

**How much can we predict
alpine plant species distribution
at a very high resolution?**



Pritzelago alpina, Photo: Marietta Wilhelm, 2006

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ABSTRACT

Plant species distribution modeling needs predictive variables that describe the modeled area. In alpine areas topographic variables influence predictions more than in lower regions. Topographic variables also influence the climatic variables. These predictive variables change over small distances. This variation can be resolved by high resolution imagery from LIDAR surveys. High resolution in topographic and climatic variables can detect microhabitats. We investigated changes in predictive power when using different topographic resolution to model 31 alpine plant species in the Western Alps of Switzerland. We ascertained plant species characteristics to explain an association to these changes in predictive power. In general, high resolution does not improve the power to predict plant species distribution. However variables from high resolution imagery describe better the niche of the species, than do variables from low resolution imagery. Dispersal capacity, plant size, and the life forms “cushion” and forb show weak and inconsistent association with the model fit and the predictive power. On larger study areas with more sampling sites these tendencies may turn out to significant aspects for the used high variable resolution.

INTRODUCTION

Mountain areas present significant challenges for modeling plant species distribution. Every massif and valley has its own climatic regime (Körner, 2003) and differs in soil material composition (Ozenda, 1985). Mountains limit dispersal of some species and present at the same time refuge for other species (Udvardy, 1969). Moreover, the influence of climatic factors and topography impacts regional species composition (Ozenda, 1985). The species composition variation between regions influences plant distribution models. These models could lose their predictive power when projected to other similar alpine areas (Randin and al., 2006). Every area needs to be modeled individually, with data on its own topographic and climatic conditions. These issues may lead to varying conclusions on the importance of environmental variables among regions.

Alpine species distribution prediction requires climatic and topographic variables. These variables become more useful with increasing elevation in the mountains (Körner, 2003), because competition between neighboring plants appears more often than facilitation (Choler et al., 2001). Competition limits plant species installations on suitable places while facilitation can favor growth and development in unsuitable regions. Therefore plants use topographic relief to find growing places protected from avalanches, extreme wind forces, and cold temperature. These factors limit plant development (Hopkins, 2003). Mean air temperature declines with elevation. But soil surface temperature at high elevations can be as hot, as those at low elevations (Körner, 2003). Even if climate variables are important for prediction of species distribution, measurements at standard climate stations do not correspond well to the microclimates to which alpine species are exposed. The interpolation of the measurements in space generates additional uncertainty (Guisan and Zimmermann, 2000). Proximal climatic measurements describe microenvironments corresponding

to plant species niches. These climatic variables may improve the accuracy and precision of distribution models of alpine plant species.

Alpine plant species are adapted to extreme environments (Körner, 2003; Billings and Bliss, 1959) or the plants grow in habitats protected from these extreme factors, for example under deep snowbanks (Billings and Bliss, 1959). High resolution of topographic variables may improve the description of microhabitats and hence the power of distribution predictions of alpine plant species. The increase of the resolution of topographic variables in distribution models does not change the predictive power of these models (Lassueur et al. 2006). Microtopographic factors influence the predictive ability at high elevation (Ozenda, 2002). There, plants show adaptation to varying topographic and climatic factors of mountain areas (Ozenda, 2002). In a modeling study, Gottfried et al. (1998) derived 1 m resolution environmental variables from aerial photography. Regardless of potential inaccuracy, high resolution improved their prediction of alpine plant species distributions. The emergent technique of airborne LIDAR allows creation of topographic variables at a high resolution (Lassueur et al., 2006). On sufficiently large areas these variables may increase the predictability of species adapted to extreme environments (Rietkerk et al., 2002).

Plant species can grow in habitats, niches, where environmental conditions do not limit development. The niche determines which species characteristics maximize plant fitness in the local environment (Ackerly et al. 2000). Extreme environments require extreme adaptations. Lassueur et al. (2006) showed that resolution does not affect prediction quality of species distribution models. The influence of microenvironment on the fit and predictive power of distribution models may be important only for a few plant species, depending on their characteristics. Some plant characteristics should therefore help to determine optimized resolution of predictive variables.

In the following study we tested two hypotheses.

- If proximal climatic variables and variables of very high resolution can improve quality of distribution prediction of alpine plant species.
- If species characteristics influence quality change in modeling with variables of different resolution.

To investigate importance of predictive variables in modeling distribution prediction, we used the presence/absence data of 31 alpine species collected in the Western Alps of Switzerland. We compared fit and predictive ability of predictive distribution models. We used generalized linear and generalized additive method. To test the influence of proximal climatic variables on quality of distribution prediction we compared distribution models containing proximal climatic variables with models containing standard climatic variables. We tested quality change of distribution prediction of models containing variables at 2 m resolution with models containing variables at 25 m resolution. Finally, we analyzed species characteristics influence in change of predicting power and model fit between distribution models with varying variable resolution.

MATERIAL AND METHODS

Study Site

The study area of Anzeindaz is a west-east oriented plateau of 25 km² located in the western Alps of Switzerland (Figure 1). This area is bordered on the North by the Diablerets Mountains and to the South by the Muveran massif. Elevation ranges from 1900 to 3210 m at the top of the Diableret peak.

The vegetation is distributed according to the typical climax of sub-alpine (meadow and grassland vegetation) and alpine belt vegetation (high-elevation taxa). In the sub-alpine zone the landscape has been modified for centuries by human activity, first by intensive wood use and then through grazing by cattle and sheep. The main effect of human use has been the lowering of timberline by several hundred meters. In the alpine zone, the vegetation is little affected by human activities. The study area holds 300 plant species, which corresponds to one tenth of the Swiss flora (Randin et al., 2006).

Vegetation data

Sampling strategy of vegetation plots

We selected the locations of the sampling plots according to a random stratified sampling strategy (Hirzel and Guisan, 2002). 36 strata were defined by combining three elevation classes (1900 – 2200 m, 2200 – 2500 m, and > 2500 m), three slope inclination classes (0° - 5°, 5° - 45°, > 45°), two aspect classes (North, South) and two topographic convexity classes (convex, concave). The stratification was done at a 2 m resolution and for each stratum we selected randomly eight pixels. We used vegetation samples collected during a previous study, as well as new plots, to complement the data. We omitted in the study insufficiently represented strata. We controlled that no strata were over represented after sampling.

We sampled 63 plots (4 m²) in August 2006. We registered the exact coordinates of the centre of each plot using a Trimble® GPS system, with an accuracy of less than 1 m after a differential post-correction (Lassueur et al., 2006). The plants of each sampling point were exhaustively inventoried (Randin et al., 2006). The previous 86 plots sampled in the summers 2002 to 2005 were sampled identically.

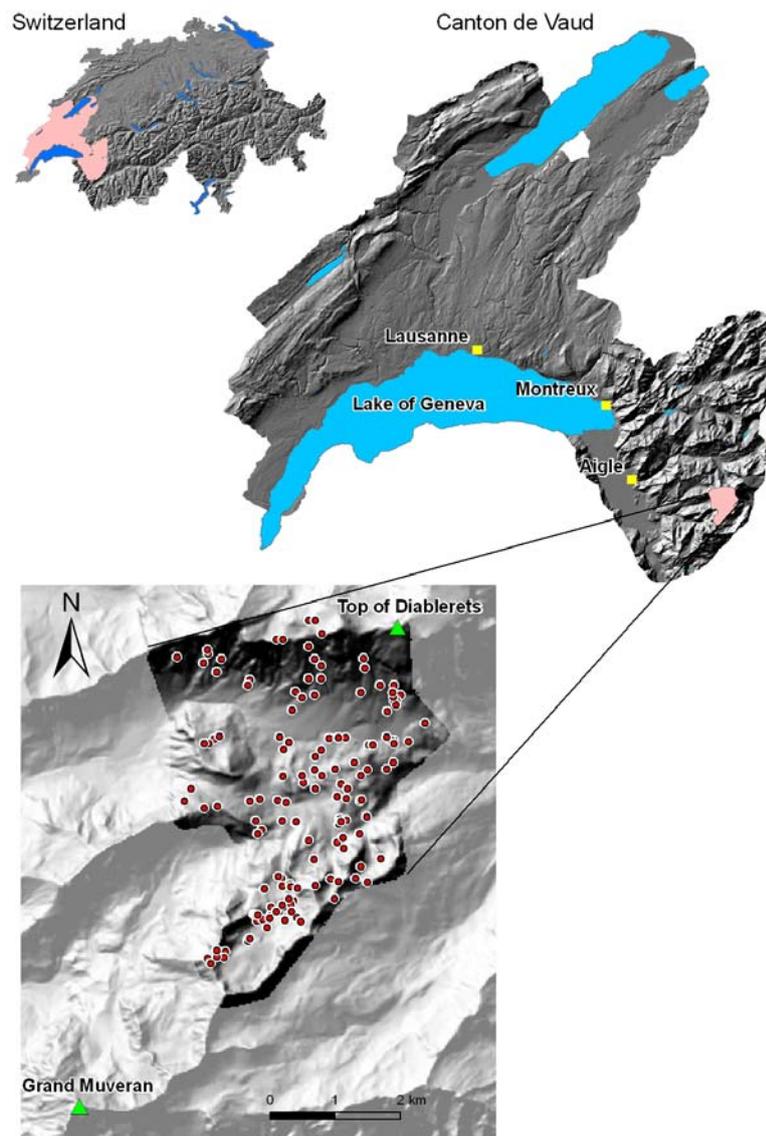


Figure 1 – Study area: This high plateau is located in the Prealps of the Canton de Vaud (Switzerland). It is situated between the Diablerets mountains and the Muveran massif. The points correspond to the 149 realized vegetation sampling sites.

Environmental data

Topographic variables

We generated two identical sets of topoclimatic environmental predictors at 2 m and 25 m spatial resolution. All spatial predictors were derived directly or indirectly from two different Digital elevation Model (DEM), one at a 25 m resolution of the Federal Office of Topography (www.swisstopo.ch) and the other with a 1 m resolution from the canton de Vaud (for the latter, see methods in Lassueur et al., 2006). In order to calculate the variables with a 2 m resolution, we resampled the 1 m resolution DEM with a bilinear interpolation algorithm (ArcGIS 9.1 software (ESRI, 2004)). The slope, profile of curvature, plan of curvature, curvature, flow accumulation, and flow length were based on the DEMs and calculated using ArcGIS. The only qualitative variable is a classification of landcover (Vector25, Swisstopo), which we classified into three categories: pastures/grassland, cliffs (solid rocks), and rockfall.

Climatic variables

We derived solar radiation for July, August and September from the DEM (Zimmermann and Kienast, 1999). We calculated moisture Index, an average atmospheric water balance, for the same period (Zimmermann and Kienast, 1999). The precipitation maps used for that are from the Swiss Federal Institute of Forest, Snow and Landscape Research (WSL). The temperature layers were based on the interpolation (Table 1) of data from 65 temperatures loggers (iButton temperature logger, model DS1921L, maxim integrated products; www.ibutton.com) that recorded from the 7th of July to the 4th of September 2006 (Figure 2). We built mean, minimum and maximum temperature maps for the surface temperatures (measured at ground surface) and for the soil temperatures (measured at 5 cm below the surface) (Figure 3) with variables at 25 m and 2 m resolution. The cap of the surface logger always faced south to seize the maximum amplitude of temperature that plant species can experience.

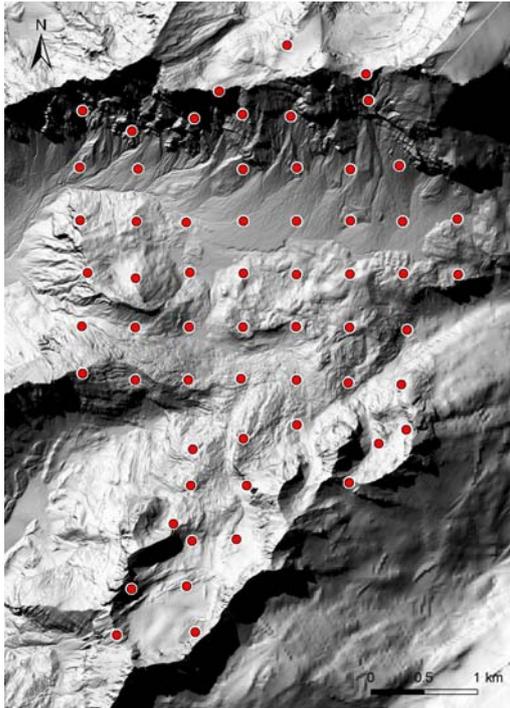


Figure 2 – Positions of the 65 temperatures loggers.



Figure 3 – Temperature logger, the cap of the surface logger is facing the South

Statistical analysis

Temperature models

Since soil and surface temperature are affected by topographic factors and texture of the soil (Körner & Paulsen, 2004) we used topographic variables for modeling proximal temperature variables. We used Gaussian generalized linear models (GLM; McCullagh and Nelder, 1989) to calculate the coefficients of each variable for the different temperatures (mean, minimum and maximum of soil and surface temperature). We constructed the models without stepwise elimination of the variables (Table 1) to conserve comparability between the temperature maps. We calculated the fit of the model (D^2 values) as the proportion of explained deviance (McCullagh & Nelder 1983).

Table 1 – Topographic and climatic variables used to interpolate temperature variables

Variables	Abbreviation	Details	References
DEM 25 m		Digital elevation model	Federal Office of Topography (Swisstopo)
DEM 1 m		Digital elevation model	Lassueur et al. (2006)
Landcover		Landcover classification	Vector25 (Swisstopo)
Global solar radiation [kJm ⁻² day ⁻¹]	Sum_srad	Monthly average of daily global solar radiation from July to September	Kumar et al. (1999)
Topographic convexity	Topo	Slope inclination	Zimmermann N. E. (unpublished) ArcGIS (ESRI, 2004)

Table 2 – Environmental and Climatic variables build to model habitat suitability of the 31 plant species. The last four variables were omitted after PCA analysis.

Variables	Abbreviation	Details	References
Topographic convexity	Topo		Zimmermann N. E. (unpublished)
Slope [degrees]		Slope inclination	ArcGIS (ESRI, 2004)
Profile curvature	Prcurv		ArcGIS (ESRI, 2004)
Flowlength	Flow_len	Length of flow to each cell	ArcGIS (ESRI, 2004)
Moisture Index [mm day ⁻¹]	Mind	Monthly average of daily atmospheric water balance from July to September	Zimmermann and Kienast (1999)
Temperature		Mean of air temperature, in 2 m height	Swiss Federal Institute of Forest, Snow and Landscape Research (WSL)
Temperature	MeanTS MinTS MaxTS	Mean, minimum and maximum temperature for ground and surface from July to September	See method in this article
Plan curvature	Picurv		ArcGIS (ESRI, 2004)
Curvature	Curv		ArcGIS (ESRI, 2004)
Flow accumulation	Flow_acc		ArcGIS (ESRI, 2004)
Global solar radiation [kJm ⁻² day ⁻¹]	Sum_srad	Monthly average of daily global solar radiation from July to September	Kumar et al. (1999)

Species prediction

We selected 31 species occurring at least 20 times in our sampling sites to build species distribution models. We used the *ade4* library in R (R Development Core Team, 2005) to make a principal component analysis (PCA; Venables, and Ripley, 2002) with all available variables (Table 2). The PCA supports our selection of the predictors (predictive variables). We eliminated correlated predictors when explaining little variance. Finally, we used four climatic and four topographic variables for plant distribution models. The climatic variables were limited to the period of temperature recording. We used mean, minimum and maximum of the surface temperature and moisture index. The environmental variables consist in slope, profile of curvature, flow length and topographic convexity. We constructed three different models. The first model (*wsl model*) contains standard climatic variables provided by the WSL and all variables are at a resolution of 25 m. For the second model (*25 m model*) proximal climatic variables substitute standard climatic variables. The third model (*2 m model*) incorporates proximal climatic variables and all variables are at a resolution of 2 m. *Wsl* models are limited to six predictors, because minimum and maximum temperatures were unavailable. We used generalized linear models and generalized additive models (GAM; Hastie and Tibshirani, 1986) to construct the models. We did the models without stepwise selection to conserve comparability between models. The models differ only in variable resolution or in type of climatic variables. To compare effects of these differences, we used area-under-the-curve measure (AUC) (Fielding & Bell 1997) and its cross-validated version with ten folds. We examined the significances of AUC-CAL and AUC-EVAL differences, with paired t-test.

We determined the influence of species characteristics (dispersal capacity, mean and maximum plant size, elevation and life form (Table 3)) on the variable resolution of the better model (2 m or 25 m). We examined the correlation of each species characteristic with the difference of models with different resolutions of variables

analyzing AUC-CAL and AUC-EVAL values of the GLM and GAM models. Spearman correlation test tests correlation significances of dispersal capacity, elevation and plant size, t-test analyzes the correlation of life forms.

Table 3 – Species characteristics used

	Definition	Classification			Reference
Dispersal capacity	Estimated dispersal distances [m] within which respectively 50, 95 and 99% of the seeds are dispersed	50%	95%	99%	Vittoz and Engler (submitted)
		1: 0.2	0.5	1	
		2: 0.4	1	5	
		3: 1.5	4	20	
		4: 15	40	200	
		5: 40	100	500	
		6: 80	200	1000	
		7: 400	1000	5000	
Maximum and mean plant size	Size of species [cm]	No classification			Aeschimann et al. (2004)
Elevation	Elevation Index	Montane, subalpine, alpine, nival			Vittoz et al. (to be submitted)
Life form		Grass, forb, cushion, shrub			Randin et al. (to be submitted)

RESULTATS

Temperature maps

The difference between the best and the worst D^2 values of the interpolated temperature variables was important. We obtained D^2 value of 0.87 for ground mean temperature and 0.86 for the surface mean temperature. The D^2 value of minimum temperature was 0.41 for surface temperature and 0.58 for the soil temperature. The D^2 of the maximum temperature is 0.41 for the ground surface and 0.34 for soil temperature. We visually observed influence of the 25 m-DEM on standard temperature interpolation (Figure 4a). The interpolation of the proximal temperature variables also shows the influence of relief structure (Figure 4b and 4c). Resolution influence on the two proximal temperature maps is less visible. We can better distinguish differences between temperature maps at different resolution on the zooms.

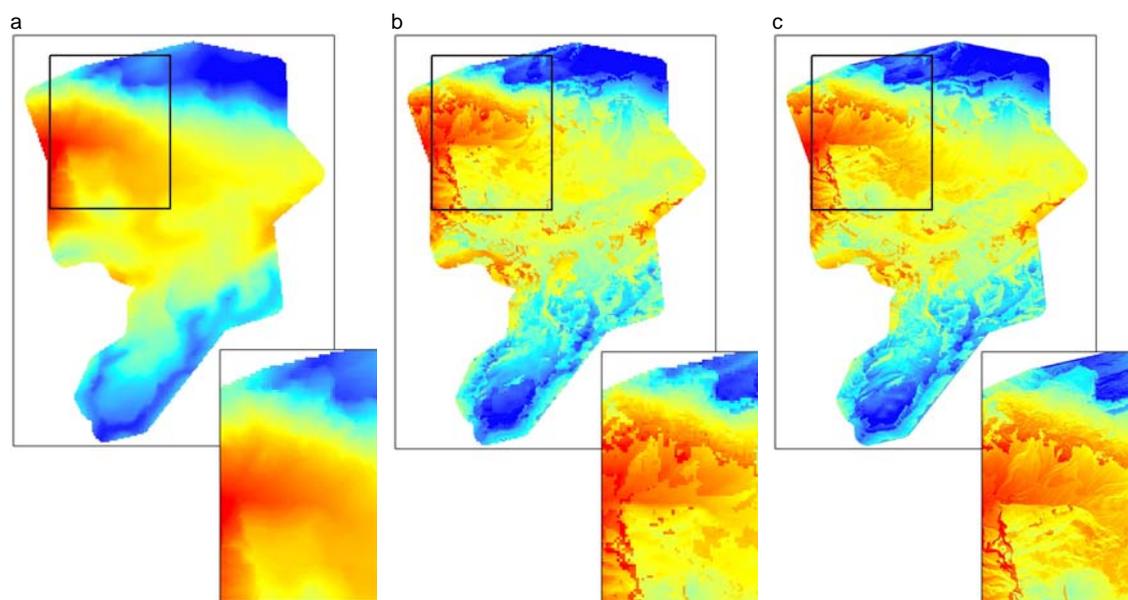


Figure 4 – Mean air / surface temperature from 7th of July to 4th of September
a. From Standard mean temperature from the WSL
b. Generated from temperature loggers with variables at 25 m resolution
c. Generated from temperature loggers with variables at 2 m resolution

Predictors' selection

Principal component analysis allowed excluding some of the possible predictors (Figure 5). The soil mean and minimum temperatures, the mean surface temperature and the solar radiations were grouped. From these positively correlated predictors, we kept only the mean surface temperature, because it explains more variance. For the same reason we also kept negatively correlated moisture index. We selected minimum and maximum surface air temperature as they seem not to be correlated with each others. We did not select maximal soil temperature due to its worse D^2 values. We modeled distribution prediction with topographic convexity, profile curvature, slope, and flow length as environmental variables. We omitted curvature and plan curvature because they are positively correlated to topographic convexity and explain less variance than last one. We also omitted flow accumulation which is correlated to flow length.

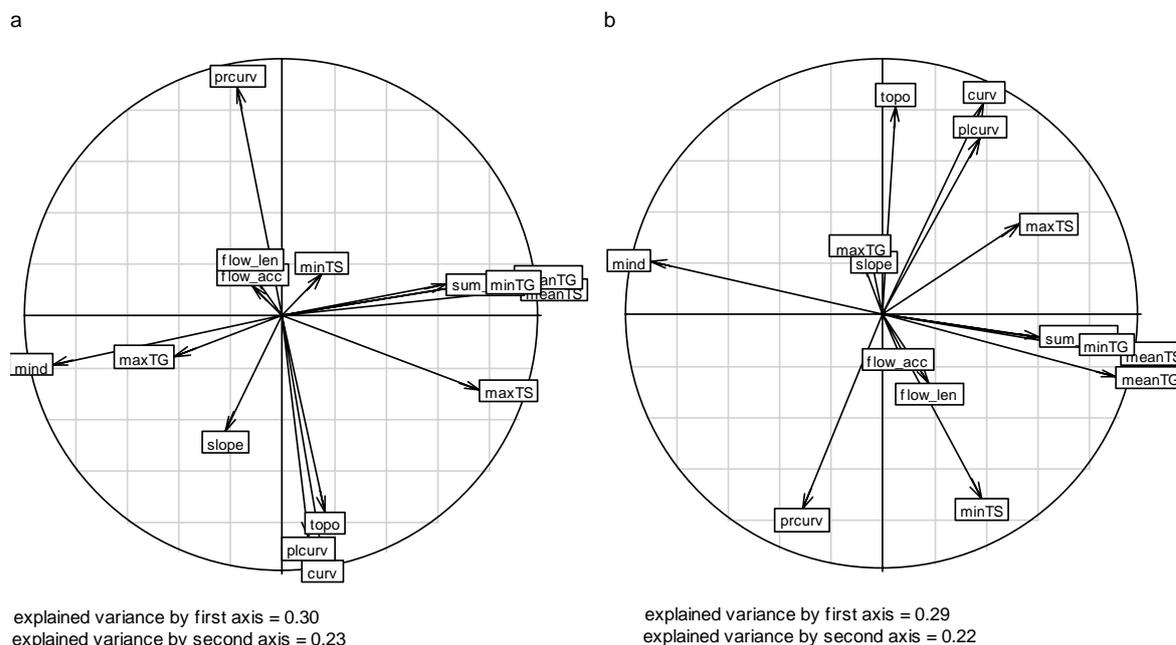


Figure 5 – Correlation circle of PCA to support the predictor selection

- with the predictors at 2 m resolution
- with the predictors at 25 m resolution

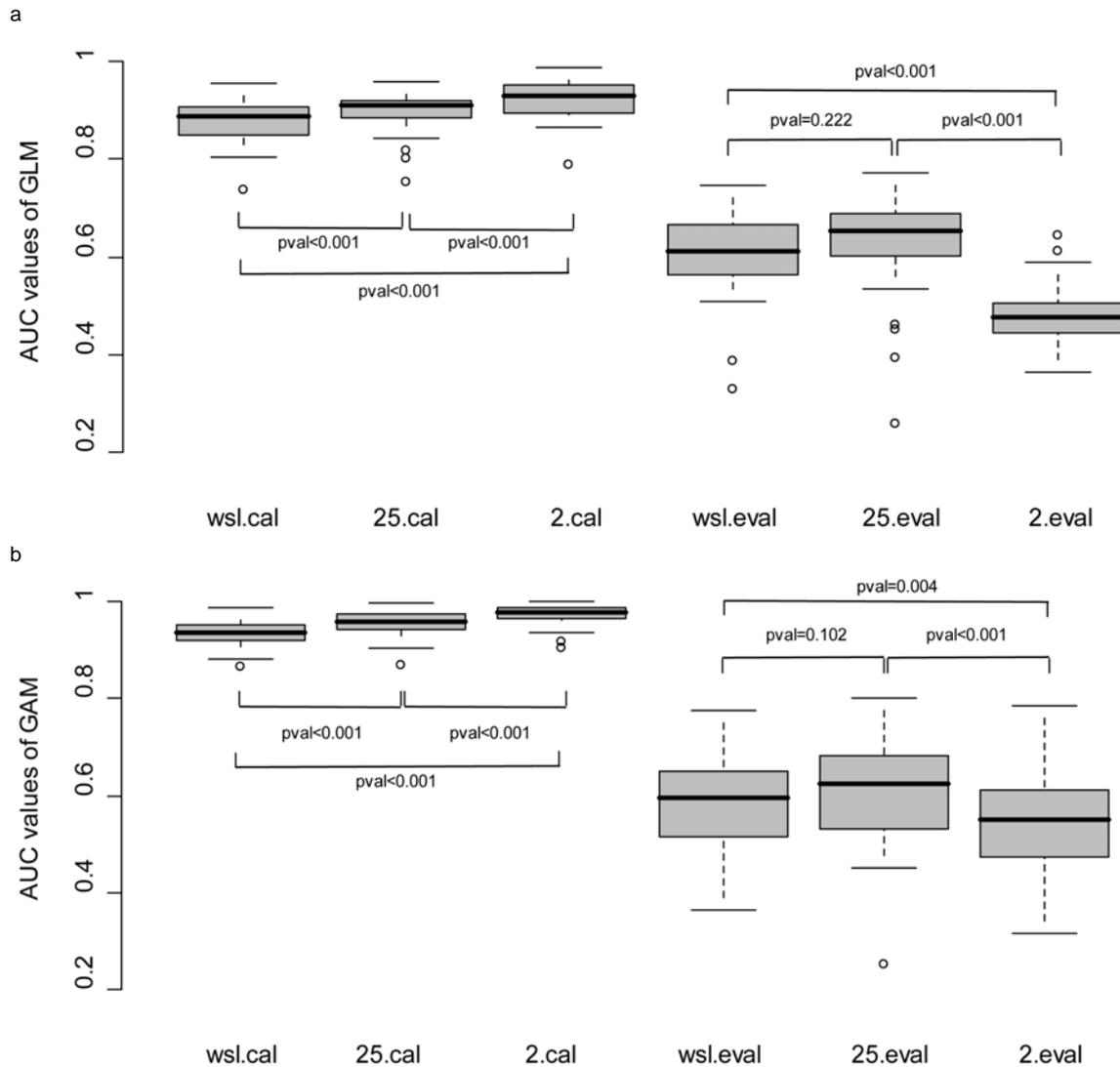


Figure 6 – Boxplot of AUC-CAL and AUC-EVAL values to compare different models

- GLM models
- GAM models

Models comparing

The boxplots (Figure 6) show the results of the comparison of the models with AUC-CAL values and AUC-EVAL values. AUC values of wsl models differ from AUC values of the 25 m models with proximal climatic variables. AUC-CAL values increase significantly using proximal climatic variables. AUC-EVAL values increase not significantly. AUC-CAL values of 2 m resolution model were significantly higher than these of the two 25 m resolution model and AUC-EVAL were significantly lower than the values of the other two models.

We compared individually AUC-CAL and AUC-EVAL values of 2 m resolution models with the values of 25 m resolution models for each species (Figure 7). The AUC-CAL value for nine species is higher when predicted with 25 m resolution predictors: *Festuca pumilla*, *Galium anisophyllum*, *Plantago artrata*, and *Poa alpina* for GLM, *Cerastium latifolium*, and *Potentilla aurea*, for GAM. *Alchemilla conjuncta*, *Ligusticum mutellina* and *Soldanella alpina* are present for GAM and GLM. AUC-EVAL values of eleven species increases using variables of 2 m resolution: *Campanula cochleariifolia*, *Cerastium latifolia*, *Saxifraga aizoides*, and *Thlaspis repens* for GLM and *Campanula scheuchzeri*, *Festuca violacea*, *Leontodon hispidus*, *Plantago alpina*, *Salix retusa*, *Saxifraga aizoides*, and *Soldanella alpina* for GAM.

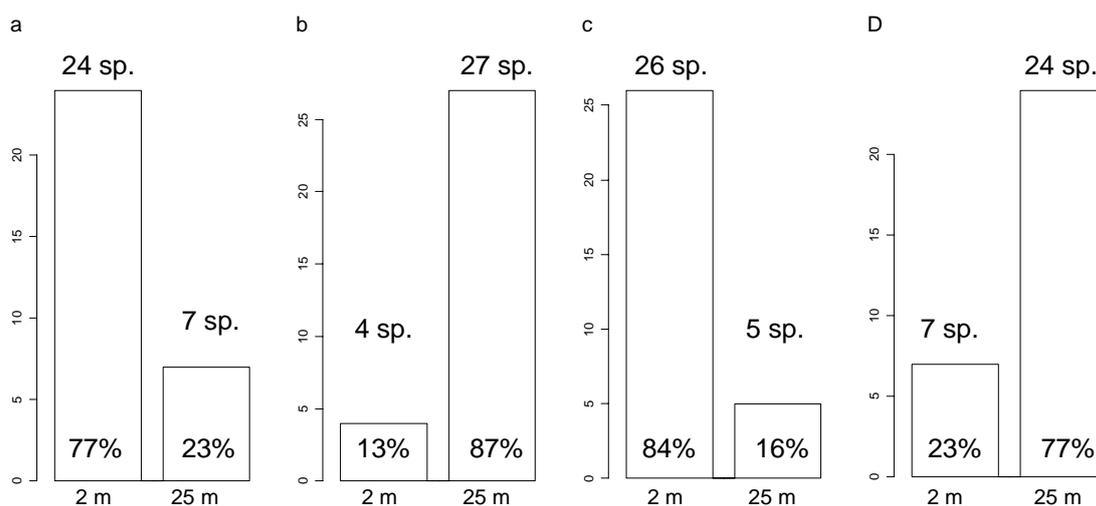
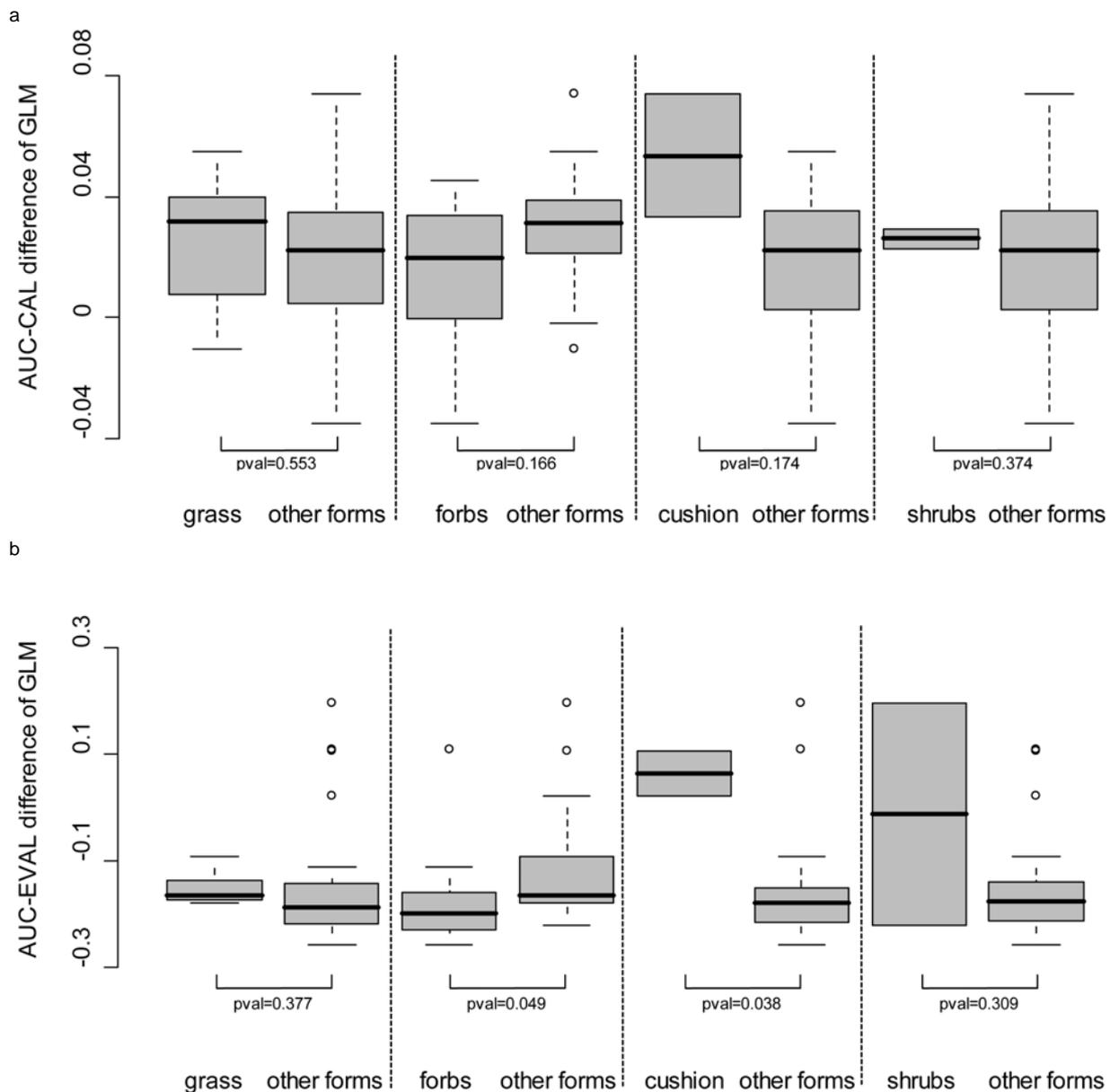


Figure 7 – Amount of species for which prediction quality improve with variable resolution of 2 m or 25 m.

- Increase of AUC-CAL values of GLM
- Increase of AUC-EVAL values of GLM
- Increase of AUC-CAL values of GAM
- Increase of AUC-EVAL values of GAM

Species characteristics

The analysis of the influence of species characteristics on AUC values of prediction models with different variable resolution reveals no significant and weak correlation. Correlation values and p-values of correlation test are shown in Appendix. Dispersal capacity of plant species is significantly ($p\text{-value} < 0.05$) or marginally significantly ($p\text{-value} < 0.1$) correlated with AUC differences. We found marginally significant p-values for correlations between plant size (mean or maximal plant size) and AUC-EVAL values differences of GAM. Elevation is not correlated significantly. Not all species



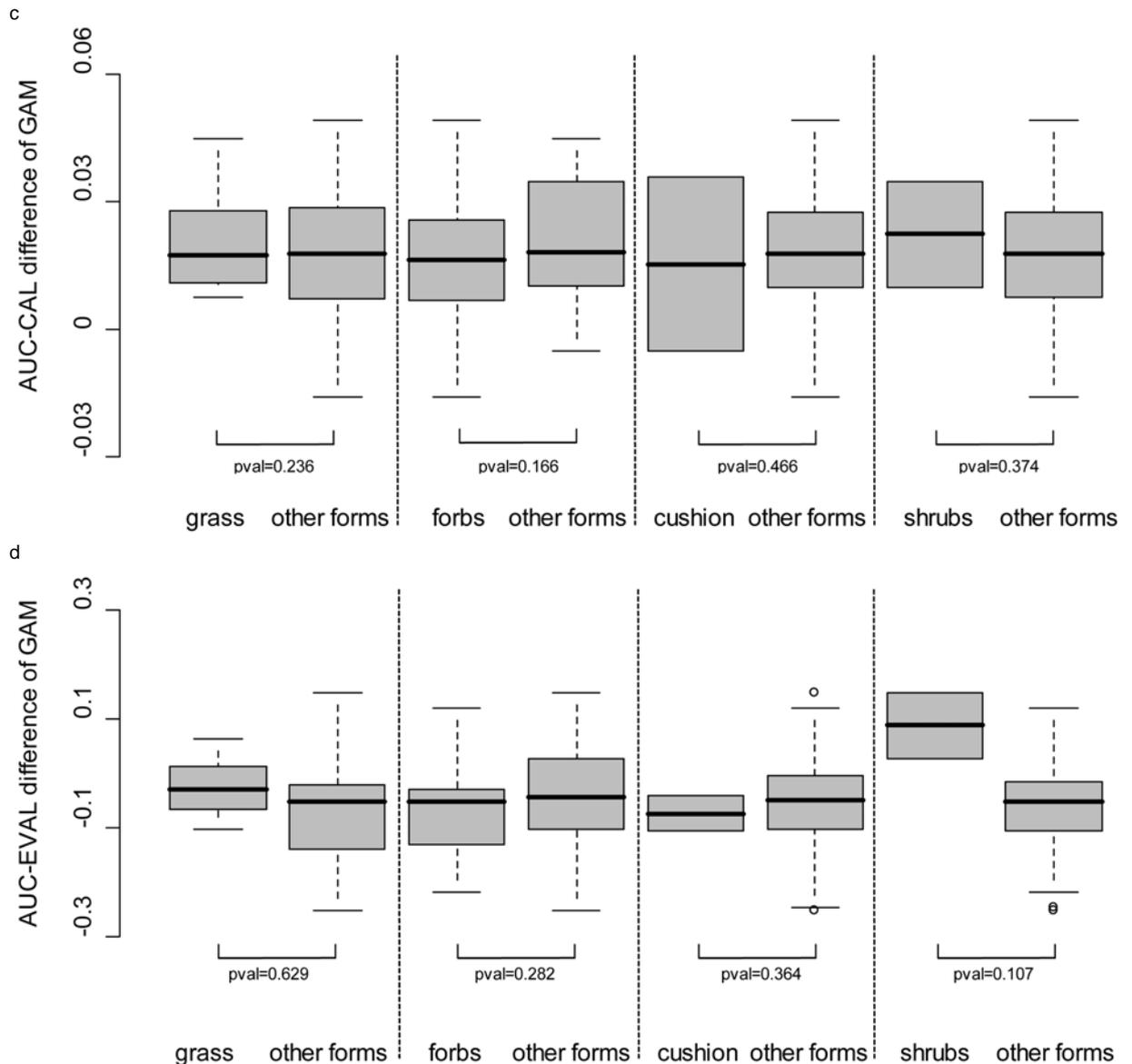


Figure 8 – Boxplot of AUC differences of variable resolutions (2 m – 25 m) of a given life form versus all other forms

- AUC-CAL differences of GLM
- AUC-EVAL differences of GLM
- AUC-CAL differences of GAM
- AUC-EVAL differences of GAM

life form does explain quality change in distribution predictions with different variable resolutions. The boxplots on Figure 8 show tendencies of influence of species life forms on AUC values. The analysis of AUC-EVAL differences of GLM models reveals significant p-values for forb and for “cushion” life form. P-values are not significant for and AUC-EVAL differences of GAM models and AUC-CAL differences.

DISCUSSION

Temperature maps

Mean ground and surface temperature maps have higher D^2 values than minimum and maximum temperatures. This statement applies for the resolution of 2 m and 25 m. Mean temperature combines measurements of the whole summer of 2006. This combination relativises extremely high or extremely low values. Temperature drops influence less mean temperatures. However maximum and minimum temperatures correspond to extreme values of the measurements. The predictability of these temperature variables decreases.

Minimum and mean soil temperature have better fitting than surface temperature. The soil temperature is influenced by texture and not by heating logger's material (Körner & Paulsen, 2004). The inertia of soil temperature is more important than of surface Temperature (Bliss, 1956); where the temperature depends on the shade of the relief or clouds and where thermal shocks occur. Maximum soil and surface temperature have worse D^2 values than other temperature predictions. Depending on soil material color, maximum soil temperature of higher elevation can reach the maximum temperature of lower elevations (Körner, 2003). Soil material and soil color present important factorial variables for soil surface temperature (Körner, 2003). They may increase the fit of temperature interpolations. Unfortunately, this kind of variables was not available for the study area.

Models comparing

Comparison of the models with variables at the same 25 m resolution reveals higher AUC values for both calibration and evaluation for the models with improved climatic variables. Proximal climatic variables improve the fit and power of models and their predictions. This can have several reasons: First, the number of measure stations we used to interpolate temperature compared to the modeled surface is higher than the

number of meteorological stations. We count 64 temperature loggers on a surface of 25 km² and 181 meteorological stations on the surface of Switzerland (41300 km²). Only seven of these stations are near the study area. We adapted the design of the logger establishment and temperature measurements with the aim to create a proximal variable for species predictions. Second, the standard temperature measures are made at on a height of 2 m from the ground to avoid microtopographic influence. Alpine plant size is not big enough to reach this height (Aeschimann, 2004). The temperature at this level is not relevant for these plants. We placed the loggers for the temperature measurements at the soil surface. Records at the soil surface or even some centimeters below ground represent the temperature that alpine plant species undergo (Körner, 2003). There, temperature influences species distribution (Hopkins, 2003). Additional, mean surface temperature is higher than mean air temperature. Maximal temperatures are higher and minimal temperatures are lower at the soil surface than in the air (Bliss, 1956). The influence of these temperature variables may also be responsible for increase of model quality with proximal climatic variables, because standard minimum and maximum temperature variables were not available.

Results show that variable resolution changes quality of distribution predictions. While AUC values at evaluation indicate better predicting power for variables at the 25 m resolution than at the 2 m resolution AUC values at calibration reveal better fit for models with variables of 2 m resolution. Variables at 2 m resolution become more precise and they describe the optimal niche for each species, based on the involved presence/absence data. High resolution improves niche description and decreases predicting potential, due to the high specificity of the niche description, which may not be equal to the real niche of species. This leads to the conclusion that high resolution over fits niches so that good prediction is not longer possible. Distribution models can even less been transferred to others equitable alpine regions or in the future (Randin et al., 2006).

Species characteristics

AUC-CAL and AUC-EVAL values for some species vary little between models of different variable resolutions. Therefore, it is interesting to show the influence of specific plant characteristics on the predicting power and fit of models with different variable resolutions: Which species possessing what kind of characteristics is linked with which variable resolution? The results of these analysis show tendencies of correlation between dispersal capacity and AUC differences. Quality of distribution prediction with variables at of 25 m resolution increases for species with long-distance dispersal capacities. The quality of the same predictions decreases for species with smaller dispersal capacities. The dispersal capacity corresponds to the radius of circle in what new plants can develop if environmental factors correspond to species niche. Only species with small-distance dispersal can profit from predictions with 2 m resolution as their seeds can not reach more than one cell of 25 m resolution. Correlations between AUC differences and the plant characteristics elevation and plant size are not significant. We can only derive following tendencies: Predictions for tall species increase with variables at 25 m resolution. Predictions for small species increase with variables at 2 m resolution. We expected increased AUC values for prediction with 2 m resolution with species of high elevation. We only examined alpine species with similar elevation index. So, the power of the correlation analysis is limited. Significant results may be deduced from analysis of species with higher elevation index differences.

Only some species life forms can explain difference of power and fit of distribution models with variables of different resolutions. Comparison between cushion plants and other life forms and the comparison between forb and other life forms give significant p-values for the AUC-EVAL differences of GLM models. For the other AUC differences tendencies are not significant. Forb plants are better predicted with distribution models with variables at 25 m resolution. The cushion life form may be

predicted with variables of 2 m resolution to increase predicting power of distribution models.

In general, species characteristics influence prediction quality changes between models with different variable resolution. The small study area could limit significance of analysis. More intensive study may have more power to reveal the importance of species characteristics on variable resolution for distribution prediction of alpine plant species.

We showed that the fit of models improved using 2 m resolution variables while their prediction capacity improved using 25 m resolution variables. Regardless this generality, models for *Alchemilla conjuncta*, *Festuca pumilla*, *Galium anisophyllum*, *Ligusticum mutellina*, *Plantago atrata*, *Poa alpina*, *Soldanella alpina*, *Cerastium latifolium*, and *Potentilla aurea* have a better fit with 25 m resolution variables. Most of these species occurs in pastures of alpine regions (Aeschimann et al., 2004). *A. conjuncta*, *G. anisophyllum*, *L. mutellina*, *P. atrata*, *S. alpina* and *P. aurea* have forbs as life form (Randin et al., in prep). *A. conjuncta*, *F. pumilla*, *G. anisophyllum*, *L. mutellina*, *P. atrata*, *P. alpina*, and *P. aurea* can disperse at long distances (Vittoz and Engler, submitted). Only *C. latifolium* does not present these characteristics. Its presence may depend on its installations on debris flow accumulations (Ozenda, 1985). Microtopographic variables do not influence this substrate. So, *C. latifolium* niche depends on an environment which's description does not change with high resolution. Variables of 2 m resolution improve prediction of following species: *Campanula cochleariifolia*, *Cerastium latifolia*, *Saxifraga aizoides*, *Thlaspis repens*, *Campanula scheuchzeri*, *Festuca violacea*, *Leontodon hispidus*, *Plantago alpina*, *Salix retusa*, *Saxifraga aizoides*, and *Soldanella alpina*. These typical alpine species occur after all on sparse environments (Aeschimann et al., 2004). *C. cochleariifolia*, *C. latifolia*, *S. aizoides*, *T. repens* live on avalanche path where a few nutrients are available. They are small species with low-distance dispersal capacities. *C.*

scheuchzeri and *S. alpina* also present these latter characteristics. Only *P. alpina* and *S. retusa* disperse far and *F. violacea* and *L. hispidus* have median dispersal values (Vittoz and Engler, submitted). The presence of *S. retusa* in this group may be due to its small size and because it grows along the ground (Aeschimann et al., 2004). It prefers wet areas which appear on topological depressions modelled by topographic convexity and profile curvature of 2 m resolution.

The variable resolution of best distribution prediction model depends on the species we want modeling. Species types should be modeled separately with optimized resolution. Higher spatial resolution does not mean higher accuracy, only smaller cells. Small plants and plants with low-distance dispersal are the only ones that seem to profit from high resolution, because their requirements are very specific, while large plants out-shadow such small differences by their own plant body. Very high resolution can easily over fit prediction models instead of improve it.

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APPENDIX

Appendix 1 – Spearman correlations between the species characteristics and the AUC-CAL or AUC-EVAL difference of the two resolutions (2 m – 25 m) and the p-values of these correlations.

AUC-CAL	GLM	p-value	GAM	p-value
Dispersion	-0.296	0.053	-0.126	0.250
Maximal size	0.124	0.253	-0.057	0.381
Mean size	0.139	0.228	-0.066	0.363
Elevation	-0.046	0.278	-0.046	0.403
AUC-EVAL				
Dispersion	-0.264	0.076	-0.322	0.039
Maximal size	-0.231	0.106	-0.199	0.141
Mean size	-0.243	0.093	-0.170	0.181
Elevation	-0.077	0.340	0.057	0.380

Appendix 2 – Abbreviations and full names of the species used for modeling distribution predictions

Abbreviation	Full species name
ANTVL	<i>Anthyllis vulneraria s.l.</i>
CACOC	<i>Campanula cochlearifolia</i>
CASCH	<i>Campanula scheuchzeri</i>
CASEM	<i>Carex sempervirens</i>
CELAT	<i>Cerastium latifolium</i>
CRAUR	<i>Crepis aurea</i>
EUMIN	<i>Euphrasia minima</i>
FEPUM	<i>Festuca quadriflora</i>
FERUB	<i>Festuca rubra aggr.</i>
FEVIO	<i>Festuca violacea aggr.</i>
GAANI	<i>Galium anisophyllum</i>
HOALP	<i>Homogyne alpina</i>
LEOHA	<i>Leontodon hispidus s.l.</i>
LIMUT	<i>Ligusticum mutellina</i>
LOCOR	<i>Lotus corniculatus</i>
NASTR	<i>Nardus stricta</i>
PHALP	<i>Phleum rhaeticum</i>
PLALP	<i>Plantago alpina</i>
PLATR	<i>Plantago atrata s.str.</i>
POALP	<i>Poa alpina</i>
POVIV	<i>Polygonum viviparum</i>
POAUR	<i>Potentilla aurea</i>
RANMO	<i>Ranunculus montanus aggr.</i>
SALRE	<i>Salix retusa</i>
SAXAI	<i>Saxifraga aizoides</i>
SECOE	<i>Sesleria caerulea</i>
SOLAL	<i>Soldanella alpina</i>
THLRE	<i>Thlaspi repens</i>
TRTHA	<i>Trifolium thalii</i>