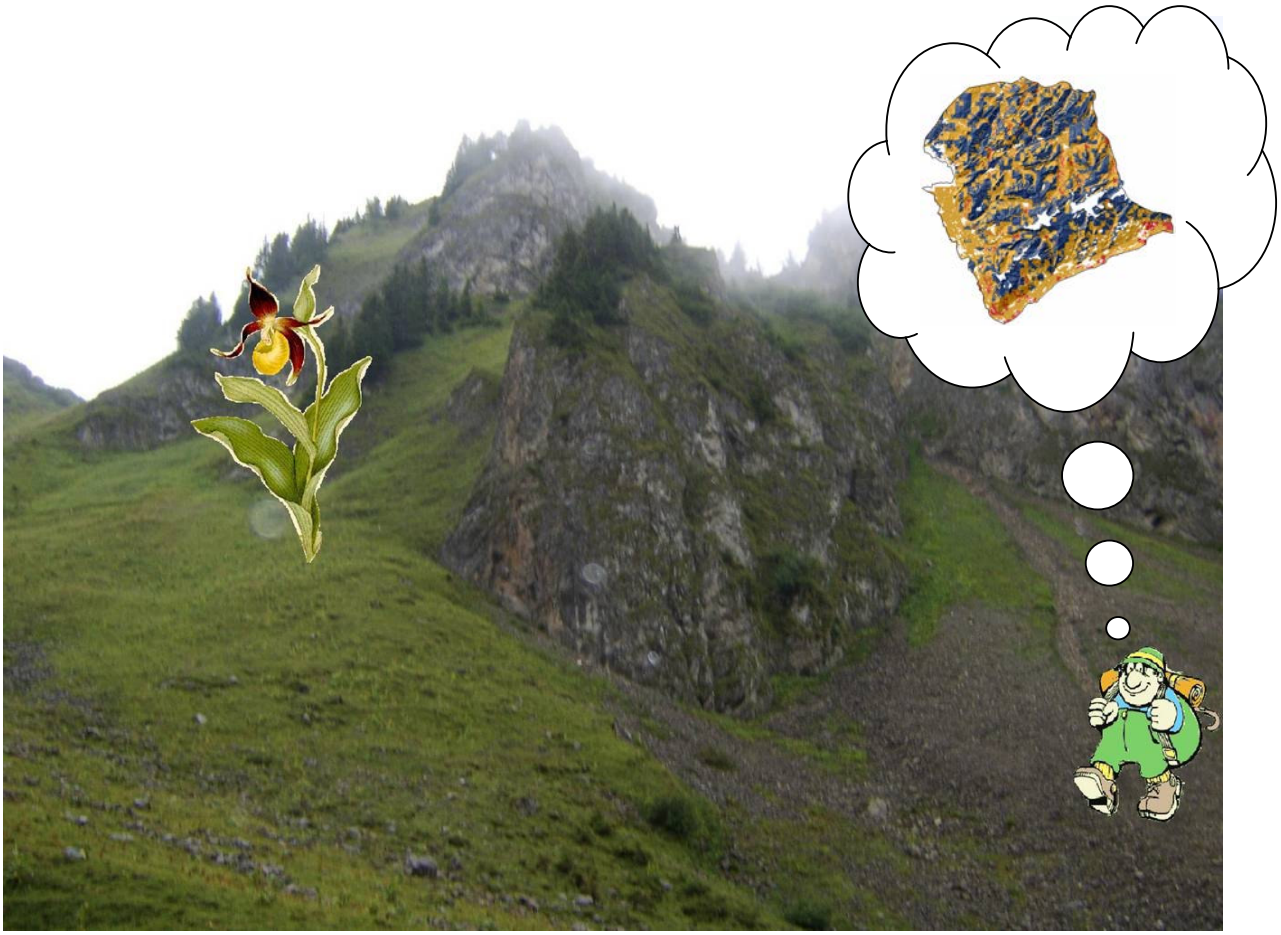
MODEL-BASED STRATIFIED SAMPLING OF RARE SPECIES



Master's Thesis

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Abstract

About one third of all plant species occurring in Switzerland are cited on the red list under the categories *vulnerable* or *extinct*. Monitoring and management of rare species are thus important issues in conservation biology. As high costs are usually associated with field work, efficient sampling strategies need to be developed. This study shows how a model-based stratified sampling strategy can improve the search for undiscovered populations of rare plant species.

The approach was developed on three endangered species, *Eryngium alpinum*, *Cypripedium calceolus* and *Scorzonera laciniata* and five common species. Spatial habitat suitability models were fitted by relating species' presence-absence data to topoclimatic predictor variables. A final categorical model resulted from the combination of models fitted by using different modeling methods at two different geographic scales. For each species, it predicted whether sites were highly favorable, fairly favorable or unfavorable. We used three different levels (30, ~250 and ~500 points) of an independent data set for calculating various validation indices.

Results showed that the probability of species' occurrence was overall largely superior in predicted suitable areas than elsewhere. However, this was better evidenced for common than for rare species. The final combined model reached better results than each of the single models (i.e. using each a distinct modeling method and scale). Fieldwork was only successful for one rare species, *Scorzonera laciniata*, for which eight new populations were found. Our results also tend to indicate that the other two rare species are very scarce in the landscape and that a model-based approach at the sampling intensity applied here cannot help discovering new populations. Yet, our results confirm overall that spatial habitat suitability models can prove useful tools to direct field sampling for rare species.

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1. Introduction

Land use, pollution and climate change lead to massive and rapid loss of biodiversity (Wilson 1992). In Switzerland, about one third of all indigenous plant and fern species are cited in the categories *vulnerable* or *extinct* on the red list (Moser *et al*. 2002). The red list evaluates the extinction likelihood of a species based upon five criteria, including extent of occurrence and area of occurrence of the species (IUCN 2001).

Mountainous regions are less influenced and threatened by habitat destruction and fragmentation through urbanization in comparison to lower regions of Switzerland. Nevertheless, human impact results in a number of threats to endangered plants in the Alps (Bauer *et al*. 2004). Picking of conspicuous flowers, even if they are under legal protection, can in some cases severely damage a population (Känzig-Schoch 1992). Intensification of agriculture in some regions and on the opposite reduction followed by reforestation in other areas leads to a loss of suitable habitat types for meadow plants (Bauer *et al*. 2004). The construction of facilities for transport and tourists and the generation of energy also have an impact on the habitat. Last but not least, the use of artificial snow in ski regions has been shown to threat the diversity of low-nutrient and dry grasslands (Kammer 2002).

In this context, rare species are especially vulnerable to extinction. Rare species are commonly defined as having a small geographic range and/or a low abundance (Thompson 2004). Rabinowitz (1981) distinguished seven forms of rarity based on range, distribution and habitat specialization. For conservation purposes it might be important to distinguish between species that have always been rare (i.e. have a natural small distribution and/or a small number of individuals) and species that have declined recently and rapidly due to human actions (Fiedler & Ahouse 1992). In addition, we might not only be interested in rare species as such, but more generally in species that are declining drastically (Schemske *et al*. 1994). However, a limited geographical distribution, like endemics, or a low number of populations makes also "naturally" rare species vulnerable to stochastic events (Fiedler & Ahouse 1992). Darwin in his book "On the origin of species" (1859) already mentioned that rarity and extinction processes are linked inseparably.

One aim in conservation biology is to monitor species for better anticipating changes in their distribution and/or abundance. This enables biodiversity managers to define and undertake the necessary

actions for the recovery of the concerned species (Hintermann *et al*. 2002). In particular, an adequate estimation of the number of individuals and the most realistic estimation of the existing population number is the basis to correctly evaluate the level of endangerment (e.g. for classification after the IUCN-criteria). In the case of rare species, it is often difficult to obtain an adequate number of samples for statistical methods, e.g. to estimate abundance, which are usually designed for large sample sizes (MacKenzie *et al*. 2004). Moreover there is often a lack of fundamental knowledge about ecological requirements of rare species. Due to their rarity, they are less often subject to research than common species. Methods adapted for rare species and fieldwork is necessary to complete our knowledge about some plants.

Sampling methods that limit fieldwork are advantageous because they allow saving time and money. Funding is an important issue in conservation biology and especially the protection of plants. In the United States for example, although nearly 50% of the 728 federally listed threatened or endangered species are plants, they received only 8% of recovery funds spend by the US fish and wildlife service (Campbell 1991).

The sampling methodology has a great influence on the success rate. Strict design based approaches, e.g. a grid based design, provide least biased estimates but such a strategy might result in too low sampling intensity to provide observations of very sparse species (McDonald 2004). Adaptive sampling methods (Smith *et al*. 2004) is efficient to increase the knowledge about one population if the location of this one population is known, but it does not provide us with any indications about the species presence in unexplored regions (McDonald 2004). On the contrary, model-based stratified sampling (MBSS) seems to be adapted in the case of rare species (Sperduto & Congalton 1996, Boetsch *et al*. 2003, Engler *et al*. 2003, Poon & Margules 2004, Edwards *et al*. 2005).

For a MBSS design, a predictive habitat suitability model is constructed, based on environmental variables and available presence and eventually absence data of the species. The model is applied to the whole study area to indicate habitat suitability for the species. Strata used for stratified sampling are defined for different levels of suitability. Additionally, habitat suitability modeling not only informs about spatial distribution but can also give some insights about the species' niche (Austin *et al*. 1990) and its ecological requirements (Austin 2002).

The construction of a predictive habitat suitability model is an important step for MBSS and consequently also the choice of the modeling method. The chance of finding new populations might be increased with a most accurate model. An approach proposed by Guisan *et al*. (in press) is to improve the model in an iterative way. The study presented in this Master's Thesis is part of a larger study investigating this model-based stratified sampling approach over several years. The objective is to create a preliminary spatial distribution model from rare species' data and topo climatic variables (step 1 in Figure 1) that will be enhanced in the next steps. The first model will be verified through fieldwork and the newly obtained points will be added to the initial sample (step 2 in Figure 1). A new model will be created from this increased sample and again will be verified in the field. These steps will be repeated several times and the model fit is supposed to increase, with the increasing number of data until an equilibrium is reached. At this point, the model cannot be improved anymore with the available predictors. In simulations of the model-based sampling approach predicting rare species' presence, promising results were obtained (Guisan *et al*. in press). The simulations were run with different sample sizes and in all cases, the number of new occurrences found was significantly greater with a model-based stratified sampling design than at random. Generally, the model improved after every iteration step until an equilibrium was reached, where additional data did not improve the model anymore (Guisan *et al*. in press).

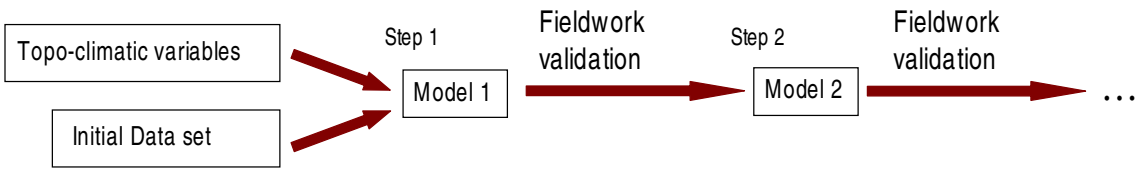


Figure 1. Figure 1 shows a simplified scheme of the global study on model based stratified sampling.

In this Master's thesis, the creation of the first model and its validation is presented. The model-based stratified sampling design aims to discover unknown populations of rare species. Four different models with different spatial scales (50m and 1km) and different techniques using presence only (ecological niche factor analysis, ENFA (Hirzel *et al*. 2002a)) or presence/absence data (generalized additive models, GAM (Hastie & Tibshirani 1986)) were combined. The larger spatial scale allowed including a greater number of presence points of the species, because not all available points had an accuracy inferior to 50m. This is especially for the rare species considerable, for which not a lot of points are available that are highly

accurate. With a larger number of points, it might be that a better adjusted model is constructed. Second, including different scales maybe allows some insights in the importance of the scale for modeling. At different scales, different sets of parameters might be important. This was the case in a study on rare plants (Wiser *et al*. 1998) where for instance solar radiation was important at 100m scale for all of the study species but not equally at a 1m scale. Moreover, it might be interesting to see if one scale fits data generally better than another one. Another point is that absence points are seldom available in databanks. It is therefore interesting to consider modeling techniques that are only based on presence points (Zaniewski *et al*. 2002) additionnaly to methods using presence and absence data. Moreover, the models are evaluated with data sets of different sample sizes to investigate wether there is an influence sample size.

The approach was tested on three rare and endangered species and additionally on five common species that served as control. Propositions are made to improve predictive distribution models of rare species.

2. Material & Methods

2.1 study area

The study area was located in the western part of Switzerland, partly covering the cantons of Vaud, Valais, Fribourg and Bern (Figure 2 a)). It is merely a mountainous region, with an elevation ranging from about 500 to about 3200 meters above sea level. It covers a surface of 2054 km² and it is part of the biogeografic regions of the Northern Alps and the Western Internal Alps. (Gonseth *et al*. 2001) The study area is included in the floristic regions of the northern Alps and Valais (Vust & Galland 2001). In the Valais, the climate is quite warm and dry, whereas in the north of the study area and in higher altitudes it is colder (Figure 2 b)). In lower altitudes of the region there are hardly any undisturbed areas left and nature has severely suffered from anthropogenic transformation at some places: At lower south faces, there are vineyards, especially in the southern part of the study area. Pastures are found more or less allover the region, sometimes even at high altitudes (Moléson and Vanil Noir). In higher altitudes, ski slopes are quite frequent. In lower region in the Valais, there is a high density of constructions, but in higher altitudes there are only some villages. However there are quite a lot of roads that make almost the whole region more or less easily accessible.

This study area was chosen because it included quite an important environmental gradient and a sufficient number of known presence points of the rare species. Moreover, a natural park project was planned in the region of the "Grand Muverans", which is partly in the cantons of Vaud and Valais. However, this project has been abandoned meanwhile.

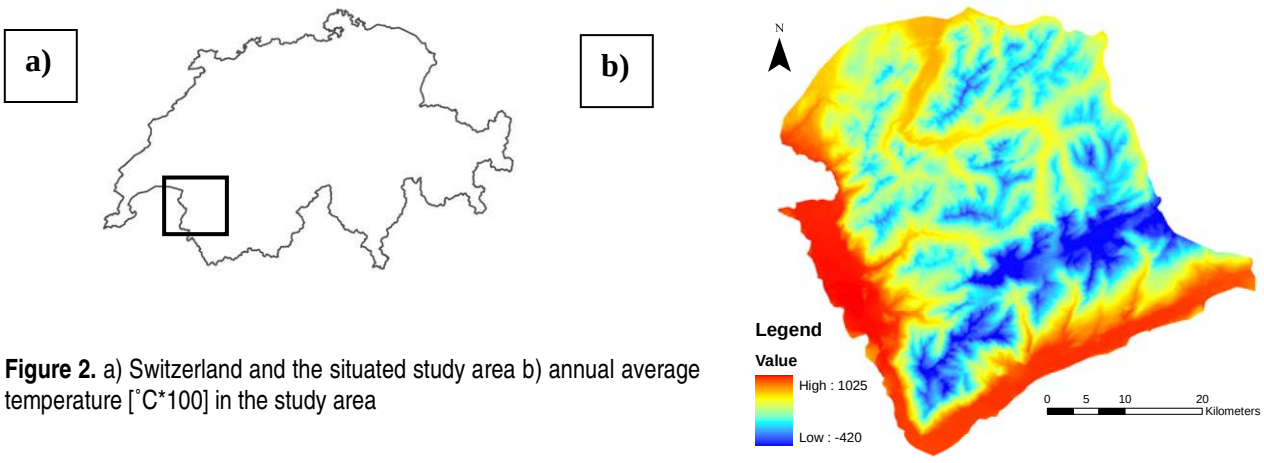


Figure 2. a) Switzerland and the situated study area b) annual average temperature [˚C*100] in the study area

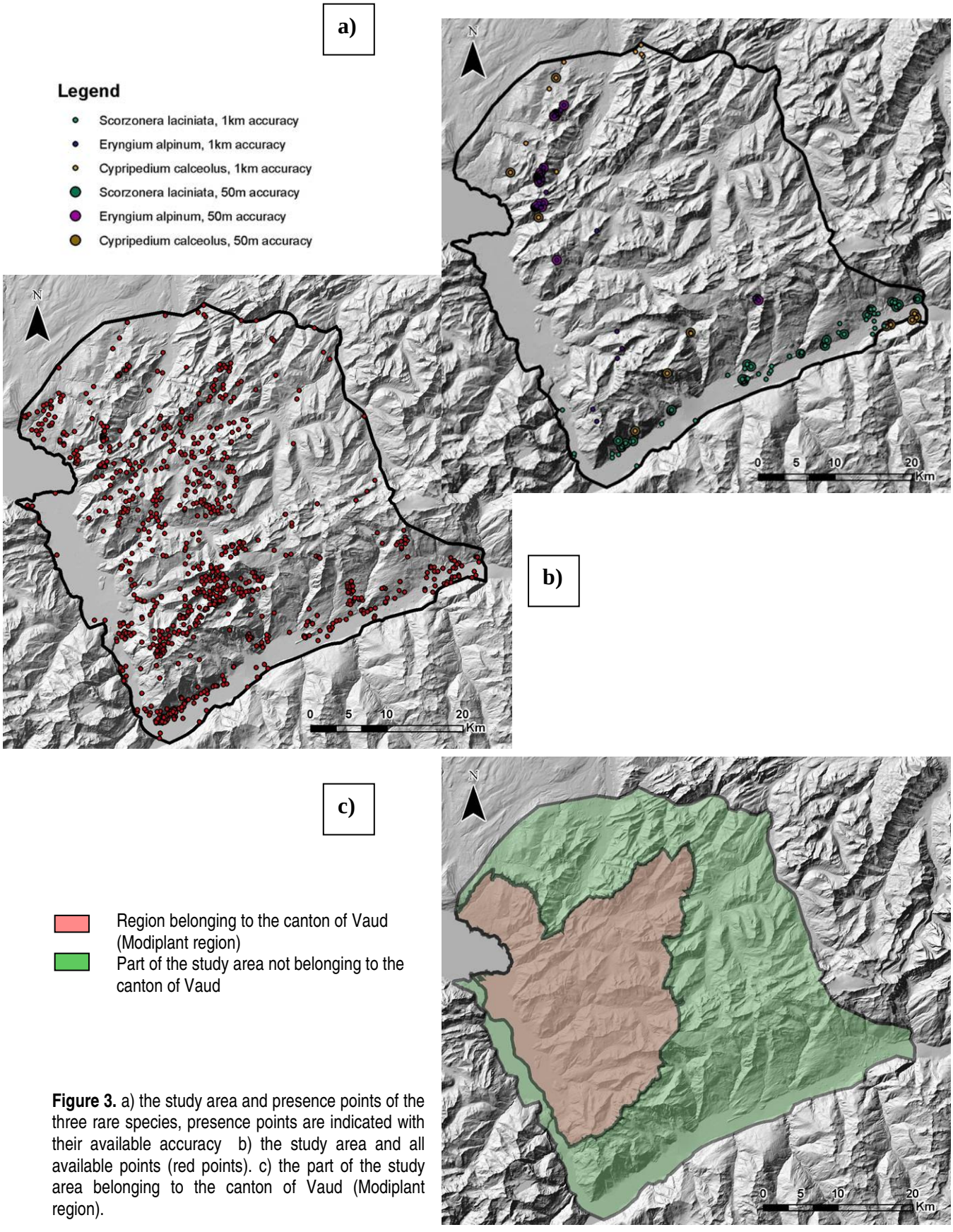


Figure 3. a) the study area and presence points of the three rare species, presence points are indicated with their available accuracy b) the study area and all available points (red points). c) the part of the study area belonging to the canton of Vaud (Modiplant region).

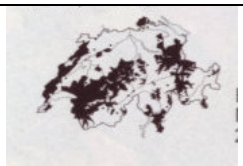
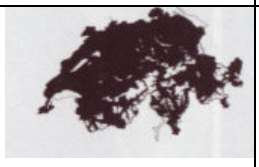
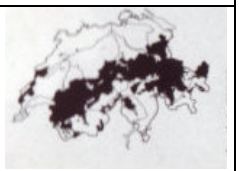
2.2 species and species data

The Swiss Floristic Network (CRSF) maintains a database with presence points of plant species in Switzerland. As they gave us data for our study area, we were able to firstly identify which rare species are present in this region and what is their abundance. Finally, the rare species are chosen after five criteria: 1. There need to be enough known presence points of the species in the study area, otherwise modeling is simply not possible. 2. The species should not be too restricted to a special biotope of the study area (like e.g. *Allium angulosum*, which is found exclusively in sump meadows). In such a case modeling cannot improve fieldwork, as the suitable areas will essentially be the biotope presence. 3. The species must not be too sporadic. For them, presences are often imprecisely known and might change regularly inside the sector of distribution. It does not appear every year and the population size fluctuates. 4. The species are supposed to have distribution that is possible to model with topo-climatic variables. 5. The species should be easily distinguishable from familiar species and not too cryptic to avoid determination error as well detection error as much as possible. The three rare and endangered species retained are *Cypripedium calceolus*, *Eryngium alpinum* and *Scorzonera laciniata* (Table 1).

For analytical purposes the study was not restricted to rare species. We hypothesized that the approach does not provide convincing results for the rare species because of their too strong rarity. In the case of no new species presences found, the methodology could not be demonstrated as useful. Five common species were therefore added and chosen after the criteria 2 – 5 of the rare species. Additionally, species were preferred that grow in about the same habitat as the rare species. These five common species serve as control for the approach. The five common species are *Anthyllis vulneraria*, *Astrantia major*, *Briza media*, *Heracleum sphondylium* and *Pulsatilla alpina* (Table 1).

Table 1. The study species and their habitats.

Rare species			
Latin name	*Cypripedium calceolus*	*Eryngium alipinum*	*Scorzonera laciniata*
Habitat type (Käsermann 1999)	Deciduous/mixed woodland, open scrub and alpine meadows	Open habitat (avalanche corridors and hayfields)	Ruderal habitat, dry meadows, vineyards
Altitudinal distribution (Käsermann 1999)	Hilly belt - subalpine 300 – 2000m	Subalpine 1400 – 2100m	Hilly belt - montane 480 – 1405m
Conditions (Käsermann 1999)	Calcareous soil	Nutrient rich and alkaline soil	Dry and sandy soil Calcareous soil
Rabinovitz Rarity Type (Broennimann *et al.* in press)	C (large range, specific to rare habitat, small populations)	A (large range, specific to rare habitat, big populations)	D (restricted range, specific to common habitat, big populations
Distribution in Switzerland (Lauber & Wager 1996)			
Global distribution (Hegi 1987)	holearctic	All over the alpine chain	From Russia to north Africa, central and southern Europe
Threats (Käsermann 1999))	-habitat distruction (forest exploitation) -picking	-picking -change in landuse, distruction and fragmentation	-successions -habitat distruction -herbicides
IUCN classification (Moser *et al.* 2002)	vulnerable	vulnerable	Near threatened
			

Common species					
Latin name	*Anthyllis vulneraria*	*Astrantia major*	*Briza media*	*Heracleum sphondylium*	*Pulsatilla alpina*
Habitat type (Lauber & Wager 1996)	Dry meadows, open forest	Mountainous meadows, clearings	meadows, oligotrophic pastures	Fat meadows, alder plantations, border of roads and forests.	meadows, oligotrophic pastures, lawn, rubble
Altitudinal distribution (Lauber & Wager 1996)	Hilly belt – montane <1600m	Montane – subalpine 700 – 2400m	Hilly belt – subalpine <2400m	Hilly belt – alpine <2400m	Subalpine- alpine 1200 – 2700m
Conditions (Hegi 1987)	Poor and calcareous soil	Sunny locations, humide soil, limestone	Sunny locations, soil fairly rich in nutriments.	Exposed locations	limestone
Distribution in Switzerland (Lauber & Wager 1996)					
					

Species data

We used data from three different databases: 1. For all of the species, **presence points** were available from the Swiss Floristic Network (CRSF) in Geneva. All the points are documented about the year of observation as well as the spatial accuracy of the point. The accuracy ranged from 25m to +/-750m. Only the points that were announced or last controlled after 1950 were used for the study. 2. From the region of the study area being in the canton of Vaud (the so-called Modiplant region), 550 non-forest vegetation plots were available. At each plot an exhaustive inventory was made in the years 2002-2004 (Randin *et al.* in press). 3. Inventory data from the project "phytoVD"(© SFFN-Vaud; regular grid sampling of one plot every 400m inside forested areas in the canton of Vaud). The points from the complete inventories were accurate because a GPS was used for locating the sites. The presence points of the rare species are shown in Figure 3 a).

The combination of these three different inventories had consequences on the spatial distribution of the data (Figure 3 b)). In particular, for the common species, presence points were almost only available for the part of the study area being in the canton of Vaud (Figure 3 c)). Common species are normally not announced to the CRSF, except if a complete inventory is made. The Prealps of the canton of Vaud have been subject to several botanical studies, whereas in the other regions exhaustive inventories are rather scarce.

Absence points as such are hardly available because people do not indicate absences to the Swiss Floristic Network. It was therefore necessary to create pseudo-absences (Zaniewski *et al*. 2002, Engler *et al*. 2004). In this study it was admitted that if a botanist discovers a rare species, he would certainly have noticed another rare species nearby and also announced its presence to the CRSF. It was therefore possible to admit that presence points of one rare species can account for absence points of another rare species. Moreover, the exhaustive inventories of Modiplant and PhytoVD (points 2 and 3) also provided reliable absences. A few absence points have also been provided by the Thesis of Dr. J. Droz (1994).

For modeling it is important to have independent data to avoid spatial autocorrelation. Spatial autocorrelation reduces the effective degrees of freedom and therefore the derived statistics are less reliable (McArdle 1990). To avoid spatial autocorrelation, presence and absence points were kept only when separated by more than 500m. This point selection also partly contributed to reduce the "spatial bias" of the points' distribution.

2.3 environmental data

The environmental variables have to describe the study area in a relevant way. They must reflect characteristical traits of the study area and be able to discriminate the niche of the species. The chosen variables are listed in the Table 2. They were chosen with respect to their estimated importance for the species. However, it must be noted that this choice was limited by the availability of variables. Some environmental factors that might be important were simply not available or not available at the right resolution.

Table 2: Environmental predictors

layer	description	units	interval	source
calcaire	Soil proportion of limestone,	-	Semi-quantitative, 6 categories	Lehmann & Ayer 2004
permeabilite	Soil permeability	-	Semi-quantitative, 5 categories	Lehmann & Ayer 2004
Gt_ch_c1	Quaternal mobile deposits	-	semi-quantitative 2 categories	Lehmann & Ayer 2004
Gt_ch_c2	Detrital rocks fines and medium	-	semi-quantitative 2 categories	Lehmann & Ayer 2004
Gt_ch_c3	limestone	-	semi-quantitative 2 categories	Lehmann & Ayer 2004
Gt_ch_c4	Fine detrital rocks (clays)	-	semi-quantitative 2 categories	Lehmann & Ayer 2004
Gt_ch_c5	Limestone magnesic and evaporites	-	semi-quantitative 2 categories	Lehmann & Ayer 2004
Srad_5to9	Mean of short wave radiations per day from May until September.	[KJ/m²/day]	[3056.25 : 29558.25]	Calculated from the DEM as the sum of direct and diffuse radiations
Slp50	slope	degrees	[0:81.5]	Derived from the DEM25
Mind_5to9	Mean monthly moisture index from May until September	[(1/10mm)/mth]	[-1195:1820.5]	Zimmermann (WSL)
topo	Topographic position (x,y) Represents the relative topographic exposition of one pixel compared to its neighbor cells	-	[-2337.5 : 1953]	Derived from the DEM25
Ndvi *	Combination of reclected red-light and near infrared light	-	[-0.557215452 : 0.759206533]	Derived from landsat ETM, Image 10/2001

*Ndvi was not included at 1km, because it was supposed to be not significant at this scale

The predictors **calcaire** and **permeabilite** derived from the Swiss geological layer. An expert indicated an index for transforming the map in a more biological interesting map that indicates proportional presence of limestone, the proportional soil permeability and structure. It is a semi-quantitative variable; six categories were defined for limestone and five for permeability. (Lehmann & Ayer 2004). Calcaire was chosen because a lot of the plants in our study prefer limestone, especially *C. calceolus* (Table 1). Soil permeability indicates water and nutrient availability. However, it must be noted that these predictors are able to distinguish global tendencies but they are maybe not precise enough for local soil characteristics.

Gt_ch_1, **Gt_ch_2**, **Gt_ch_3**, **Gt_ch_4** and **Gt_ch_5** were also derived from the Swiss geological layer. These layers describe the structure and to a certain extent the soil of a site. Soil characteristics are important for plants, because there are some types that are richer in nutriments and retain water better.

Srad_5to9 describes the quantity of solar radiations in kJ per day (Zimmermann & Kienast 1999). It is a proximal variable and has a direct influence on plant growth. Growth depends on the obtained energy.

Slp50, describing the slope, is derived from the digital elevation model and is an indirect variable. The content of water and nutriments in the soil might be inferior at steep slopes due to drainage and soil stability might be inferior at steep slopes.

Mind_5to9 is a variable with a direct influence on plants. It is obtained by subtraction of the potential average daily evapotranspiration from the mean daily precipitations (Zimmermann & Kienast 1999). Positive values indicate high water availability in the environment. Negative values are obtained when the precipitations cannot counterbalance the potential evapotranspiration which results in an environment with water deficiency. This variable is important for plants because it informs about water resources which are essential for plant growth. Sites with a negative value might be favorable for xérophilous plants.

The variable **Topo** expresses the relative position of the site compared to the local environment. The variable presents a surrogate for the characteristics micro and meso climatic and edaphic. Positive values indicate local tops that are rather exposed to wind and sun. The soil layer might be shallow, nutrient poor and rather dry. Negative values indicate hollows, where there is a better protection from wind, a soil rather deep and rich in nutrients and water accumulation. However, this variable does not distinguish between sites with a homogenous slope and flat sites. In both cases, the variable has a value close to 0 but the conditions are different at the sites.

The normalized difference vegetation index (**NDVI**; Rouse 1973, Rouse *et al*. 1974) describes the vegetation of the study area. It is derived from the landsat satellite images of October 2001. It is calculated with a relationship of two spectral bands (band 4 = near infrared and band 3 = red) that permits best to discriminate different vegetation types.

$$NDVI = \frac{(PIR - R)}{PIR + R} = \frac{band4 - band3}{band4 + band3}$$

Potential values range from -1 to +1, high values indicate high vegetative productivity and negative values indicate low vegetative productivity.

2.4 experimental design

For all plants, the same modeling scheme was applied to make the results comparable (Figure 4). The detailed steps are explained below.

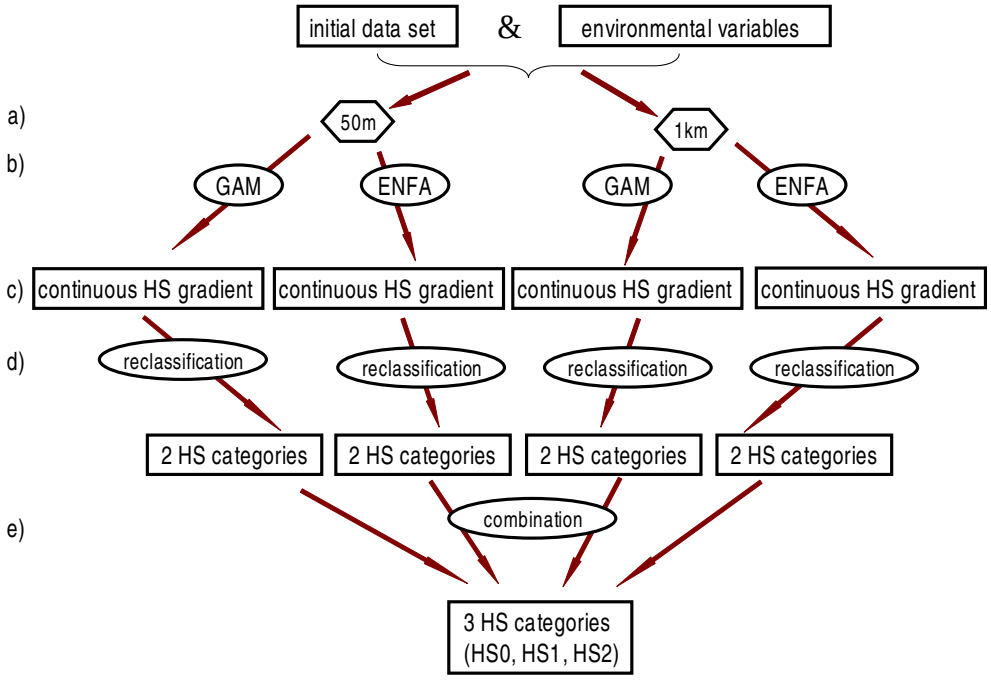


Figure 4. This figure shows the design of modeling approach that was used in this study. = maps; = methods. a) spatial scale, b) modeling method, c) continuous habitat suitability (HS) maps, d) reclassification of the continuous habitat suitability maps e) combination of the four maps. a)-e) are explained in the text.

2.4.1 preparation of data

Table 3 presents the number of presence and absence points available. It includes the points with an accuracy of at least 50m and all points that were known with an accuracy of less than 1km.

Table 3. For each of the studied species: number of presence and absence points used for the models at the two scales

Species		Presence points (50m/1km)	Absence points (50m/1km)
rare species	*Cypripedium calceolus*	14/25	553/388
	Eryngium alpinum	43/79	546/362
	Scorzonera laciniata	31/81	550/377
common species	*Anthyllis vulneraria*	199/200	2272/531
	Astrantia major	479/484	1879/338
	Briza media	206/212	2166/500
	Heracleum sphondylium	892/909	1686/1673
	Pulsatilla alpina	195/197	1817/475

At the 50m scale, presences and absences were rasterised, which means, if several points fell in one pixel, they counted only as one presence. At the 1km scale absences were always raterised except for

Heracleum sphondylium (because there were about the same number of presences and absences). Presences however were not rasterised at this scale for the GAM (Generalized additive models; more explanations in 2.4.2) to not reduce their number. At the 1km scale for the ENFA (ecological niche factor analysis; more explanations in 2.4.2), the number of presences were counted per pixel, which means that we had a quantitative response variable. The predictors were also prepared at two different scales (Figure 4. a)), 50m and 1km.

2.4.2 modeling methods (Figure 4, b))

We used two different types of modeling methods: GAMs (generalized additive models) that use presence and absence data and ENFA (ecological niche factor analysis), a presence only method.

Presence-absence models

Generalized additive models (GAM) are an extension of generalized linear models (GLM: McCullagh & Nelder (1989)), which are an extension of the classical regression of ordinary least squares. They are used when the response curve of the Y variable does not have a parametric shape (GAM: Hastie and Tibshirani (1986)). GAMs were chosen for this study because they fit generally more precisely the available data than GLMs (Lehmann *et al*. 2002a). Also, in the case of rare species we expect the predictor response curve of the species to be complex. However, GAMs are criticized to fit maybe in some cases too closely (overfitting) the data and are consequently more restrictive in suggesting new sites (Lehmann *et al*. 2002a). It is important to consider the degrees of freedom used to construct the models to avoid overfitting (i.e. number of predictors included in the model and shape response curve). This concerns especially rare species, for which only a few presences are available.

The GAMs were constructed using the GRASP library (Generalized Regression Analysis and Spatial Prediction, Lehmann *et al*. 2002b) in Splus (Insightful Corp.). This step of modeling includes a step of model validation. In fact, different models were constructed (for GAMs) and retained a different predictor set. Validation is necessary to classify models according to their accuracy and to keep only the best one.

It is important to note that regarding the number of absences (Table 3) we see that there was a bias. Absences were therefore weighted in the GAMs, in a way that the total number of presences had the same weight as the total number of absences (with GRASP). Moreover the predictors must not be

correlated. Including correlated variables in the models induces inclusion of redundant information and prevents other variables, explaining other variance, from being included in the model. A correlation matrix was created to eliminate highly correlated variables. The correlation matrix of the retained variables is in Appendix C. In general, proximate predictors having a direct influence on the species were preferred to distant predictors.

Models were selected with three different automatic stepwise selection mechanisms, AIC (Akaike Information Criterion, Akaike 1973), BIC (Bayesian Information Criterion, Schwarz 1978) and the Cross-Validation and with two different degrees of freedom for the variables (3 and 4). For all the models several indices were calculated: Kappa (Cohen 1960), weighted Kappa (Cohen 1968) and Minimal Predicted Area (MPA, Engler *et al.* 2004) at several levels. According to these criteria, the best model was kept.

Presence only methods

The ecological niche factor analysis (ENFA) (Hirzel *et al.* 2002a) compares the ecological niche of the species (though of the presence points) with the environment. Similarly to a principal component analysis, ENFA reduces the environmental variables into new, uncorrelated axes. The first factor describes the marginality of the species niche compared to the environment (study area). The following factors are called specialization factors and describe the niche breadth, the tolerance, of the species. The ENFA provided for all species a marginality and a tolerance index value. The variables used for ENFA were standardized, to uniform their values, and the radiation-variable was also transformed with a Box-Cox transformation (to normalize a sample; Sokal & Rohlf, 1981). The BIOMAPPER software (version 2·1; Hirzel *et al.* 2002b) is used for the construction of the ENFA and the derived habitat suitability maps.

2.4.3 model reclassification and combination

For each of the species, four single models were obtained: Two GAMs, one with a 50m accuracy and one with a 1km accuracy, and two ENFA with 50m and 1km precision. (Figure 4 c)). Their values ranged from 0 to 1, where 1 indicates a maximum of habitat suitability and 0 a minimum. To facilitate comparison, the obtained habitat suitability maps were reclassified using a threshold. Pixels with values above the threshold predict presences and values below absences (Figure 4 d)). The threshold for

transforming the obtained continuous models was defined separately for each of the models. The weighted Kappa (Cohen 1968) seemed to be the most adapted method to define the threshold of GAMs for transformation results into binary maps, as it is less sensitive to unequal presence/absence occurrence than the Kappa index. The weighted Kappa attributes different weights to the observations. The weight to be attributed was previously investigated with simulations (Le Lay & Engler, unpublished results). The most adapted weighting factor in our case is the ration between the observed presences and the observed absences (p. 19, WF = (a+c)/(b+d)). The threshold to create the binary map for the ENFA habitat suitability maps were defined using the graphs and methods offered by the BIOMAPPER software (In particular the continuous Boyce index, Hirzel *et al.* submitted). Biomapper offers also a visual interpretation by classifying the pixels of the zone in different habitat suitability classes. The number of presence points per class is also counted. The definition of the threshold is a trade-off by defining it as low as possible to include a maximum number of presence points and as high as possible to restrict the as favorable predicted area.

The four reclassified binary models were combined (overlayed) and resulted into three different layers (habitat suitability classes) (Figure 4 e)): The layer where all of the four models predicted absence of the species (HS0), the layer where all of the models predicted presence of the species (HS2) and, finally, the layer where at least one but not all of the models predicted presence (HS1). A mask was applied to the model to eliminate the zones were the species are surely not present. This concerns the zones of towns and villages as well as lakes, rivers and glaciers.

2.4.4 Preparing fieldwork: random stratified sampling

We applied a random stratified sampling to validate the models. In each layer (HS0, HS1, HS2), 20 points were selected randomly. Of these 20 points, only 10 were verified in the field. To avoid spatial correlation, these 10 points were chosen if possible to be distributed over the whole zone and at a distance of at least 500m. Finally, there are for each species a total of 30 sample points controlled, ten in each layer (HS0, HS1, HS2). To combine the different habitat suitability maps and select the points, ArcGIS software (ESRI Inc., Redlands, CA, USA) was used.

2.4.5 Fieldwork

Fieldwork took place from May until the beginning of November 2005. Species were sampled, if possible, during the flowering season to exclude determination and detection error as much as possible. At every sample point, the same scheme was applied. Instead of searching exactly at the site of the randomly selected point, the point was placed in a natural area (i.e. really reflecting topo-climatic characteristics and not the influence of human activities) supposed to be typically for the species and above all a natural area because we wanted to validate a topopclimatic model i.e. reducing the effect of human impact. Exceptionally, we went up to about 200m away from the selected point if necessary. Presence or absence for every study species was determined in a 50m². Additionally, if one of the species was seen on the way, between two sampling points, the coordinates were taken as well. It is to note that the sampling method of the single models is in this study not independent. The sampling of one single model is dependant on the other three models of the species.

2.5. evaluation methods

Three different levels were defined for model evaluation: 1) the 30 points sampled specifically for the species, based on the species' model 2) all the points sampled for all of the species (about 250) and 3) all of the available points (i.e. all points of level two, all presence points made where the species was seen randomly and presence and absence points of other people doing fieldwork this summer in this region and that were following the method of searching in a 50m²). The points at this third level were converted into 50m and 1km maps. Consequently, if there are several points in one pixel they count only as one. When there were presence and absence points in one pixel, the pixel counted as presence. In the second layer, there were also about 20 points with a distance less than 1km from the next point, but anyway all the points were kept for evaluation. The evaluation with this three levels permits to see if the number of points, intensity of search, has an influence on the models' evaluation result. Second, the search method is different at the three levels. At the first level, the quality of the points is superior to the second and the third. With quality I mean that the points are adapted for one species and they respect the experimental design, i.e. an equal number of sample points in each layer. One can ask if it is more efficient to focus on quality or quantity of the points. However, at the second level, the collected data are not completely independent because they depend on the models of the other species. For *Scorzonera laciniata*, the number of collected

points in different habitat suitability classes was therefore visually compared to the number of pixels of the study area in the different habitat suitability classes for the ENFA models. All evaluation procedures were preformed in the R software (R 2.00; A Language for Data Analysis and Graphics © 2004).

Evaluation of reclassified models

The reclassified models were evaluated using the **Kappa index** (Cohen 1960) and the **weighted Kappa index** (Cohen 1968) from the contingency table. The weighted Kappa was obtained by equalizing the number of presence and absence predictions. This seems more adequate in this situation where we want about the same search effort in both layers. It would not be objective to say that there are more presences rightly predicted only because there were more points sampled in the as presence predicted areas for example. Each model was separately valued at all of the three levels. The combination of models was valued by using solely the layers HS0 and HS2.

Contingency table:

		observed	
		1	0
predicted	1	a	b
	0	c	d

Kappa = $\kappa = \frac{2 \cdot ((a \cdot d) - (b \cdot c))}{((a+b) \cdot (b+d) + (c+d) \cdot (a+c))}$

weighting factor = $WF = \frac{(c+d)}{(a+b)}$

weighted Kappa = $weighted\kappa = \frac{2 \cdot ((WF \cdot a \cdot d) - (WF \cdot b \cdot c))}{((WF \cdot a + WF \cdot b) \cdot (WF \cdot b + d) + (c+d) \cdot (WF \cdot a + c))}$

Evaluation of continuous models

For the evaluation of the continuous models, the **AUC** "area under the curve" and the **Gini coefficient** (Copas 1999) were calculated. They take into account the values of sensitivity and the specificity of the models calculated each time after changing in steps of 0.05 the cut-off point for reclassification into a binary presence-absence map. It is visualized with the ROC-plot (Receiver Operating Characteristic, Fielding & Bell 1997), where sensitivity (true positives) is plotted against [1- specificity]

(proportion of false positives). By computing the area under the curve thus defined, a value ranging from 0.5 to 1 is obtained. The AUC is equal to 1 if the model is discriminating perfectly presence and absence and close to 0.5 if the model predictions do not differ significantly from random predictions. We transform the AUC value in the Gini Coefficient. The advantage of the Gini Coefficient is that the scale is between 0 and 1 which allows an easier interpretation and comparison with other coefficients. Only the single models are evaluated with the AUC. It is not possible to evaluate the combination of the models in this way.

Gini Coefficient = AUC' = $2 \cdot (AUC - 0.5)$

Comparison of the model predictions

The Kappa coefficient was calculated between the predictions of the GAM and ENFA at the same scale. This enabled the estimation of the difference of prediction between the two maps. It was calculated using ArcGIS software (ESRI Inc., Redlands, CA, USA) to transform the grid maps into IDRISI layers and IDRISI software (Eastman 1997) to provide the contingency table.

2.6 spatial quality of the predictions for the common species

In Figure 3 b) it is visible that most of the known points are in the part of the study area belonging to the canton of Vaud (Modiplant region, Figure 3 c)). Consequently, the resulting models are supposed to be better adjusted to this zone than to the other regions of the study area. This concerns the absence points, but especially also the data available for the five common species. The models of the common species were therefore somehow extrapolated in the rest of the zone. To see whether there was a difference between the predictions in the two sub-regions (Modiplant and no Modiplant region), the Kappa and weighted Kappa coefficient were calculated as well as the AUC and the AUC' for the continuous models seperately for the two different regions. The data of the third level were used for this comparison. A paired t.test was performed when the data was normally distributed, otherwise the non parametric Wilcoxon test for paired data, to see if the difference between the two zones is significant.

3. Results

3.1. initial models

A) *patterns of spatial predictions*

Figure 5a and 5b show the reclassified single models for the rare species *Scorzonera laciniata* and the common species *Briza media*. The predicted absence zone was larger for the rare species than for the common species. In Table 3 the percentage of presence and absence zones predicted by the models is listed. For *B. media* the models predict about 50% of the study area as presences. For *S. laciniata*, only 5-15% of the zone was predicted as presence.

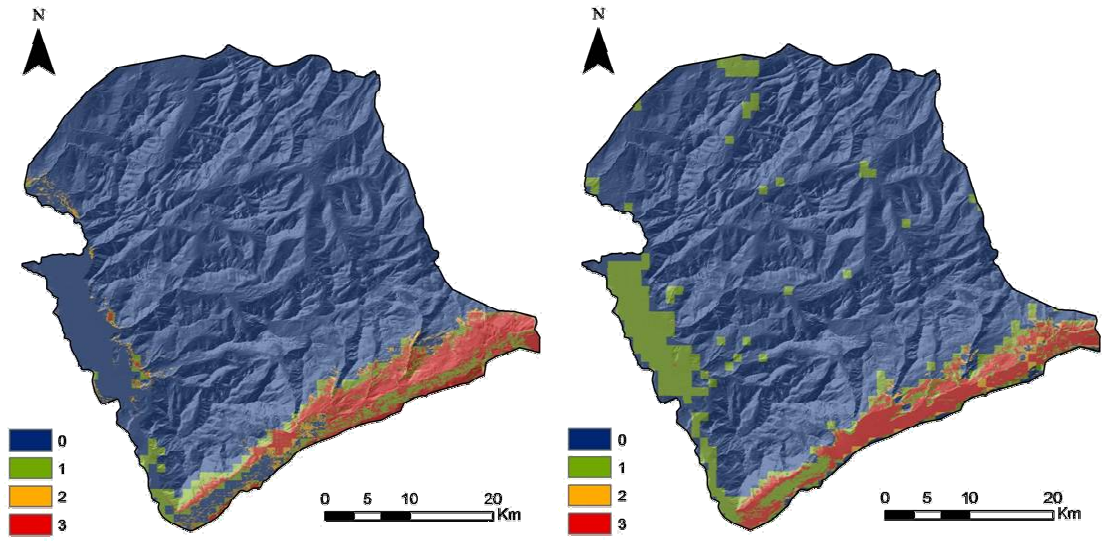


Figure 5a. Single reclassified models for *S. laciniata*. Gam on the left, Enfa on the right. 0 = both models predict absence; 1 = the model at 1km resolution predicts presences and the model at 50m resolution absence; 2 = the model at 1km resolution predicts absence and the model at 50m resolution presence; 3 = both models predict presence. White zones = mask (glaciers, rivers, lakes, urban areas).

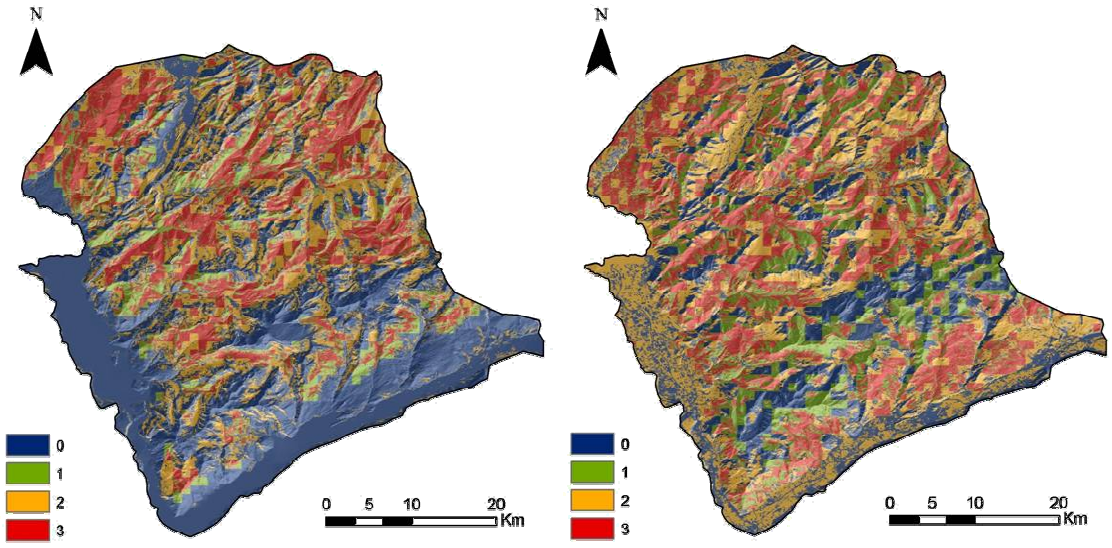


Figure 5b. Single reclassified models for *B. media*. Gam on the left, ENFA on the right**.** 0 = both models predict absence; 1 = the model at 1km resolution predicts presences and the model at 50m resolution absence; 2 = the model at 1km resolution predicts absence and the model at 50m resolution presence; 3 = both models predict presence. White zones = mask (glaciers, rivers, lakes, urban areas).

Table 3. Relative surface of the predicted presence and absence zones in the study area. 0 = absence; 1 = presence**.** Reclassification threshold based on the weighted Kappa.

Cypripedium calceolus	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
0	0.78	0.78	0.71	0.67
1	0.22	0.22	0.29	0.33

Eryngium alpinum	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
0	0.92	0.81	0.85	0.87
1	0.08	0.19	0.15	0.13

Scorzonera laciniata	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
0	0.93	0.90	0.95	0.85
1	0.07	0.10	0.05	0.15

Briza media	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
0	0.56	0.65	0.46	0.52
1	0.44	0.35	0.54	0.48

Combined models

Figure 6 shows the combined models. The zone HS0, where all models predict absence, was much larger for the three rare species than for the five common species.

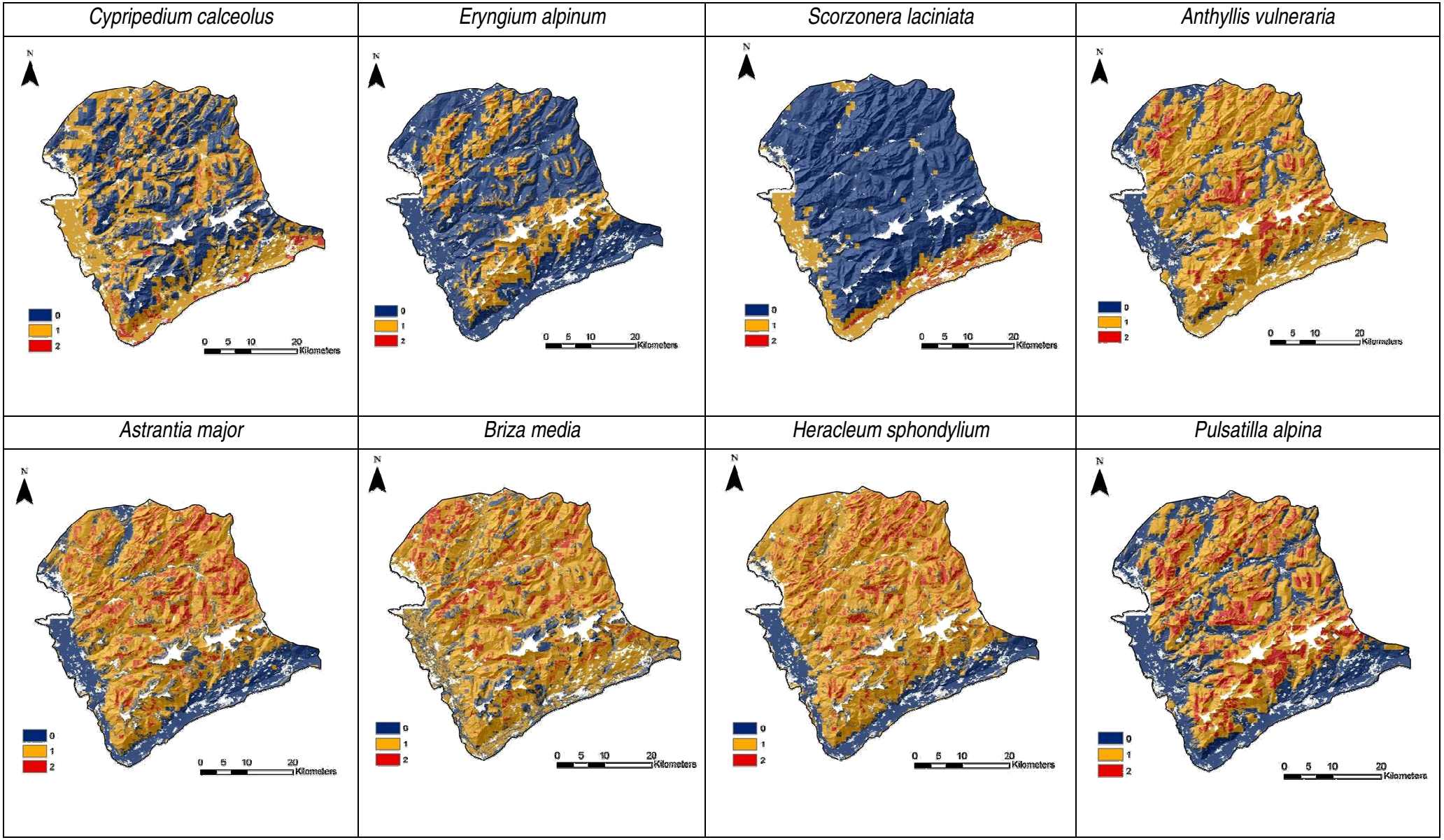


Figure 6. The combined models of all species with three habitat suitability classes. 0 = HS0; 1 = HS1; 2 = HS2 (in 2.4.3).

For the combined models, the three categories HS0, HS1 and HS2 had a different relative importance. Figure 7 shows the percentage of the study area for the three categories HS0, HS1 and HS2. The highly suitable surface (HS2) was larger for the common than for the rare species. The surface with fairly suitable habitat (HS1) was in general very large. The surface HS1 was larger for the common species than the rare species, too, except for *Pulsatilla alpina*. The non suitable surface (HS0) was larger for the rare species. The relationship HS2:HS1 is greatest for Scorzonera laciniata (3/15), but lowest for *Cypripedium calceolus* and *Eryngium alpinum*.

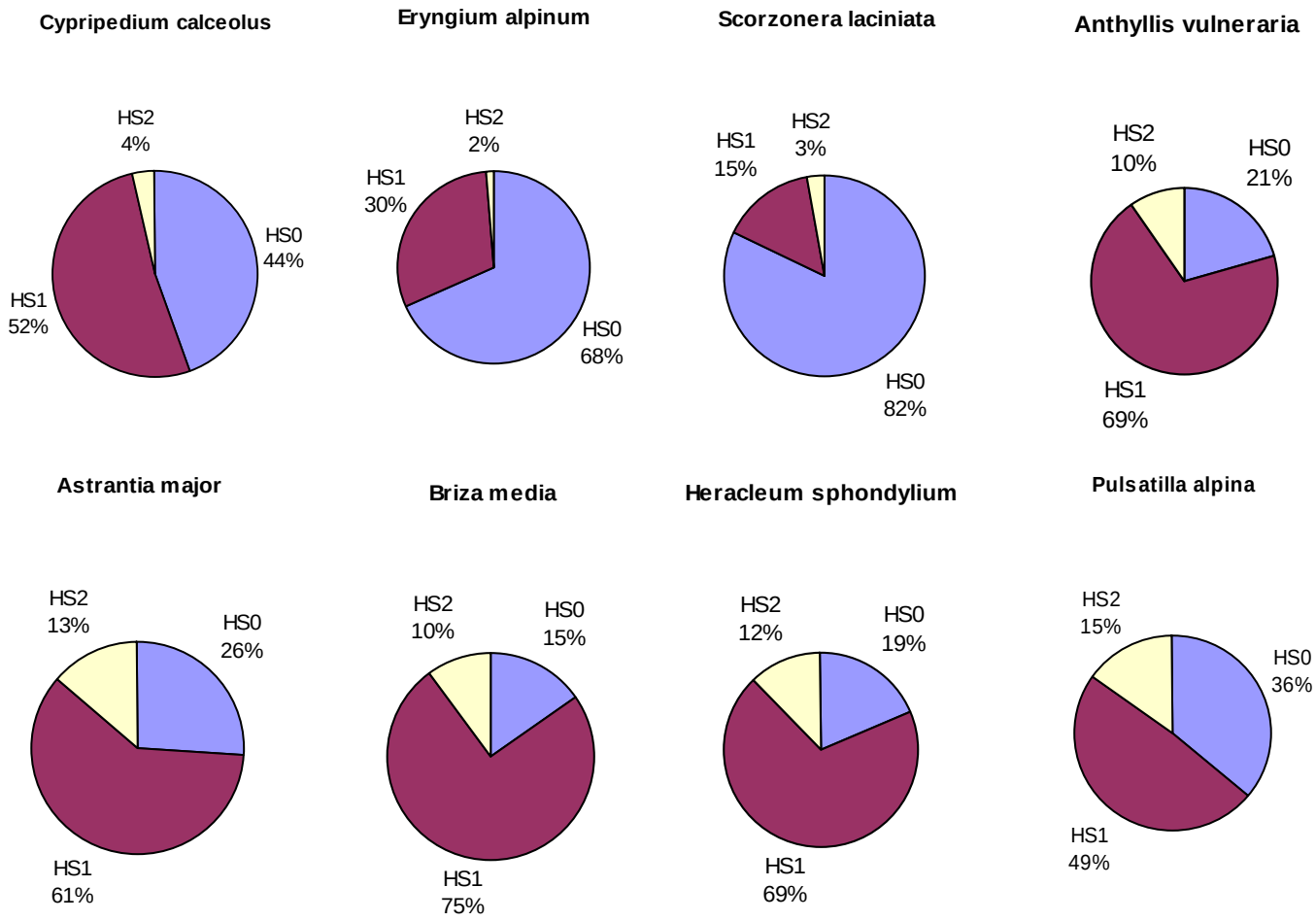


Figure 7. Model predictions of the combined models for all species. Percentage of the study area predicted as HS0, HS1 and HS2.

The Kappa index values were calculated between two model predictions, with GAM and ENFA, at the same scale. Table 4 lists the results. The model predictions with the two different modeling methods were very different for *Anthyllis vulneraria*. There was not a lot of correspondence between the different

model predictions of *Briza media* and *Heracleum sphondylium*, either. *Scorzonera lacinata* and *Pulsatilla alpina* had the most corresponding model predictions.

Table 4. Comparison of model predictions at the same scale with the Kappa index.

	Kappa GAM 50m-ENFA 50m	Kappa GAM 1km-ENFA 1km
Cypripedium calceolus	0.34	0.36
Eryngium alpinum	0.22	0.45
Scorzonera laciniata	0.55	0.50
Anthyllis vulneraria	0.07	0.09
Astrantia major	0.25	0.42
Briza media	0.13	0.25
Heracleum sphondylium	0.17	0.30
Pulsatilla alpina	0.47	0.43

B) *Ecological niche characteristics*

Different predictors were important for the different species. In Table 5, the important variables for the rare species are listened. The climatic variables were generally more important than the geological variables.

Table 5. Environmental predictors explaining the larger part of variance of distributions in our study area. For the GAM, the table shows all the retained predictors and for the ENFA, the most important predictors were selected. The predictors are explained in 2.3, Table 1. Mind = mind_5to9; Slp = slp 50; srad = srad_5to9; Perm = permeabilité; Calc = Calcaire; Gt_c1 = Gt_ch_c1; Gt_c2 = Gt_ch_c2; Gt_c3 = Gt_ch_c3; Gt_c4 = Gt_ch_c4; Gt_c5 = Gt_ch_c5;

Cypripedium calceolus

a)	**Mind**	**Slp**	**Srad**	**Topo**	**Perm**	**Calc**	**ndvi**	**Gt_c1**	**Gt_c2**	**Gt_c3**	**Gt_c4**	**Gt_c5**
GAM 50m	X	X			X							
GAM 1km	X	X	X			X			X			X
ENFA 50m		X		X	X	X						
ENFA 1km						X		X		X		

Eryngium alpinum

	Mind	**Slp**	**Srad**	**Topo**	**Perm**	**Calc**	**ndvi**	**Gt_c1**	**Gt_c2**	**Gt_c3**	**Gt_c4**	**Gt_c5**
GAM 50m	X				X	X	X					
GAM 1km	X	X	X		X				X			
ENFA 50m	X		X	X			X					
ENFA 1km	X	X			X							X

Scorzonera laciniata

	Mind	Slp	Srad	Topo	Perm	Calc	ndvi	Gt_c1	Gt_c2	Gt_c3	Gt_c4	Gt_c5
GAM 50m	X	X			X		X					
GAM 1km	X	X				X						
ENFA 50m	X		X	X								
ENFA 1km	X		X			X				X		X

Cypripedium calceolus: In the GAMs, the moisture index and slope were retained at both scales. The predictor slope was included in all models except the ENFA at 1km. Calcaire was retained in all models except the GAM at 50m. Permeability was retained in both models at a 50m scale. Topography was only retained in the ENFA at 50m but explained quite a lot of variance in this model.

Eryngium alpinum: The moisture index was retained in all four models. Slope was only important at 1km and the ndvi at 50m. Permeability was important in all models except the ENFA at 50m scale. Radiation was important for the GAM 1km and the ENFA 50m.

Scorzonera laciniata: Moisture index seem to be important and was retained in all four models. Limestone was important at 1km scale. Radiation was retained in the ENFA models and slope only in the GAM models.

The ENFA provided marginality and tolerance factors at both scales for all species (Table 6). At both scales, marginality was superior for the rare species to the common species. On the other hand, tolerance was inferior for the rare species to the common species.

Table 6: marginality and tolerance factors (from the ENFA)

Species	Marginality 50m	Tolerance 50m	Marginality 1km	Tolerance 1km
Cypripedium calceolus	0.695	0.21	0.8	0.295
Eryngium alpinum	0.954	0.253	1.041	0.212
Scorzonera laciniata	1.272	0.339	1.291	0.504
Anthyllis vulneraria	0.404	0.872	0.542	0.344
Astrantia major	0.222	0.644	0.324	0.597
Briza media	0.324	0.683	0.274	0.694
Heracleum sphondylium	0.229	0.745	0.233	0.758
Pulsatilla alpina	0.654	0.655	0.759	0.547

3.2. model evaluation

For all species, 30 points were sampled, 10 in each layer (HS0, HS1, HS2). Figure 8 shows the distribution of all sample points.

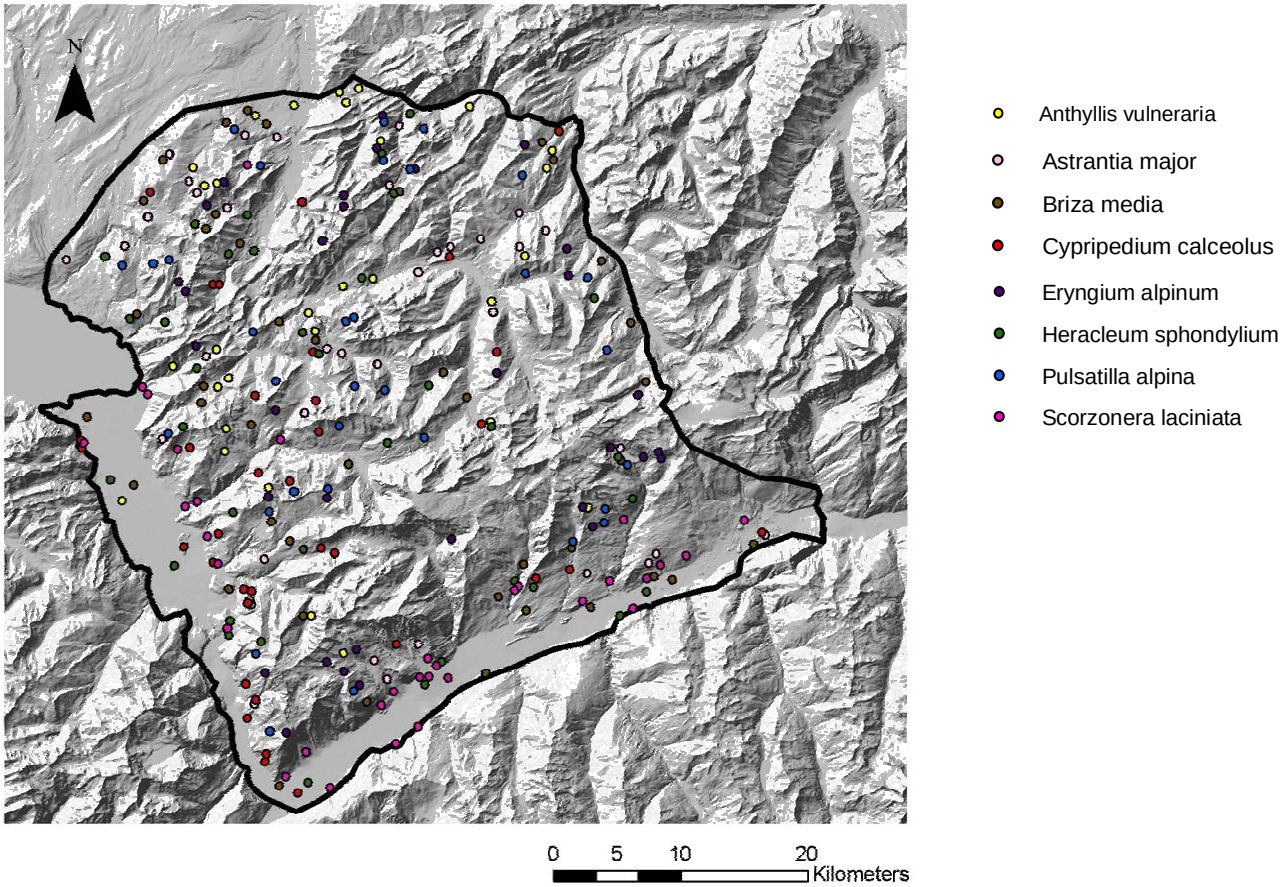
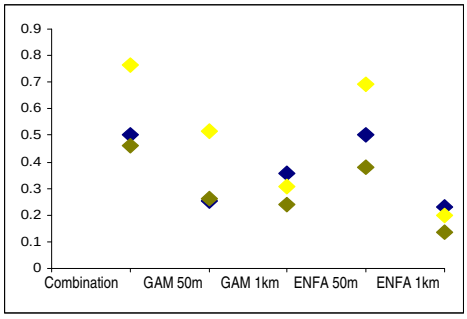


Figure 8. The study area and the 30 sample points of all species.

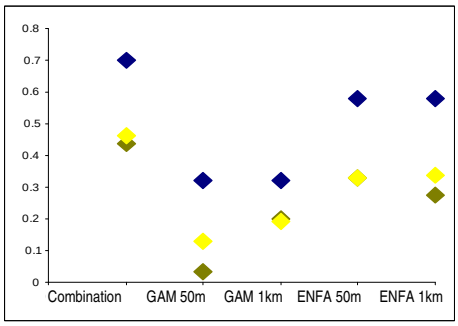
Eight new presence sites of *Scorzonera laciniata* were found. For *Eryngium. alpinum* and *Cypripedium calceolus*, however, no new populations were discovered. The coefficients that were used in this study are equal to 0 when there are no presences for evaluation. Graphs are therefore not shown for *E. alpinum* and *C. calceolus*. Evaluation at all three levels show that the combination of the models always performed better than the single models at all levels with the Kappa and the weighted Kappa and for all species, except *E. alpinum* and *C. calceolus*. Figure 9 shows the evaluation results for *S. laciniata*, *Anthyllis vulneraria* and *Pulsatilla alpina*. The complete evaluation results are listed in Appendix A.

Kappa

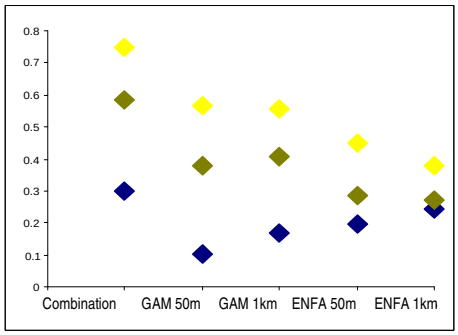
Scorzonera laciniata



Anthyllis vulneraria

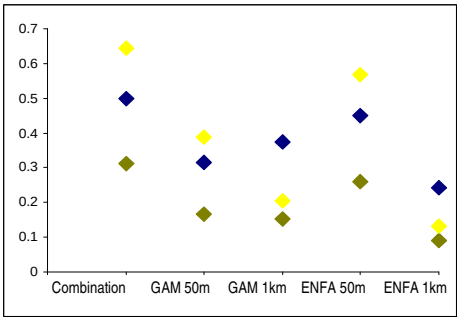


Pulsatilla alpina

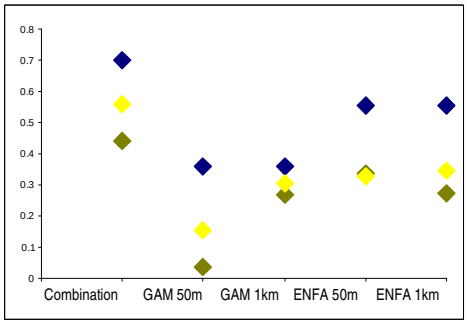


Weighted Kappa

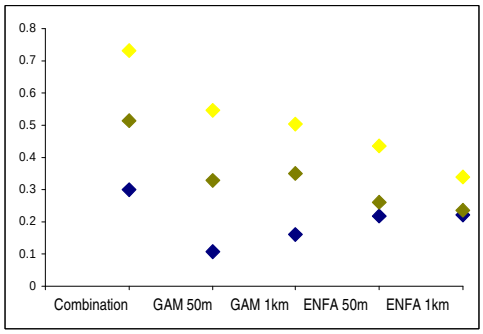
Scorzonera laciniata



Anthyllis vulneraria

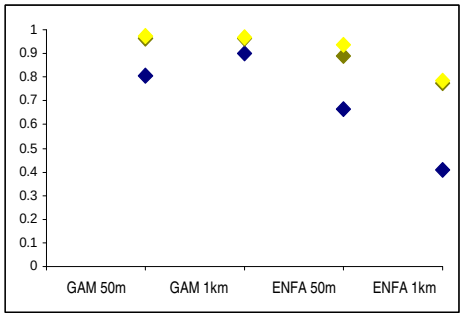


Pulsatilla alpina

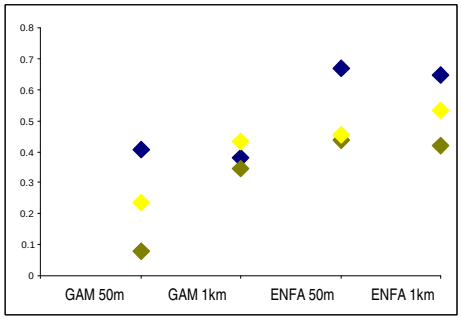


AUC'

Scorzonera laciniata



Anthyllis vulneraria



Pulsatilla alpina

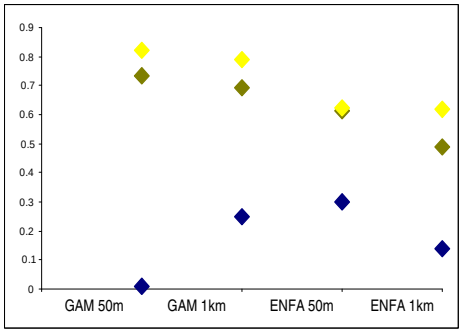


Figure 9: Graphs of the Kappa, the weighted Kappa and the AUC' for all models of 3 species. Kappa and weighted Kappa: 1 = combination; 2 = GAM 50m; 3= GAM 1km; 4 = ENFA 50m; 5 = ENFA 1km. AUC': 1 = GAM 50m; 2= GAM 1km; 3 = ENFA 50m; 4 = ENFA 1km. Level 1 = blue; level 2 = light green; level 3 = yellow.

To visualize the results for the single models, a model ranking was made. It was made separately for each level and for each evaluation index. Table 7 contains the result.

Table 7. model ranking for all species.

		best model	2nd model	3rd model	4th model
Scorzonera laciniata					
level 1	Kappa	ENFA 50m	GAM 1km	GAM 50m	ENFA 1km
level 1	Wkappa	ENFA 50m	GAM 1km	GAM 50m	ENFA 1km
level 1	AUC	GAM 1km	GAM 50m	ENFA 50m	ENFA 1km
level 2	Kappa	ENFA 50m	GAM 50m	GAM 1km	ENFA 1km
level 2	Wkappa	ENFA 50m	GAM 50m	GAM 1km	ENFA 1km
level 2	AUC	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
level 3	Kappa	ENFA 50m	GAM 50m	GAM 1km	ENFA 1km
level 3	Wkappa	ENFA 50m	GAM 50m	GAM 1km	ENFA 1km
level 3	AUC	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km

		best model	2nd model	3rd model	4th model
Anthyllis vulneraria					
level 1	Kappa	ENFA	ENFA	GAM	GAM
level 1	Wkappa	ENFA	ENFA	GAM	GAM
level 1	AUC	ENFA 50m	ENFA 1km	GAM 50m	GAM 1km
level 2	Kappa	ENFA 50m	ENFA 1km	GAM 1km	GAM 50m
level 2	Wkappa	ENFA 50m	ENFA 1km	GAM 1km	GAM 50m
level 2	AUC	ENFA 50m	ENFA 1km	GAM 1km	GAM 50m
level 3	Kappa	ENFA 1km	ENFA 50m	GAM 1km	GAM 50m
level 3	Wkappa	ENFA 1km	ENFA 50m	GAM 1km	GAM 50m
level 3	AUC	ENFA 1km	ENFA 50m	GAM 1km	GAM 50m

		best model	2nd model	3rd model	4th model
Astrantia major					
level 1	Kappa	GAM 50m	ENFA 1km	GAM 1km	ENFA 50m
level 1	Wkappa	GAM 50m	ENFA 1km	GAM 1km	ENFA 50m
level 1	AUC	GAM 50m	GAM 1km	ENFA 1km	ENFA 50m
level 2	Kappa	GAM 1km	GAM 50m	ENFA 50m	ENFA 1km
level 2	Wkappa	GAM 1km	ENFA 50m	GAM 50m	ENFA 1km
level 2	AUC	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m
level 3	Kappa	GAM 1km	GAM 50m	ENFA 50m	ENFA 1km
level 3	Wkappa	GAM 1km	GAM 50m	ENFA 50m	ENFA 1km
level 3	AUC	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m

		best model	2nd model	3rd model	4th model
Briza media					
level 1	Kappa	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m
level 1	Wkappa	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m
level 1	AUC	GAM 1km	GAM 50m	ENFA 50m	ENFA 1km
level 2	Kappa	GAM 50m	GAM 1km	ENFA 1km	ENFA 50m
level 2	Wkappa	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
level 2	AUC	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m
level 3	Kappa	GAM 50m	GAM 1km	ENFA 1km	ENFA 50m
level 3	Wkappa	GAM 50m	GAM 1km	ENFA 1km	ENFA 50m
level 3	AUC	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m

		best model	2nd model	3rd model	4th model
Heracleum sphondylium					
level 1	Kappa	ENFA 50m	ENFA 1km	GAM 50m	GAM 1km
level 1	Wkappa	ENFA 50m	ENFA 1km	GAM 50m	GAM 1km
level 1	AUC	ENFA 50m	GAM 1km	ENFA 1km	GAM 50m
level 2	Kappa	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m
level 2	Wkappa	GAM 1km	GAM 50m	ENFA 1km	ENFA 50m
level 2	AUC	GAM 1km	ENFA 1km	GAM 50m	ENFA 50m
level 3	Kappa	ENFA 1km	GAM 1km	ENFA 50m	GAM 50m
level 3	Wkappa	ENFA 1km	GAM 1km	ENFA 50m	GAM 50m
level 3	AUC	ENFA 1km	GAM 1km	ENFA 50m	GAM 50m

		best model	2nd model	3rd model	4th model
Pulsatilla alpina					
level 1	Kappa	ENFA 1km	ENFA 50m	GAM 1km	GAM 50m
level 1	Wkappa	ENFA 1km	ENFA 50m	GAM 1km	GAM 50m
level 1	AUC	ENFA 50m	GAM 1km	ENFA 1km	GAM 50m
level 2	Kappa	GAM 1km	GAM 50m	ENFA 50m	ENFA 1km
level 2	Wkappa	GAM 1km	GAM 50m	ENFA 50m	ENFA 1km
level 2	AUC	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
level 3	Kappa	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
level 3	Wkappa	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km
level 3	AUC	GAM 50m	GAM 1km	ENFA 50m	ENFA 1km

Best model = model that had the highest value with the respective evaluation index;
2nd model = model that had the second highest value with the respective evaluation index;
3rd model = model that had the third highest value with the respective evaluation index
4th model = model that had the lowest value with the respective evaluation index

Level 1 = 30 points
Level 2 = ~ 250 points
Level 3 = ~ 500 points

Comparison of the three levels (level 1 = 30 points, level 2 = ~250 points, level 3 = ~500 points)

For *Scorzonera laciniata*, the GAM 50m performed better at the second and the third level than GAM 1km, but not at the first level. *Anthyllis vulneraria* has the inverse trend than *S. lacinata*. At the first and the second layer, ENFA 50m was better than ENFA 1km, but not at the third level for *A. vulneraria*. Concerning *Astrantia major*, it shows no difference between the second and the third level except one change for the weighted Kappa, but the first level was quite different. The same is the case for *Briza media*. *Heracleum sphondylium* showed at all three levels different rankings. Also for *Pulsatilla alpina*, the second and third level evaluations were more similar compared to the first level.

Comparison of the different spatial scales (50m resolution vs. 1km resolution)

There is no global trend identifiable whether one resolution performs better than the other. Concerning *Scorzonera laciniata*, the models at a 50m scale is better when the same modeling method is used. The same is the case for *Pulsatilla alpina* at the second and third level. For *Heracleum sphondylium*, except at the first level, models at 1km scale performed better.

Comparison between modeling methods (GAM – ENFA)

There are different results depending on the species. For *Anthyllis vulneraria*, ENFA models always performed better than GAMs. For *Briza media*, GAMs always performed better than ENFA. For *Pulsatilla alpina*, GAMs performed better than ENFA except at the first scale. For *Heracleum sphondylium*, ENFA models performed better than GAMs at the third level, where as at the second level, GAMs performed better.

Comparison of the different evaluation methods (Kappa – weighted Kappa – AUC)

The Kappa index values and the weighted Kappa index values ranked the models in the same way, except in three cases: At level 2 for *A. major* and *B. media*. The AUC ranked the models in a different way than the Kappa indices in some cases.

Graphics of the number of sample points per strata

In the example of *Scorzonera laciniata* the points at the second and the third level seem to be more or less distributed in the same way like the number of pixels of the zone in each HS class (Figure 10).

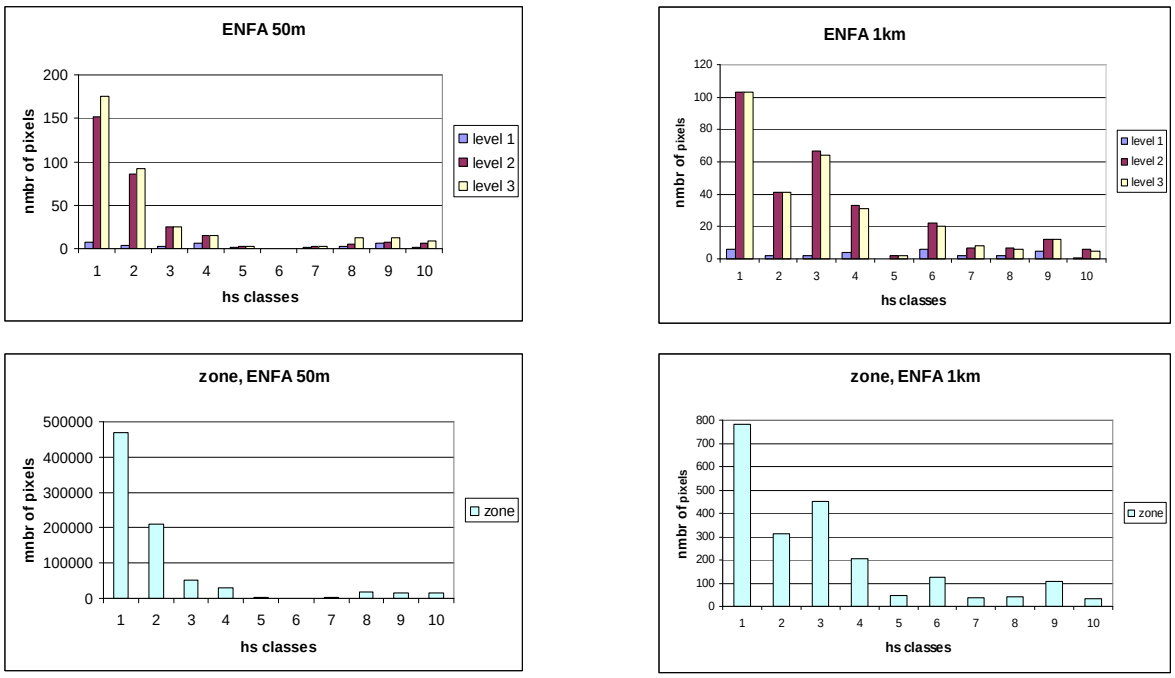


Figure 10. The number of pixels sampled per habitat suitability class for *S. laciniata* and the number of pixels of the zone (= study area) in each habitat suitability class of the ENFA at 50m precision and 1km precision. 1 = 0-10; 2 = 10-20; 3 = 20–30; 4 = 30–40; 5 = 40–50; 6 = 50–60; 7 = 60–70; 8 = 70–80; 9 = 80-90; 10 = 90–100.

3.3. results of the spatial quality of the predictions for the common species

The average Kappa index over all models for all five species is greater for the Modiplant region than for the rest of the zone, although not significantly (t.test: p-value = 0.19). The average weighted Kappa index over all models for all five species is greater for the Modiplant region than for the rest of the zone, too, but not significantly greater either (t.test: p-value = 0.14). Concerning the AUC and AUC' evaluations, the average values of all models and all species are nearly the same in both regions and even slightly greater for the "extrapolated" predictions. When regarding each species separately, it is observable that for *Pulsatilla alpina* and *Anthyllis vulneraria* spatial bias in data has an effect for all modeling methods except ENFA 1km of *A. vulneraria*. For *Heracleum sphondylium*, *Briza media* and *Astrantia major*, spatial bias had not a negative effect. The complete results are listed in Appendix B.

4. Discussion

4.1. initial models

A) *patterns of spatial predictions*

Two cases are to be discussed: 1) the predictions of the single models and 2) the predictions of the final combined models.

1) For all the rare species, the reclassified single models present absences zones far larger to the predicted presences zones (Figure 5, Table 3). For *Scorzonera laciniata*, predicted presence zones range from 5%(ENFA 50m) - 15%(ENFA 1km) of the study area, 22 - 33 % for *Cypripedium calceolus* and 8 – 19% for *Eryngium alpinum* (Table 3). In comparison, common species have more equitable areas, models for *B. media* predict up to 54 % of the study area as presence (ENFA 50m) (Table 3). This means that, in the study area, fewer sites fit the characteristics of the sites where the rare species were observed than for the common species. Common species have either a larger realized niche or are specialized for a common habitat type in the study area.

2) Similarly, for the combined models, the zone HS2, where all four models predict species' presence, is much smaller for the rare species than for the common species (Figure 6). HS2 covers 2-4% of the study area for the rare species and 10-15% for the common species. Combining models lead thus to a reduction of the predicted high suitable area. The size of the HS1 layer can be seen as surrogate for correspondence among the models, because HS1 is the area where the models predict differently. The HS1 layer encompasses 52% of the study area for *C. calceolus*, 30% for *E. alpinum* and 15% for *S. laciniata*, but for the common species it ranges from 49% to 75% (Figure 7). However, it is not distinguishable from this layer if there is only one single model that does not correspond with the other three or if they are all four slightly different. It seems that the models for the rare species globally correspond better than the models of the common species, especially for *S. laciniata*. The comparisons with the Kappa index of the two models at the same scale show that the models of the rare species indeed have a higher value (Table 4). Also the models of *Pulsatilla alpina* correspond quite well. Nevertheless, for the rare species, most of the zone is predicted as absence in all models, which results in a large zone HS0. As the Kappa index is sensitive to prevalence of the evaluated classes the large predicted absence areas may influence the results. When we look at the relationships between the HS2 and HS1, it appears that *S. laciniata* and *P. alpina* have the best

relationship (i.e. the smallest HS1 compared to HS2). *C. calceolus* and *E. alpinum* actually have the largest HS1 zones compared to their HS2 zones (Figure 7), which means that the in predicted presence zones of various models do not match well. The predicted presence zones are the most important parameter in our approach, as our aim is to find new locations of rare species. In cases of mismatch models, one interpretation might be that the models have fitted different parts of the species' niche, as shown by the different variable sets retained in the models. In this case, combining models is a good method for improving predictive power. Otherwise, if differences mostly come from differences between GAM and ENFA results, interpretation has to be found in presence/absence vs. presence only modeling. If presences are not located in sites not highly contrasted from the global environment (here described by its topo-climatic characteristics), the ENFA might have difficulties in separating suitable habitats from unsuitable areas. The more one species distribution is easily discriminated with the variables used, the more the models are supposed to converge.

B) *Ecological niche characteristics*

The environmental predictors retained in the models vary according to the scales and the modeling methods used. For the ENFA models, there are more variables retained but only the most important ones will be discussed. On the base of the correlations they highlight, the results help in describing the functional relationships between a species and its environment (Austin *et al*. 1990). This information might be helpful for understanding and improving modeling of rare species.

Cypripedium calceolus: In the GAMs, the moisture index and slope were retained at both scales. In literature it is pointed out that *C. calceolus* grows in shady areas and only in higher altitudes in full sunlight (Käsermann 1999). Moisture might be an important determining factor for presence of the species. The predictor slope was included in all models except the ENFA at 1km. The relationship with the slope however, is not directly obvious, because *C. calceolus* is found in forests without slope, but also on sunny slopes in higher altitude. However, in our study region, mainly forests occupy steep areas. In the evenly areas, open system dominates and human activities are more present. Calcaire was retained in all models except the GAM at 50m. Calcaire was expected to be an important predictor because the species is known to grow predominantly on calcareous soils (Kull 1999), as indicated in the name. Permeability was retained in both models at a 50m scale. The species' requirement for this parameter might be local. Topography was

only retained in the ENFA at 50m but explained quite a lot of variance in this model. NDVI was never retained and neither were the two Boolean predictors detrital rocks and fine detrital rocks. The NDVI, which describes the vegetation type, was maybe not important because the species grows in forests, but also seldom in more open habitat. The NDVI is therefore not adapted for the species. Figure 11 shows that the variance of the species' distribution is about the same as the variance of the study area. The predictor is consequently not adapted to discriminate the niche of the species in this study area. Globally, our results are thus consistent with the general knowledge of the species.

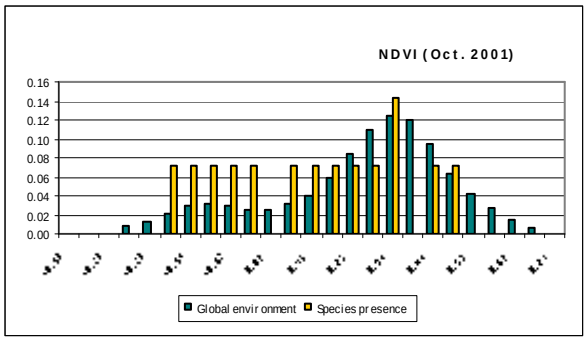


Figure 11. *Cypripedium calceolus* distribution of the NDVI. Frequency distribution of the *Cypripedium calceolus* occurrences (yellow) and the frequency distribution of the global environment (green) per ndvi-value class. The frequency distributions of the other predictors is in Appendix D.

Eryngium alpinum: The predictor moisture index was retained in all four models. The species is found in areas where it is exposed to full sunlight, but at rather cool sites (Käsermann 1999) and moist soils (Landolt 1977). The moisture index might be correlated with this favorability. Figure 12 shows that occurrences are situated at location with a rather high moisture index value compared to the study area. Also the solar radiation variable, which is linked to exposition to full sunlight, was important for the GAM 1km and the ENFA 50m. The NDVI was retained in both 50m precision models. *E. alpinum* grows preferably in megaphorbies and sites rather rich in vegetation (Käsermann 1999) that might be quite well distinguished with the NDVI. Slope was only important at 1km, although it is sometimes mentioned, that *E. alpinum* grows preferably on steep slopes (Hegi 1987). Permeability was important in all models except the ENFA at 50m scale.

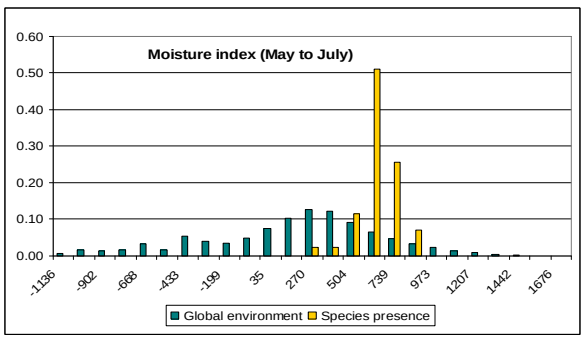


Figure 12. ***Eryngium alpinum* distribution of moisture index**. Frequency distribution of the *Eryngium alpinum* occurrences (yellow) and the distribution of the global environment (green) per moisture index class. The frequency distribution of the other predictors is in Appendix D.

Scorzonera laciniata: Moisture index seem to be important and was retained in all four models. *S. laciniata* is known to grow on rather dry soils (Käsermann 1999) and moisture is therefore an important predictor for the species presence. Limestone was important at 1km scale. Radiation was retained in the ENFA models. This is in coincidence with literature, where it is mentioned that the plant seems quite light loving (Brandes 1994). In the study area, the sites where *S. laciniata* was identified during the last years are clearly located in a topo-climatic region highly contrasted with the rest of the area. The models succeed in highlighting this contrast.

At the scale of our study region, moisture index and solar radiation appear as key factors for the niche of the rare species. Moisture index is a proximate variable that has a direct impact on the species because it informs about water availability (Zimmermann & Kienast 1999). Also solar radiation seemed to be important for determining a species' presence. The geological structure variables were seldom important. These variables are possibly not precise enough (Booleans) to describe the sites and to determine importance for the species. The other interpretation is that the soil characteristics are not a limiting factor for the study species in this area. The predictors retained in the models are not only dependant on the species requirements, but also on their variability in the study area, the characteristics of the sites for which we have the species' presence information and, finally, the variability of these predictions in the study area (i.e. the available environment). There might be one factor that is indispensable for the species, but as it is more or less constant in the whole study area, it is not adapted to discriminate the niche of the species. However, these parameters were taken into account when determining the study area.

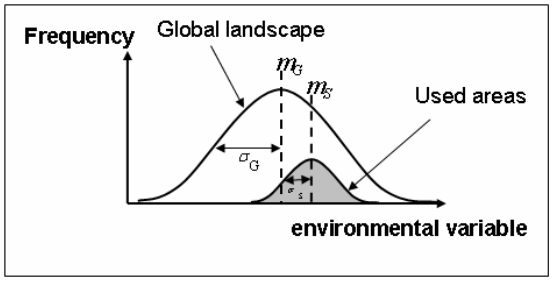
An underlying assumption of static spatial distribution modeling is that the species is in equilibrium with the environment (Guisan & Zimmermann 2000). The three rare species are supposed to occur in their entire climatic favorable habitat, i.e. they have reached their pseudo-equilibrium. For instance, *Cypripdedium calceolus* is distributed over whole Europe (Table 1). Interpreting the results of the HS models can thus be considered as valuable at a global scale. However, at a local scale, suitable areas might not be occupied for other reasons than topoclimatic patterns. These patterns, not included in the present models, are responsible for the remnant not explained variance.

Marginality and Tolerance factors of the ENFA

The rare species have higher marginality scores than the common species (Table 6). This means that the mean of their habitat characteristics was far from the mean of the study area patterns; rare species occur in rather marginal habitat (Figure 13). At the 1km scale, where more points were available, marginality was higher than on the 50m scale and it is therefore admitted that the higher marginality of the rare species is not due to the lower number of data compared to the common species. Similarly, the tolerance factor, which describes the extent of the niche (Figure 13), was lower for rare species than for the common species (Table 6). This confirms our hypothesis that the realized niche of rare species is rather specialized and smaller than those of common species. This observation is valid even at global topo-climatic scale. This specialization might be partly the cause of their rarity (Kunin & Gaston 1993, Thompson *et al.* 1999). However, we must keep in mind that these results describe the realized niche of the species and not the fundamental niche. In a study on lichen for instance, the investigated rare species had not narrower physiological tolerance than the common species and that the physiological tolerance was broader than indicated by the range of where rare species actually occurred (Clevitt 2002). Species interactions (biological interactions) and physiological limitations encountered earlier in the life cycle (dispersal, recruitement) might limit the real distribution of the species (Bossuyt *et al.* 2004). Another theory says that rare species might be more competitive in highly suitable areas whereas they are outcompeted in fairly suitable areas (Cain 1940). Rare species may only occupy sites closer to their physiological optimum and this results in a small, specialized realized niche. Due to their higher tolerance and competivity, common species might occupy a greater proportion of favorable habitat and be able to colonize also suboptimal habitat, conferring them an advantage for dispersal and establishment.

Marginality and specialisation are visualised in Figure 13.

Species 1



Species 2

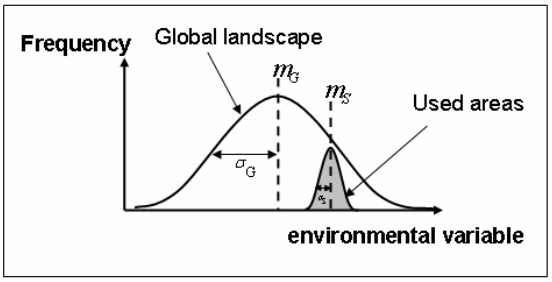


Figure 13: In white is the frequency distribution of the study area and in grey the frequency distribution of one species (1 and 2). σs = is the variance of the species' distribution, σG is the variance of the global landscape, *m*s = mean of the species' distribution, *m*G = mean of the distribution of the global landscape. Marginality indicates the difference between *m*s and *m*G. Tolerance informs about the variance of the species' distribution compared to the environmental gradient. Species 2 occurs in a rather marginal habitat compared to the study area and Species 1. Species 2 is less tolerant than species 1. (adapted from Le Lay, 2002).

4.2. evaluation

The main result coming from the evaluation steps is that the combined-models perform better than any of the single models (Figure 9, Appendix A). This conclusion is effective for all species. The models' accuracy, when comparing evaluation levels, modeling methods and spatial scales are less contrasted.

comparison of the three evaluation levels (30 points, ~250 points, ~500 points)

In the model performance ranking (Table 7) the second and the third level are generally similar, whereas the first level was often quite different than the second and the third level. Validation with 30 points might be insufficient for representing completely the variance of the species' requirements in this quite large study area. Moreover, it is possible that stochasticity, coming from the local adaptations of the species, plays an important role. Consequently, the evaluation results obtained at level 1 might be less reliable than the results of the levels 2 and 3.

In simulations of the iterative MBSS approach run with 30, 60 and 120 points sample size, the models (GAMs) improved in all cases but they actually improved more with a 60 than at 30 points sample

size (Guisan *et al*. In press). To completely assess the efficiencies of the sampling levels, there should be new models made and validated. This will be done in a further step of the whole project (Figure 1). Comparing the new models made with the different point sets with the first model will show if there is a lot of improvement with more points. This will also help in comparing results coming from real data to these made from simulations. However, here, not only the number of points has an influence, but also their "quality". The points at level 1 were sampled especially for the species, in a more or less typical habitat. The points at level 2 and 3 were not completely designed for validating predictions of the same focus species (see 2.4.6). An example of the number of pixels of the zone in each HS class and the number of species' data is shown in Figure 10. *Scorzonera laciniata* data of the second and the third layer was distributed in the same way as the HS classes in the ENFA at 1km and ENFA at 50m. This result suggests that it might not influence that much that the sampling of the points was not completely independent.

Comparison of the different spatial scales (50m resolution vs. 1km resolution)

Map resolution influences model results of rare species, as the models constructed at the larger scale are based on more presence points, which were not available at the smaller resolution (Table 3). However, looking at the result for *Scorzonera lacinata*, it seems that a smaller resolution provides better results, even though more than twice as many presence points were used at the 1km scale. It might be that this depends on the species traits and on the variables used, at which scale a model fits better. By contrast, *Heracleum sphondylium* has better results with models at 1km scales. At a larger scale, other mechanisms might influence the distribution of the species than at a smaller scale. Ecological factors determining species' abundance include environmental variability, intraspecific density, interspecific competition, herbivory, mutualisms, pathogens, pollinators and dispersal (Schemske *et al*. 1994) and they influence at different scales. Also, at a small scale, predictors describing the local site characteristics, solar radiations might be important (Barry 1992) and soil characteristics. In some cases, the predictors used in this study may rather explain the large scale mechanisms.

Another explanation are the environmental variables. At a 50m resolution they are more precise, express better the local characteristics of the sites and express why a site is favorable or not at a local scale. At 1km, the information is smoothed and is maybe more adapted for a larger study area (e.g. Switzerland or Europe).

Comparison between modeling methods (GAM – ENFA)

The underlying question of comparison between GAM and ENFA is to assess the effect of using presence only vs. presence/absence data on rare species models. Including absence data can increase the discriminance (Zaniewski *et al*. 2002) of the model but only if they are true absences that reflect low habitat quality. If the species is for other reasons absent than low habitat quality, inclusion does not improve the model (Hirzel *et al*. 2001) and might decrease their accuracy. Our results show that for very common species that occur in various habitat types, GAMs are too restrictive. For *Anthyllis vulneraria* and *Heracleum sphondylium*, ENFA models are better. These species have both several subspecies and are very common. It was pointed out that presences only methods, like ENFA, predict spatial distributions that are close to the fundamental niche of the species (Zaniewski *et al*. 2002). *H. spondylium* and *A. vulneraria* might have a realized niche that is close to their fundamental niche.

For *Pulsatilla alpina* inversely, GAMs performed better at higher levels and *P. alpina* is rarer than the other common species and is actually protected in several cantons including Bern, Fribourg and Vaud. Also for *Briza media*, the GAMs were always better than the ENFA models. *B. media* and *P. alpina* might be more specific to a habitat. *B. media* is predominantly a species of calcareous grasslands (Dixon 2002). Absences might present true absences and increase the predictability of the model.

As conclusion, suitability of presence-only or presence/absence models might largely depend on the species traits. If a rare species is often absent from good quality habitats due to competition, dispersal or picking (Benayas 1999), absences are not real "true" absences in the sense of topo-climatic influence (Pullinam 2000, Figure 1 D, dispersal limitation). In this case, including absences might compromise the model and it might be better to use a presence only method. Otherwise, if the species is specialized (niche limitation), absences are true absences; they probably reflect the low frequency of suitable habitat. The same is the case, if a species is rare because it is only competitive in optimal habitat. In this case, including absences might increase the predictability of a model.

Sensibility of models' evaluation

For evaluation, three different indices were used. Differences occur because the indices are not calculated in the same way. The Kappa index value is sensitive to the prevalence of data (Fielding & Bell

1997). The weighted Kappa is a measure that attributes different weights to the data and should therefore be robust to prevalence. However, our results show that generally the model ranking does not change between the Kappa and the weighted Kappa evaluation (Table 7). The rightness of the ranking is therefore underlined. Nevertheless, the AUC evaluation ranked the models differently than the Kappa values a few times (Table 7). Although there are these slight differences, both evaluation methods are taken into account for the discussion.

If we want to statistically test in our study whether the combination of models always performs better than single models, a bootstrap should be made to obtain a standard error. However, this result still has to be regarded critically because sampling of the single models (i.e. GAM 50m/GAM1km/ENFA50m/ENFA1km) was not independent (see 2.4.6). Also, the model ranking only says if one model is better or worse than another, but it does not say anything about if there is a big difference or not and does not test significance of the difference.

Regarding the influence of spatial quality of the initial data set, it derives that it does not in all cases decreases accuracy of the model. Differences between the evaluations of the region where a lot of data was available (Modiplant region) and the rest of the study area were not significant (3.3, Annex B). However, these general results are maybe not of primary importance. A more detailed investigation of this pattern, for each species, shows that spatial bias of the initial data set only matters in the case of *Anthyllis vulneraria* and *Pulstilla alpina*. The overall results obtained for these to species, might therefore be less accurate than if the points of the initial data set were better spatially distributed.

4.3 discussion of the rare species

Eryngium alpinum and *Cypripedium calceolus*

During fieldwork in summer 2005, no new populations were found for *Eryngium alpinum* and *Cypripedium calceolus*. There are different explanations likely why our sampling approach did not work out for those two species. 1) First, both species are classified as *vulnerable* in the red list (Moser *et al*. 2002) and it might be that the species has such a low abundance that there are no other populations in the study area. Also, the region of the canton of Vaud (Figure 3 c)) has been investigated rather well in previous

studies already. 2) Second, populations close to roads are probably known and indicated to the Swiss Floristic Network (CRSF). Both species are very conspicuous and considered as flagship species for the Alps and for conservation. 3) In our approach, we followed a specific sampling scheme. At each site, about the same amount of time was spent. Also, the sites were chosen randomly. Only 10 points were sampled in the highly suitable predicted area, which was perhaps a too low sampling intensity 4) Furthermore, the predictions were too large to accurately predict the highly suitable sites. The highly suitable zone for the *E. alpinum* covers about 410 km² (2% of the area) and for *C. calceolus* even 820 km² (4% of the area). It might be that important parameters for species' presence and that define the ecological niche are not included. Otherwise, it is also possible that the species is frequently absent from favorable habitat due to dispersal problems. *E. alpinum* has been identified as week disperser with a dispersal distance of about 1m (Gaudeul & Till-Bottraud 2004). 5) Moreover there are certainly anthropogenic factors that influence absence of the species in apparently suitable habitat. One considerable point is picking of individuals. *C. calceolus* grows in small populations (Hegi 1987) and to poach one or two individuals might affect largely the extinction likelihood of the population. Also for *E. alpinum*, although the populations are sometimes quite large (Hegi 1987), picking was identified as one of the most important threats (Käsermann 2000). 6) Also, there might be a problem of scale that a 50m resolution and especially a 1km resolution is simply too large for predicting the rare species in our study area. These resolutions are possibly more adapted for modeling the species at a large scale. The distribution of *E. alpinum* was successfully modeled at the scale of Switzerland (Engler *et al*. 2004, Guisan *et al*. in press). It might be that at a local microhabitat contains important features for determining presence and absence of a species (Bossuyt *et al*. 2004). 7) Genetic differentiation of populations between mountain ranges evoque local adaptations (Wiser *et al*. 1998) and consequently slightly varying niche. *C. calceouls* and *E. alpinum* populations might be quite isolated and this genetic factor can be pronounced. Moreover, factors determining abundance and rarity of species include the amount of heterozygosity and allelic diversity (Schemske *et al*. 1994). Genetic factors cannot be taken into account in these types of spatial distribution models used in this study. It was suggested that the decline of *E. alpinum* might be partly due to loss of genetic diversity (Gaudeul 2002).

Scorzonera laciniata

For S*corzonera laciniata* the sampling approach worked out quite well. It has some, for our study, favorable characteristics compared to *Eryngium alpinum* and *Cypripedium calceolus*. First, *S. laciniata* is

more frequent according to one rarity-classification scenario, where it was even classified as common (Brönnimann *et al*. in press). Also, *S. laciniata* occurs only in the Valais (at least, there have not been found any populations elsewhere in Switzerland yet) (Lauber & Wagner 1996). Although the predicted high suitability area covers a large area of about 615km² (3%), it was aggregated and almost only situated in the Valais (Figure 5). Consequently, search effort was higher in this region. Furthermore, it has to be pointed out that the populations of *S. laciniata* are typically growing in vineyards (Käsermann 1999). This has the advantage that the suitable areas generally are easily accessible by car and second, that prospectation is quite simple and quick, too, by walking along the vines. Additionally, *S. laciniata* preferably grows in vineyards poor in ground vegetation and is therefore easily detectable. Comparatively, *C. calceolus* grows in the forest and in small populations which decreased its detectability especially during the non flowering season. Finally, *S. laciniata* might benefit in some way from human activities. *S. laciniata* is apparently a poor competitor and human impact, for instance modest use of herbicides in vineyards, result in decreasing competition. However, intensive use of herbicides was identified as one of the greatest threats to *S. laciniata* (Käsermann 1999). The results show that the models for *S. laciniata* fit better than those of the other species (Figure 7 and Table 4). This might indicate that the topo-climatic variables explain quite well the distribution of *S. laciniata*. This might be due to the climatic specificity of this part of the Valais. At a finer scale, including only the Valais, it might be more difficult to obtain an accurate model. Furthermore, *S. laciniata* has fruits that are especially adapted for wind dispersal. *S. laciniata* might therefore not be dispersal limited and, in case of local extinction, rapidly recolonize suitable habitat.

4.4 perspectives

Sampling effort

Sampling effort might be increased for rare species, especially when the species is cryptic, and this has to be integrated in the planning. It has been stated that new discovered populations of rare species are mostly in mountain regions which are difficult to access and in remote peripheral areas, e.g. Jura. (Bäumler *et al*. 2005). Searching in more remote areas might provide better results, as they are less known and less disturbed. Increased search effort in the highly suitable areas adds a bias statistically. This is a problem when the objective of the study is purely methodological, but from the conservation point of view, of course, it is better to do so. In the case of conspicuous species, an idea is to use binoculars to investigate

slopes quickly and without having to climb. This increases the efficiency of prospecting (Garcia *et al*. 2002). A further proposition is to contact local people that might have some additional knowledge about presences of rare plant species. This might also provide understanding of the species' habitat and historical features. There might be populations that are discovered but that have never been mentioned to the Swiss Floristic Network (CRSF). This approach however, is globally only of use for species that are conspicuous, well known also among non specialists and easily determined. For *E. alpinum* and *C. calceolus*, such an approach might furnish additional data. Also an inquiry among farmers, foresters and mountain associations might provide additional information.

Predictors

To choose the right **predictors** for modeling is primordial, not only for rare species. Deepened knowledge about the ecological requirements of the species helps identifying the factors influencing the species' niche (Austin *et al*. 1990). *Scorzonera laciniata* especially, is a species of which, due to its rareness, hardly any indications about its ecology are published (Brandes 1994) and it is also mentioned that there is limited knowledge about its population biology (Käsermann 1999). Variables that determine the niche at a large scale, as for example climate, but also limiting factors at small scale explain rarity. This might also include variables such as human activity and pollination (Schemske *et al*. 1994).

In a study on modeling four rare plant species, important predictors were investigated in models of two different scales, 100m and 1m. At the macroscale, **potential solar radiation** important predictor as well as the predictors **fracturing index** (a semi-quantitative variable defining the degree of fracturing) and **iron axis** (of a PCA) (Wiser *et al*. 1998). This underlines the importance of the direct variable potential solar radiation, which was also important for predicting rare species in our study. The fact that iron was quite important suggests that in our case, a more detailed soil analysis might provide more enlightenment about a species' niche requirements. The importance of landscape structure (measured as for instance mean patch size and Shannon-Wiener diversity index of landscape), similar to the fracturing index, was also investigated in another study on rare species richness (Luoto 2000) and appeared to be significantly related to rare species richness. There was no such predictor included in our study and including it might provide useful insights.

Predictors that are important for species' richness might also be important for modeling one single species. It was pointed out that for modeling alpine plant species richness, climatic variables like **temperature** and **potential evapotranspiration**, seem to be the most important predictors (D. Moser *et al*. 2005). This is in coincidence with our study, where moisture and solar radiations were apparently more important than geological features. However, In another study on prealpine calcareous grassland communities, the most important factor determining floristic composition was **lithology** (a qualitative variable with five categories of geological cover) and the second most important **grazing intensity** (Barbaro *et al*. 2004). The importance that was given to the geological variable, might suggest, that in our case, the geological predictors were just not precise enough to contribute to the models, but still important for rare plant species. The study also underlines the importance of landuse and that such a predictor might increase accuracy of a predictive model. Anthropogenic factors can be taken into account in the model, either in form of a predictor as surrogate in the model or a mask that can be applied after modeling. To mask habitat might improve the evaluation of a model, by restricting the favorable area and consequently permitting to concentrate the search in the field. Including landuse and especially **pastures**, in the habitat suitability model of *E. alpinum* might improve its accuracy. Especially at a small scale, land use has been shown to be an important predictor for community distribution (Fisher 1994). Unfortunately, a detailed land use map is not available for the whole region. An idea might be to create a spatial distribution model for pastures using topo-climatic variables and include this afterwards in the model of the species.

Instead of landuse, **landownership** can provide a surrogate predictor. The necessary data might be easier obtained than for landuse. A study in Canada investigated the effect of Landownership (Lovett-Doust *et al*. 2003). Public land has been identified to contain more rare species. Private areas are often pastures and privately owned land under more intensive economic pressure than public owned land and biodiversity in privately owned land is linked with purpose of the ownership. There are factors indirectly related to landownership, for example public land is larger and less fragmented (Lovett-Doust *et al*. 2003).

C. calceolus has been identified to be sensible to some types of **forest exploitations** (Terschuren 1998). Including a **land use** map with forest exploitation method, if available, might improve the model. For *S. laciniata*, herbicide use in the vineyards might provide a useful predictor at a very local scale.

Soil parameters might be determinant for a species presence (Wiser *et al*. 1998). In general, this predictor does not exist and can therefore not be included in a model before extensive fieldwork is made to obtain soil data. We included categorical soil parameters, but this was a map based on an expert opinion

and it was perhaps not precise enough to discriminate local patterns. Preliminary analyses showed that soil parameters (e.g. amount of nitrogen, limestone, copper) can partly explain presence vs. absence of species (Verchère & Ulrich 2006, Legris 2006). Nevertheless, it is difficult to model the spatial variation of these variables. Values can be simply interpolated, but this provides smoothed information.

Eryngium alpinum is a week disperser. Including dispersal in a dynamic HS model might improve information about the spatial distribution of the species. An approach for this is for example the program MigClim (Engler, in prep) which takes habitat suitability of a pixel and distance to other pixels into account.

Modeling method

An important issue when modeling rare species is to chose an adapted modeling **method**. The most obvious and difficult problem for rare species is to find a method that circumvents the problem of few presence data. One approach, which was used in this study, is to make several models and combine them for limiting each of their bias. This was for example successfully made in a study on the red squirrel, where an environmental model and a locational model were combined with a Bayesian approach (Pereira & Itami, 1991). Different sets of parameters might be important at different scales in determining a species' presence. By making models at two different scales and by combining them afterwards, both sets of parameters are included in the final predictive map. In this way it is possible to include more parameters than with a simple GAM, where the number of predictors that can be used is dependant on the number of presence points. Also, it is supposed that there is not one single modeling method that fits in all cases. By combining several methods, the different advantages of each one of the methods might be combined. Even if there was one method that "better" than another one, we ignore it and the chances of success are increased by combining the methods. Besides, with the combination of models the favorable zone becomes restricted which is more realistic in the case of rare species

An idea that was suggested is to identify it the species is associated with another, more common species. Presence of this common species could be used as surrogate for the rare and especially cryptic species and the presence points used for model construction. This was successfully accomplished in a study on five rare lichen species. For four of the five species, model-based sampling resulted in a two- to fivefold gain in detection rate compared to observed detection rates (Edwards *et al*. 2005).

Type of rarity

Distinguishing between different types of rarity may help to improve modeling of such rare events (Edwards *et al*. 2005). So-called urban species, which occur in large populations, are supposed to be easier to model compared to satellite species (a species with a patchy distribution, but locally abundant) and rural species (a species that is patchy and scattered distributed throughout its range (Edwards *et al*. 2005). Species that are rare principally because they have a small fundamental niche might by easier to model if the predictors that determine the niche are available. High specialization makes their environment rather Boolean (i.e. suitable/unsuitable) than slowly ranging form suitable to unsuitable). There might be one key factor that determines their presence. On the other hand, species that are rare mainly due to complex biological interactions or dispersal are more difficult to model. In the introduction it was mentioned that we might distinguish between intrinseque rarity versus recent decline due to human actions. Intrinsequely rare species might be easier to model with the type of models used here (with topo-climatic variables), because human impact is in some cases difficult to estimate.

Model-based stratified sampling

Model-based stratified sampling is a promising sampling method for rare species, despite of some difficulties in our study mentioned above. By creating a model to predict species occurrence derived from environmental data, it is somehow formalized what an experienced field biologist would do in his mind. By following such a procedure, this kind of research for new populations is made accessible for people without experience in this domain. Also, there might be a factor that determines species presence that is not evident at the first sight and which might be included in the model. From the scientific point of view, such a method is an advantage because it makes search repeatable (Poon & Margules 2004). Moreover, such a stratified sampling design might avoid a bias in data. To estimate distribution for example, it might be inefficient to depend upon chance discoveries.

There are several other studies published recently where model-based stratified sampling was used to find new locations of rare species. In a study on the rare species *Coix gasteenii* and *Jedda multicaulis* in Australia, bioclim models were used to predict occurrences of unknown populations. No new population was found for *Jedda multicaulis,* however, search for this species was often limited by restricted access to the favorable area. One new population was found of *Coix gasteenii* (Poon & Margules 2004). In a research on

the rare species *Cardamine clematitis*, a model based on the Mahalanobis distance was created and used to stratify the study area. The model predicted reliably the absence of the species in unsuitable areas, but also in apparently suitable habitats the species was frequently absent. There might be other factors than site quality responsible for this result or insufficient data resolution for fine-scale habitat characteristics (Boetsch *et al*. 2003). The rare orchid *Isotria medeoloides* has also been subject to a study. Two different overlay models were created, on with equal weight for all predictors and one with different weights for the predictors, depending on a chi-square evaluation between sites with and without orchid. Nine populations of *Isotria medeoloides* were discovered (Sperduto & Congalton 1996).

Nevertheless, it is important to be aware of the limitations of habitat suitability modeling. Small sample size and uneven occurrence are likely to distort a model. Furthermore, biological interactions may be pronounced in rare species because this might be the cause of rarity (Kunin & Gaston 1993). Many factors influence the success of the modeling approach and perhaps it might never be possible to reach the same threshold of model quality for rare species as obtained with simulations (Guisan *et al*. in press). There will always be a variance in species' distribution that cannot be explained, but with the iterative model-based sampling approach, this unexplained variance might be reduced.

5. Conclusion

1. All species were successfully modeled with topo-climatic variables and different modeling methods. The suitable area was larger for the common than for the rare species.
2. Some species were better modeled using presence only data and others using presence/absence data.
3. The combination of models achieved better results in the evaluation than all of the single models. The importance of the approach is therefore confirmed.
4. Probability of occurrence was overall largely superior in suitable areas than elsewhere for the common species and *Scorzonera laciniata*. 8 new populations of *S. laciniata* were discovered, all in highly suitable habitat, where as for *Eryngium alpinum* and *Cypripedium calceolus* no new populations were found.
5. This sampling approach can be of great importance for conservation managers. When models are accurate, they can help both in finding rare species' populations and protecting the most suitable areas.

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Appendix A. All validation results.

Species	Model	Level	Kappa	Weighted Kappa	AUC	AUC'
Cypripedium calceolus	combined	1	0.00	0.00	NA	NA
Cypripedium calceolus	combined	2	0.00	0.00	NA	NA
Cypripedium calceolus	combined	3	0.00	0.00	NA	NA
Cypripedium calceolus	GAM 50m	1	0.00	0.00	0.00	0.00
Cypripedium calceolus	GAM 50m	2	0.00	0.00	0.00	0.00
Cypripedium calceolus	GAM 50m	3	0.00	0.00	0.00	0.00
Cypripedium calceolus	GAM 1km	1	0.00	0.00	0.00	0.00
Cypripedium calceolus	GAM 1km	2	0.00	0.00	0.00	0.00
Cypripedium calceolus	GAM 1km	3	0.00	0.00	0.00	0.00
Cypripedium calceolus	ENFA 50m	1	0.00	0.00	0.00	0.00
Cypripedium calceolus	ENFA 50m	2	0.00	0.00	0.00	0.00
Cypripedium calceolus	ENFA 50m	3	0.00	0.00	0.00	0.00
Cypripedium calceolus	ENFA 1km	1	0.00	0.00	0.00	0.00
Cypripedium calceolus	ENFA 1km	2	0.00	0.00	0.00	0.00
Cypripedium calceolus	ENFA 1km	3	0.00	0.00	0.00	0.00
Eryngium alpinum	combined	1	0.00	0.00	NA	NA
Eryngium alpinum	combined	2	0.00	0.00	NA	NA
Eryngium alpinum	combined	3	0.00	0.00	NA	NA
Eryngium alpinum	GAM 50m	1	0.00	0.00	0.00	0.00
Eryngium alpinum	GAM 50m	2	0.00	0.00	0.00	0.00
Eryngium alpinum	GAM 50m	3	0.00	0.00	0.00	0.00
Eryngium alpinum	GAM 1km	1	0.00	0.00	0.00	0.00
Eryngium alpinum	GAM 1km	2	0.00	0.00	0.00	0.00
Eryngium alpinum	GAM 1km	3	0.00	0.00	0.00	0.00
Eryngium alpinum	ENFA 50m	1	0.00	0.00	0.00	0.00
Eryngium alpinum	ENFA 50m	2	0.00	0.00	0.00	0.00
Eryngium alpinum	ENFA 50m	3	0.00	0.00	0.00	0.00
Eryngium alpinum	ENFA 1km	1	0.00	0.00	0.00	0.00
Eryngium alpinum	ENFA 1km	2	0.00	0.00	0.00	0.00
Eryngium alpinum	ENFA 1km	3	0.00	0.00	0.00	0.00

Species	Model	Level	Kappa	Weighted Kappa	AUC	AUC'
Scorzonera laciniata	combined	1	0.50	0.50	NA	NA
Scorzonera laciniata	combined	2	0.46	0.31	NA	NA
Scorzonera laciniata	combined	3	0.76	0.65	NA	NA
Scorzonera laciniata	GAM 50m	1	0.25	0.32	0.90	0.81
Scorzonera laciniata	GAM 50m	2	0.26	0.17	0.98	0.97
Scorzonera laciniata	GAM 50m	3	0.52	0.39	0.99	0.97
Scorzonera laciniata	GAM 1km	1	0.36	0.38	0.95	0.90
Scorzonera laciniata	GAM 1km	2	0.24	0.15	0.98	0.96
Scorzonera laciniata	GAM 1km	3	0.31	0.21	0.99	0.97
Scorzonera laciniata	ENFA 50m	1	0.50	0.45	0.83	0.67
Scorzonera laciniata	ENFA 50m	2	0.38	0.26	0.95	0.89
Scorzonera laciniata	ENFA 50m	3	0.69	0.57	0.97	0.94
Scorzonera laciniata	ENFA 1km	1	0.23	0.24	0.70	0.41
Scorzonera laciniata	ENFA 1km	2	0.14	0.09	0.89	0.78
Scorzonera laciniata	ENFA 1km	3	0.20	0.13	0.89	0.79
Anthyllis vulneraria	combined	1	0.70	0.70	NA	NA
Anthyllis vulneraria	combined	2	0.44	0.44	NA	NA
Anthyllis vulneraria	combined	3	0.46	0.56	NA	NA
Anthyllis vulneraria	GAM 50m	1	0.32	0.36	0.70	0.41
Anthyllis vulneraria	GAM 50m	2	0.03	0.03	0.54	0.08
Anthyllis vulneraria	GAM 50m	3	0.13	0.15	0.62	0.24
Anthyllis vulneraria	GAM 1km	1	0.32	0.36	0.69	0.38
Anthyllis vulneraria	GAM 1km	2	0.20	0.27	0.67	0.35
Anthyllis vulneraria	GAM 1km	3	0.19	0.30	0.72	0.43
Anthyllis vulneraria	ENFA 50m	1	0.58	0.56	0.83	0.67
Anthyllis vulneraria	ENFA 50m	2	0.33	0.34	0.72	0.44
Anthyllis vulneraria	ENFA 50m	3	0.33	0.33	0.73	0.46
Anthyllis vulneraria	ENFA 1km	1	0.58	0.56	0.82	0.65
Anthyllis vulneraria	ENFA 1km	2	0.28	0.27	0.71	0.42
Anthyllis vulneraria	ENFA 1km	3	0.34	0.34	0.77	0.53

Species	Model	Level	Kappa	Weighted Kappa	AUC	AUC'
Astrantia major	combined	1	0.80	0.80	NA	NA
Astrantia major	combined	2	0.59	0.59	NA	NA
Astrantia major	combined	3	0.64	0.64	NA	NA
Astrantia major	GAM 50m	1	0.67	0.68	0.88	0.77
Astrantia major	GAM 50m	2	0.30	0.30	0.74	0.48
Astrantia major	GAM 50m	3	0.32	0.33	0.76	0.52
Astrantia major	GAM 1km	1	0.53	0.53	0.87	0.73
Astrantia major	GAM 1km	2	0.37	0.37	0.79	0.58
Astrantia major	GAM 1km	3	0.41	0.42	0.79	0.59
Astrantia major	ENFA 50m	1	0.46	0.46	0.65	0.29
Astrantia major	ENFA 50m	2	0.30	0.30	0.70	0.40
Astrantia major	ENFA 50m	3	0.32	0.32	0.71	0.43
Astrantia major	ENFA 1km	1	0.66	0.66	0.80	0.60
Astrantia major	ENFA 1km	2	0.27	0.27	0.71	0.41
Astrantia major	ENFA 1km	3	0.28	0.28	0.72	0.45
Briza media	combined	1	0.70	0.70	NA	NA
Briza media	combined	2	0.64	0.64	NA	NA
Briza media	combined	3	0.62	0.62	NA	NA
Briza media	GAM 50m	1	0.60	0.60	0.86	0.71
Briza media	GAM 50m	2	0.40	0.40	0.72	0.44
Briza media	GAM 50m	3	0.37	0.37	0.72	0.45
Briza media	GAM 1km	1	0.68	0.72	0.86	0.72
Briza media	GAM 1km	2	0.38	0.40	0.76	0.52
Briza media	GAM 1km	3	0.33	0.34	0.75	0.50
Briza media	ENFA 50m	1	0.46	0.46	0.74	0.48
Briza media	ENFA 50m	2	0.15	0.16	0.60	0.21
Briza media	ENFA 50m	3	0.13	0.14	0.59	0.18
Briza media	ENFA 1km	1	0.48	0.49	0.71	0.43
Briza media	ENFA 1km	2	0.16	0.16	0.65	0.31
Briza media	ENFA 1km	3	0.16	0.16	0.64	0.29

Species	Model	Level	Kappa	Weighted Kappa	AUC	AUC'
Heracleum sphondylium	combined	1	0.60	0.60	NA	NA
Heracleum sphondylium	combined	2	0.38	0.38	NA	NA
Heracleum sphondylium	combined	3	0.34	0.35	NA	NA
Heracleum sphondylium	GAM 50m	1	0.36	0.38	0.58	0.16
Heracleum sphondylium	GAM 50m	2	0.21	0.22	0.64	0.28
Heracleum sphondylium	GAM 50m	3	0.11	0.13	0.61	0.21
Heracleum sphondylium	GAM 1km	1	0.28	0.29	0.65	0.29
Heracleum sphondylium	GAM 1km	2	0.24	0.24	0.67	0.34
Heracleum sphondylium	GAM 1km	3	0.19	0.20	0.65	0.30
Heracleum sphondylium	ENFA 50m	1	0.57	0.57	0.71	0.42
Heracleum sphondylium	ENFA 50m	2	0.17	0.18	0.64	0.28
Heracleum sphondylium	ENFA 50m	3	0.15	0.15	0.63	0.27
Heracleum sphondylium	ENFA 1km	1	0.45	0.44	0.61	0.23
Heracleum sphondylium	ENFA 1km	2	0.19	0.20	0.67	0.33
Heracleum sphondylium	ENFA 1km	3	0.28	0.27	0.73	0.47
Pulsatilla alpina	combined	1	0.30	0.30	NA	NA
Pulsatilla alpina	combined	2	0.58	0.51	NA	NA
Pulsatilla alpina	combined	3	0.75	0.73	NA	NA
Pulsatilla alpina	GAM 50m	1	0.10	0.11	0.50	0.01
Pulsatilla alpina	GAM 50m	2	0.38	0.33	0.87	0.74
Pulsatilla alpina	GAM 50m	3	0.57	0.55	0.91	0.82
Pulsatilla alpina	GAM 1km	1	0.17	0.16	0.63	0.25
Pulsatilla alpina	GAM 1km	2	0.40	0.35	0.85	0.69
Pulsatilla alpina	GAM 1km	3	0.56	0.50	0.90	0.79
Pulsatilla alpina	ENFA 50m	1	0.20	0.22	0.65	0.30
Pulsatilla alpina	ENFA 50m	2	0.28	0.26	0.81	0.61
Pulsatilla alpina	ENFA 50m	3	0.45	0.44	0.81	0.62
Pulsatilla alpina	ENFA 1km	1	0.24	0.22	0.57	0.14
Pulsatilla alpina	ENFA 1km	2	0.27	0.24	0.74	0.49
Pulsatilla alpina	ENFA 1km	3	0.38	0.34	0.81	0.62

Appendix B. Results of the spatial quality of the predictions for the common species.

Modipl = part of the study area belonging to the canton of Vaud; *NoModipl* = part of the study area not belonging to the canton of Vaud.

	Kappa		weighted Kappa		AUC		AUC'	
	Modipl	***NoModipl***	***Modipl***	***NoModipl***	***Modipl***	***NoModipl***	***Modipl***	***NoModipl***
Anthyllis vulneraria								
Combination	0.49	0.26	0.60	0.28	NA	NA	NA	NA
Gam 50m	0.25	-0.07	0.32	-0.07	0.71	0.45	0.42	-0.09
Enfa 50m	0.40	0.24	0.40	0.24	0.75	0.71	0.50	0.42
Gam 1km	0.24	0.11	0.41	0.17	0.75	0.64	0.50	0.28
Enfa 1km	0.31	0.35	0.31	0.35	0.76	0.79	0.51	0.58
Astrantia major								
Combination	0.63	0.66	0.63	0.67	NA	NA	NA	NA
Gam 50m	0.30	0.36	0.30	0.36	0.72	0.79	0.45	0.58
Enfa 50m	0.28	0.36	0.28	0.36	0.69	0.74	0.39	0.48
Gam 1km	0.41	0.43	0.41	0.44	0.78	0.81	0.55	0.63
Enfa 1km	0.30	0.25	0.30	0.26	0.72	0.72	0.43	0.45
Briza media								
Combination	0.59	0.65	0.62	0.63	NA	NA	NA	NA
Gam 50m	0.38	0.36	0.38	0.35	0.73	0.71	0.46	0.42
Enfa 50m	0.05	0.25	0.06	0.25	0.58	0.63	0.16	0.27
Gam 1km	0.31	0.35	0.32	0.37	0.73	0.78	0.45	0.55
Enfa 1km	0.14	0.20	0.14	0.20	0.62	0.67	0.25	0.35
Heracleum sphondylium								
Combination	0.24	0.44	0.26	0.45	NA	NA	NA	NA
Gam 50m	0.06	0.17	0.07	0.20	0.54	0.69	0.08	0.38
Enfa 50m	0.08	0.25	0.08	0.24	0.53	0.71	0.06	0.42
Gam 1km	0.16	0.22	0.17	0.23	0.60	0.70	0.20	0.39
Enfa 1km	0.25	0.31	0.24	0.30	0.72	0.73	0.43	0.46
Pulsatilla alpina								
Combination	0.85	0.57	0.82	0.57	NA	NA	NA	NA
Gam 50m	0.66	0.42	0.63	0.42	0.95	0.86	0.89	0.71
Enfa 50m	0.48	0.41	0.46	0.40	0.82	0.76	0.63	0.52
Gam 1km	0.64	0.44	0.57	0.41	0.94	0.84	0.87	0.69
Enfa 1km	0.45	0.29	0.40	0.26	0.84	0.75	0.68	0.51

Appendix C: Correlation matrix of the predictors for 1km and 50m used for the ENFA, performed in the BIOMAPPER software (Hirzel *et al*. 2002b).

Correlation matrix for the predictors at 1km accuracy

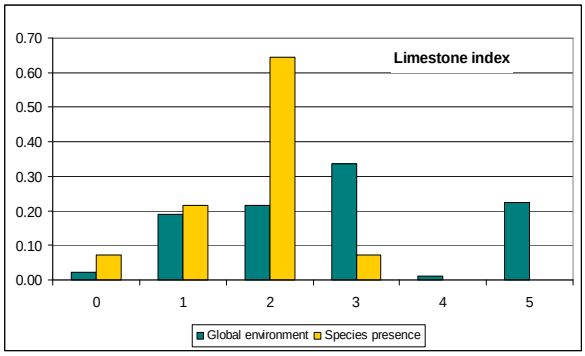
	calcaire	gt_ch_c1	gt_ch_c2	gt_ch_c3	gt_ch_c4	gt_ch_c5	mind_5to9	permeabilite	slp50	srad_5to9
calcaire	1	-0.696	-0.066	0.856	0.318	-0.06	0.402	0.03	0.496	-0.24
gt_ch_c1		1	-0.333	-0.517	-0.389	-0.02	-0.543	0.448	-0.634	0.229
gt_ch_c2			1	-0.398	-0.276	-0.079	0.093	0.084	-0.015	0.112
gt_ch_c3				1	0.157	-0.098	0.352	-0.063	0.478	-0.239
gt_ch_c4					1	-0.119	0.292	-0.559	0.364	-0.227
gt_ch_c5						1	-0.036	-0.108	0.007	0.052
mind_5to9							1	-0.418	0.59	-0.46
permeabilite								1	-0.451	0.151
slp50									1	-0.54
srad_5to9										1

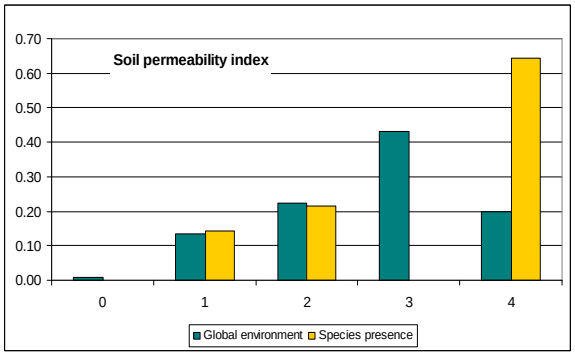
Correlation matrix for the predictors at 50m accuracy

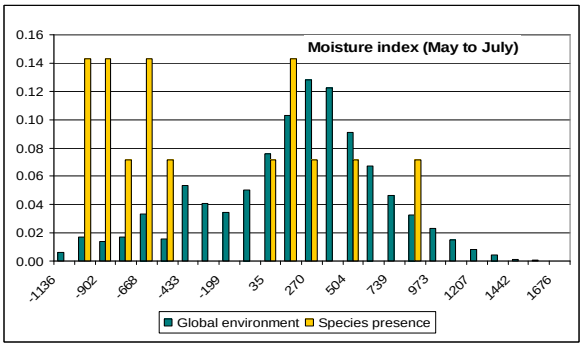
	calcaire	permeabilite	mind_5to9	ndvi	slp50	srad_5to9	topo
calcaire	1	0.213	0.295	-0.224	0.359	-0.145	0.2
permeabilite		1	-0.298	0.078	-0.26	0.08	-0.072
mind_5to9			1	-0.468	0.523	-0.487	0.227
ndvi				1	-0.287	0.459	-0.044
slp50					1	-0.479	0.191
srad_5to9						1	0.032
topo							1

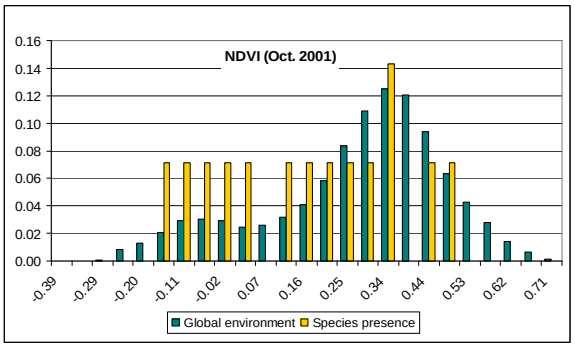
Appendix D: Frequency distribution of species' occurrences (yellow) and the frequency distribution of the global environment (green).

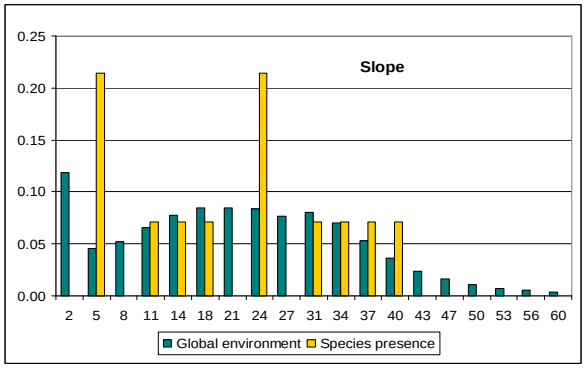
Cypripedium calceolus

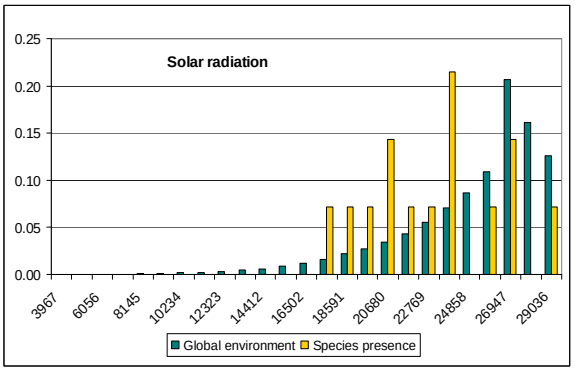


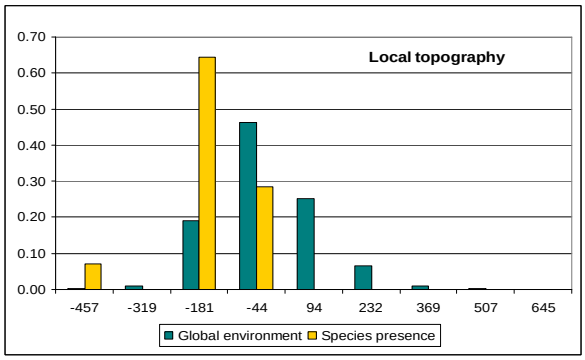




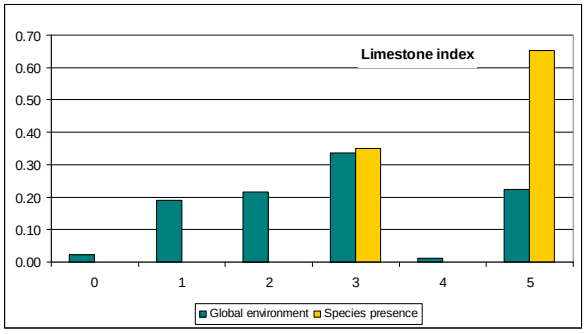


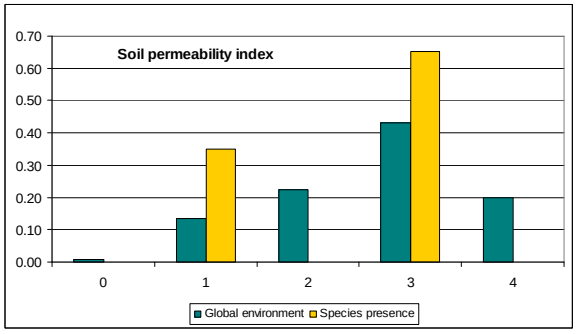


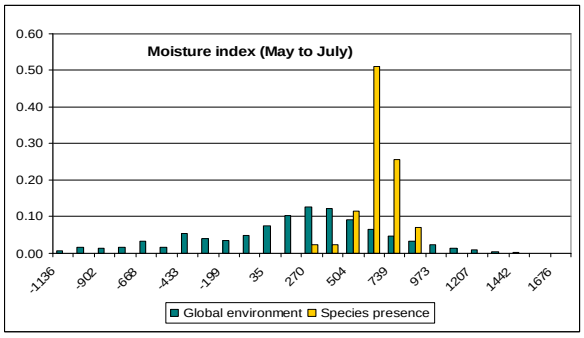


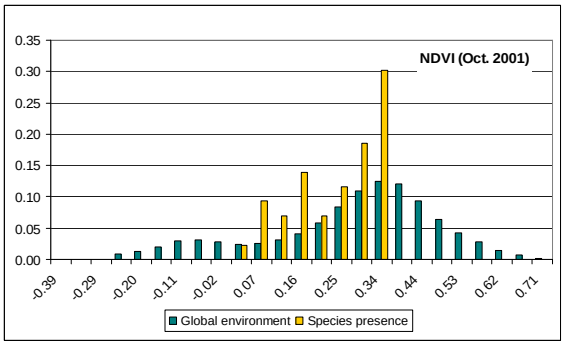


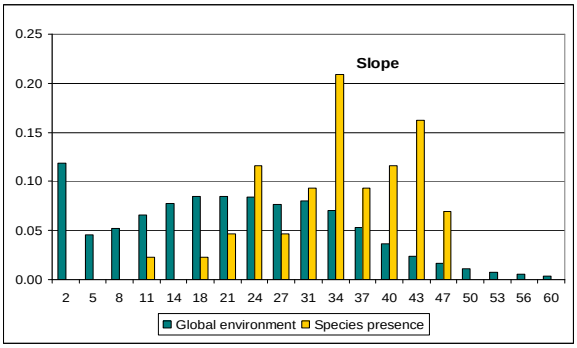
Eryngium alpinum

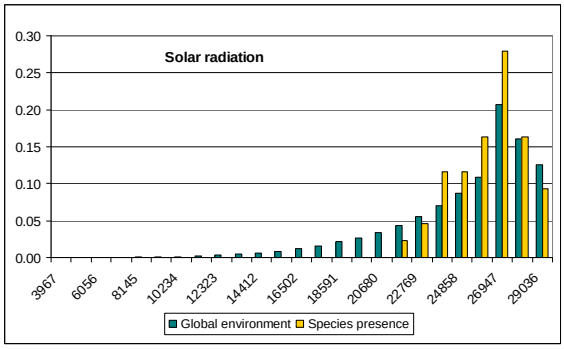


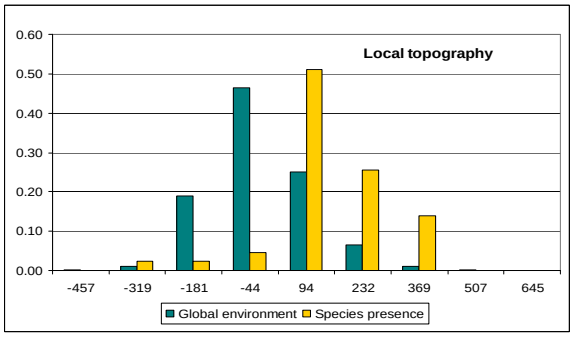




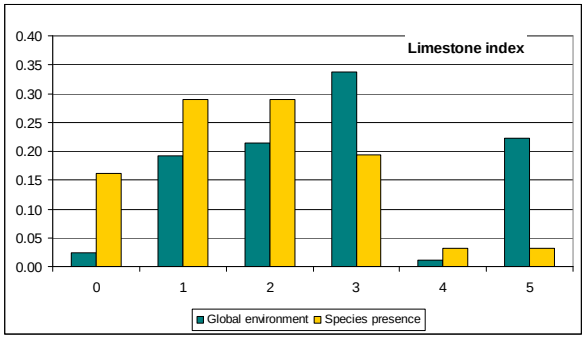


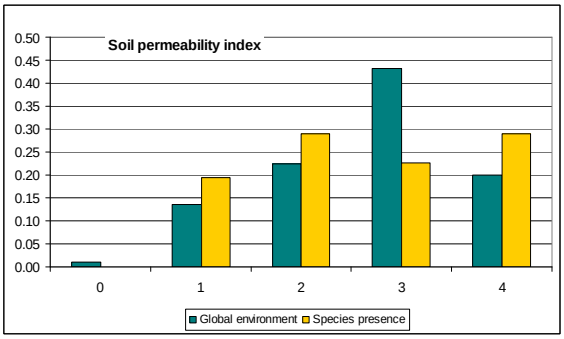


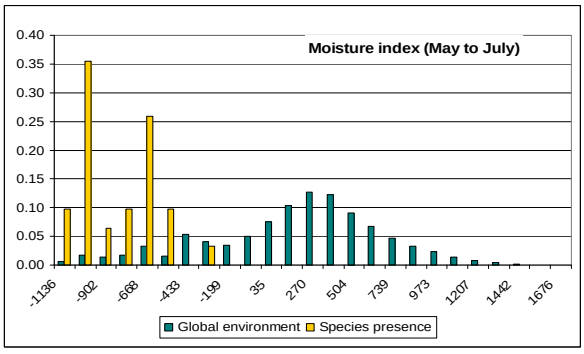


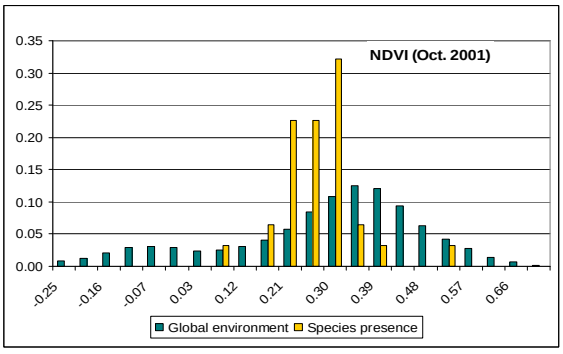


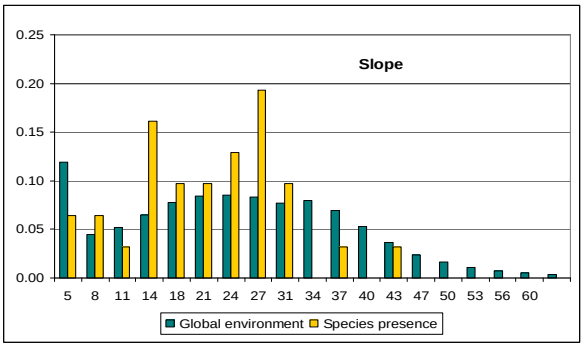
Scorzonera laciniata

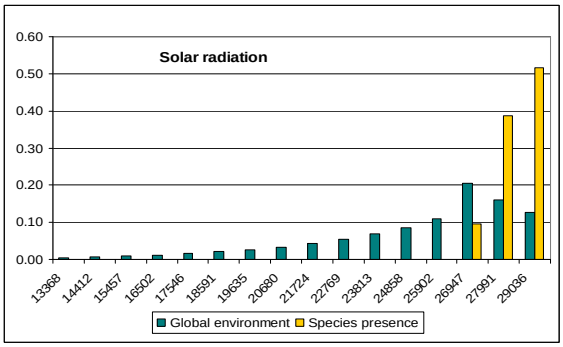


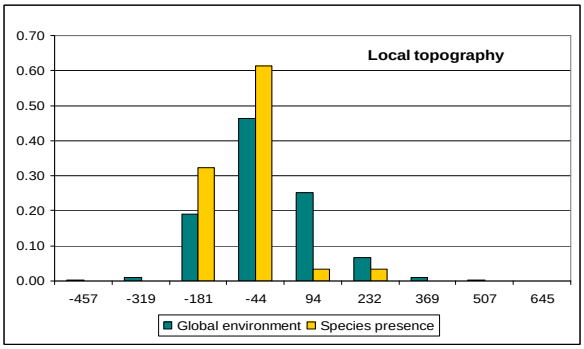












VU *Cypripedium calceolus* L. – Sabot de Vénus – *Orchidaceae*

Tiré de HESS & AL. 1976-1980

Description

Plante de 15-60 (70) cm de haut, rhizome rampant, prolif rant souvent en touffes. 2-4 feuilles ovales-elliptiques longues de 6-18 cm, embrassantes, vert clair, nervures saillantes. Une fleur, plus rarement 2-3. P rigone brun pourpre, les deux s pales inf rieurs tant soud s sur une partie de leur longueur en une pi ce r fl chie sous le labelle, le sup rieur dress en visi re au-dessus du labelle, et les deux p tales lat raux vrill s tal s r fl chis atteignant 5 cm de long. Labelle tr s grand renfl en sabot, long de 3-4 cm, sans peron. Colonne 2 tamines fertiles et un staminode (st rile). Floraison 5-6(-7). Chromosomes 2n = 20, 22.

Ecologie et sociologie

Le sabot de V nus cro t sur des sols secs ou fra cheur fluctuante, meubles, riches en bases, neutres mod r ment acides, humus de type moder, limoneux ou argileux, sur calcaires ou dolomie. En Suisse, il pr f re des habitats semi-ombrag s et tendant une certaine s cheresse estivale: for ts claires de feuillus mixtes (rablaies et autres for ts de ravin, h traies x rophiles orchid es) ou de r sineux (pin des et peuplements d'ifs), brousses claires jusqu' l' tage du pin couch . Dans les Alpes il peut coloniser, presque en pionnier, des sols graveleux-caillouteux, condition qu'ils soient assez riches en terre fine. A l'ombre il ne supporte la concurrence que sur des sols assez riches tandis qu'au soleil il n'appara t que sur des sols pauvres. Les sols de ses stations foresti res sont frais humides et biologiquement tr s actifs de l'automne au printemps, c'est- -dire pendant sa p riode de repos. Pendant cette p riode la teneur en nutriments disponibles est relativement lev e et le sabot de V nus conna t des processus m taboliques importants. La porosit (et une forte a ration) du sol semble aussi d terminante.

Collin enne subalpine avec un optimum l' tage monagnard, l'esp ce va de 300 2000 m d'altitude en Suisse (2200 m dans le Trentin, Italie).

Cypripedium calceolus est relativement ubiquiste: K NZIG (comm. litt.) cite 14 associations pour la Suisse seulement. Un optimum clair se situe n anmoins dans le *Cephalanthero-Fagenion* TX. 55 et sous les couverts transparents de l'*Erico-Pinion* BR.-BL. in BR.-BL. et al. 39. L'esp ce appara t en outre dans plusieurs associations du *Fagion,* du *Galio-Abietenion* OBERD. 62, des *Quercetalia pubescenti-petraeae* BR.-BL. 31, des *Origanetalia vulgaris* TH. M LL. 61 et d'alliances apparent es.

Milieu naturel: 6.2.1 (6.4.1)

Valeurs indicatrices: F2wR5N2H3D4L3T3K3.

Particularités de l'espèce

Ce g ophyte pr sente une fleur-trappe: un insecte attir par le grand labelle jaune glisse et tombe dans le sabot; prenant appui sur deux marches de poils succulents (correspondant deux zones translucides visibles sur la paroi du sabot), il peut ressortir, mais en effleurant les pollinies, qu'il emporte ainsi jusqu'au stigmate collant d'une autre fleur o il sera tomb dans le m me pi ge. Cette pollinisation implique surtout des abeilles solitaires (*Andrena* sp.) et d'autres petits insectes robustes. La maturation dure quatre mois, les premiers fruits sont m rs d but octobre. Le taux de fructification est faible (20-30%), on admet donc que la pollinisation crois e est obligatoire. Le sabot de V nus d pend de champignons symbiotes sp cifiques (mycorhizes) pour sa germination, mais l' ge adulte il est totalement ind pendant. Il ne commence fleurir qu'au bout de six dix ans et peut vivre plus de vingt ans. Le rhizome conserve son pouvoir de d bourrement probablement pendant des ann es voire des d cennies. Aucun hybride n'est connu en Europe. La germination de graines ex situ peut tre obtenue par un proc d sophistiqu , puis le reste de la culture est relativement facile. La transplantation (ill gale) de la nature dans un jardin se solde pratiquement toujours par la mort des plantes. On trouve dans le commerce des cultivars d'aspect identique mais mieux adapt s la culture.

Distribution générale et menaces

Le sabot de V nus est un l ment floristique eurasiatique (sub)continental, subm ridional bor al. Il est r parti (mais clairsem) surtout en Europe septentrionale, centrale et orientale. Son aire s' tend jusqu'en Sib rie et en Chine entre 45 et 60°N. En Am rique du nord vivent des taxons tr s apparent s. La limite occidentale court du delta du Rh ne au sud de la Belgique par l'est de la France; des avant-postes isol s se trouvent dans les Pyr n es (E, F) et dans le nord de l'Angleterre. Sinon l'esp ce manque en Islande, en Belgique, en Hollande, dans de nombreuses r gions littorales et dans l'essentiel de la r gion m diterran enne. Elle atteint au nord le 70e parall le et au midi le nord de l'Italie et de la Hongrie, la Roumanie et le Don. De petits avant-postes se trouvent dans les Abruzzes (I), les Rhodopes (BG) et en Crim e.

Stations les plus proches: Savoie, Haute-Savoie (Sal ve, Franclens, maintes localit s des Alpes L maniques et d'Annecy), Jura (tr s rare), Alsace (Rosenau, introduit?) (F), plaine du Haut-Rhin (Kaiserstuhl), Baar (p. ex. H fingen), Wutach, Hegau (p. ex. Ramberg), Jura souabe, r gion du Lac de Constance, avant-pays alpin (D), Vorarlberg, Liechtenstein (p. ex. Triesenberg, entre Steg et Malbun), Tyrol (p. ex. Trafoi, vall e de l'Inn pr s de la fronti re), Dolomites, Valteline, Pi mont (rare), Val d'Aoste (I).

Menaces: A maints endroits l'esp ce a r gress ou disparu. Dans pratiquement toute l'Europe elle est menac e ou fortement menac e.

Statut de protection

CH: Liste rouge, protection int grale; F, D, A, FL, (I); CB, EU/FFH.

Distribution et menaces en Suisse

Le sabot de V nus tait r parti dans de larges secteurs du Plateau et des Pr alpes. Il se trouvait en outre surtout en Valais central, dans le Binntal (VS), le Val Bedretto (TI), les centre des Grisons et en Basse-Engadine (GR). Il manquait par contre dans les secteurs siliceux des Alpes centrale et m ridionales, dans le canton de Gen ve et dans de larges portions du Jura. Actuellement, il existe encore dans le canton de Schaffhouse, dans des secteurs des Pr alpes, en Valais central, dans le centre des Grisons et en Basse-Engadine, o il est un peu plus r - pandu. Ailleurs il est rare. En Romandie il ne subsiste que quelques rares stations.

Menaces: Sur le Plateau et dans le Jura, l'esp ce a fortement r gress et se trouve tr s menac e. Dans les Pr alpes et les Alpes la situation est meilleure. Quant aux types de menaces et aux mesures envisager, on peut consulter K NZIG 1996: 5.4/5.5. En moyenne l'esp ce est tenue pour menac e. Suivant les r gions elle est seulement rare (p. ex. aux Grisons) ou au contraire menac e d'extinction (p. ex. Suisse occidentale).

Evolution des populations: recul l ger mod r dans les Alpes mais fort sur le Plateau et dans le Jura. Actuellement ce recul est partiellement ralenti par des mesures de protection.

Responsabilité

La responsabilit de la Suisse l' chelle internationale est moyenne.

Christoph Käsermann

Menaces	Mesures
fermeture du couvert, ombre, embroussaillement	coupes d' claircie et d broussaillage; favoriser des essences transparentes comme le fr ne et le pin
construction de pistes et de routes foresti res	informer les communes responsables; respecter les populations existantes
pacage en for t	enclore les populations menac es; tout au plus un pacage extensif
installations touristiques	pas de nouvelles installations; cr er des r serves naturelles
sylviculture intensive (passage de machines de d bardage, monocultures, plantation d'essences trang res la station)	adopter localement une sylviculture de peuplements clairs et ouverts; cr er des r serves naturelles foresti res, des lots de vieux arbres et des zones gestion conservative; laisser le bois dans les stations ou le d barder seulement sur sol gel
cueillette, arrachage, pi tinement par les chasseurs d'images	nouvelles r serves de flore; panneaux d'information; cl turer les secteurs menac s ou les surveiller pendant la floraison
changement du r gine hydique, abaissement de la nappe phr atique	favoriser ou restaurer l' coulement naturel des eaux
carence de connaissances en dynamique des populations et en cologie	clarifier les facteurs d terminants de la r partition , la relation symbiotique champignon/plante et ses rapports avec les facteurs biotiques et abiotiques, la prolif ration clonale, le rapport entre la dynamique de la population et les changements de l'habitat, etc.
populations restreintes et isol es	protection des stations (plan de zones); contr les p riodiques; visite de toutes les populations anciennes (plus mentionn es depuis 1980); garantir le suivi de l'efficacit des mesures

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Projets et contacts

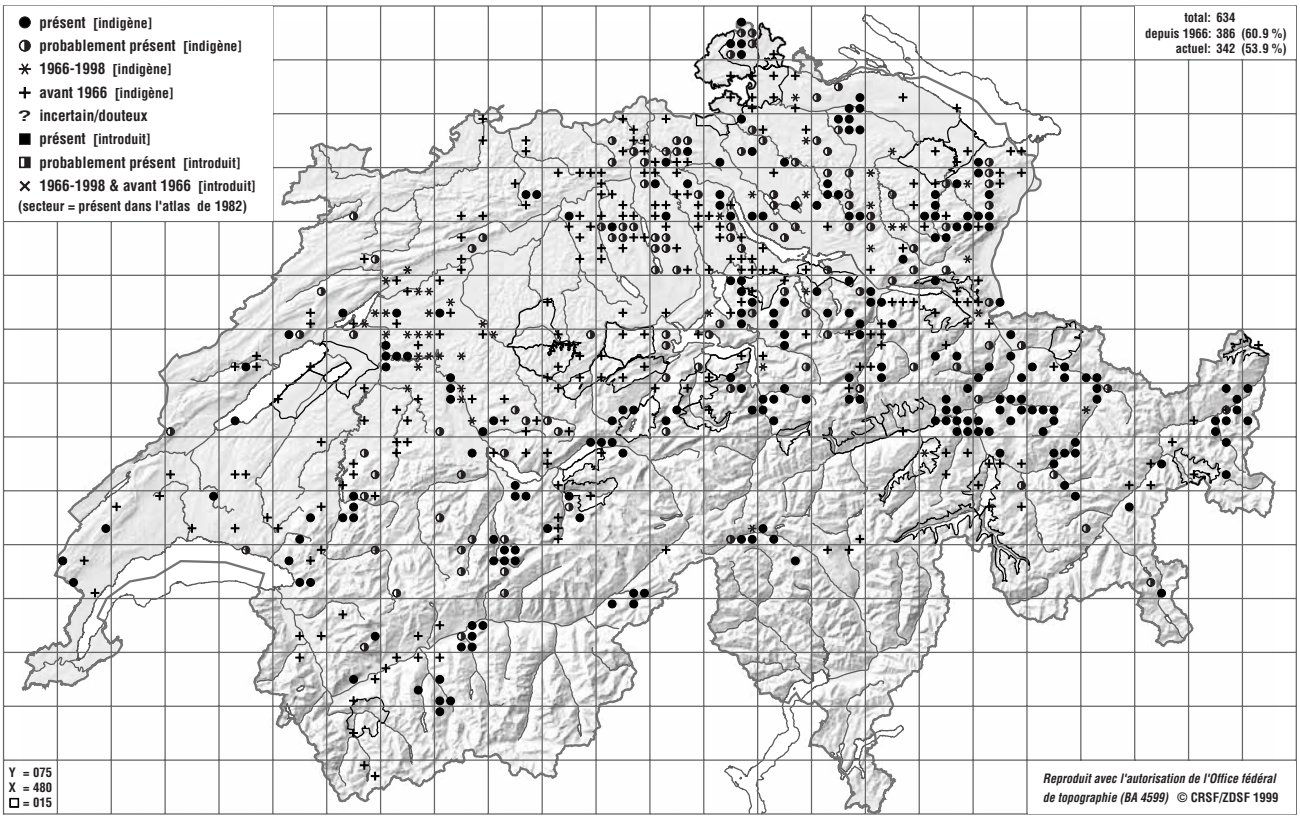
URS K NZIG, SIGMAPLAN, Thunstrasse 91, 3006 Bern.

VU ***Cypripedium calceolus*** L. – Sabot de Vénus – *Orchidaceae*

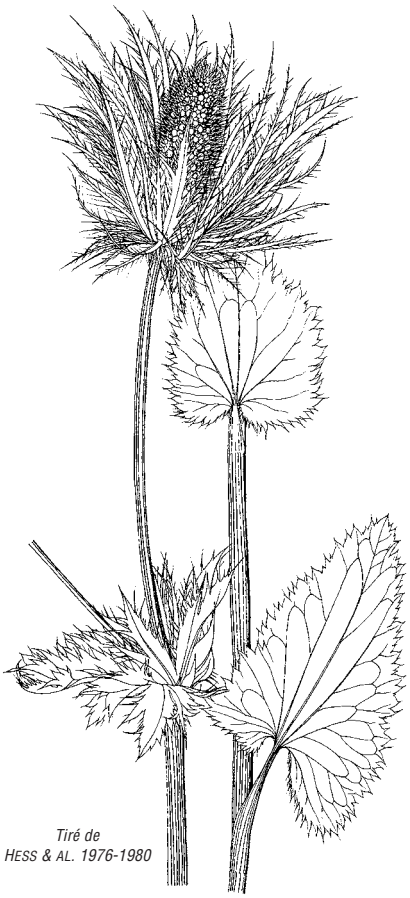
JU 1	PL 2	AN 3	AIO 4	AIE 5	AS 6
EN	**EN**	**VU**	**VU**	**LR(nt)**	**EN**

F	D	FL	A	I
à. surv.	**3+/VU**	**R**	**3r!/VU**	**VU**

Monde	CH
	VU/V



VU *Eryngium alpinum* L. – Chardon bleu – *Apiaceae*



Tiré de HESS & AL. 1976-1980

Description

Plante de 30-100 cm de haut. Feuilles radicales atteignant 25 cm, p tiol es, indivises, triangulaires-cord es et grossi rement dent es. Feuilles caulinaires sup rieures digit es, dent es-acicul es. Bract es bleues pennatilob es lobes termin s par des aiguillons, d passant l'inflorescence et mimant le p rigone d'une fleur compos e unique. Fleurs bleues de moins de 5 mm, sessiles et serr es sur un axe oblong, l'ombelle ainsi transform e en une massue atteignant 6 cm. P tales plus courts que les s pales. Fruit marqu de l g res c tes longitudinales garnies d'un rang d' cailles aigu s. Floraison 7-8(9). Chromosomes 2n = 16.

Ecologie et sociologie

Le chardon bleu cro t sur des sols frais, assez riches en nutriments, profonds, calcaires (tr s rarement pauvres en calcaire) et souvent argileux dans des pentes rocailleuses ensoleill es et en g n ral raides. Il pr f re des microbiotopes frais dans des Wildheuplanggen ou sur des bancs rocheux, des formations riches en phorbes tendant la m gaphorbiaie et des boulis grossiers. Il appara t m me parfois dans des brousses de pins couch s et des aulnaies vertes.

En Suisse, il est subalpin(-alpin) et va de 1400 2100 m d'altitude (de 1000 2500 en France).

Eryngium alpinum se rencontre principalement dans le *Caricion ferrugineae* BR.-BL. 31 (p. ex. dans le *Campanulo-Laserpitietum latifoliae* B - GUIN 72 du Jura fran ais) et dans des groupements apparent s l'*Adenostylion alliariae* BR.-BL. 25 et au *Calamagrostion* LUQ. 26. Dans les Alpes suisses il a aussi t mentionn dans l'*Eryngio-Centauretum rhaponticae* SUTTER 78, au Parc national de la Vanoise (F) dans le *Polygono bistortae-Eryngietum alpini* GEHU 84 (*Polygono-Trisetion* BR.-BL. et TX. ex MARSCH. 47 n. inv. TX. et PRSG. 51). Il doit se trouver en outre dans le *Festucetum spadiceae*. Quant aux formations des sites de foin des rochers (Wildheuplanggen) et des bancs rocheux, elles sont difficiles classer.

Milieu naturel: 4.3.3 (5.2.3)

Valeurs indicatrices: F3R4N4H3D4L4T2K2.

Particularités de l'espèce

Cet h micryptophyte a des caract res spectaculaires: le dimorphisme foliaire, l'orientation de l'inflorescence suivant le cours du soleil et le fait que l'involucre finement dentel ne s'ouvre qu'apr s le lever du soleil et se referme la nuit ou par temps frais. La r partition du chardon bleu a un caract re typiquement relictuel: il ne se trouve plus que dans des endroits quasi inaccessibles. C'est qu'autrefois cette plante embl matique des Alpes tait souvent cueillie ou arrach e par des collectionneurs, et qu'en plus elle est peu comp titive en p turage. Elle est cultiv e un peu partout (depuis au moins 1560 en Allemagne). La culture et la multiplication sont faciles.

Distribution générale et menaces

Cet end mique ouest-pr alpin va des Alpes maritimes par le Vorarlberg jusqu'aux Karawanken et aux Alpes juliennes avec un centre de r partition dans les Alpes occidentales. Il se rencontre en outre dans le Haut Jura fran ais, les montagnes illyriennes (Croatie, Bosnie, Mont n gro) et peut- tre dans les Tatra (SK). Par ailleurs il a t introduit ou s'est chapp de jardins maints endroits.

Stations les plus proches: Hautes Alpes (p. ex. environ 18 stations dans le Parc national des Ecrins), Is re (Belledonne, Oisans, Valjouffrey) Savoie (Bauges, Beaufortin, Haute Maurienne, Pralognan en Tarentaise), Haute-Savoie (Chablais: p. ex. Val d'Abondance, massif du Mont de Grange, des Cornettes de Bise et du Chauff , Bellevaux au massif du Roc d'Enfer; Alpes d'Annecy: p. ex. Montmin, Parmelan; les Contamines-Montjoie), Haut Jura fran ais (Reculet, Col de Crozet, Colomby de Gex) (F), Vorarlberg (disparu? autrefois plusieurs stations dans le Gamperdonatal, Br ggelealp pr s de Brand), Liechtenstein (Sareiserjoch-St. Rochus), Alpes carniques, Alpes cottiennes (p. ex. haut Val Stura) (I).

Menaces: Cette esp ce attractive est class e rare l' chelle mondiale (UICN 1998), mais dans de nombreux pays elle est d j menac e.

Statut de protection

CH: Liste rouge, protection int grale; F, (A), (I); CB, EU/HFF.

Distribution et menaces en Suisse

Le chardon bleu poss de plusieurs secteurs actuels de r partition dispers s, avec une pr - dominance dans les Pr alpes valaisannes, vaudoises et fribourgeoises: Chablais autour du Lac de Tanay (VS), des Rochers de Naye (VD) par les Verraux jusqu'au Mol son (FR). Il existe quelques autres stations en Valais (Val d'Illiez, La Creusaz sur Les Mar cottes, Catogne [naturalis], Sanetsch), dans les cantons d'Unterwald et Uri (Melchthal, environs d'Engelberg), dans le Alpstein au Seealpsee (SG) et aux Grisons (Gafiental St. Ant nien, sur Langwies, Nufenen). Dans le Chablais valaisan entre le Grammont et le Vallon du Trient il pourrait bien exister d'autres petites populations inconnues. Les populations de la r gion de Charmey (FR), de la Vall e d'Anzeindaz (VD), de la Dent de Morcles et du L tschental (VS), de l'Oltschiburg au S du Lac de Brienz (BE), du Safiental sur Schiers, Saas et Tschiertschen (GR) n'ont pas t confirm es depuis longtemps d j , mais elles existent peut- tre encore. L'esp ce est cultiv e dans les jardins et les cimeti res, d'o elle se r pand facilement dans la nature. Elle a par ailleurs souvent t introduite par des amis de la nature dans des biotopes naturels: c'est ainsi que les populations du Jura l'est de La D le [Marais des Amburnex (VD) et Creux du Van (NE) tout au moins], du Pilate (LU) et du Rigi (SZ) ne sont certainement pas autochtones. A Sedrun et Tschamutt (GR) le chardon bleu est cultiv en grand pour le commerce.

Menaces: En Suisse l'esp ce a besoin de formations v g tales peu perturb es, elle semble mal supporter le pacage pr coce (avant la maturation de ses fruits) et tout changement de mode d'esploitation. Si l'on y ajoute l'attractivit de la plante et le faible effectif des populations, l'esp ce doit tre consid r e comme menac e dans l'ensemble du pays. Hormis les Pr alpes occidentales (VS, VD, FR), elle est m me fortement menac e voire menac e d'extinction.

Evolution des populations: recul moyen jusqu'au milieu du si cle, l ger aujourd'hui.

Responsabilité

La Suisse a une forte responsabilit l' chelle internationale.

Christoph Käsermann

Menaces	Mesures
changements de mode d'exploitation	maintenir la fauche traditionnelle; ne pas r exploiter des surfaces favorables qui ont t longtemps laiss es en friche; contrats d'exploitation
pacage trop pr coce	pacage seulement en automne (apr s la fructification) et extensif, sinon cl turer
embroussaillement	d broussailler
constructions (quipements touristiques, routes, canalisations)	planification soign e et respectueuse de l'esp ce dans tous les cas
cueillette, arrachage	panneaux d'interdiction de cueillette; r serves de flore; surveillance locale au moment de la floraison
exigu t du secteur de r partition, isolement des populations	protection de toutes les stations (plan de zones); contr les r guliers, carr s permanents; multiplication ex situ de mat riel de chaque secteur; essayer une r introduction exp rimentale suivie scientifiquement; cartographie d taill e des stations (1:250) hormis celles des Pr alpes occidentales; garantir le suivi de l' fficacit des mesures

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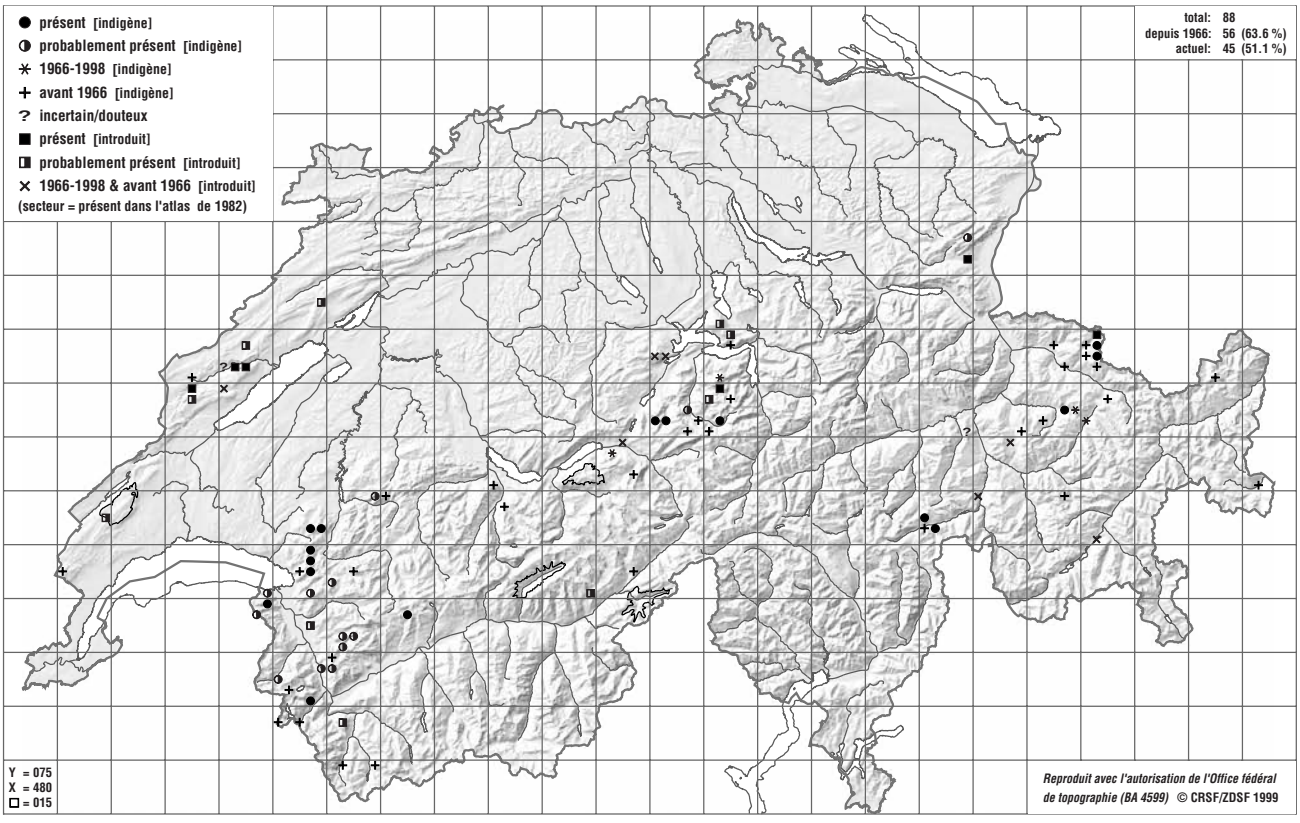
VU ***Eryngium alpinum*** L. – Chardon bleu – *Apiaceae*

JU 1	PL 2	AN 3	AIO 4	AIE 5	AS 6
EN*		**VU**	**EN**	**EN**	

F	D	FL	A	I
V	**–**	**R**	**3/VU**	**VU**

Monde	CH
R	**VU/V**



LR(nt) *Scorzonera laciniata* L. s. str. – Scorsonère en lanière – *Asteraceae*

Synonyme: *Podospermum laciniatum* (L.) DC.

Tiré de HESS & AL. 1976-1980

Description

Plante de 10-50 cm, annuelle hivernante. Tige rameuse, glabre comme les feuilles ou pubescente, en g n ral scabre. Feuille pennatis qu e segments distants lin aires-lanc ol s, le lobe apical un peu plus large. Capitules solitaires longuement p doncul s. Involucre de 10-15 mm la floraison, puis atteignant 40 mm, octogone. Fleurs jaune clair, de m me longueur que l'involucre. Fruit de 8-13 mm (support inclus), t tragone pourvu d'un support creux assez pais et plus clair. Aigrette plusieurs rangs de soies plumeuses. Floraison 5-7. Chromosomes 2n = 14.

Ecologie et sociologie

Ce scorson re est une rud rale typique qui pousse en groupes parfois fugaces sur des sols secs, en g n ral calcaires et sablonneux-argileux, dans des situations chaudes en t tendance continentale. On le trouve au bord des chemins, sur des talus de route, dans des vignobles ou en bordure, dans de jeunes friches, dans des champs de c r ales, sur des murs et des digues et dans les prairies arides lacunaires. En Allemagne on la trouve aussi dans des tr fli res, dans des terrains ± salins, dans des rochers et des boulis, et l'est galement dans des steppes.

En Europe centrale il est pratiquement limit l'aire de la vigne. Collin en-montagnard, il va de 480 1405 m (peut- tre 1460 m Vispertminen) d'altitude en Suisse (0-1900 m en Italie).

En Allemagne centrale l'esp ce est li e aux *Agropyretalia intermedii repentis* M LL et G RS 69 et au *Dauco-Melilotion* G RS 66: elle y colonise des zones de transition la terre nue. En Valais, selon WALDIS (1987), elle est r pandue dans le *Setario-Veronicetum politae* OBERD. 57, dans les friches du *Caucalido-Adonietum flammae* TX. 50 (ex OBERD. 59) et dans d'autres associations rud rales. En outre elle appara t marginalement dans des stations perturb es de *Mesobromion erecti* BR.-BL. et MOOR 38 em. OBERD. 57 et dans le *Festucion vallesiacae* KLIKA 31. Dans les vignobles elle se trouve dans des groupements pauvres en esp ces, presque toujours associ e *Tragopogon dubius* SCOP., parfois *Artemisia absinthium* L. et diverses esp ces d'*Amaranthus*.

Milieu naturel: 4.6.1

Valeurs indicatrices: F2wR4N3H3D5+L4T5K4.

Particularités de l'espèce

Ce th rophyte bisannuel est an mochore et entomophile mais l'auto-pollinisation est aussi possible. Si la plante est brout e et ne peut pas fleurir, il arrive qu'elle devienne vivace: sous un fort abroutissement la racine s' paissit et la plante devient gazonnante et produit plusieurs tiges florif res. La culture est pour l'instant inconnue, mais elle est certainement possible.

Distribution générale et menaces

El ment subm diterran en-sarmate, ce scorson re atteint sporadiquement le nord de la France, le sud du B n lux et de l'Allemagne septentrionale, la Boh me (CZ), le Bassin Pannonien (A, H) et la Russie centrale et va l'est par le Caucase jusqu l'Alta . La limite m ridionale passe par le Maroc, l'Espagne, l'Italie, la Dalmatie (HR) et les Balkans.

Stations les plus proches: Savoie (Maurienne et Tarentaise), Haute-Savoie (adventice La Menoge) (F), Bade-Wurtemberg (nord de la r gion de collines de loess et de calcaires du Haut-Rhin, Wurmlingen et Weipertshofen), Bavi re (au N d'Augsburg et l'E de Schweinfurt) (D), Val d'Aoste et nord de l'Italie (manque dans le Trentin-Haut Adige et en Lombardie) (I).

Menaces: Dans le nord de son aire l'esp ce a r gress par la dynamique naturelle, la destruction de biotopes et l'usage des herbicides. Au nord des Alpes elle a disparu maints endroits. Mais en Allemagne orientale et dans le sud-est de l'Europe elle n'est pas menac e.

Statut de protection

CH: Liste rouge; D.

Distribution et menaces en Suisse

Ce scorson re n'est jamais apparu qu'en Valais, dans la vall e du Rh ne entre Vernayaz et Vi ges, dans les vall es des Dranses, dans le bas Val d'H rens et les basses vall es de la Vispa. Aujourd'hui on peut mentionner au moins les localit s suivantes: vignoble de Fully et le long de la route de Fully Eulo, NE de Mazembroz, Charrat, Conthey, Venth ne, Veyras, pied du Mt. d'Orge Pont de la Morge, SE de Grimisuat et Chandolin de Savi se, sur St. L onard, Lens, sur la station de Granges-Lens, sous Chermignon, Salgesch, W et E de Varen, W de Lo che, Brentjong sur Lo che, Turtig et dans le Val d'H rens Longeborne, Vernami ge et St. Martin. D'autres localit s pas encore contr l es mais vraisemblables sont T rbel, Stalden, Emd, Visperterminen et peut- tre Sembrancher. Il existe en outre une indication douteuse pour B le. Il est certain que le Valais poss de d'autres stations non mentionn es et que l'esp ce, quoique rare, est assez largement r pandue dans la vall e principale. La sous-esp ce *calcitrapifolia* (VAHL) MAIRE a peut- tre exist (1865) dans la Valle Maggia Linescio (TI).

Menaces: l'esp ce a d'abord fortement r gress cause des destructions de biotopes, du changement de mode d'exploitation et de l'intensification de la viticulture. Mais depuis 2 d cennies, malgr l'exploitation intensive et l'usage des herbicides, elle a repris et s'est un peu tendue. Les causes de cette progression, qui doivent tenir aux m thodes viticoles autant qu'aux l g res d rives climatiques, sont encore inconnues et devraient tre tudi es.

Evolution des populations: recul assez fort, puis r tablissement et l g re progression depuis environ 15 ans.

Responsabilité

Comme les Alpes avoisinent la limite nord de l'aire, la Suisse a une responsabilit moyenne l' chelle de l'arc alpin.

Christoph Käsermann

Menaces	Mesures
mode d'exploitation du vignoble: sous-semis d'herbe, mulch, sarclage, traitement aux herbicides, fumure	dans le vignoble: pas de sous-semis d'herbe; pas de b chage profond; peu de mulch; limiter les herbicides (attention: ils favorisent peut- tre l'esp ce en liminant ses concurrentes !); n'adopter des mesures qu'en posant des objectifs de protection larges tenant compte des autres esp ces rares
am liorations fonci res du vignoble, alt rations du terrain, nivellement du relief	maintenir la structure traditionnelle du vignoble (l'esp ce a rarement t trouv e dans de grandes parcelles nivel es et intensives)
traitement aux herbicides et entretien des bords de routes	exclure les herbicides; pargner les stations
travaux de g nie civil	conserver les stations; informer les responsables
fort pacage	all ger la charge des p turages trop intensifs (en particulier Vernami ge)
irrigation par aspersion	viter d'arroser les stations comprises dans des prairies et des p turages; maintenir l'exploitation traditionnelle
concurrence	poursuivre les interventions qui limitent la concurrence: perturbations ad quates du tapis v g tal, travaux du sol et de la vigne
abandon/intensification de la culture c r ali re	maintenir un mode cultural extensif qui favorise les adventices rares (en particulier Brentjong)
embroussaillement	d broussailler si n cessaire
fauche trop pr coce	ne pas faucher avant juillet (talus de routes)
populations restreintes et isol es	contr les tous les 5-10 ans pour pouvoir intervenir en cas de r gression; suivi de l'efficacit des mesures
carence de connaissances en dynamique des populations et auto cologie	initier un travail de dipl me ou une th se sur ce sujet pour pouvoir favoriser l'esp ce de mani re ad quate

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LR(nt) ***Scorzonera laciniata*** L. s. str. – Scorsonère en lanière – *Asteraceae*

JU 1	PL 2	AN 3	AIO 4	AIE 5	AS 6
			LR(nt)		

F	D	FL	A	I
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Monde	CH
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