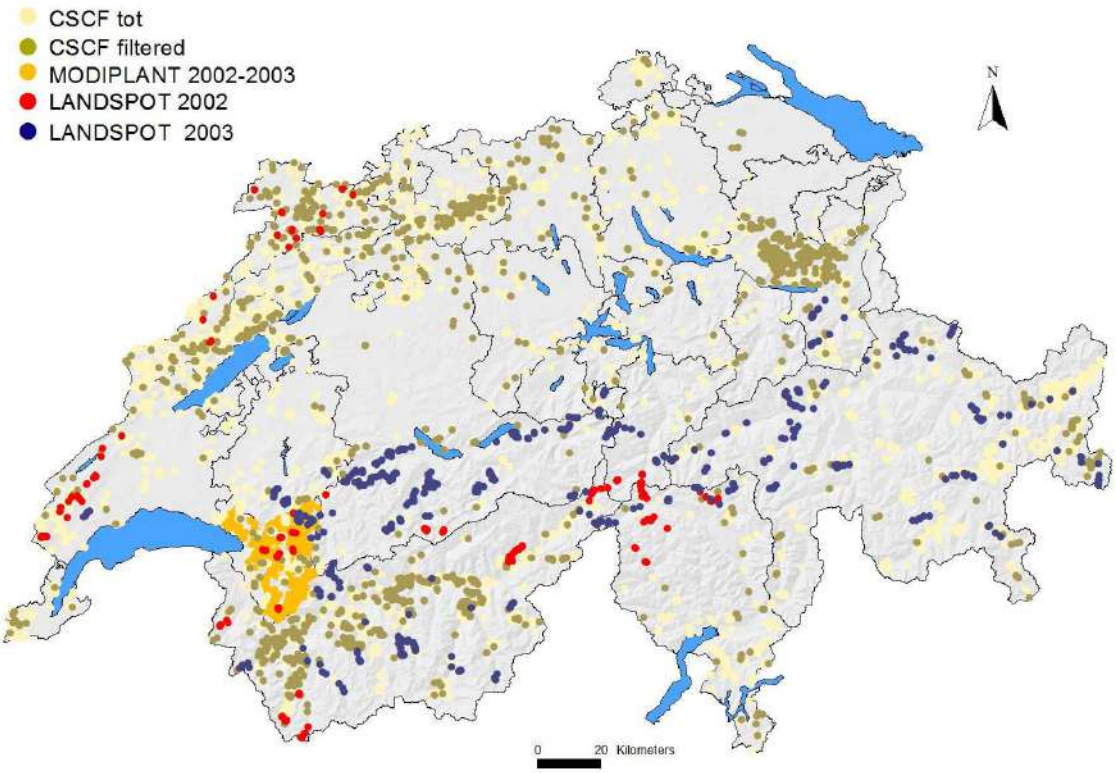


Figure A3. 1 Distribution across Switzerland of Landspot (this thesis) sampling sites visited during summer 2002 (red dots) and summer 2003 (blue dots), Modiplant sampling sites (orange dots) and habitat records extracted from the CSCF database (yellow dots= all records; green dots= records located on or in the direct vicinity of a point evaluated for the Swiss land use statistics).

FIELD WORK 2003

The survey of 'open habitats' continued during summer 2003. For this second campaign, the sampling design was improved in order to be more efficient in the field. The new sampling strategy was based on maps of the potential distribution of the target vegetation units obtained by expert models (Annex 1.2). Sampling plots were once again centred on the same points considered for the Swiss land use statistics. Land use information was however not used to stratify the sampling because already integrated in the expert models predicting the potential distribution of the different grassland communities. Expert models allowed creating a composite map to be used in the field with all the vegetation communities potentially present at a given site (Figure A3. 2).

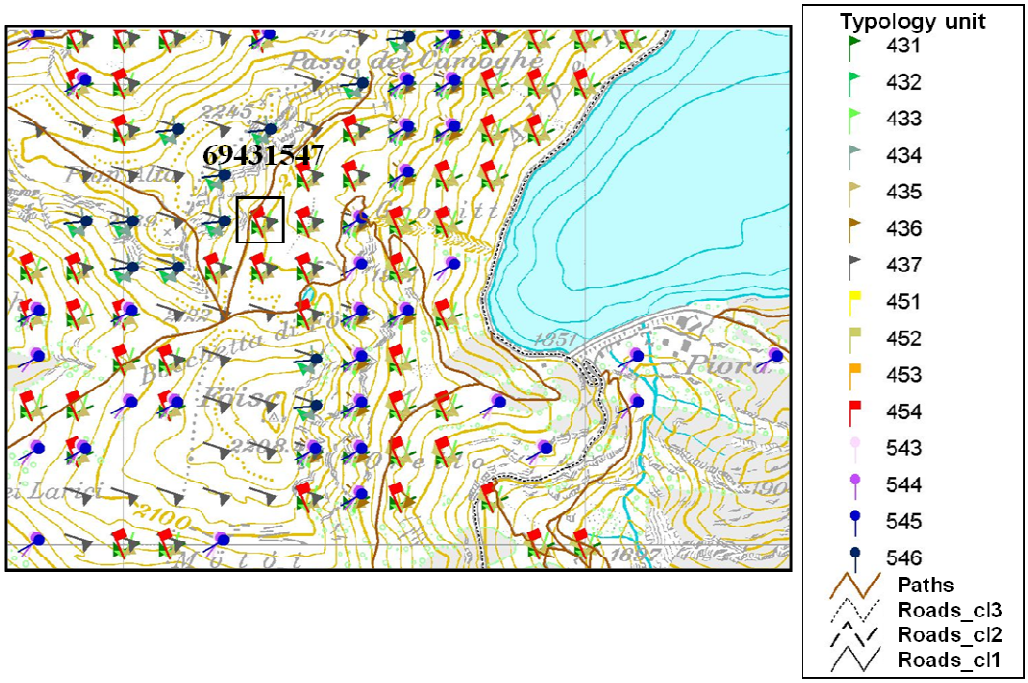


Figure A3. 2 Example of a map used in the field. For each point at the intersections of a 100m grid are indicated the phytosociological units (according to Delarze et al., 1998) that can potentially be found at that site. The randomly selected point to survey is surrounded by a square in the map and the code '69431547' indicates that the point is to be found at the Swiss coordinates < 694300 ; 154700>.

In order to obtain a sample representative of all the environmental conditions characterizing the Swiss territory, the sampling was stratified using the Swiss Environmental domains (SED, Annex 2) at the 50 groups level. A further improvement was made by optimizing the time needed to reach the sampling units. This was achieved by retaining only the sites that are located in a buffer of 250 m around the roads of category 1 (main roads) down to category 3 (public roads, small rural or forest roads) or in a buffer of 150 m around the paths of category 5 and 6 (Swisstopo: Vector 25) and characterized by a slope inferior to 35°. In Switzerland the road and path networks are very well developed also in the mountainous regions, the high density and the large buffer thus allowed reaching

either by car or by foot all the different vegetation communities that were to be prospected. Sites to be prospected were only chosen in patches with a minimum surface of 5 hectares of the right land use categories. To summarize, the random selection of the sites to be sampled in the field was thus performed on the population of points that i) had at least a probability of 50% of sheltering the target habitat, ii) were located within a 250/150 m buffer around roads/paths, iii) were characterized by a slope inferior to 35°, and iv) were located in a 5 hectare patch of a favourable land use category. The selection was made randomly within the preselected population of points and with a minimum number (5) within each environmental domain.

As a result of the improved sampling strategy the second season of survey for 'open habitats' was much more efficient than the first one and allowed to survey 464 supplementary field units scattered across the entire Swiss territory over the period 6 June – 29 August 2003. The geographic locations of sampled units are shown in Figure A3. 1. The records of this second field season were integrated in the Landspot Access database (Annex 4) and a decision-support system added to the database allowed to assign a phytosociological unit to the relevés that could not be classified in the field. As a general conclusion, the field sampling was much more efficient in this second field campaign thanks to the targeting trough expert models and the stratification by environmental domains.

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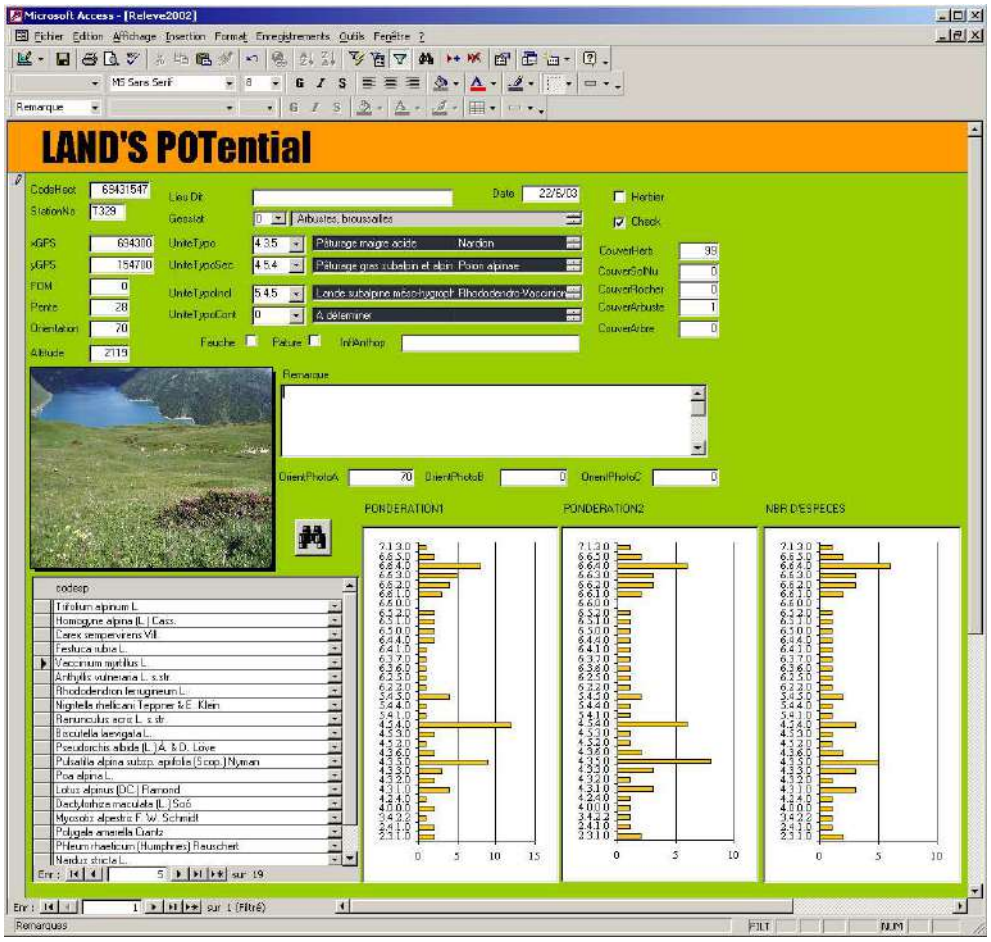
ANNEX 4: LANDSPOT DATABASE AND DECISION-SUPPORT SYSTEM

An Access database was created for storing data collected in the field. Information on each sampled site can be visualized in a form containing a picture of the site, the list of plant species recorded in the plot, site measurements and three decision-support graphs assisting in the classification of the relevé and the assignment of a phytosociological unit (as described in Delarze et al., 1998). The decision-support system was developed within the framework of the Landspot project (this thesis) and is based on histograms representing the total score obtained for each possible phytosociological unit for the site. Points are assigned to each unit according to the number of species that belong to it, weighted by the exclusivity (characteristic vs accompanying species) and dominance (dominant vs non dominant) of the species in the unit. Three different systems of weighting were considered: with 'Ponderation 1', species are weighted according to their exclusivity and their dominance; with 'Ponderation 2' species are weighted only according to their exclusivity; and finally the third system simply apply the same weight of 1 to all the species. A phytosociological unit or a mixture of several units can thus be attributed to each relevé according to the totalized score.



ANNEX 5: DOWNSCALING LAND USE FROM AVAILABLE DATA SOURCES USING NEAREST NEIGHBOURS AND EXPERT SYSTEMS

Anthony Lehmann[1*], Ramona Maggini[2], Christian Lehmann[3], John R. Leathwick[4]

[1] Swiss Centre for Faunal Cartography (CSCF), Terreaux 14, CH-2000 Neuchâtel, Switzerland

[2] Department of Ecology & Evolution (DEE), Biosphore building, University of Lausanne, CH-1015 Lausanne, Switzerland

[3] State of Geneva (DEAL), CP 22, CH-1211 Geneva 8, Switzerland

[4] National Institute of Water and Atmospheric Research, PO Box 11115, Hamilton, New Zealand

Produced in collaboration with Dr Anthony Lehmann while at CSCF.

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A5.1 ABSTRACT

A downscaled land use map was obtained by blending two inputs: the Swiss topographic base map at a 1:25000 scale with a national land use/cover classification obtained from aerial photo-interpretation on a regular lattice of points with a grid spacing of 100m. The grain size of the resulting land use map was increased by a factor of 16 to reach a resolution of 25m, while the number of land use categories increased from 24 in the base map to 59 in our result. A case-based method analysing each pixel in turn was used. It combines an inverse distance spatial weighting of 36 nearest neighbours and an expert system of correspondence between input base map categories and possible output land use types. The developed algorithm was written as a C++ code that reads and writes GIS grid layers containing more than 64 millions pixels. Downscaling allows combining the geographic precision of existing base maps with the thematic details of photo-interpreted land use information. Improved land use maps allow more precise watershed analyses, improved species and habitat distribution modelling, the construction of dynamic models of species migration, and robust assessment of land use changes.

Keywords

Land cover, land use, downscaling, geographic information system, aerial photo interpretation, topographic map, inverse distance weighting, expert system, Switzerland

A5.2 INTRODUCTION

In many disciplines downscaling is used to derive local scale maps from information available at coarser scales. Climatologists refer to statistical downscaling (Wilby and Wigley 1997) to describe this general approach that has been used widely with temperature and precipitation e.g. (Huth 2002; Coulibaly et al 2005), but also with wind speed (Bogardi and Matyasovszky 1996) or air humidity (Huth 2005). In turn, downscaled climatic information are used in many different applications such as hydrological modelling (Muller-Wohlfeil et al 2000; Wilby et al 2000; Wood et al 2004), species distribution models (Lehmann et al 2002a), and geological risk assessments (Dehn et al 2000).

Several statistical approaches have been used for downscaling. For instance, Bardossy et al (2005) used fuzzy rule-based models to predict frequency distributions of daily precipitation, Burger and Chen (2005) compared regression methods to derive river runoff from large scale climatic scenarios, Biau et al (1999) used geostatistical methods (kriging) to estimate rainfall, and Coulibaly et al (2005) investigated the use of temporal neural networks to downscale temperature and precipitation.

Downscaling is not restricted to climatic data and has been used with remote sensing data to derive, for instance, soil moisture maps (Crow et al 2000). Species distribution modelling can also be defined as a general downscaling approach that predicts species distributions from point observations combined with spatially-explicit environmental predictors (Lehmann et al 2002a,b). The term “downscaling” can also be used when creating a land use map from combined input layers at various scales. For example, Remm (2004) used case-based predictions to map the distribution of habitat classes from Landsat 7 ETM imagery, greyscale and colour orthophotos, an elevation model, digital base map and soil map.

Case-based algorithms are problem solving methods that learn from experiences at a low level of generalisation (Aha 1998). They can be considered as an Artificial Intelligence method that derives results from the data as directly as possible, without the formulation of an intermediate model. Machine learning specialists distinguish between *lazy* learning that typically combine information during the problem solving phase, and *eager* learning that tend to derive a generalization and forget about raw observations after the learning phase (Aha 1998). Remm (2004) argued that case-based methods represent a promising alternative for a large range of downscaling problems, such as habitat mapping and the prediction of species potential distributions, especially with large and complex datasets where generalisation is difficult.

Land use maps are critical in many applications such as watershed analyses (Mander et al 2000; Hormann et al 2005), land use impact on stream ecology (Snyder et al 2003), species and habitat distribution modelling (Oja et al 2005), dynamic modelling of species migration (Boone and Hunter 1996; Akçakaya 2001), reserve site selection (van Langevelde et al 2000), impact assessment on biodiversity (Crist et al 2000), land use planning (Theobald et al 2000) or monitoring of land use changes (Bock et al 2005). Precise land use information is also the base of sustainable development assessment (Mander et al 2005) that are based on structural (both temporal and spatial) and functional (social, ecological, economical) attributes of landscapes. Another challenge in landscape ecology is to deal adequately with spatial scales (Whittaker et al 2001) so as to select the appropriate scale for the problem under study when relating ecological processes to landscape patterns.

Although land use and land cover maps are increasingly made available through remote sensing or photo-interpretation classifications, traditional base maps of Switzerland have been available for more than a century and are now provided in digital format. Land use maps derived from remote sensing classification often have a “salt and pepper” appearance that does not meet end user demand (Bock et al 2005). Land use derived from aerial photo interpretation can define many different classes of land use/cover classes. National base maps usually lack the thematic details that can be obtained from aerial photo-interpretation, but they generally have an excellent geographic precision to define landscape patches and linear features.

In this paper, we present a *lazy* learning method, which could be assimilated to a case-based approach, for downscaling land use information from a 100m lattice of points to a 25m resolution grid, taking advantage of an existing 1:25000 digital base map and building an expert system defining possible correspondences between the base map and land use categories.

A5.3 DATA

A5.3.1 Land use statistics

The most reliable source of land use/cover information in Switzerland is a photo-interpretation dataset that assigns one of 74 categories of land uses to the lower-left corner of each 100m grid cell (Swiss Federal Office of Statistics: Geostat, area statistics). This map (Landuse100) is therefore not a comprehensive land use map, because its categories (Figure A5.3) are assigned to points at the intersections of a 100m grid rather than indicating the predominant landuse for each hectare square. It was developed as a source of land use statistics over relatively large zones rather than as a land use map per se. It tends however to be often used as a land use map in many applications (e.g. Gellrich and Zimmermann 2006) and remains the most exhaustive source of land use information for Switzerland. Two time periods are presently available (1979-1985 and 1992-1997), and a new version is under preparation (2004-2009).

A5.3.2 National base map (land cover)

The Swiss Federal Office of Topography provides digital versions of national topographic base maps at a 1:25000 scale as a landscape model in a vector format (Swisstopo: Vector25, primary surfaces). This land cover information is defined in 24 categories (Figure A5.2). Data from linear features such as rivers, roads and trains can also be obtained separately. The national base maps is the geographically most precise source of land cover information for the entire country (precision = 3-8 m) and is partially updated every year.

A5.3.3 Digital elevation model

Switzerland has a 25m resolution digital height model (Swisstopo: DHM25) developed by the Swiss Federal Office of Topography by interpolating between 10 m isolines of altitudes (vertical precision = 1.5 - 10m). Altitude is central in any GIS analyses because information such as slope, orientation, topographic position or flow accumulation can be directly derived from DEM (Horsch 2003).

Elevation is also highly correlated with air temperature, which in turn drives many natural phenomena and human activities, and therefore land use.

A5.3.4 Resolution

All available datasets were rasterized either at a 25m and/or 100m resolution in order to allow raster overlays between them. With 42000 km^2, Switzerland can be described with approximately 4 million pixels at a 100m resolution and with 64 million pixels at a 25 m resolution.

A5.4 METHODS

A5.4.1 General algorithm

The general idea used for downscaling the existing land use information from 100 m to 25 m relies on the combination of the geographic precision of the 1:25000 national topographic base map rasterized at 25m and the detailed land use categories obtained from land use statistics available at 100 m (Figure A5.1). The detailed algorithm uses inverse distance weighting combined with an expert system (Figure A5.2) to assign acceptable land use categories at a finer scale. The main steps are:

Data preparation:

1/ Rasterize a land use grid at 100m resolution from points out of the Landuse100 statistics

2/ Convert to NA land use categories that correspond to linear features (rivers, roads, trains)

3/ Rasterize the primary surfaces of the land cover vector base map at a 25m resolution (BaseMap25)

Main process (p1):

4/ Visit each BaseMap25 pixel

5/ According to expert system table (Figure A5.2), select those categories that could be elected for the current pixel. In some rare case, assign the only possible value (then go to point 10).

6/ Select among the 36 nearest Landuse100 neighbours those with acceptable categories.

7/ Calculate the inverse distance to each neighbour

8/ Sum up the inverse distances for each category

9/ Assign the category with higher score to the BaseMap25 pixel or, in case of lack of decision, assign a best replacement choice from the expert system table

10/ Repeat steps 4 to 11 for each BaseMap25 pixel

Optional process (p2):

11/ Replace categories wherever river, road or train linear segments are available from BaseMap25.

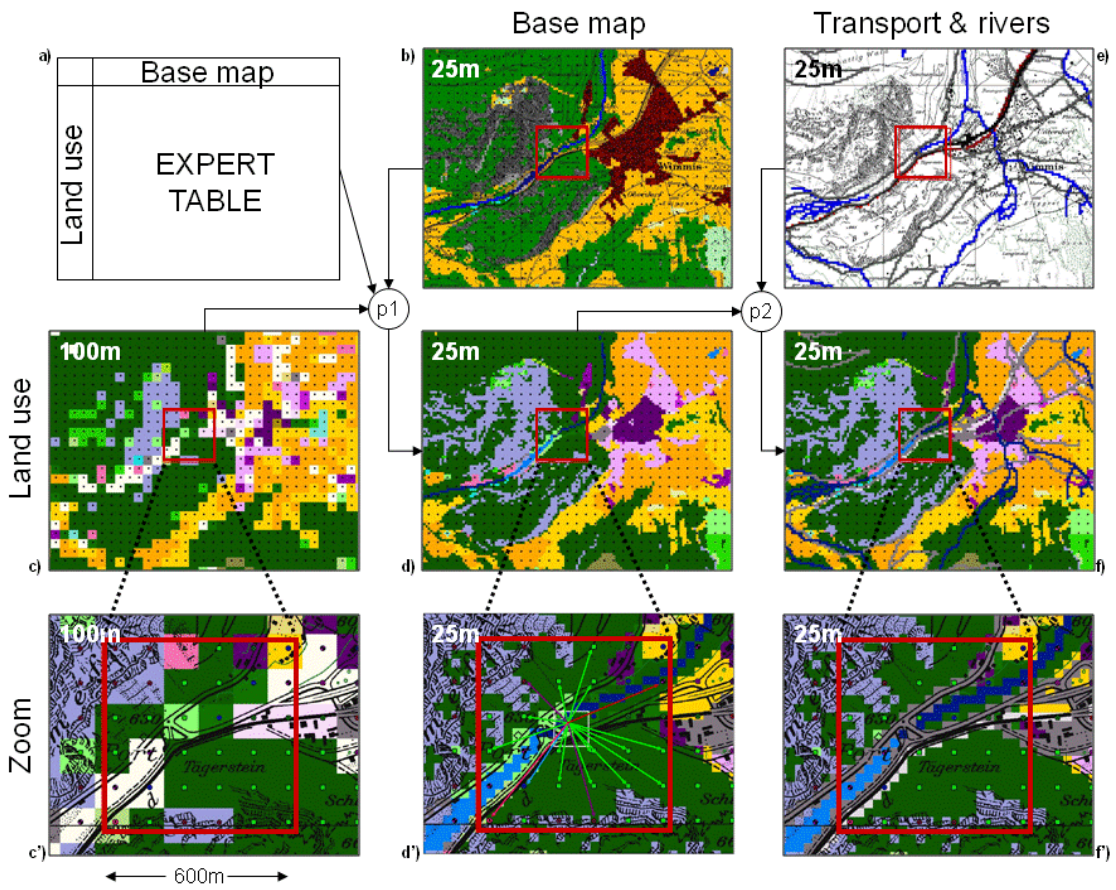

Figure A5. 1 Downscaling land use information from 100m to 25m resolution using inverse distance weighting, expert knowledge, national base map, transport and river information at 25m. a) expert system, b) 1:25'000 base map, c) and c') hectare land use information d) and d') downscaled land use, e) 1:25'000 rivers and roads, f) and f') adding rivers and roads to downscaled land use at 25m resolution.

A5.4.2 Detailed algorithm for inverse distance weighting

First a scaled distance to each 36 Landuse100 point around the pixel under investigation is calculated in the three spatial dimensions.

(1) $d_j(i) = (|\, x25_i - x100_j \,| / range.x25) + (|\, y25_i - y100_j \,| / range.y25) + (|\, alt25_i - alt100_j \,| / range.alt25)$

where *j* spans from 1 to 36 nearest neighbours and *i* represents each visited pixel at a 25m resolution.

Second the inverse distances are summed up by land use types

(2) $D_k(i) = \sum_{j=1}^{36} (\lambda_j(k) / d_j(i))$ where $\lambda_j(k) = \begin{cases} 1 \;\; if \;\; landusetype_j = k \\ 0 \;\; otherwise \end{cases}$

Finally, the category scoring the highest sum of inverse distance is attributed to the pixel under investigation.

(3) $$K(i) = \underset{k}{greatest}(D_k(i))$$

A5.4.3 Expert system

An expert system was used to constrain the possible choices when using information from BaseMap25 to select the most appropriate Landuse100 category (Figure A5.2). For instance, if a forest patch is defined for a particular site in BaseMap25, the expert system constrains the choice of Landuse100 categories to include only that related to forest. Furthermore, the expert system can also select a certain Landuse100 category when the distance based algorithm fails to make a clear selection because of the lack of appropriate land use categories within the search neighbourhood.

		BaseMap 25																											
	DEFINITIONS	Other type land cover	Forest	Habitation zone	Lake	River	Shrub	Open forest	Marshland in forest	Marshland	Orchard	Gravel pit	Rock	Stone drain in forest	Stone drain	Seedbed	Vignard	Quarry	Clay quarry	Marshland in open forest	Marshland and shrub	Stone drain and shrubs	Track on hard coating	Track on grass	Stone drain in open forest	Glacier	Concrete dam	Stone drain on glacier	Green dam
CODE	Landuse 100	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
9	Forest fresh cuts	1	1																										
10	Other forest	1	1				1	1																					
11	Normal dense forest		3																										
12	Open forest (on unproductive areas)	1	1					3																					
13	Open forest (on agricultural areas)	1	1					1																					
14	Forest stripes, edges	1	1					1																					
15	Brush forest	1	1				3	1														1							
16	Scrub vegetation	1					1	1														1							
17	Groves, hedges																												
18	Clusters of trees (on agricultural areas)	1	1					1																					
19	Other woods	1	1					1																					
20	Ruins																												
21	Industrial buildings																												
23	Buildings in recreational areas																												
24	Buildings in special urban areas																												
25	One- and two-family houses																												
26	Terraced houses																												
27	Blocks of flats																												
28	Agricultural building																												
29	Unspecified buildings																												
31	Motorways																												
32	Green motorway environs																												
33	Roads and paths																												
34	Parking areas	1		1																									
35	Railway station grounds	1		1																									
36	Railway lines																												
37	Airports	1																					2						
38	Airfields, green airport environs	1																						3					
41	Industrial ground			1																									
45	Land around 25			1																									
46	Land around 26			1																									
47	Land around 27			1																									
48	Land around 28	1		1																				1					
49	Land around 29			3																									
51	Sport ground	1		1																				1					
52	Garden allotments	1		1																									
53	Camping, caravan sites	1		1																									
54	Golf courses	1		1																									
56	Cemeteries	1		1																									
59	Public parks	1		1																									
61	Other energy building	1		1																									
62	Other supply or waste treatment plants	1		1																							2		2
63	Waste water treatment plants	1		1																									
64	Discharges	1		1								1						1	1										
65	Quarries, mines, dumps	1		1								3						3	3										
66	Construction sites	1		1																									
67	Green railway environs	1		1																									
68	Green road environs	1		1																									
69	River shores																												
71	Regular vineyards	1															3												
72	'Pergola' vineyards	1															1												
73	Extensive vines	1															1												
75	Intensive orchards	1									3																		
76	Rows of fruit trees	1									1																		
77	Scattered fruit trees																												
78	Horticulture	1														2													
81	Favourable arable land and meadows	1																											
82	Other arable land and meadows	1																											
83	Farm pastures	1																											
84	Brush meadows and farm pastures	1					1																						
85	Mountain meadows	1																											
86	Brush alpine pastures	1					1	1														1							
87	Remote and steep alpine meadows and pastures	1																											
88	Favourable alpine pastures	1					1	1																					
89	Rocky alpine pastures	1					1	1														1							
90	Glacier																									3		1	
91	Lake				2																								
92	River					2																							
93	Dam																												
95	Wetlands	1	1				1	1	3	3										3	3								
96	Water shore vegetation	1					1	1	1	1										1	1								
97	Unproductive grass and shrubs	1					1	1														1			1				
98	Avalanche protections																												
99	Bare rock												2	2	2							3			3	1		3	

Figure A5. 2 Expert system showing the possible authorized Landuse100 categories withinBaseMap25 units. (1) represents possible choices, (2) unique choice, and (3) the best replacement choice in case of lack of decision. 15 land use categories remain unmatched (in dark grey). 4 categories correspond to linear features that are treated separately (light grey).

A5.4.4 C++ code reading and writing grids

Although the algorithm used was relatively simple, it required the carrying out of extensive calculations on several large grids, e.g., the 25 m resolution grid for Switzerland contains approximately 64 million pixels. To our knowledge, implementing this algorithm in a regular GIS package would be either impractical or at least very slow. We therefore developed C++ code that

directly reads and writes data in ESRI grid format, using the ESRI GridIO library. This code allowed processing of the entire 64 million pixels grid in about 20 minutes.

A5.5 RESULTS

Results from the land use downscaling are best appreciated at a regional scale (Figure A5.3), where the map produced by our expert system keeps the geographic precision of the original BaseMap25 map, but now defines at higher definition of categories, going from 25 categories in BaseMap25 to 59 categories in the final result. 74 categories are originally found in Landuse100 but some groupings were done on some less important categories (e.g. buildings). The new map has a much finer grain and can hereafter be used for GIS overlays at much finer scales, where the 16-fold increase in the density of pixels gives substantially improved results. Fine scale details on roads and river networks were also maintained whereas they are often difficult to represent adequately in coarse resolution raster formats.

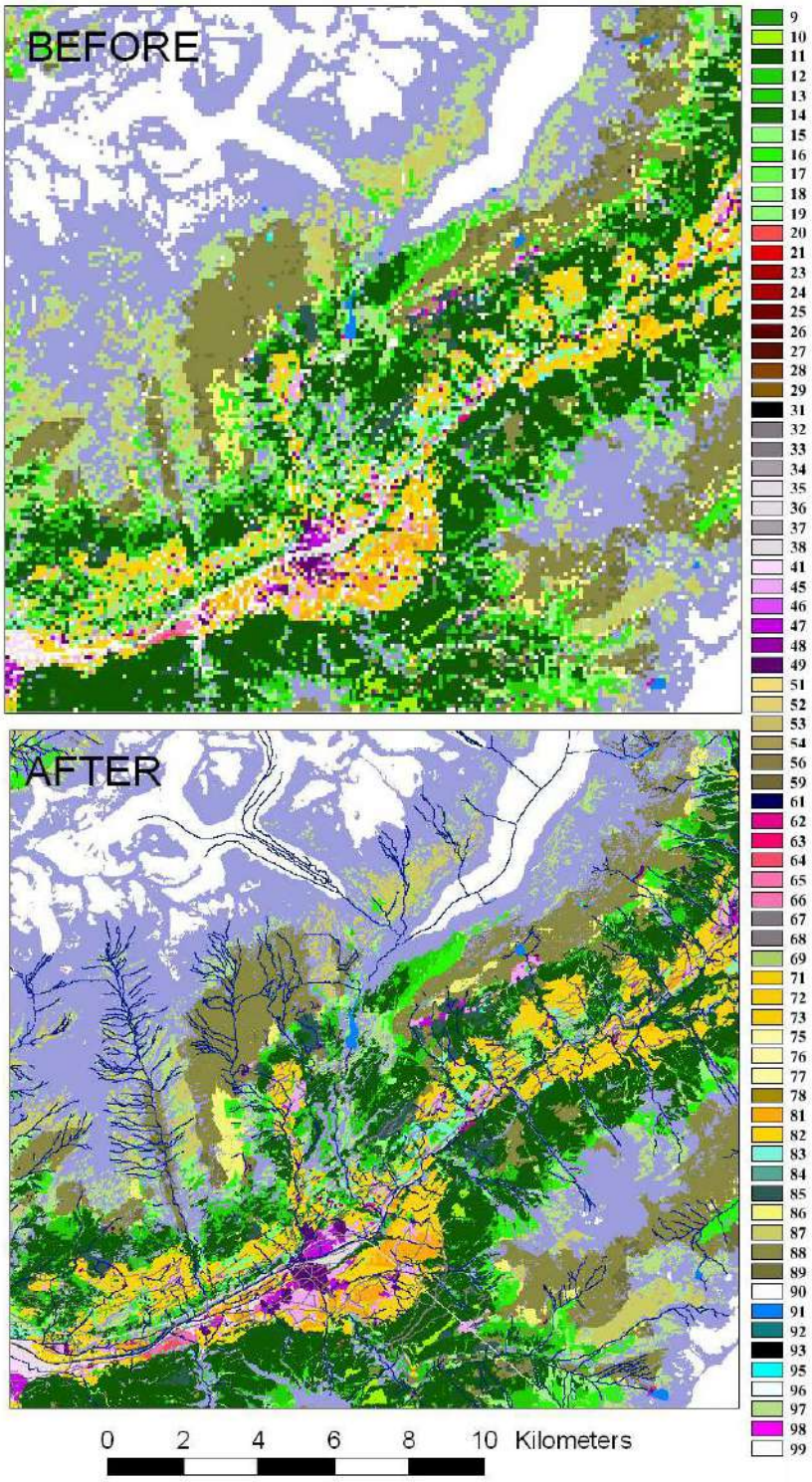

Figure A5. 3 Result of land use downscaling from 100m to 25m in the Riederalp region in Switzerland (see Figure A5.2 for legend interpretation).

The average percentage of similarity evaluated between the original points found in the Landuse100 statistics and the resulting Landuse25 classifications is 83% when assessed without roads, rivers and railways, and 77% when assessed with these linear features (Figure A5.4). Most categories have a correspondence of 80% or greater, and the lowest correspondences were for linear features such as

freeways (31), roads (33), railways (36) and rivers (92). Categories from the Landuse100 classification that show zero correspondence are those that were not predicted such as building of different types (20 to 29), groves (17), river shores (69), avalanche protections (98), dam (92) and scattered fruit trees (77) (Figure A5.4).

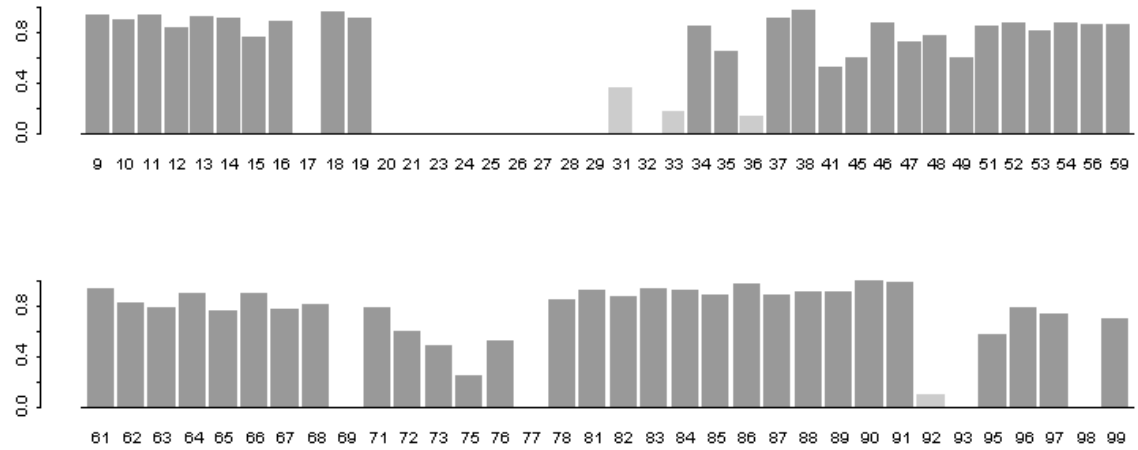

Figure A5. 4 Percentage of similarity between 74 original classes (Landuse100) and 59 downscaled classes (Landuse25).

A5.5 DISCUSSION

The method presented in this study is a general approach that can be used to downscale different type of geographic information such as results from photo interpretation, remote sensed image classification, or vegetation and soil maps. The general idea is to use the nearest precise point observations to define the attribute of a pixel at a finer resolution within an area defined by a precise land cover map with low attribute information value. Other co-variables such as remote sensing reflectance from different bands (e.g., NDVI), topographic position, slope or orientation could also be used to calculate the closest average distance between competing land use categories.

In the example presented here, the use of a national topographic base map at a 1:25000 scale to define main land cover areas guarantees a perfect overlay with administrative maps. Indeed, base maps are now widely available in digital format and are used generally as reference maps in most studies and field work. The possibility of matching the geometry defined by base maps with our resulting land use categories reinforces the chance of acceptance of the final product by end users. However, some recent changes in land use that might be visible from remote sensing images could be lost if they involved changes between incompatible land use categories as defined by the expert table.

Our approach also avoids the “salt and pepper” effect often found with remote sensing classifications (Bock et al 2005), except with object oriented classifications (Ivits et al 2005). We believe that our approach could be particularly useful to smooth land use maps obtained from remote sensing classifications. In such case, the land use statistics would be replaced by the land use classification

obtained from supervised or unsupervised remote sensing classification, whereas the land cover map will remain the national base map.

The relatively high proportion (83%) of exact matches between the land use category recorded at Landuse100 grid points and the corresponding point at 25m resolution is particularly encouraging. Discrepancies appear to result mainly from the change of scale and geometric precision brought in by the 1:25000 base maps. A visual check confirms that most divergences occur most frequently along boundaries of land use change and along linear features. By using an inverse distance calculation to choose the best candidate land use for each pixel we greatly favoured the maintenance of input land use categories at an observed location in the final result.

The approach could be used at finer scale by rasterizing for instance the topographic maps at 10m instead of 25m, or using a regional map at a finer scale (1:10000). Getting precise land use information is crucial for calculating landscape indices such as those obtained from FRAGSTAT (McGarigal and Marks 1995). As demonstrated by Uuemaa et al (2005) changing grain size can have a significant effect on many landscape metrics. Therefore one should be very careful about the scale at which a given landscape metrics is meaningful, and what grain size of land use maps is best adapted, as there is no single land use scale which is "best" for observing and managing changes in land-used patterns (Verburg and Veldkamp 2004).

The implementation of a cased-based reasoning algorithm in a C++ code proved to be a very efficient approach, given the very large number of pixels (64 million), but required the development of purpose-written software. The provision of tools for implementing case based approach within existing GIS packages would certainly be very useful for many applications. One such tool has been developed by Remm (2004) using Microsoft Visual Studio.NET, and this can predict several response types (binomial, multinomial, continuous and complex) based on continuous and categorical predictors.

Riitters (2005) cites the practical tradeoff between generality, precision and realism proposed by Levins (1966), where generality and realism should be maximized at national scales, and precision optimized at local scales. Indeed, the use of the same raw data to develop models at different scales will enhance thematic and geographic comparisons between disciplines and across scales. Methods to upscale and downscale data are therefore central to local, national and global environmental assessments.

A5.6 CONCLUSIONS

Downscaling allowed combining the geographic precision of existing topographic base maps with the thematic details of photo-interpreted land use information. Improved land use maps open the door to more precise watershed analyses, species and habitat distribution modelling, species dynamic models of migration or land use changes assessment. Precise land use information is also the base to develop sustainable development indicators defining structural and functional attributes of landscapes.

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