Predicting the potential spatial distributions of epiphytic lichen species at the landscape scale

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Abstract: The potential spatial distributions of six epiphytic lichen species were assessed in Switzerland (41 000 km^2) as a function of various key climatic drivers and forest types using logistic regression models. *Cetrelia cetrarioides* is 'near threatened', *Lobaria pulmonaria* is 'vulnerable', and *Graphis scripta*, *Hypogymnia physodes*, *Lecanora cadubriae*, *Letharia vulpina* are not endangered according to the Red List assessment based on IUCN criteria. Lichen presence and absence were derived from the SwissLichens database that contains spatially explicit information on both species presence and absence.

The spatial lichen niches are predicted with R^2 values between 0·5 and 0·75 and AUC values between 0·63 and 0·94. Model evaluation shows that the models perform well.

Lichenologists reviewed the spatial predictions of lichen species on the basis of their expert knowledge and concluded that parsimonious regression models may suffice for successful prediction of the potential spatial niche distributions of epiphytic lichen species.

Key words: AUC, bioclimate, *Cetrelia cetrarioides*, GINI coefficient, GLM, *Graphis scripta*, *Hypogymnia physodes*, *Lecanora cadubriae*, *Letharia vulpina*, *Lobaria pulmonaria*, predictive distribution model, ROC, Switzerland

Introduction

Data availability on species distributions at the landscape-scale is often limited, as the collection of quality data is costly (Bowker 2000), or limited for infrequent, inconspicuous, or less broadly known taxa (Berg *et al.* 2004; Edwards *et al.* 2005; Martinez *et al.* 2006). However, when conducting landscape-scale surveys or monitoring projects for the development of effective management and conservation strategies, a sufficient quantity of data is required to estimate or model species frequencies and distributions (Maina & Howe 2000; Edwards *et al.* 2005; Lavergne *et al.* 2005). Thus, adequate detection of species occur-

rences or abundances to derive baseline information is needed for ecological conservation or management strategies. One possible strategy involves the development of predictive models which generate potential spatial distributions of species as a function of point observations. The models yield continuous probability surfaces of species occurrence in the modelled biophysical and geographic space. Thus, although frequently restricted due to limited data availability, the approach may be important in generating and testing hypotheses about landscape-scale spatial distribution potentials of infrequent, inconspicuous, or less broadly known taxa such as lichens or bryophytes (Kadmon & Heller 1999; Berg *et al.* 2004; Edwards *et al.* 2005; Martinez *et al.* 2006). Methodologically, statistical tools available to correlate species with their habitats include General Linear Models, General Additive Models, or CART models

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(Guisan & Zimmermann 2000; Thuiller *et al.* 2003; Guisan & Thuiller 2005).

It has been claimed that climate is a major driver of species distributions across Europe (Thuiller *et al.* 2004). Thus, climate and its variability have been widely applied in ecological research that quantifies species spatial biotic responses as a function of environmental drivers (Zimmermann & Kienast 1999; Bolliger *et al.* 2000; McKenzie *et al.* 2003) or land-use (Easterling *et al.* 2001; Dirnböck *et al.* 2003; Dullinger *et al.* 2003a; Dullinger *et al.* 2003b). It has also been used to estimate potential spatial distributions of a variety of animal habitats and taxa, e.g., insects (Bonn & Schröder 2001) and molluscs (Kadmon & Heller 1999; Berg *et al.* 2004).

In this paper, we identify the potential spatial niche distributions of six epiphytic lichen species as a function of key climatic drivers and major forest types in Switzerland. The resulting species distribution models may be used further either to complete existing lichen surveys by identifying areas where the species has not previously been observed (Edwards *et al.* 2005), or to delineate species-specific, spatially explicit occurrence hotspots. Spatial niche modelling of lichen species has only rarely been done (Edwards *et al.* 2005; Martinez *et al.* 2006). Many lichen species occupy specific microenvironmental niches (e.g., rain-exposed surface of a trunk), and are known to be sensitive towards environmental change (Wirth 1992). Thus, assessing lichen-specific niche potentials is important in estimating the degree of sensitivity to change, although the poikilohydric properties of lichens may complicate modelling mainly by purely environmental variables. Four out of the six lichen species considered here are not currently threatened (*Graphis scripta*, *Hypogymnia physodes*, *Lecanora cadubriae*, *Letharia vulpina*), one is near threatened (*Cetrelia cetrarioides*), and one species is vulnerable (*Lobaria pulmonaria*) according to the Red List assessment for Switzerland following IUCN criteria (Scheidegger *et al.* 2002).

Material and Methods

Study area

Switzerland covers an area of approximately 41 000 km², of which 12 300 km² is forested (Statistisches Jahrbuch der Schweiz 1997). The climate is temperate humid, but there is a strong regional variation due to the effects of mountains. Conditions range from an intra-alpine dry and continental climate (Central Alps) to an oceanic regime at higher (Northern Alps, Jura Mountains) and low elevations (Plateau). The southern alpine part of Switzerland is dominated by an insubrian climate type with relatively mild and dry winters and warm-humid summers (Fig. 1).

Study species

Six lichen species were selected to provide examples of characteristic distribution ranges along altitudinal and climate gradients in Switzerland (Table 1). *Lobaria pulmonaria* (L.) Hoffm., and *Cetrelia cetrarioides* (Duby) W. Culb. & C. Culb) represent species which occur predominantly in oceanic climates and *Letharia vulpina* (L.) Hue represents species occurring in continental climates. *Lecanora cadubriae* (Massal.) Hedl. *Hypogymnia physodes* (L. Nyl.) and *Graphis scripta* (L.) Ach. are observed across all major bioclimatic regions of Switzerland, but their distribution ranges differ with respect to altitude. *Hypogymnia physodes* is widespread at altitudes between 1000–1600 m asl, and *Graphis scripta* occurs mainly at altitudes between 600–1000 m a.s.l.

Data on presence/absence of lichens, or more specifically, detection/non-detection, were obtained from the SwissLichen database (Stofer *et al.* 2003). The data were collected between 1989 and 2000 and for each observation, the species name, coordinates, elevation, status of protection, number of specimens found, and name of most frequent hosts (tree, shrub) were recorded. The database encompasses 557 epiphytic lichen species across Switzerland selected from systematic design and non-systematic purposive sampling approaches. The design sampling is based on a stratified random sample across Switzerland and is a measure of both lichen presence and absence. Lichen observations from purposive sampling originated from non-systematic sampling performed by amateur and professional lichenologists who collected lichens in specific areas mainly for qualitative, floristic purposes. Lichen data originating from purposive sampling are thus presence only data with a strong subjective bias.

For this study, both sampling methods (systematic design and purposive) were combined. Data from the designed sampling strategy relies on plots of 500 m² located on the 1 km intersections of the Swiss coordinate system. The database contains a total of 826 plots for the purpose of long-term observations. The plots were pre-stratified according to the presence of forest (two strata), altitudinal gradients (six strata) within the five major regions of Switzerland (Jura Mountains (98), Plateau (189), Northern Alps (132), Alps (336), and Southern Alps (71 sampling plots)). Within these strata, the plot selection was performed randomly. For each
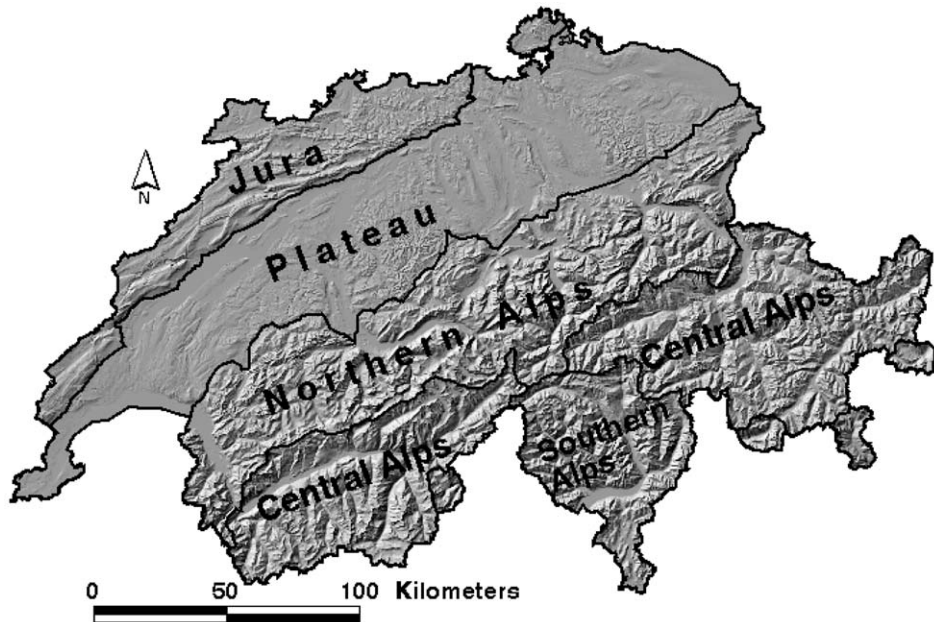
Fig. 1. The study area of Switzerland and its five major bioclimatic regions.

plot, lichen-species' presence and absence were recorded. Lichen observations derived from the purposive sampling strategy relied on a 20 × 20 km grid and lichen floristic data derived from the literature. These data mirror species presence only. For a more detailed description of the sampling strategies see Dietrich *et al.* (2000) and Scheidegger *et al.* (2002).

Species distribution modelling

We used logistic regression with a logit link function to predict the spatial distribution of lichen species as a function of various climatic variables and forest types. Logistic regression is well established in ecological research and has been widely used to predict species probability surfaces from presence/absence data for species distribution modelling (Bartlein *et al.* 1986; Brown 1994; Mladenoff *et al.* 1995; Guisan *et al.* 1998; Bolliger *et al.* 2000; Guisan & Zimmermann 2000; Guisan & Hofer 2003; McKenzie *et al.* 2003). The predicted response surfaces take values of probability of presence between 0 and 1. Low probabilities of occurrence (close to 0) indicate sites of potentially unsuitable ecological niches. High values (close to 1) specify potentially suitable ecological niches for the corresponding lichen species. However, probabilities of presence are no indication of species frequency, or difficulty and time requirements to successfully detect a species in a predicted habitat.

Use and limitations of species distribution modelling have been discussed elsewhere (Guisan & Zimmermann 2000; Hampe 2004; Segurado & Araujo 2004; Guisan & Thuiller 2005) and will not be repeated here.

Climatic variables

Independent predictors included thermic (summer frost frequency, degree day sum) and hygric variables (yearly precipitation sum, water budget in July), as well as measures of continentality (global radiation in March and July, Gams angle) (Table 2). The variables used in this study are described in detail in Zimmermann and Kienast (1999) and Bolliger *et al.* (2000). All climatic variables are available as raster maps, based on spatially interpolated data from standardized meteorological records derived from the national network and digital elevation models (DEM) on a 25 m resolution. Monthly averages were used for degree days and precipitation (mm) for the period between 1961 and 1990. The climatic measurements were spatially interpolated using local thin plate spline functions (Franke 1982; Mitas & Mitasova 1988). To obtain an estimate of the local climatic properties and the local climatic variability relevant for each geographic location, we calculated mean, standard deviation, maximum, and minimum within a 1 × 1 km rectangular neighbourhood.

The thermic variables include degree-days and summer frost frequency. Degree-days are calculated as the sum of degrees above a 5 °C threshold for a whole year (Zimmermann & Kienast 1999). Summer frost frequency expresses the number of frost events during the frost-sensitive time of the year. A frost event is defined by a fall in temperature below zero if it was preceded by a period of temperatures >3 °C during the frost sensitive period of the year (Bolliger *et al.* 2000).

TABLE 1. *Morphological and ecological characteristics and Red List status of the six lichen species studied (status after Scheidegger et al. 2002)*

Species	Growth form	Red List status in Switzerland	Main altitudinal range (min/max) [m a.s.l.]	Habitat	Colonized tree species
Cetrelia cetrarioides	Foliose	Near threatened	1000–1600	Relatively oceanic sites with high precipitation rates, often in old woodlands but also on free-standing trees	Deciduous trees, mainly *Acer pseudoplatanus* and *Fagus silvatica*
Graphis scripta	Crustose	Least concern	600–1000	Moderately to deeply shadowed smooth bark in forests and on free-standing trees at humid sites	Deciduous trees, mainly *Fagus silvatica* and *Fraxinus excelsior*
Hypogymnia physodes	Foliose	Least concern	1000–1600	On siliceous rocks, trees and other acidic substrata, over a wide range of habitats	Conifers and deciduous trees, mainly *Picea abies* and *Abies alba*
Lecanora cadubriae	Crustose	Least concern	1000–1600	Cold, relatively continental sites, mainly in forests	Conifers, mainly *Larix decidua* and *Picea abies*
Letharia vulpina	Fruticose	Least concern	1000–1600	Cold, well lit sites on very acidic bark in forests and open habitats	Conifers, mainly *Larix decidua* and *Pinus cembra*
Lobaria pulmonaria	Foliose	Vulnerable	1000–1600	Relatively oceanic sites with high precipitation rates, often in old woodlands but also on free-standing trees	Deciduous trees, mainly *Acer pseudoplatanus* and *Fagus silvatica*

TABLE 2. *Description of climatic variables used in regression models*

Climatic variable	Abbreviation	Minimum	Maximum	Mean
Summer frost frequency (0·01 nday)	Sfro	0	8154	92·3
Degree day sum (day*deg*10)	Dgd	0	3712	1728·8
Yearly precipitation sum (0·01 mm yr^{-1})	Nann	4326	5189	14135·7
Water budget in July (0·01 mm mth^{-1})	Wb$_{Jul}$	− 42	265	74.5
Radiation in March and July [kJ day^{-1} (monthly avg.)]	R$_{Mar.}$, R$_{Jul.}$	R$_{Mar.}$: 0	9578	3689·2
		R$_{Jul.}$: 0	10165	6721·3
Gams angle (unitless)	Kig	47	726	452·7

Hygric variables include mean yearly precipitation sum and water budget in July. The water budget in July is calculated as the difference between the precipitation sum and the potential evapotranspiration in July. Potential evapotranspiration is calculated from the empirical formula of Turc (1961). For calculation details, see Zimmermann and Kienast (1999).

Measures of continentality include radiation for the months March and July and Gams angle. Potential direct solar radiation was estimated from the empirical formula of Müller (1984). The Gams angle gives a general estimate of landscape-scale weather patterns with sensitivity to regional differences based on precipitation and temperature regimes at given elevations (Zimmermann & Kienast 1999).

Forest types

Data for forest types across Switzerland were derived from BFS (BFS 1990/1992). The data has a resolution of 25 m and relies on 11 geometrically and radiometrically corrected Landsat-5 TM scenes, generated between 1990 and 1992 (BFS 1990/1992). First, the satellite images were classified into forest/non-forest using a maximum likelihood classifier (BFS 1990/1992). Second, the 11 Landsat-5 TM scenes were categorized into four forest types: coniferous (90–100% conifers), mixed coniferous (50–90% conifers), mixed deciduous (10–50% coniferous) and deciduous (0–10% coniferous), also using maximum likelihood classifier (BFS 1990/1992). The classification has an overall accuracy of 91·8% (BFS 1990/1992).

Model fitting

The dependent variable of the logistic regression models was observed lichen species presence and absence from the SwissLichens database (Tables 1 & 3). Lichen species presence/absence was geographically intersected with the independent climatic variables (mean, standard deviation, minimum, and maximum) and forest types. This data set was then subjected to the logistic regression (stepwise selection), where thresholds for entry or stay were set at a level of significance of 0·05 and relied on minimal correlation of the variables (<0·5) as assessed by a correlation matrix.

Model evaluation

Accuracy of the predicted lichen models. Confusion matrices were used to evaluate the accuracy of the predicted versus the observed presence or absence of a species. Confusion matrices are 2 × 2 cross-tabulations of the proportions of correct model predictions for presence (sensitivity) and absence (specificity) with respect to the observed data (Fielding & Bell 1997). The matrices may be assessed using a discrete threshold identified to benchmark species presence versus absence, or they may be threshold independent.

Threshold-dependent approaches include the Kappa statistics (Cohen 1960), which identify species presence and absence discretely by measuring the proportion of agreement. A threshold-independent method to assess the degree to which species presence and absence were predicted correctly relied on AUC (Area Under the Curve) statistics derived from ROC (Receiver Operating Characteristics) plots (Fielding & Bell 1997). Here, we applied a modified version of the AUC, the Gini coefficient (AUC′) (Copas 1999). The AUC′ takes values between 0 and 1, where 0 indicates no prediction success and 1 indicates high prediction success for both presence and absence.

Predictive ability of the lichen models. Ideally, an independent data set is used to test a model's predictive ability. Because we did not have such a data set, a tenfold cross-evaluation was applied (Verbyla & Litvaitis 1989). Cross-validated models were then assessed by AUC′$_{eval}$ values (mean and standard deviation), and compared to the predictions originating from the full calibration data set (AUC′$_{cal}$). AUC′$_{eval}$ was calculated using SimTest (Zimmermann 2001).

Results

Model evaluation

Model R^2 for all six lichen species ranged between 0·4 and 0·75 (Table 3). The climatic variables included measures related to continentality (radiation, Gams angle),

TABLE 3. *Numbers of observations and quantitative assessments of logistic regression model performance for each lichen species studied*

| | Number of observations | | | Model | | | | Test statistics for the calibrated models | | | Test statistics for the evaluated models | |
| | | | | Bioclimatic variables | | | Forest variables | | | | | |
Lichen species	Presence	Absence	Total	Thermic	Hygric	Continentality		R^2_{cal} (Nagelkerke)	AUC_{cal}	AUC'_{cal}	AUC_{eval}	AUC'_{eval}
Cetrelia cetrarioides	169	817	986	$Sfro_s$	$Nann_s$ $WbJu_s$ $WbJu_{min}$	–	Non-forest Mixed deciduous Deciduous	0·54	0·90	0·80	0·78++	0·56++
Graphis scripta	397	695	1092	$Sfro_s$	–	$RJul_{min}$ Kig_{min}	–	0·56	0·63	0·60	0·82++	0·63++
Hypogymnia physodes	671	616	1289	$Sfro_s$	–	$RJul_{max}$	Coniferous	0·40	0·80	0·60	0·80++	0·60++
Lecanora cadubriae	66	802	868	$Sfro_s$	$Nann_{max}$	$RJul_{max}$	Non-forest	0·65	0·94	0·88	0·90+	0·90++
Letharia vulpina	78	799	877	$Sfro_s$	$WbJu_{max}$ $WbJu_s$	Kig_{max}	–	0·75	0·86	0·72	0·90+	0·63+++
Lobaria pulmonaria	146	824	970	Dgd_m $Sfro_s$	–	–	Non-forest	0·55	0·90	0·80	0·90+	0·80++

$Sfro_s$=standard deviation of summer-frost frequency, Dgd_m=mean of degree day sum, $WbJum_{max}$=maximum of water budget in July, $WbJu_{min}$=minimum of water budget in July, $WbJu_s$=standard deviation of water budget in July, $Nann_{max}$=maximum of annual precipitation, $Nann_s$=standard deviation of annual precipitation, $RJul_{min}$=minimum of July radiation, $RJul_{max}$=maximum of July radiation, Kig_{min}=minimum of Gams angle, Kig_{max}=maximum of Gams angle, R^2=Nagelkerke's R^2, AUC_{cal}=Area Under the Curve for the calibrated model, AUC_{eval}=Area under the curve for the evaluated model, AUC'_{cal}=Gini coefficient for the calibrated model, AUC'_{eval}=Gini coefficient for the evaluated model. Statistical tests for the evaluated models: n=10, means, standard deviation categorised as +<0·01, ++0·01–0·1, +++>0·1.

hygric (July water budget, annual precipitation), and thermic factors (summer frost frequency, degree days). Of these variables, the standard deviation, minimum, and maximum were often more important than the means (Table 3). The forest types entering the regressions encompassed mixed deciduous, deciduous, coniferous and non-forest.

For five species models, the threshold-independent indicator for model accuracy for the full calibration data set (AUC$'_{cal}$) ranged between 0·60 and 0·88, indicating satisfactory to good discrimination between predicted and observed species presence and absence (Table 3). Thus, the pattern of the predictive ability of the lichen distribution models is very similar to the one observed for the model calibrated with the full data set.

Potential spatial distribution of epiphytic lichen species

The potential spatial distributions of *Graphis scripta* and *Hypogymnia physodes* are broad with high probabilities of occurrence in the Jura mountains, the Plateau, and in the Northern and Southern part of the Alps (Fig. 1, Fig. 2B & C). *Hypogymnia physodes* and *Graphis scripta* are both ubiquitous with high probabilities of occurrence in all major bioclimatic ranges of Switzerland, including the Central Alps (Fig. 1, Fig. 2C). Whereas *Hypogymnia physodes* covers low and higher altitudes, *Graphis scripta* has low probabilities of occurrence at higher altitudes (Fig. 2B & C). *Cetrelia cetrarioides* and *Lobaria pulmonaria* exhibit high probabilities of occurrence throughout the Jura mountains, and the Northern and Southern Alps with likelihood of lower occurrence on the Plateau (Fig. 1, Fig. 2A & F). This indicates that these species occur predominantly at higher elevations (montane zone, <1500 m a.s.l.) in suboceanic climates (Northern Alps, Jura). The predicted and observed spatial distributions of *Letharia vulpina* are restricted to the higher elevations of the Central Alps (Fig. 1, Fig. 2E). Similarly, empirical evidence suggests that *Lecanora cadubriae* is also primarily observed in the Central Alps (Fig., 1, Fig. 2D), but, in

contrast to *Letharia vulpina*, however, this species is also observed and predicted to occur in the Northern Alps, although with rather low probabilities of occurrence. (Fig. 1, Fig. 2D).

Discussion

Spatial predictive models for lichen species

We successfully predicted the occurrence of lichen species as a function of exogeneous environmental characteristics. The approach assesses statistical relationships between the response variable and the explanatory variables to predict the species in previously not sampled geographical space. For inconspicuous or rare species, this often means that the data for the response variable originates from different sampling strategies in order to increase the number of observations to allow modelling. For our approach, we combined data from a systematic design and from purposive data sampling. Although the focus of this paper was to test how well the data extrapolated to unsampled regions, future research should assess possible effects of the data sampling strategies. A recent paper by Edwards *et al.* (2006) provides evidence that the selection of explanatory variables as well as the prediction accuracy of a model may depend on the sampling strategy of the dependent variable.

It is typically assumed in spatial distribution models that a few parsimonious environmental variables suffice to predict species distributions (e.g., climate, topography) (Bolliger *et al.* 2000; Bolliger *et al.* 2000; Guisan & Theurillat 2000; Thuiller *et al.* 2003; Edwards *et al.* 2006). Among environmental drivers, climate is referred to as a resource predictor and has been used extensively for predicting species distributions (Bolliger *et al.* 2000; Guisan & Hofer 2003) at the landscape and the continental scale (Holdridge 1947; Woodward 1987). The simplification of predicting species distributions using only a few environmental variables holds true in environments such as those the Alps where the vegetation is likely
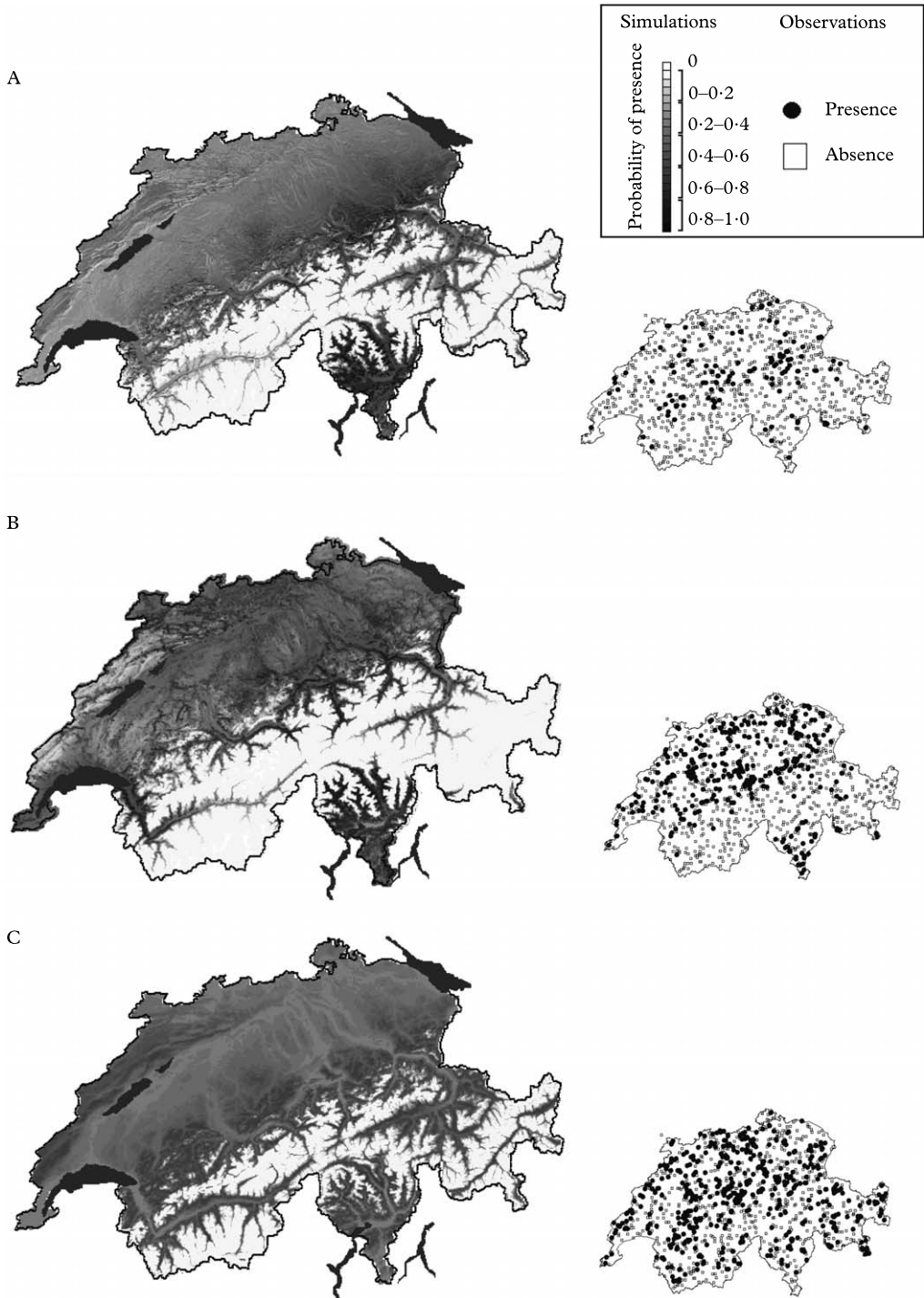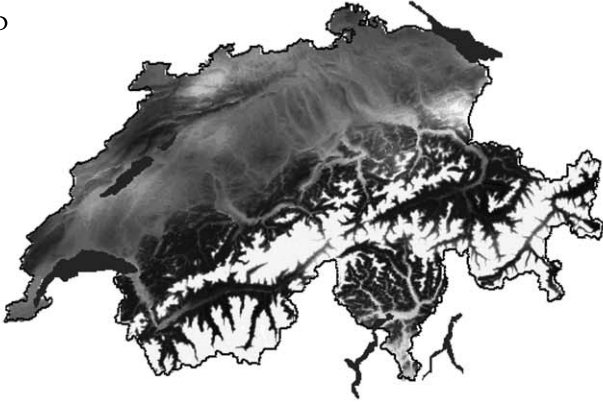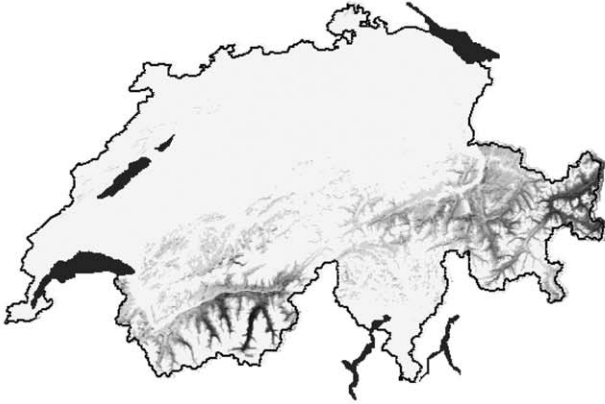
FIG. 2. A–F. Potential habitat distribution maps for six epiphytic lichen species. A, *Cetrelia cetrarioides*; B, *Graphis scripta*; C, *Hypogymnia physodes*.
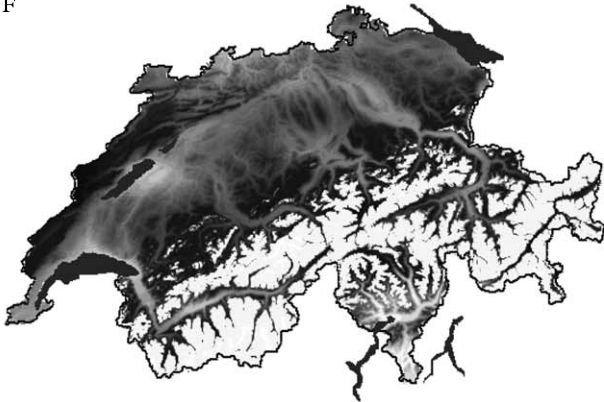
D

E

F

FIG. 2. Continued. D, *Lecanora cadubriae*; E, *Letharia vulpina*; F, *Lobaria pulmonaria*.

to be primarily driven by environmental variables (e.g., temperature) at the mesos-cale. Certainly, the credibility of the models and the resulting plausibility of the predicted spatial lichen distributions depend largely on the availability and quality of the input data sets used for model calibration. The climatic variables used here rely on about 400 climate stations across Switzerland. Most of the stations are located at lower elevations. This bias is addressed and partly compensated for by applying a high-resolution 25 m DEM that accounts for the complex topography in a mountainous area. All climatic variables are long-term climatic records (30 year monthly normals) that have been used in various studies in Switzerland (e.g. global change: Zimmermann & Kienast 1999; Bolliger *et al.* 2000; Bolliger *et al.* 2000).

Interestingly, our results suggest that climatic minima, maxima, and standard deviations are of greater relevance in explaining species occurrences than mean values. However, by using climate variables with a 1 km^2 resolution, local-scale climatic characteristics cannot be accounted for. For example, in the northern-most part of Switzerland there are some isolated occurrences of *Lobaria pulmonaria* which are not accurately predicted by the model. Overall, this region is characterized by a dry and warm local climate quite untypical for *Lobaria pulmonaria*. However, the species occurs in locally more humid climates such as ravines, local topographic variability or coppice with standard forests, which favour *Lobaria pulmonaria* populations. These particular local climatic conditions cannot be assessed with geographically aggregated variables. On the other hand, the occurrence of species with a limited regional distribution is likely to be overestimated by the simulation presented here. *Letharia vulpina* and *Lecanora cadubriae* are both frequent in subalpine forests in continental regions of the Alps but were not reported from the Jura mountains. For *Letharia vulpina* the simulation correctly predicts high probabilities of presence in the Central Alps of the cantons of Valais and Graubünden. Some rather isolated regions in the Northern and Southern Alps were

correctly predicted. However, the extremely small and scattered islands in the Jura mountains where the simulation predicts a low probability of presence for the species at the highest altitudes, the species probably does not occur owing to chorological reasons (SwissLichens). The simulation of *Lecanora cadubriae* distribution predicts rather high probabilities of presence on the Plateau and on the Jura mountains. Generally, *Lecanora cadubriae* has a distribution pattern that is similar to *Letharia vulpina* except for more outposts in the northern Alps. However, this species does not occur on the Plateau and the Jura mountains, for chorological, rather than for climatological reasons.

Epiphytic lichens are well known to be sensitive to host tree species and forest structure and management (Barkman 1958; Dietrich & Scheidegger 1996; Uliczka & Angelstam 1999; Ihlen *et al.* 2001; Johansson & Ehrlén 2003; Pykälä 2004). Although the forest types used here characterized very crudely the habitat requirements of the lichen species examined, for four out of the six species the forest types were important for modelling the species distributions. The simulation gives an accurate prediction of the distribution of *Hypogymnia physodes* and *Graphis scripta*, two species that are good colonizers with a broad tree species spectrum.

Another limitation of the regression modelling approach is that endogeneous drivers such as biotic interactions (e.g., competition), feedback, or various aspects of species-specific life-history attributes (e.g., dispersal ability) are not usually accounted for by spatial regression models (Bolliger *et al.* 2000; Guisan & Zimmermann 2000). Thus, the modelling approach does not consider species specific life-history attributes of the biota. In addition, it is suggested that lichen responses to climatic conditions depend on the physiological state of the lichen (Scheidegger & Schroeter 1995). Models could be improved by accounting for local forest structure, composition and disturbance history (Kalwij *et al.* 2005; Werth *et al.* 2006; Werth *et al.* 2006), or life-history attributes, but such data are not usually available in the required resolution or scale.

This constraint is rather common in spatial distribution modelling. Although these limitations may lead to truncated response curves (Hirzel *et al.* 2001), or to inconsistent model performances that vary across geographical space, most approaches assess species distributions using surrogates (e.g., temperature). This is particularly true for large-scale study areas with strong environmental gradients (e.g., Switzerland with strong altitudinal gradients) which drive major vegetation patterns (Zimmermann & Kienast 1999; Bolliger *et al.* 2000). The interpretation of the distribution maps are thus a large-scale assessment without claiming detailed interpretations on life-history details.

Model performance using threshold independent indicators suggests that the spatial distribution of the biotic input data has a significant effect on the statistical accuracy and the predictive success of the output. This effect is independent of the number of lichen observations used for model calibration. *Letharia vulpina*, with 78 observations and the rarest species considered, is a species restricted to the continental high-elevation range and exhibits the highest model performance compared with the other five species (Table 3). Discrimination between presence and absence of a geographically defined species distribution pattern is predicted better than for a widely distributed species. Correspondingly, the Gams angle, a continentality-specific variable becomes important with *Letharia vulpina*. Furthermore, the predicted distribution of *Letharia vulpina* is presumably less impacted by any human disturbances since this species occurs in the subalpine part of the central and southern Alps which exhibit rather low human populations. The predicted niche of this species may thus approach its realised niche under current climatic conditions. In contrast, the modelled niche of the threatened *Lobaria pulmonaria* (Scheidegger & Clerc 2002), although clearly defined by thermic variables (degree days, summerfrost), has been affected by human activities such as forest management, especially in the lowlands (Clerc *et al.* 1992). Thus, some areas with

certain combinations of environmental variables under which this species could occur are presumably not occupied at the moment. Without any human activities we assume that *Lobaria pulmonaria* would have higher probabilities of occurrence on the Plateau (more upland regions).

Implications for lichen conservation and management

While high-quality data are often available throughout a study area for many conspicuous taxa, at least in non-tropical and so-called developed countries, for less prominent taxa such as lichens data are often sparse. Even regional distributions might not be well known because of the lack of lichenologists in many countries (Wolseley 1995). The lack of knowledge of species distributions may prevent their allocation to red-list categories defined by IUCN (2001). For example, the extent of occurrence in a region and its temporal trend are very important measures for assessing the conservation status of a species. However, measuring the extent of occurrence by a minimum convex polygon as proposed by IUCN (2001) can result in poor estimates if the geographic distribution of the species is not well sampled. Furthermore, in a geographically highly structured country such as Switzerland, with very different climatic regions and strong environmental gradients where suitable habitat patches are often quite distant from each other, the estimates of the extent of occurrence by minimum convex polygons are much too large. This may lead to an inappropriately low red-list status of the species (see also Burgman & Fox 2003). In such cases, niche-based models such as developed here may yield more realistic estimates of the extent of occurrence than the actual data, provided that the thresholds to transfer the probability maps into binary maps are chosen sensibly.

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