# Introduction of Snow and Geomorphic Disturbance Variables into Predictive Models of Alpine Plant Distribution in the Western Swiss Alps

Authors: Randin, Christophe F., Vuissoz, Grégoire, Liston, Glen E., Vittoz, Pascal, and Guisan, Antoine

Source: Arctic, Antarctic, and Alpine Research, 41(3) : 347-361

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-41.3.347

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research on 02 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

*Arctic, Antarctic, and Alpine Research, Vol. 41, No. 3, 2009, pp. 347–361*

# Introduction of Snow and Geomorphic Disturbance Variables into Predictive Models of Alpine Plant Distribution in the Western Swiss Alps

*Christophe F. Randin*§*
*Grégoire Vuissoz**
*Glen E. Liston*†
*Pascal Vittoz*‡ *and*
*Antoine Guisan**

*Department of Ecology and Evolution, Laboratory for Conservation Biology, ECOSPAT group, University of Lausanne, CH-1015 Lausanne, Switzerland
†Cooperative Institute for Research in the Atmosphere, Colorado State University, Fort Collins, Colorado 80523-1375, U.S.A.
‡Faculty of Geosciences and Environment, University of Lausanne, CH-1015, Lausanne, Switzerland
§Corresponding author: Christophe.Randin@unil.ch

## Abstract

Indirect topographic variables have been used successfully as surrogates for disturbance processes in plant species distribution models (SDM) in mountain environments. However, no SDM studies have directly tested the performance of disturbance variables.

In this study, we developed two disturbance variables: a geomorphic index (GEO) and an index of snow redistribution by wind (SNOW). These were developed in order to assess how they improved both the fit and predictive power of presence-absence SDM based on commonly used topoclimatic (TC) variables for 91 plants in the Western Swiss Alps. The individual contribution of the disturbance variables was compared to TC variables. Maps of models were prepared to spatially test the effect of disturbance variables.

On average, disturbance variables significantly improved the fit but not the predictive power of the TC models and their individual contribution was weak (5.6% for GEO and 3.3% for SNOW). However their maximum individual contribution was important (24.7% and 20.7%). Finally, maps including disturbance variables (i) were significantly divergent from TC models in terms of predicted suitable surfaces and connectivity between potential habitats, and (ii) were interpreted as more ecologically relevant.

Disturbance variables did not improve the transferability of models at the local scale in a complex mountain system, and the performance and contribution of these variables were highly species-specific. However, improved spatial projections and change in connectivity are important issues when preparing projections under climate change because the future range size of the species will determine the sensitivity to changing conditions.

DOI: 10.1657/1938-4246-41.3.347

## Introduction

Mountain ecosystems are likely to be sensitive to global warming because of area reductions with increasing elevation (Guisan et al., 1995; Theurillat et al., 1998; Theurillat and Guisan, 2001; Diaz et al., 2003; Beniston, 2006). A recent global assessment of the potential impacts of climate change on these ecosystems predicts that they will experience unprecedented rates of warming during the 21st century, two to three times greater than observed during the 20th century (Nogués-Bravo et al., 2006).

In the last decade, species distribution models (SDM; Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005) have become efficient tools that provide a rapid estimate of the potential impacts of climate change on plant distributions (Bakkenes et al., 2002; Thomas et al., 2004; Thuiller et al., 2005). These tools statistically relate multiple abiotic habitat characteristics (*sensu* Kearney and Porter, 2004) with observed species occurrences, thus fitting the original definition of the Hutchinsonian environmental niche without explicitly requiring a mechanistic link between environmental gradients and population fitness (Guisan and Thuiller, 2005; Araujo and Guisan, 2006). In this study, using presence-absence data for 91 species, we intend to quantify the importance of two disturbance variables—a geomorphic index and a snow distribution index—in order to predict plant species distribution, compared to a set of commonly used topoclimatic variables. The following aspects make our study novel: (i) process-based disturbance variables specific to mountain systems were developed to improve predictions of plant distribution, and (ii) a statistical framework to test the contribution of these variables was also constructed.

Alpine environments, with their large landscape variability, represent a modeling challenge for plant species distribution (Guisan et al., 1998). The conic shape of mountains with large altitudinal gradients generate variations in temperature, including growing-season temperature, rainfall regime, contrasting energy fluxes between exposed and shaded faces and high variations in ultraviolet light (Seastedt et al., 2004). These factors are thought to explain much of the observed diversity of plant species distribution patterns.

One crucial task when building species distribution models is selecting the environmental predictor variables. These variables can be classified as indirect, direct, or resource variables (Fig. 1; Austin and Heyligers, 1989; Huston, 1994; Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). Indirect variables, such as altitude, slope and curvature, can only influence plant distributions through their correlation with variables that express variations in temperature and moisture that have a direct

1523-0430/09 $7.00

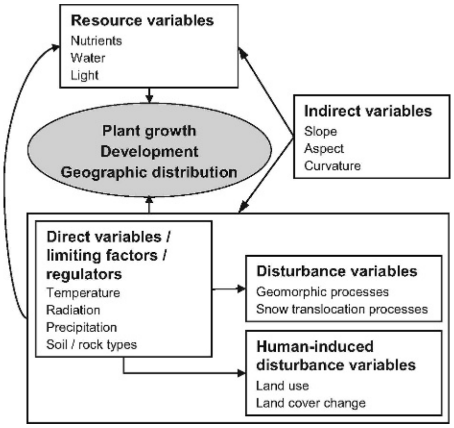

**FIGURE 1. Hierarchical modeling framework of resource, direct, and indirect variables used in species distribution models (adapted from Guisan and Thuiller, 2005).**

physiological impact on plants (Fig. 1). Temperature and rainfall are direct variables, while resource variables are those that are consumed by plants, e.g. nitrogen (Fig. 1; Austin, 2006).

At the micro- to local scale in mountain environments, models based on indirect predictors like topography can still provide accurate predictions. However, at the meso- to global scale, like Switzerland and other large areas, models based on indirect predictors lose power compared to models based on more proximal predictors (Guisan and Hofer, 2003; Guisan and Thuiller, 2005). This is because, at these scales, the same indirect predictor values at distant sites can translate into very different values for the more proximal predictors (i.e. direct or resource gradients), due to major climatic or geologic differences that take place between entire regions within the modeled area. Hence, although models fitted with indirect predictors at the local scale can still provide accurate predictions for the same area, they might lack the power to predict other areas, i.e. they can show weak transferability (Randin et al., 2006).

In order to generate models of plant distribution in alpine systems that have both high predictive power and good transferability to other areas, we need to develop and use variables that have a direct physiological effect on species or constitute resources used by the species (Fig. 1; Austin, 1980, 1985, 2006; Austin et al., 1984; Austin and Heyligers, 1989; Guisan and Zimmermann, 2000). A limited number of studies have used resource variables to project the geographic distribution of plant species, and in these rare cases, a limited set of tree species in complex dynamic simulations was used (Aassine and El Jai, 2002; Lischke et al., 2006; Schumacher and Bugmann, 2006). The main limitation of using resource variables is the lack of spatially explicit data (Austin and Meyers, 1996). In contrast, direct variables have been widely and successfully used to predict vegetation distribution in mountain regions (Guisan et al., 1998; Guisan and Theurillat, 2000; Dirnböck et al., 2003; Dullinger et al., 2004; Randin et al., 2006). However, disturbance variables (*sensu* Guisan and Thuiller, 2005; see Fig. 1) also have a direct impact on plant species distribution and have been neglected in most modeling studies even when the geomorphic control of vegetation was already demonstrated (Jenny, 1941; Walsh et al., 1994, 2003; Butler et al., 2003, 2007).

At high elevations in mountain areas, like those found in the alpine and nival vegetation belts of the Swiss Alps, the rugged landscape configuration leads to active and dynamic hydromechanical processes, like geomorphic ones. These processes affect vegetation at the local scale (Burga, 1999) but also modify the species diversity at a larger scale (Nichols et al., 1998). Geomorphic processes like rock slides, avalanches, or solifluction (Johnson and Billings, 1962; Erschbamer, 1989; Malanson et al., 2002; Körner, 2003) are processes that have an important impact on the soil surface and strongly drive the distribution of plant species and communities. Some adaptive traits of plant species are highly correlated with the conditions encountered in extremely disturbed situations, such as large root networks on moving rock slides (Jonasson and Callaghan, 1992).

In the alpine landscape, the spatial and temporal distribution (depth, persistence) of snow cover is influenced by topography and wind (Greene et al., 1999; Liston et al., 2000; Tappeiner et al., 2001). The snow cover itself determines species composition and spatial vegetation patterns (Walsh et al., 1994; Körner, 2003). Snowpack limits the length of the growing season (Billings and Bliss, 1959) but also offers protection against climatic stress, particularly wind desiccation (Schaefer and Messier, 1995), and constitutes a direct reservoir of nutrients for plant growth (Bowman, 1992). Snow also affects soil and vegetation moisture levels and can represent a severe stress factor through its dynamic effects, like avalanche paths or wind-induced snow translocation (Erschbamer, 1989; Körner, 2003). As a result, its overall effect is to decrease plant productivity (Billings and Bliss, 1959) and photosynthetic activity (Körner, 2003).

Topographic position (Gottfried et al., 1998; Guisan et al., 1998; Gottfried et al., 1999; Guisan and Theurillat, 2000; Dirnböck et al., 2003), drainage surface (Leathwick et al., 1998), or distance to ridges (Moore et al., 1991; Dirnböck et al., 2002) have been used as surrogates for disturbance processes in plant distribution modeling studies. Most of these studies were conducted in mountain environments (Gottfried et al., 1998, 1999; Guisan et al., 1998; Guisan and Theurillat, 2000; Dirnböck et al., 2003). Land-use and land-use change scenarios were only used in one SDM study of a mountain region in Austria (Dirnböck et al., 2003). Snow cover has been used in a few studies in the Alps (Guisan and Theurillat, 2000; Dirnböck and Dullinger, 2004; Randin et al., 2006), but we are not aware of any study that uses a physical, mechanistic map of snow redistribution by wind as an input variable in plant species distribution models. Geomorphic processes have never been included in SDM. Finally, thus far, SDM studies have never quantified the importance of disturbance compared to other variables.

# Methods

## *STUDY AREA*

The study area of Anzeindaz (46°15′ to 46°18′N, 7°7′ to 7°11′E) is a west-east–oriented plateau of 25 km$^2$ located in the western Alps of Switzerland (Fig. 2a). This area is bordered to the North by the Diablerets massif and to the South by the Muveran massif. Elevation ranges from 1900 to 3210 m at the top of the Diableret peak. Annual temperature and precipitation vary from 1°C and 1800 mm at 1900 m to −5°C and 2600 mm at 3000 m along the elevation gradient (Bouët, 1985). The soil parent material is mainly calcareous.

The lowest part of the Anzeindaz study area is just below the natural treeline ecotone. However, centuries of wood exploitation and cattle grazing have lowered this ecocline (Villaret, 1973; Gehrig-Fasel et al., 2007). Trees are now absent from the area since subalpine and alpine grasslands are still grazed by cattle every summer. This probably has little effect on the composition

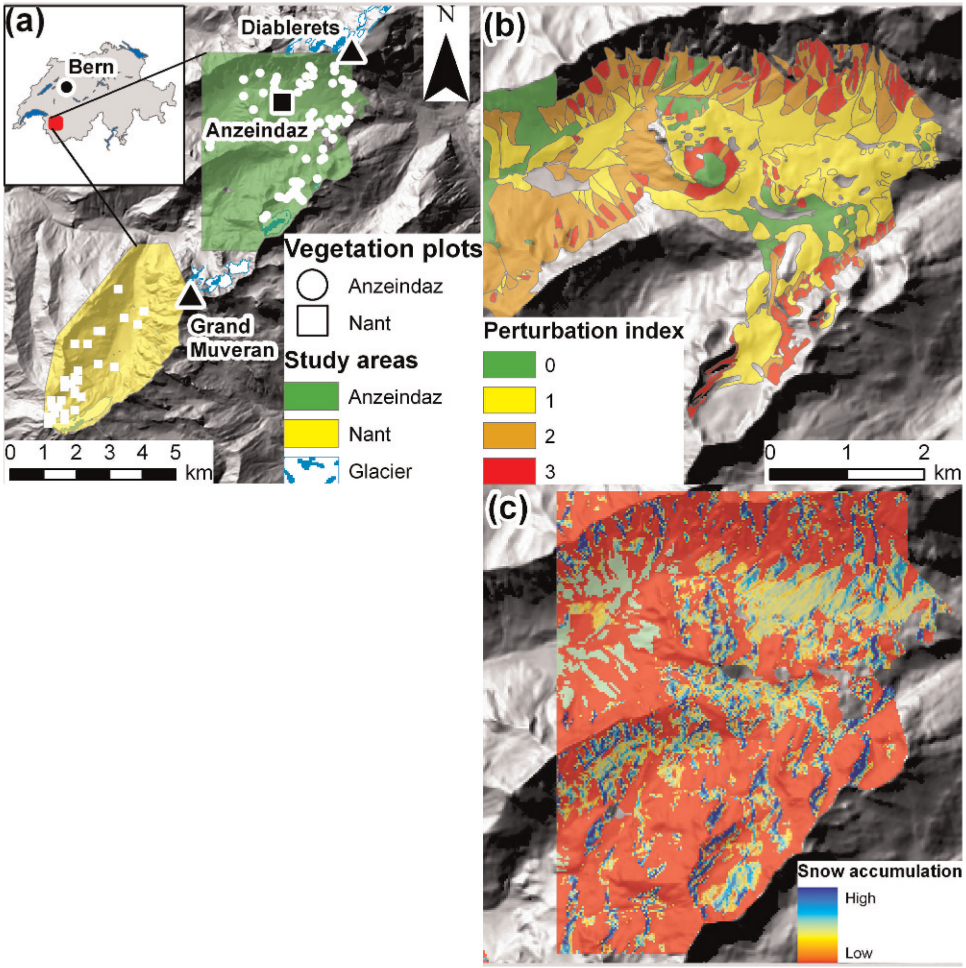

**FIGURE 2.** **(a) Geographic location of the study area with Anzeindaz and Nant regions. Nant is used for an independent evaluation of model maps of (b) the geomorphic index and (c) the snow distribution, which are used as predicting variables in distribution models.**

of alpine meadows. The study area of Anzeindaz contains 300 plant species, which corresponds to one-tenth of the Swiss flora (Villaret, 1973; Aeschimann and Burdet, 1994).

This area is also well known by geographers because of its wide range of geomorphic processes, and several studies have provided detailed geomorphic maps of the area (Loye and Pahud, 1996; Rappaz and Hunziker, 1996).

A small valley in the area, the Vallon de Nant, was used as an independent evaluation area for validating the predictive models (Fig. 2a). This area is similar to the Anzeindaz study area and is a good representation of the alpine environment. In addition, mean and standard deviation of species prevalence in Anzeindaz and Nant are comparable (mean = 0.231 with SD = 0.095 in Anzeindaz and mean = 0.197 with SD = 0.128 in Nant). However, the Vallon de Nant has geographic peculiarities and less slope and aspect variation than the calibration area due to its unique south-north orientation. Nevertheless, this area was chosen because of the availability of geomorphic maps (Phillips, 1993).

### *SPECIES DATA*

During the summers of 2002–2003, 49 vegetation plots were sampled in Anzeindaz (as part of the sampling of a larger area; see Randin et al., 2006) following a random-stratified sampling strategy restricted to non-woody vegetation (grassland, rock, and scree). Stratification was completed using elevation, slope, aspect, and simplified classes of geology. Plots were 64 $m^2$ (8 × 8 m), and the presence of all species growing on this surface was recorded. We registered the exact coordinates of the center of each plot using a Geoexplorer 3 Trimble GPS system, with an accuracy of less than 1 m after differential post-correction. A second random-stratified sampling was performed during the summer of 2004, which especially focused on geomorphic units and provided 32 additional plots. The 91 species that occurred in more than 10 plots were used in the analyses (Appendix). Nomenclature follows Aeschimann and Heitz (1996). The Nant data set was collected during the summers of 2002–2003 using the same random-stratified sampling strategy. This data set is composed of 31 vegetation plots of 64 $m^2$ with presence-absence records for the same 91 species.

### *CLIMATIC AND TOPOGRAPHIC VARIABLES*

Climate data were derived from the national meteorological stations at different altitudes. Long-term monthly means for average temperature (°C) and sum of precipitation (mm) for the period 1961–1990 were used. Climatic data were spatially interpolated with a 25 m DEM (Swisstopo, 2001), and thus all derived data were also at this resolution of 25 m. The method of computation and a description of the variables are given in Zimmermann and Kienast (1999) and Zimmermann et al. (2007). In this study, we used three climatic and two topographic variables (Table 1) expected to be of greatest ecophysiological significance for plants (Guisan and Zimmermann, 2000; Pearson et al., 2002; Körner, 2003; Guisan and Thuiller, 2005). Days with temperatures above 0°C were derived from interpolated daily temperatures and summed for the growing season (Zimmermann and Kienast, 1999). Moisture index was calculated as the difference between precipitation and evapotranspiration, and expressed the amount

**TABLE 1**

**Topographic and climatic variables used in the present study to model the distribution of species.**

| Variables | Units | Details | Method | References |
|---|---|---|---|---|
| Temperature degree days | $^{\circ}C * day * yr^{-1}$ | Sum of days multiplied by daily mean temperature >0°C | ArcInfo AML | Zimmermann and Kienast (1999) |
| Moisture index (average of monthly values June–August) | $mm * day^{-1}$ | Monthly average of daily water balance (precipitation-evapotranspiration) | ArcInfo AML | Zimmermann and Kienast (1999) |
| Global solar radiation (sum over the year) | $kJ * m^{-2} * yr^{-1}$ | Daily global solar radiation | ArcInfo AML | Zimmermann et al. (2007) |
| Slope | degrees | Slope inclination | DEM, ArcInfo, GRID routine | ESRI (2005) |
| Topographic position | Unitless | Concave vs. convex land surface | ArcInfo AML | Zimmermann et al. (2007) |

of soil water potentially available at a site. The sum of mean daily values for the months of June, July, and August and the annual amounts of potential global solar radiation were also calculated. Topographic position (Zimmermann et al., 2007) and slope (ESRI, 2005) were derived from the DEM. Positive values of topographic position represent relative ridges, tops, and exposed sites, whereas negative values indicate sinks, valleys, or toe slopes.

### *GEOMORPHIC DISTURBANCE VARIABLE*

Published geomorphic maps of Anzeindaz and Nant (Phillips, 1993; Rappaz and Hunziker, 1996) were first digitalized using ArcGIS 9.1 software (ESRI, 2005). Geomorphic units were then merged into three classes to produce an index of geomorphic disturbance (GEO; Fig. 2b) that has a potential impact on plant species and is characterized by relative age of deposits, speed of movements, scale, frequency, soil, and vegetation cover (Table 2).

### *SNOW DISTURBANCE VARIABLE*

The snow distribution index (SNOW) was made with the physically based numerical SnowTran-3D snow transport model (SnowTran-3D; Liston and Sturm, 1998), using the 25 m DEM and average dominant wind data. Local wind direction and intensity was calculated in a quasi-physically based meteorological model (MicroMet; Liston and Elder, 2006b). An initial layer of 1 m of uniform snow was then applied to the whole area and SnowTran-3D was run to simulate areas of snow accumulation and wind erosion. Snow was blown for 5 days with an average dominant wind of 280° at 15 m $s^{-1}$ (data provided by MeteoSwiss). The resulting snow-depth distribution was divided by the original 1 m of uniform snow, producing a map indexing snow redistribution by wind. Index values ranged between 0 and positive infinite values, with values above 1 indicating snow accumulation, values below 1 indicating snow erosion and null values indicating complete erosion (Fig. 2c).

### *MODELING FRAMEWORK*

The steps of the analyses are summarized in Figure 3. A topoclimatic model (TC model) was first calibrated in the Anzeindaz study area for each species. The geomorphic variable (GEO) and the snow variable (SNOW) were added separately to the TC model (resulting in the GEO and SNOW models,

**TABLE 2**

**Classification of geomorphologic units by their relative age of deposits, speed of movements, scale, frequency, soil, and vegetation cover.**

| | Geomorphic perturbations | | | |
|---|---|---|---|---|
| | No perturbation | Low | Medium | High |
| | 0 | 1 | 2 | 3 |
| Age of deposits | Absence of deposit | Ancient deposits | Recent deposits | Recent deposits |
| Speed and type of movement | Absence of movements | Slow movements | No movements but occasional impacts of rock deposits/slow movements with mechanic constraints on root system | High and impact of rocks and snow/slow movements with mechanic constraints on root system |
| Scale | — | — | Occasionally at a large scale (affecting an entire slope) | Usually at a large scale and affecting an entire slope |
| Frequency | — | — | Episodic events for rock fall and gravity accumulation, yearly cycle/dynamic for solifluction and active glacial deposit | Yearly cycles/dynamic (e.g. spring avalanche, mudflow after summer storm) |
| Soil | Developed soil | Developed soil but hygric stress due to the rock texture | Sparse developed soil | Absence of soil |
| Vegetation cover | High vegetation cover | High vegetation cover | Sparse vegetation cover with small patches | Patches of vegetation only composed of few individuals of highly specialized species |
| Initial units of geomorphic maps | Soil on stabilized rock | Stabilized glacial deposit<br>Stabilized dejection cone<br>Lapiaz | Rock fall<br>Gravity accumulation<br>Solifluction<br>Active glacial deposit | Avalanche paths<br>Rock scree<br>Active rock glacier |

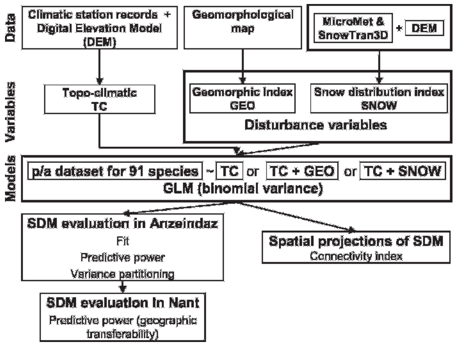

**FIGURE 3. Analytical framework of the study (SDM = species distribution model).**

respectively). The fits of the TC models were compared to those of the GEO and SNOW models. We also compared the predictive power of TC models with GEO and SNOW models using: (1) a cross-validation procedure on the training data set (Anzeindaz), and (2) a fully independent evaluation on the test data set (Nant). We used variation partitioning to quantify the independent contribution of TC, GEO, and SNOW variables. Finally, TC, GEO, and SNOW models calibrated in Anzeindaz were implemented into a geographic information system (GIS) to produce potential habitat maps of presence-absence for each species. The connectivity of the predicted maps derived from the TC models was then compared to those of the GEO and SNOW models. Finally, a set of species was selected to illustrate the difference in spatial projections between the models.

### *STATISTICAL ANALYSES*

All statistical analyses were performed in R version 2.6.1 (R Development Core Team, 2007) and the Design packages available on the R website (http://cran.r-project.org). Analyses were run on all species that occurred more than 10 times in the training data set (91 plant species; Appendix).

For each species, a generalized linear model (GLM; McCullagh and Nelder, 1989) with a binomial variance and a logistic link function was fitted using presence-absence as the response variable and climate and topographic variables as predictors (TC model). An Akaike information criterion (AIC)-based stepwise procedure in both directions was used to select the most significant predictors (Akaike, 1973). Predictor values were allowed up to second-order polynomials (linear and quadratic terms), with the linear term being forced in the model each time the quadratic term was retained. In a second step, the geomorphic index and the index of snow distribution by wind were independently added to the TC model to produce the GEO and SNOW model.

### *MODEL FIT*

The model fit was estimated using the adjusted geometric mean squared improvement $R^2$ (Cox and Snell, 1989; Nagelkerke, 1991). This $R^2$ was rescaled for a maximum of 1 and adjusted for both the number of observations and predictors in the model.

### *MODEL PREDICTIVE POWER*

The predictive power of GLM was first evaluated by running a tenfold cross-validation (van Houwelingen and Le Cessie, 1990) on the training data set. During the cross-validation procedure, the original prevalence of the presence and absence of the species in the data set was maintained in each fold.

Comparisons of predictions from the cross-validation (probability scale) and observations (presence-absence) were based on the area under the curve (AUC) of a receiver-operating characteristic plot (ROC; Fielding and Bell, 1997). AUC accepts values between 0 and 1, with 0.5 meaning no agreement; 0 representing an inverse relationship (errors better predicted); and 1 representing a perfect agreement.

Secondly, an external evaluation was made by predicting all models of the Nant data set and comparing predictions and observations with the AUC values. This represents a fully independent evaluation, as recommended by Fielding and Haworth (1995) or Vaughan and Ormerod (2003), and an estimate of the generality and the geographic transferability of the models (Randin et al., 2006). Since the independent evaluation area (Nant) does not provide a sufficient number of sampling plots (31 plots) for a robust evaluation (Vaughan and Ormerod, 2003), it can only be used as an indicative and explorative test set for evaluating model predictions.

### *VARIATION PARTITIONING*

A variation partitioning approach (Borcard et al., 1992) based on partial correlation analyses was used to quantify the deviance added by the GEO or SNOW variable in the TC model. This approach allows variation to be partitioned into four identifiable fractions of deviance, including (1) pure topoclimatic, (2) shared topoclimatic and geomorphic (or snow cover), (3) pure geomorphic (or snow cover) and (4) unexplained variation. The adjusted geometric mean squared improvement $R^2$ was used as an estimator of the explained deviance without adjustment for the number of observations and predictors.

### *POTENTIAL HABITAT MAPS*

Maps of spatial projections of TC, GEO, and SNOW models were prepared for species with an AUC that was improved by the GEO or SNOW variable in the GLM of the cross-validation evaluation. Spatial projections of GLM were reclassified into presence-absence using a ROC-optimized threshold that jointly maximized the percentage of presence and absence that was correctly predicted (i.e. the probability $P_{fair}$ is where sensitivity = specificity; Liu et al., 2005). A mask based on forests, roads, urbanized areas, and rivers was applied to avoid prediction of the species in impossible situations.

Three maps were prepared for some exemplar species, based on (1) TC model, (2) GEO (or SNOW) model, and (3) their difference. Map 3 was prepared by subtracting maps 1 and 2 (i.e. TC – GEO, or TC – SNOW).

### *INDEX OF CONNECTIVITY*

An index was developed to compare the connectivity between suitable habitat projections of the TC and GEO/SNOW models of species for which the predictive power of the TC model was improved by the GEO/SNOW variable. We hypothesized that the model improvement by these variables would lead to a higher fragmentation of the projected potential suitable habitats as proposed by Patten and Knight (1994).

Let $\mathrm{CS}_i$ be the number of cells predicted to be suitable in a 3 × 3 cell moving window around a suitable focus cell $i$. Let $\mathrm{CT}_i$ be the total number of cells in the 3 × 3 cell window around the focus

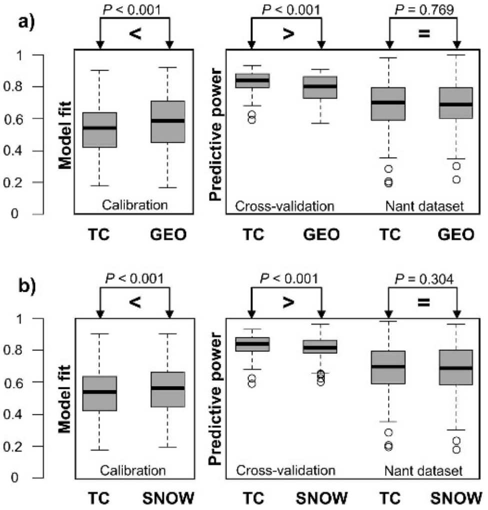

**FIGURE 4. Boxplots of model fit ($R^2$ on the calibration data set) and predictive power (AUC from cross-validation and from the Nant data set) of the three models. (a) TC = topoclimatic, GEO = with geomorphic index, (b) TC = topoclimatic, SNOW = with snow distribution index. The $P$ values indicate the significance of the Wilcoxon signed rank tests between models. The $>$ or $<$ symbols indicate the direction of the test.**

cell *i*. $CT_i$ reaches a maximum of 8 if cells have not been removed by the mask. We calculated the connectivity index *CI* as follows:

$$CI_{GLM} = \frac{\left(\sum_{i=1}^{N} \frac{CS_i}{CT_i}\right)}{N} \qquad (1)$$

The connectivity index reaches a maximum value of 1 when all cells surrounding the focus suitable cell are also suitable. The change in potential suitable surface and connectivity between TC and GEO/SNOW models was quantified using the Wilcoxon signed-rank test, treating the sample as if it were grouped by species.

## Results

### DIFFERENCE IN MODEL FIT AND PREDICTIVE POWER

The boxplot (Fig. 4) showed that the fits of the model were, on average, significantly higher for models including geomorphic and snow disturbance variables (GEO and SNOW models), compared to pure topoclimatic models (TC models). The highest level of improvement reached 25.1% for the GEO model of *Hippocrepis comosa* and 21.6% for the SNOW model of *Agrostis rupestris*.

By contrast, the predictive power of the TC models evaluated by cross-validation remained significantly higher than GEO and SNOW models. The improvement by geomorphic and snow disturbance variables was modest but significant, reaching up to 9.7% and 8.3% for *Pedicularis verticillata*, respectively.

On average, there was no significant differences in the predictive power between TC and GEO models and between TC and SNOW models (Fig. 4) when evaluation was performed in the independent study area (Nant). In addition, the predictive power, although remaining low overall in Nant, revealed greater improvements than the internal validation for some species, reaching 13.8% for the GEO model of *Dryas octopetala* and 15.4% for the SNOW model of *Saxifraga paniculata*.

### VARIATION PARTITIONING

The contribution of the geomorphic index in the explanation of additional deviance in topoclimatic models was weak on average (5.6%, Table 3). Nonetheless, it reached 24.5% in the best model for *Hippocrepis comosa* (Fig. 5). The contribution of the snow index was, on average, also weak (3.3%), with a maximum independent contribution of 20.7% for the model of *Agrostis rupestris* (Table 3; Fig. 5).

### POTENTIAL HABITAT DISTRIBUTION MAPS AND CONNECTIVITY

The geomorphic index improved the predictive power of 23 species, whereas 19 species were improved by the snow distribution index.

When considering the subset of 23 species, the connectivity between cells with suitable habitat significantly decreased when the geomorphic index was added to the TC model (Wilcoxon signed-rank test: $P < 0.001$). The same decrease in connectivity was observed for the subset of 19 species when the snow distribution index was added to the TC model (Wilcoxon signed-rank test: $P < 0.001$).

Based on model performance, four species were selected to illustrate spatial projections from presence-absence models (Appendix). *Agrostis capillaris* and *Galium megalospermum* were selected to show the improvement gained by the geomorphic index. *Sedum atratum* and *Silene acaulis* were selected to demonstrate improvement by the snow distribution index. The resulting maps can be compared with those of the two disturbance variables in the study area (Figs. 2b and 2c).

Comparisons of spatial projections of TC and GEO models (Fig. 6; Table 4) showed that the occurrence of *A. capillaris* was predicted more often on surfaces with low or no geomorphic perturbations. On the contrary, *Gallium megalospermum* was predicted more often on surfaces with medium to high perturbations. When comparing TC and SNOW models, boxplots (Fig. 7) showed that the occurrence of *Sedum atratum* was predicted more often on areas with a high accumulation of snow, whereas *Silene acaulis* was predicted exclusively on surfaces with low snow

**TABLE 3**

**Percentage of mean, minimum, and maximum of the contribution for each identifiable fraction of GEO and SNOW models separated by the variation partitioning method. TC = topoclimatic.**

| | Geomorphic index (GEO) | | | | Snow distribution index (SNOW) | | |
|---|---|---|---|---|---|---|---|
| | Mean | Min | Max | | Mean | Min | Max |
| TC | 36.3 | 14.4 | 76.0 | TC | 55.0 | 16.7 | 88.0 |
| GEO | 5.6 | 0.3 | 24.5 | SNOW | 3.3 | 0.0 | 20.7 |
| TC+GEO | 18.9 | −6.4 | 47.8 | TC+SNOW | 0.2 | −14.9 | 10.2 |
| Unexplained | 39.2 | 7.0 | 78.0 | Unexplained | 41.6 | 8.6 | 76.6 |

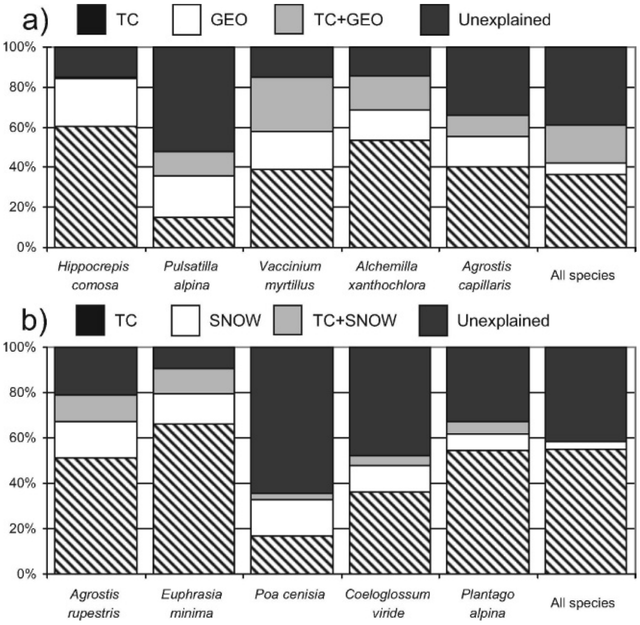

**FIGURE 5. Fraction of explained deviance (independent contribution) among the target variables (TC = topoclimatic variables alone, GEO/SNOW = geomorphic index or snow distribution index alone, [TC + GEO]/[TC + SNOW] = joint contribution of TC with GEO or SNOW and unexplained deviance by the model) for the five species having the highest $R^2$ for (a) the geomorphic index and (b) the snow distribution index separated by the variation partitioning.**

accumulation when the snow distribution index was included into the TC model of the two species. These differences were both significant (Wilcoxon signed-rank test; $P < 0.001$).

## Discussion

In this study, we quantified the importance of two disturbance variables—a geomorphic index (GEO) and a snow distribution index (SNOW)—in models of alpine plant species distribution, compared to more commonly used topoclimatic variables (TC). Model fit and predictive power were significantly improved by the two disturbance variables for some species. However, on average, predictive power was not improved across the entire set of 91 species. Hence, the contributions of these variables were species-specific, with significant improvements of up to 30% (fit) and 10% (predictive power) for some species.

### *MODEL FIT AND PREDICTIVE POWER OF DISTURBANCE VARIABLES*

On average, GEO and SNOW significantly improved the models' fit. However, their predictive power, as evaluated by cross-validation, remained significantly lower than topoclimatic models. One reason for the weak overall evaluation of models that incorporate the geomorphic index may reside in the development of the underlying geomorphic maps. Geomorphic processes were delimited on the map by large adjacent polygons but had no transition zones between them. Since these abrupt limits do not exist in nature, the use of a continuous perturbation index should be more powerful than the semi-quantitative index used in this study. Another problem with the geomorphic maps is that the geographer did not initially define their units in relation to vegetation. A different classification that predicts vegetation patterns could prove beneficial. This situation highlights the problem of using existing and available data for a purpose other than what they were originally intended (Yoccoz et al., 2001).

The low predictive performance of the snow distribution index illustrates the difficulty of capturing the complex processes of snow distribution in mountain systems. Patterns of snow accumulation were not only generated by the dominant wind translocation, but also by avalanches or more complex wind translocation pathways. Due to the steep slopes and the high elevation amplitude (up to 1300 m) found within the study area, avalanches could explain the patterns of snow distribution in Anzeindaz and Vallon de Nant. Moreover, snow beds and exposed ridges represent landscape features that are already considered in models with topography. Consequently, topoclimatic variables commonly used in SDMs may be sufficient to capture the main geomorphic influences on the vegetation. In addition, the dominant wind that was blown in order to distribute the snow on the landscape is not necessarily the wind that really shapes the snow after snowfalls at the microscale.

Several studies have recommended the use of direct or disturbance variables instead of indirect variables in SDM (Guisan and Thuiller, 2005) as a way to ensure better model transferability in space or time (Randin et al. 2006). However, to our knowledge, no study has formally tested the predictive power of disturbance variables in a remote area. Surprisingly, the average predictive power of the GEO and SNOW models was low when evaluated in the remote area of Nant, even though Nant is very close to Anzeindaz. One explanation for the GEO variable could be that the quality of existing maps of geomorphology as vegetation predictors strongly depends on the interpretation of the landscape made by geographers. Thus, artificial differences between the two geomorphological maps of Anzeindaz and Nant may have been generated by the different interpretations of two geographers. However, this does not explain the low predictive power of the SNOW variable that has been generated using standardized numerical simulations in both study areas. Thus, the explanation we support is the difference in interactions between topography, climate, and geomorphic processes that occur in the two study areas (see Villaret, 1973; Loye and Pahud, 1996; Rappaz and Hunziker, 1996 for Anzeindaz; and Dutoit, 1984; Phillips, 1993 for Nant). Anzeindaz is a west-east–oriented valley, whereas Nant is south-north–oriented. This difference leads to different climatic and energetic contrasts that partly control geomorphic processes and also to distinct snow distribution patterns by wind. Edaphic and geologic differences in combination with climate may also lead to different morphology in avalanches or debris flow (Butler and Walsh, 1990). Therefore, our results show the difficulty of generating a set of spatially ecologically meaningful disturbance variables that can be generalized to a complex mountain environment, even at the local scale.

When evaluated in Nant, the predictive power of TC and GEO/SNOW models were, on average, the same. First, this may demonstrate that evaluation in a remote area is a severe method for all sets of variables. Second, this finding may also show that both direct and disturbance variables are not sufficient to ensure transferability at the local scale in a mountain environment. Thus, when considering a high-elevation ecosystem at this scale, the need to shift to models that incorporate resource variables and transport processes of nutrients should be emphasized, as already proposed by Seastedt et al. (2004) with the landscape continuum model (LCM).

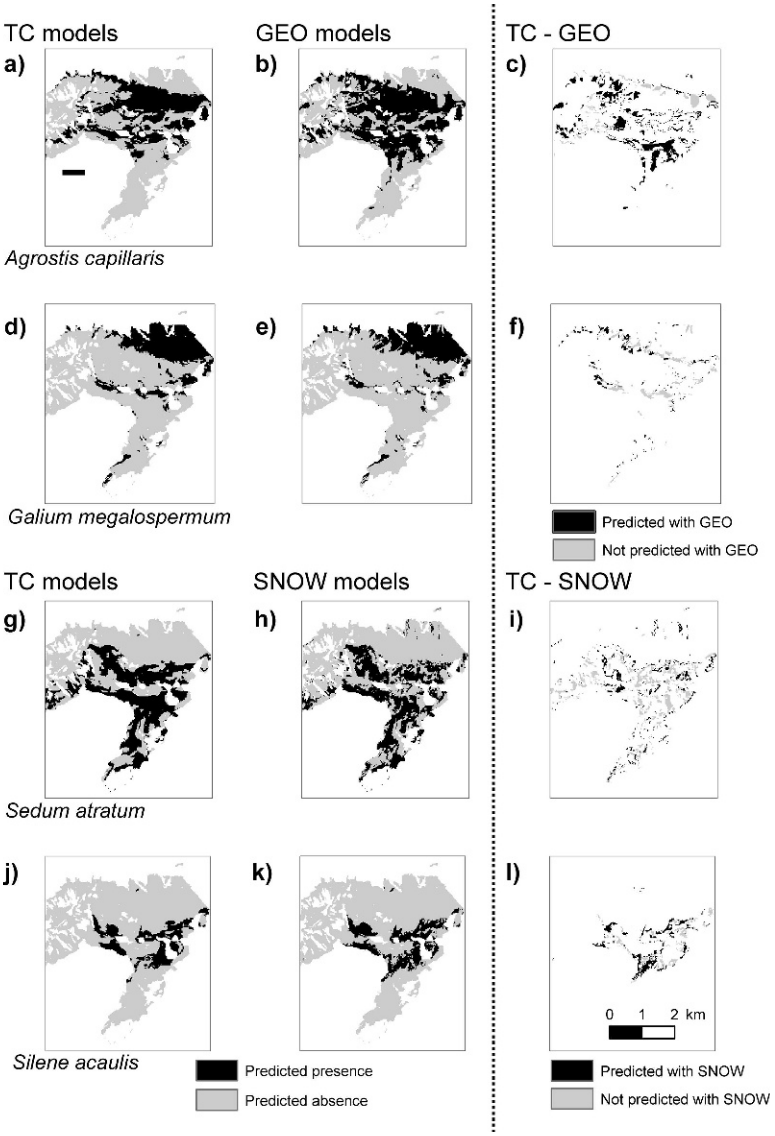

**FIGURE 6. Potential filtered habitat maps for the four exemplar species: (a–c) *Agrostis capillaris*, (d–f) *Galium megalospermum*, (g–i) *Sedum atratum*, and (j–l) *Silene acaulis*. The three maps for each species correspond (by column) to (a, d, g, j) TC models, (b, e, h, k) GEO or SNOW models, and (c, f, i, l) the difference between TC and GEO or SNOW models.**

### *VARIATION PARTITIONING*

The strong influence of topoclimatic variables when added to TC models could explain the low average contribution of both disturbance variables (5.6% and 3.3% for the GEO and SNOW variables, respectively), as highlighted by the variance partitioning results. Indeed, the intensity of geomorphic processes (i.e. screes, solifluction, and avalanche paths; Butler and Walsh, 1990; Walsh et al., 2003) as well as snow redistribution patterns (Liston and Sturm, 1998; Liston and Elder, 2006a), are highly controlled by topoclimatic attributes. However, what is supposedly improved in geomorphic and snow predictors is that slope, curvature, radiation, or precipitation also act in combination with edaphic or geologic characteristics (Butler et al., 2003). Our results tend to suggest that more refinement is needed in the preparation of geomorphic and snow predictors in alpine environments.

In contrast, the maximum contributions of GEO and SNOW variables in models were important, reaching 24.5% and 20.7%, respectively. This suggests that geomorphic disturbances and snow are only critical and dominant spatial drivers for a part of the plant species in alpine systems, as already shown in previous studies (Erschbamer, 1989; Walker et al., 1993; Patten and Knight, 1994; Butler et al., 2007).

**TABLE 4**

**Difference in spatial projections when adding the GEO variable in TC models.**

| | *Agrostis capillaris* | | | *Gallium megalospermum* | | |
|---|---|---|---|---|---|---|
| | | % predicted with GEO | | | % predicted with GEO | |
| Classes of geomorphic disturbance | Surface unchanged km$^2$ | + | − | Surface unchanged km$^2$ | + | − |
| No perturbations (0) | 0.67 | 123.4 | 0.0 | 1.29 | 0.0 | 17.2 |
| Low perturbations (1) | 4.50 | 11.2 | 0.0 | 4.77 | 1.2 | 3.7 |
| Medium perturbations (2) | 2.02 | 0.0 | 18.8 | 2.15 | 11.4 | 0.0 |
| High perturbations (2) | 1.73 | 7.9 | 0.0 | 1.75 | 0.8 | 6.0 |

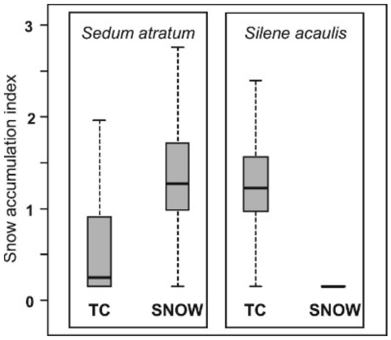

**FIGURE 7. Boxplots of the simulated snow distribution index for the potential occurrences predicted with TC and SNOW models for *Sedum atratum* and *Silene acaulis*. Difference between the snow distribution index of occurrences predicted with TC and SNOW were significantly different (Wilcoxon test: $P < 0.001$).**

### *SPECIES GEOGRAPHIC PROJECTIONS*

The contrasted results between the low average contribution of GEO and SNOW for the complete data set and the high contribution reached by individual species show the limits of such a global view on the most common species in a region. A minority of the species was influenced by the disturbances, and the impact of the GEO and SNOW variables on the models strongly differs between species. For instance, *Agrostis capillaris* is a species that has a large ecological tolerance and is mainly found in exploited colline to subalpine meadows and pastures (Aeschimann et al., 2005). This species can be occasionally and locally abundant but is generally never dominant and avoids perturbations. As expected, the GEO models more often predicted suitable habitats for this species in areas without perturbation (+123%). On the contrary, *Gallium megalospermum* is a species typically found in the calcareous screes of subalpine and alpine zones (Aeschimann et al., 2005). Its potential suitable habitats were more often predicted correctly in areas with medium perturbations (+11.4%) and less often in areas without perturbations (−17.2%). *Sedum atratum* is found in calcareous snow beds, whereas *Silene acaulis* prefers southern slopes and windy ridges (Braun-Blanquet, 1975). The divergence of SNOW models projections compared to TC models for these species was consistent with field observations, since *Sedum* was predicted significantly more often in areas of high snow accumulation and *Silene* was predicted in low accumulation sites.

### *DISTURBANCE VARIABLES FOR SPATIAL PROJECTIONS UNDER CLIMATE CHANGE*

As shown by significant changes in the connectivity of spatial projections of GEO and SNOW models, disturbance variables in topoclimatic models might remain as important factors to include in SDM when they are used to derive projections of the impacts of climate change on plant species and diversity. For the set of species sensitive to GEO and SNOW variables, geomorphic perturbations and snow distribution can be facilitators or inhibitors, thus acting as barriers or corridors for plant dispersal, as proposed by Butler (2001). Therefore, the migration rate of pioneer species from low altitudes, which are adapted to mechanical perturbations, could be accelerated, whereas populations of species found at high elevations would continue to be found at low elevations in some abyssal situations where low competition is regulated by perturbation. Moreover, rockfalls caused by the degradation of permafrost are likely to increase in a warmer climate (Gruber et al., 2004), thus leading to changes in connectivity or barriers for sensitive species.

### *FURTHER IMPROVEMENT*

Expert approaches in GIS, advanced remote sensing techniques or high resolution DEM (i.e. LIDAR) may be used to more precisely determine the intensity of geomorphic perturbation (Tarboton, 1997; Meissl, 2001; Walsh et al., 2003; Noetzli et al., 2006). For example, the size and spatial organization of stones in a rockslide may provide information about the intensity and frequency of the perturbation events that occurred.

The snow distribution model used in this study was only based on a single climatic variable: the dominant wind. Therefore, the simulation of snow distribution used to derive our index only represented one possible realization, without any associated variation. More complex physical models of snow distribution should be tested in the future (Gurtz et al., 1999; Liston and Elder, 2006a) that are based on (1) several simulation runs, (2) more thorough observed climatic data recorded over longer periods, and (3) more complex processes of snow formation and melting. In addition, the use of physical models should be encouraged as a surrogate to remote sensing data (Dirnböck et al., 2003) in SDM study because they can be easily projected under climate change scenarios (see Randin et al., 2009, for implementation).

Vegetation feedback on snow distribution should also be considered when using such models (Hiemstra et al., 2002; Liston and Elder, 2006a). Depending on their height, vegetation patches can contribute greatly to snow redistribution by wind in combination with topographic attributes and improve physical model prediction at a fine scale and high resolution when included as a spatial layer (Hiemstra et al., 2002).

Statistical models of species' distribution were fitted using species presence-absence data. In further studies, models could be fitted using abundance data, since this could sensibly change the results. A recent study that tested the effect of various land-use (a form of human disturbance) treatments on plant species distribution showed that abundance is ecologically more informative than simple presence/absence data (Randin et al., in press). Similarly, using ordinal models, Dirnböck et al. (2003) showed that land use could explain up to 50% of variation in species abundance.

In this study, we did not test for significant AUC improvement like Delong et al. (1988), based on the papers from Hanley and McNeil (1982, 1983), and recently used by Thuiller et al. (2003). With their method, the areas under the curve of each of the two nested models are directly compared, which could be an alternative to our analytical framework.

Finally, the causes of the low numbers of models that were improved by the disturbance variables and the high variability among species cannot be directly seen from our results. However, aspects of our results can be used to identify potential reasons (i.e. species traits) and propose hypotheses to guide further investigations.

## Conclusion

Overall, the contributions of disturbance variables were, on average, low, but highly dependent on the species considered. In the mountain area, geomorphic variables proved to be important for some species.

Most models fitted with geomorphic and snow variables failed to predict in the remote area, thus suggesting that it is difficult to obtain spatially explicit and ecologically meaningful disturbance variables at the local scale.

Whether or not disturbance variables are considered can yield important changes in surface area and connectivity predicted by species distribution models. Changes in projected surfaces were interpreted as ecologically relevant when the two disturbance variables were considered. This is an important issue when preparing climate change projections, because the species' range size maintained in the future will determine the species sensitivity to changing conditions.

Further studies should develop a continuous geomorphic index based on more ecologically meaningful units of geomorphology. These studies should also consider using more complex models of snow distribution, even at the expense of longer computing times.

## Acknowledgments

This study was supported by the Centre de Conservation de la Nature (SFFN) of the Canton de Vaud, the Swiss National Science Foundation (SNF Grant No 3100A0-110000), and the European Commission (FP6 projects ECOCHANGE and MACIS). We thank all the people who helped with the field work in the Swiss Western Alps within the MODIPLANT project, particularly Stéfanie Maire and Dario Martinoni, as well as Séverine Widler, Chantal Peverelli, Valentine Hof, Lorenzo De Stefani, Roxane Milleret, Anny and Willy Berra, Christian Parisod, and Stéphanie Spahr. We also thank Dr. Emmanuel Reynard and Christophe Lambiel for their useful comments on the manuscript. Randin and Guisan greatly benefited from interactions with colleagues within the Swiss National Centre for Competence in Research (NCCR) "Plant survival in natural and agricultural ecosystems" (http:// www.unine.ch/nccr).

## References Cited

Aassine, S., and El Jai, M. C., 2002: Vegetation dynamics modelling: a method for coupling local and space dynamics. *Ecological Modelling*, 154: 237–249.

Aeschimann, D., and Burdet, H. M., 1994: *Flore de la Suisse et des territoires limitrophes. Le nouveau Binz.* Second edition. Neuchâtel: Le Griffon, 597 pp.

Aeschimann, D., and Heitz, C., 1996: *Index synonymique de la flore de Suisse et territoires limitrophes*. Genève: CRSF, 317 pp.

Aeschimann, D., Lauber, K., Moser, D. M., and Theurillat, J.-P., 2005: *Flora Alpina*. Paris: Belin.

Akaike, H., 1973: Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*, 60: 255–265.

Araujo, M. B., and Guisan, A., 2006: Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33: 1677–1688.

Austin, M. P., 1980: Searching for a model for use in vegetation analysis. *Vegetatio*, 42: 11–21.

Austin, M. P., 1985: Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics*, 16: 39–61.

Austin, M. P., 2006: Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling*, 200: 1–19.

Austin, M. P., and Heyligers, P. C., 1989: Vegetation survey design for conservation: gradsec sampling of forests in northeast New South Wales. *Biological Conservation*, 50: 13–32.

Austin, M. P., and Meyers, J. A., 1996: Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. *Forest Ecology and Management*, 85: 95–106.

Austin, M. P., Cunningham, R. P., and Fleming, P. M., 1984: New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio*, 55: 11–27.

Bakkenes, M., Alkemade, J. R. M., Ihle, F., Leemans, R., and Latour, J. B., 2002: Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, 8: 390–407.

Beniston, M., 2006: Mountain weather and climate: a general overview and a focus on climatic change in the Alps. *Hydrobiologia*, 562: 3–16.

Billings, W. D., and Bliss, L. C., 1959: An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology*, 40: 388–397.

Borcard, D., Legendre, P., and Drapeau, P., 1992: Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045–1055.

Bouët, M., 1985: *Climat et météorologie de la Suisse romande*. Lausanne: Payot.

Bowman, W. D., 1992: Inputs and storage of nitrogen in winter snowpack in an alpine ecosystem. *Arctic and Alpine Research*, 24: 211–215.

Braun-Blanquet, J., 1975: Fragmenta Phytosociologica Raetica I: Die Schneebodengesellschaften (Klasse der Salicetea herbaceae). *Jahresbericht der Naturforschenden Gesesellschaft Graubünden*, 96: 42–71.

Burga, C. A., 1999: Vegetation development on the glacier forefield Morteratsch (Switzerland). *Applied Vegetation Science*, 2: 17–24.

Butler, D. R., 2001: Geomorphic process-disturbance corridors: a variation on a principle of landscape ecology. *Progress in Physical Geography*, 25: 237–248.

Butler, D. R., and Walsh, S. J., 1990: Lithologic, structural, and topographic influences on snow-avalanche path location, eastern Glacier National Park, Montana. *Annals of the Association of American Geographers*, 80: 362–378.

Butler, D. R., Malanson, G. P., Bekker, M. F., and Resler, L. M., 2003: Lithologic, structural, and geomorphic controls on ribbon forest patterns in a glaciated mountain environment. *Geomorphology*, 55: 203–217.

Butler, D. R., Malanson, G. P., Walsh, S. J., and Fagre, D. B., 2007: Influences of geomorphology and geology on alpine treeline in the American West—More important than climatic influences? *Physical Geography*, 28: 434–450.

Cox, D. R., and Snell, E. J., 1989: *The Analysis of Binary Data.* Second edition. London: Chapman and Hall.

Delong, E. R., Delong, D. M., and Clarkepearson, D. I., 1988: Comparing the areas under 2 or more correlated receiver operating characteristic curves—A nonparametric approach. *Biometrics*, 44: 837–845.

Diaz, H. F., Grosjean, M., and Graumlich, L., 2003: Climate variability and change in high elevation regions: past, present and future. *Climatic Change*, 59: 1–4.

Dirnböck, T., and Dullinger, S., 2004: Habitat distribution models, spatial autocorrelation, functional traits and dispersal capacity of alpine plant species. *Journal of Vegetation Science*, 15: 77–84.

Dirnböck, T., Hobbs, R. J., Lambeck, R. J., and Caccetta, P. A., 2002: Vegetation distribution in relation to topographically driven processes in southwestern Australia. *Applied Vegetation Science*, 5: 147–158.

Dirnböck, T., Dullinger, S., and Grabherr, G., 2003: A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, 30: 401–417.

Dullinger, S., Dirnböck, T., and Grabherr, G., 2004: Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology*, 92: 241–252.

Dutoit, A., 1984: La végétation de l'étage subalpin du vallon de Nant. PhD dissertation. University of Lausanne, Lausanne, Switzerland.

Erschbamer, B., 1989: Vegetation on avalanche paths in the Alps. *Vegetatio*, 80: 139–146.

ESRI, 2005, ARCInfo Version 9.1. Redlands, California: Environmental Systems Research Institute, Inc.

Fielding, A. H., and Bell, J. F., 1997: A review of methods for the assessment of prediction errors in conservation presence-absence models. *Environmental Conservation*, 24: 38–49.

Fielding, A. H., and Haworth, P. F., 1995: Testing the generality of bird-habitat models. *Conservation Biology*, 9: 1466–1481.

Gehrig-Fasel, J., Guisan, A., and Zimmermann, N. E., 2007: Treeline shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science*, 18: 571–582.

Gottfried, M., Pauli, H., and Grabherr, G., 1998: Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Arctic and Alpine Research*, 30: 207–221.

Gottfried, M., Pauli, H., Reitter, K., and Grabherr, G., 1999: A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity & Distributions*, 5: 241–251.

Greene, E. M., Liston, G. E., and Pielke, R. A., 1999: Simulation of above treeline snowdrift formation using a numerical snow-transport model. *Cold Regions Science and Technology*, 30: 135–144.

Gruber, S., Hoelzle, M., and Haeberli, W., 2004: Permafrost thaw and destabilization of Alpine rock walls in the hot summer of 2003. *Geophysical Research Letters*, 31: article L13504.

Guisan, A., and Hofer, U., 2003: Predicting reptile distributions at the mesoscale: relation to climate and topography. *Journal of Biogeography*, 30: 1233–1243.

Guisan, A., and Theurillat, J.-P., 2000: Assessing alpine plant vulnerability to climate change: a modeling perspective. *Integrated Assessment*, 1: 307–320.

Guisan, A., and Thuiller, W., 2005: Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8: 993–1009.

Guisan, A., and Zimmermann, N. E., 2000: Predictive habitat distribution models in ecology. *Ecological Modelling*, 135: 147–186.

Guisan, A., Holten, J. I., Spichiger, R., and Tessier, L., 1995: *Potential Ecological Impacts of Climate Change in the Alps and Fennoscandian Mountains*. Genève: Conservatoire et Jardin botaniques.

Guisan, A., Theurillat, J. P., and Kienast, F., 1998: Predicting the potential distribution of plant species in an alpine environment. *Journal of Vegetation Science*, 9: 65–74.

Gurtz, J., Baltensweiler, A., and Lang, H., 1999: Spatially distributed hydrotope-based modelling of evapotranspiration and runoff in mountain basins. *Hydrological Processes*, 13: 2751–2768.

Hanley, J. A., and McNeil, B. J., 1982: The meaning and use of the area under a receiver operating characteristic (Roc) curve. *Radiology*, 143: 29–36.

Hanley, J. A., and McNeil, B. J., 1983: A method of comparing the areas under receiver operating characteristic curves derived from the same cases. *Radiology*, 148: 839–843.

Hiemstra, C. A., Liston, G. E., and Reiners, W. A., 2002: Snow redistribution by wind and interactions with vegetation at upper treeline in the Medicine Bow Mountains, Wyoming, USA. *Arctic Antarctic, and Alpine Research*, 34: 262–273.

Huston, M. A., 1994: *Biological Diversity: the Coexistence of Species on Changing Landscapes*. Cambridge: Cambridge University Press.

Jenny, H., 1941: *Factors of Soil Formation*. New York: McGraw-Hill.

Johnson, P. L., and Billings, W. D., 1962: Alpine vegetation of Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecological Monographs*, 32: 105–135.

Jonasson, S., and Callaghan, T. V., 1992: Root mechanical properties related to disturbed and stressed habitats in the Arctic. *New Phytologist*, 122: 179–186.

Kearney, M., and Porter, W. P., 2004: Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, 85: 3119–3131.

Körner, C., 2003: *Alpine Plant Life.* Second edition. Berlin: Springer.

Leathwick, J. R., Burns, B. R., and Clarkson, B. D., 1998: Environmental correlates of tree alpha-diversity in New Zealand primary forests. *Ecography*, 21: 235–246.

Lischke, H., Zimmermann, N. E., Bolliger, J., Rickebusch, S., and Loffler, T. J., 2006: TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*, 199: 409–420.

Liston, G. E., and Elder, K., 2006a: A distributed snow-evolution modeling system (SnowModel). *Journal of Hydrometeorology*, 7: 1259–1276.

Liston, G. E., and Elder, K., 2006b: A meteorological distribution system for high-resolution terrestrial modeling (MicroMet). *Journal of Hydrometeorology*, 7: 217–234.

Liston, G. E., and Sturm, M., 1998: A snow-transport model for complex terrain. *Journal of Glaciology*, 44: 498–516.

Liston, G. E., Winther, J. G., Bruland, O., Elvehoy, H., Sand, K., and Karlof, L., 2000: Snow and blue-ice distribution patterns on the coastal Antarctic Ice Sheet. *Antarctic Science*, 12: 69–79.

Liu, C. R., Berry, P. M., Dawson, T. P., and Pearson, R. G., 2005: Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28: 385–393.

Loye, E., and Pahud, P.-F., 1996: *Levé géomorphologique de Solalex-Anzeindaz*. MSc thesis. Institut de Géographie, Facultés des Lettres, University of Lausanne, Lausanne, Switzerland.

Malanson, G. P., Butler, D. R., Cairns, D. M., Welsh, T. E., and Resler, L. M., 2002: Variability in an edaphic indicator in alpine tundra. *Catena*, 49: 203–215.

McCullagh, P., and Nelder, J. A., 1989: *Generalized Linear Models.* Second edition. London: Chapman and Hall.

Meissl, G., 2001: Modelling the runout distances of rockfalls using a geographic information system. *Annals of Geomorphology*, 125: 129–137.

Moore, D. M., Lees, B. G., and Davey, S. M., 1991: A new method for predicting vegetation distributions using decision tree analysis in a geographic information system. *Environmental Management*, 15: 59–71.

Nagelkerke, N. J. D., 1991: A note on a general definition of the coefficient of determination. *Biometrika*, 78: 691–692.

Nichols, W. F., Killingbeck, K. T., and August, P. V., 1998: The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. *Conservation Biology*, 12: 371–379.

Noetzli, J., Huggel, C., Hoelzle, M., and Haeberli, W., 2006: GIS-based modelling of rock-ice avalanches from alpine permafrost areas. *Computational Geosciences*, 10: 161–178.

Nogués-Bravo, D., Araújo, M., Errea, M. P., and Martinez-Rica, J. P., 2006: Exposure of global mountain systems to climate warming during the 21st century. *Global Environmental Change*, 17: 420–428.

Patten, R. S., and Knight, D. H., 1994: Snow avalanches and vegetation pattern in Cascade Canyon, Grand Teton National Park, Wyoming, USA. *Arctic and Alpine Research*, 26: 35–41.

Pearson, R. G., Dawson, T. P., Berry, P. M., and Harrison, P. A., 2002: SPECIES: A spatial evaluation of climate impact on the envelope of species. *Ecological Modelling*, 154: 289–300.

Phillips, M., 1993: *Géomorphologie du Vallon de Nant*. MSc thesis. Institut de Géographie, Facultés des Lettres, University of Lausanne, Lausanne, Switzerland.

R Development Core Team, 2007: R 2.6.1. A language and environment. < http://cran.r-project.org>.

Randin, C. F., Dirnbock, T., Dullinger, S., Zimmermann, N. E., Zappa, M., and Guisan, A., 2006: Are niche-based species distribution models transferable in space? *Journal of Biogeography*, 33: 1689–1703.

Randin, C. F., Engler, R., Normand, S., Zappa, M., Zimmermann, N. E., Pearman, P. B., Vittoz, P., Thuiller, W., and

Guisan, A., 2009: Climate change and plant distribution: local models predict high-elevation persistence *Global Change Biology*, 15: 1557–1569.

Randin, C. F., Jaccard, H., Vittoz, P., Yoccoz, N. G., and Guisan, A., in press: Land use improves spatial predictions of plant abundances but not occurrences in a mountain landscape. *Journal of Vegetation Science*.

Rappaz, F., and Hunziker, J.-L., 1996: *Levé géomorphologique d'Anzeindaz*. MSc thesis. Institut de Géographie, Facultés des Lettres, University of Lausanne, Lausanne, Switzerland.

Schaefer, J. A., and Messier, F., 1995: Scale-dependent correlations of arctic vegetation and snow cover. *Arctic and Alpine Research*, 27: 38–43.

Schumacher, S., and Bugmann, H., 2006: The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. *Global Change Biology*, 12: 1435–1450.

Seastedt, T. R., Bowman, W. D., Caine, T. N., McKnight, D., Townsend, A., and Williams, M. W., 2004: The landscape continuum: a model for high-elevation ecosystems. *Bioscience*, 54: 111–121.

Swisstopo, 2001. DHM25: Das digitale Höhenmodell der Schweiz: Bern: Bundesamt für Landestopographie.

Tappeiner, U., Tappeiner, G., Aschenwald, J., Tasser, E., and Ostendorf, B., 2001: GIS-based modelling of spatial pattern of snow cover duration in an alpine area. *Ecological Modelling*, 138: 265–275.

Tarboton, D. G., 1997: A new method for the determination of flow directions and upslope areas in grid digital elevation models. *Water Resources Research*, 33: 309–319.

Theurillat, J. P., and Guisan, A., 2001: Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change*, 50: 77–109.

Theurillat, J.-P., Felber, F., Geissler, P., Gobat, J.-M., Fierz, M., Fischlin, A., Küpfer, P., Schlüssel, A., Velluti, C., and Zhao, G.-F., 1998: Sensitivity of plant and soil ecosystems of the Alps to climate change. *In* Cebon, P., Dahinden, U., Davies, H. C., Imboden, D., and Jäger, C. C. (eds.), *Views from the Alps. Regional Perspectives on Climate Change*. London: MIT Press, 225–308.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., and Williams, S. E., 2004: Extinction risk from climate change. *Nature*, 427: 145–147.

Thuiller, W., Araujo, M. B., and Lavorel, S., 2003: Generalized models vs. classification tree analysis: predicting spatial distributions of plant species at different scales. *Journal of Vegetation Science*, 14: 669–680.

Thuiller, W., Lavorel, S., Araujo, M. B., Sykes, M. T., and Prentice, I. C., 2005: Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102: 8245–8250.

van Houwelingen, J. C., and Le Cessie, S., 1990: Predictive value of statistical models. *Statistics in Medicine*, 9: 1303–1325.

Vaughan, I. P., and Ormerod, S. J., 2003: Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. *Conservation Biology*, 17: 1601–1611.

Villaret, P., 1973: Flore et végétation d'Anzeinde. *Mémoires de la Société vaudoise des Sciences naturelles*, 15: 139–145.

Walker, D. A., Halfpenny, J. C., Walker, M. D., and Wessman, C. A., 1993: Long-term studies of snow-vegetation interactions. *Bioscience*, 43: 287–301.

Walsh, S. J., Butler, D. R., Allen, T. R., and Malanson, G. P., 1994: Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation Science*, 5: 657–672.

Walsh, S. J., Butler, D. R., Malanson, G. P., Crews-Meyer, K. A., Messina, J. P., and Xiao, N. C., 2003: Mapping, modeling, and visualization of the influences of geomorphic processes on the alpine treeline ecotone, Glacier National Park, MT, USA. *Geomorphology*, 53: 129–145.

Yoccoz, N. G., Nichols, J. D., and Boulinier, T., 2001: Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16: 446–453.

Zimmermann, N. E., and Kienast, F., 1999: Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *Journal of Vegetation Science*, 10: 469–482.

Zimmermann, N. E., Edwards, T. C., Moisen, G. G., Frescino, T. S., and Blackard, J. A., 2007: Remote sensing-based predictors improve distribution models of rare, early successional and broadleaf tree species in Utah. *Journal of Applied Ecology*, 44: 1057–1067.

*MS accepted February 2009*

# APPENDIX

**Model fit ($R^2$), model predictive power ($AUC$) for the three models (TC = topoclimatic; GEO = topoclimatic model with the geomorphic variable; SNOW = topoclimatic model with the snow variable) and independent contribution (deviance, $R^2$) of the three groups of variables (TC = topoclimatic variables; GEO = geomorphic variable; SNOW = snow variable) in the variation partitioning analysis.**

| | | $R^2$ (Anzeindaz data set) | | | AUC by cross-validation (Anzeindaz data set) | | | AUC with the Nant dataset (transferability) | | | Variation partitioning with GEO ($R^2$) | | | | Variation partitioning with SNOW ($R^2$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Names | Occurrences | TC | GEO | SNOW | TC | GEO | SNOW | TC | GEO | SNOW | TC | GEO | TC + GEO | Unexplained | TC | SNOW | TC + SNOW | Unexplained |
| *Adenostyles glabra* | 20 | 0.588 | 0.575 | 0.623 | 0.846 | 0.752 | 0.857 | 0.875 | 0.881 | 0.911 | 0.368 | 0.004 | 0.251 | 0.377 | 0.640 | 0.041 | −0.021 | 0.340 |
| *Agrostis rupestris* | 10 | 0.478 | 0.555 | 0.694 | 0.785 | 0.801 | 0.817 | 0.767 | 0.700 | 0.800 | 0.247 | 0.088 | 0.270 | 0.395 | 0.662 | 0.207 | −0.145 | 0.275 |
| *Agrostis capillaris* | 19 | 0.495 | 0.636 | 0.495 | 0.853 | 0.902 | 0.807 | 0.607 | 0.690 | 0.607 | 0.403 | 0.151 | 0.105 | 0.341 | 0.502 | 0.013 | 0.006 | 0.479 |
| *Alchemilla conjuncta* aggr. | 41 | 0.629 | 0.656 | 0.619 | 0.838 | 0.859 | 0.821 | 0.767 | 0.767 | 0.763 | 0.507 | 0.038 | 0.159 | 0.296 | 0.629 | 0.001 | 0.037 | 0.333 |
| *Alchemilla xanthochlora* aggr. | 22 | 0.678 | 0.835 | 0.689 | 0.914 | 0.870 | 0.847 | 0.896 | 0.738 | 0.888 | 0.537 | 0.151 | 0.166 | 0.146 | 0.698 | 0.017 | 0.005 | 0.280 |
| *Alchemilla glabra* aggr. | 14 | 0.201 | 0.173 | 0.194 | 0.681 | 0.569 | 0.666 | 0.867 | 0.867 | 0.800 | 0.161 | 0.004 | 0.060 | 0.775 | 0.234 | 0.013 | −0.013 | 0.766 |
| *Androsace chamaejasme* | 18 | 0.595 | 0.622 | 0.602 | 0.847 | 0.725 | 0.863 | 0.433 | 0.400 | 0.433 | 0.237 | 0.039 | 0.389 | 0.335 | 0.622 | 0.016 | 0.003 | 0.359 |
| *Anthoxanthum odoratum* aggr. | 23 | 0.501 | 0.493 | 0.564 | 0.806 | 0.791 | 0.840 | 0.767 | 0.767 | 0.653 | 0.323 | 0.011 | 0.228 | 0.437 | 0.594 | 0.067 | −0.043 | 0.382 |
| *Anthyllis vulneraria* s.l. | 32 | 0.733 | 0.768 | 0.757 | 0.909 | 0.800 | 0.873 | 0.620 | 0.600 | 0.667 | 0.425 | 0.041 | 0.335 | 0.200 | 0.773 | 0.028 | −0.014 | 0.213 |
| *Asplenium viride* | 10 | 0.454 | 0.483 | 0.455 | 0.846 | 0.754 | 0.807 | 0.810 | 0.833 | 0.798 | 0.302 | 0.047 | 0.178 | 0.472 | 0.384 | 0.015 | 0.097 | 0.504 |
| *Bartsia alpina* | 20 | 0.576 | 0.687 | 0.615 | 0.820 | 0.843 | 0.816 | 0.758 | 0.764 | 0.709 | 0.341 | 0.114 | 0.267 | 0.278 | 0.630 | 0.046 | −0.022 | 0.346 |
| *Aster bellidiastrum* | 26 | 0.502 | 0.583 | 0.490 | 0.835 | 0.856 | 0.817 | 0.606 | 0.633 | 0.606 | 0.217 | 0.093 | 0.310 | 0.381 | 0.492 | 0.002 | 0.034 | 0.472 |
| *Botrychium lunaria* | 10 | 0.000 | 0.054 | 0.061 | 0.474 | 0.480 | 0.390 | 0.500 | 0.620 | 0.694 | 0.000 | 0.089 | 0.000 | 0.911 | 0.000 | 0.085 | 0.000 | 0.915 |
| *Campanula barbata* | 10 | 0.616 | 0.631 | 0.607 | 0.845 | 0.800 | 0.820 | 0.967 | 0.967 | 0.967 | 0.356 | 0.027 | 0.289 | 0.328 | 0.636 | 0.001 | 0.009 | 0.354 |
| *Carduus defloratus* s.str. | 19 | 0.383 | 0.361 | 0.387 | 0.786 | 0.698 | 0.767 | 0.703 | 0.710 | 0.697 | 0.362 | 0.003 | 0.052 | 0.583 | 0.426 | 0.020 | −0.012 | 0.567 |
| *Campanula scheuchzeri* | 39 | 0.538 | 0.533 | 0.536 | 0.845 | 0.836 | 0.815 | 0.641 | 0.714 | 0.662 | 0.339 | 0.013 | 0.234 | 0.414 | 0.579 | 0.010 | −0.006 | 0.418 |
| *Carex sempervirens* | 35 | 0.771 | 0.810 | 0.777 | 0.911 | 0.819 | 0.907 | 0.489 | 0.524 | 0.522 | 0.477 | 0.043 | 0.316 | 0.164 | 0.712 | 0.011 | 0.082 | 0.195 |
| *Carlina acaulis* subsp. *caulescens* | 12 | 0.410 | 0.483 | 0.470 | 0.771 | 0.702 | 0.804 | 0.785 | 0.746 | 0.715 | 0.413 | 0.088 | 0.027 | 0.472 | 0.491 | 0.070 | −0.051 | 0.490 |
| *Cerastium latifolium* | 12 | 0.458 | 0.442 | 0.461 | 0.836 | 0.830 | 0.845 | 0.658 | 0.669 | 0.692 | 0.438 | 0.005 | 0.034 | 0.523 | 0.435 | 0.016 | 0.037 | 0.512 |
| *Leucanthemum vulgare* aggr. | 16 | 0.419 | 0.445 | 0.425 | 0.827 | 0.766 | 0.758 | 0.892 | 0.885 | 0.892 | 0.406 | 0.045 | 0.056 | 0.492 | 0.460 | 0.020 | 0.002 | 0.518 |
| *Cirsium spinosissimum* | 23 | 0.277 | 0.309 | 0.277 | 0.690 | 0.689 | 0.699 | 0.812 | 0.804 | 0.783 | 0.306 | 0.058 | −0.011 | 0.647 | 0.310 | 0.019 | −0.015 | 0.686 |
| *Coeloglossum viride* | 12 | 0.335 | 0.394 | 0.449 | 0.764 | 0.653 | 0.796 | 0.586 | 0.586 | 0.466 | 0.186 | 0.080 | 0.166 | 0.568 | 0.397 | 0.125 | −0.045 | 0.524 |
| *Crepis aurea* | 20 | 0.632 | 0.638 | 0.687 | 0.897 | 0.857 | 0.910 | 0.573 | 0.567 | 0.533 | 0.382 | 0.019 | 0.269 | 0.331 | 0.695 | 0.060 | −0.044 | 0.289 |
| *Deschampsia cespitosa* | 10 | 0.377 | 0.460 | 0.368 | 0.765 | 0.720 | 0.701 | 0.850 | 0.823 | 0.850 | 0.488 | 0.097 | −0.064 | 0.479 | 0.426 | 0.007 | −0.002 | 0.569 |
| *Dryas octopetala* | 18 | 0.566 | 0.587 | 0.591 | 0.844 | 0.801 | 0.835 | 0.207 | 0.345 | 0.233 | 0.233 | 0.035 | 0.366 | 0.366 | 0.540 | 0.033 | 0.059 | 0.368 |
| *Euphorbia cyparissias* | 11 | 0.673 | 0.801 | 0.737 | 0.897 | 0.899 | 0.901 | 0.919 | 0.931 | 0.919 | 0.760 | 0.126 | −0.062 | 0.176 | 0.627 | 0.066 | 0.071 | 0.237 |
| *Euphrasia minima* | 17 | 0.691 | 0.761 | 0.869 | 0.908 | 0.899 | 0.968 | 0.818 | 0.848 | 0.755 | 0.460 | 0.076 | 0.246 | 0.218 | 0.855 | 0.173 | −0.149 | 0.121 |
| *Festuca quadriflora* | 20 | 0.388 | 0.398 | 0.377 | 0.806 | 0.737 | 0.757 | 0.196 | 0.214 | 0.179 | 0.232 | 0.032 | 0.172 | 0.564 | 0.394 | 0.005 | 0.009 | 0.592 |
| *Festuca rubra* aggr. | 28 | 0.695 | 0.718 | 0.708 | 0.892 | 0.917 | 0.877 | 0.670 | 0.634 | 0.652 | 0.331 | 0.033 | 0.380 | 0.257 | 0.722 | 0.019 | −0.012 | 0.271 |
| *Festuca violacea* aggr. | 11 | 0.291 | 0.292 | 0.303 | 0.668 | 0.629 | 0.717 | 0.623 | 0.579 | 0.689 | 0.244 | 0.027 | 0.083 | 0.646 | 0.307 | 0.029 | 0.020 | 0.645 |
| *Galium anisophyllon* | 35 | 0.701 | 0.746 | 0.763 | 0.880 | 0.877 | 0.860 | 0.866 | 0.796 | 0.862 | 0.376 | 0.050 | 0.355 | 0.219 | 0.787 | 0.062 | −0.057 | 0.208 |
| *Galium megalospermum* | 24 | 0.665 | 0.728 | 0.681 | 0.876 | 0.831 | 0.853 | 0.700 | 0.653 | 0.727 | 0.609 | 0.068 | 0.082 | 0.241 | 0.682 | 0.023 | 0.009 | 0.287 |
| *Geum montanum* | 15 | 0.616 | 0.655 | 0.662 | 0.879 | 0.866 | 0.878 | 0.707 | 0.724 | 0.586 | 0.350 | 0.049 | 0.285 | 0.315 | 0.612 | 0.052 | 0.024 | 0.313 |
| *Gentiana campestris* s.str. | 19 | 0.563 | 0.593 | 0.581 | 0.820 | 0.820 | 0.809 | 0.538 | 0.638 | 0.469 | 0.151 | 0.043 | 0.444 | 0.361 | 0.576 | 0.027 | 0.020 | 0.377 |
| *Gentiana purpurea* | 10 | 0.704 | 0.759 | 0.707 | 0.845 | 0.718 | 0.890 | 0.698 | 0.698 | 0.681 | 0.470 | 0.060 | 0.256 | 0.214 | 0.731 | 0.010 | −0.005 | 0.264 |
| *Gentiana verna* | 19 | 0.589 | 0.577 | 0.608 | 0.869 | 0.768 | 0.844 | 0.798 | 0.821 | 0.726 | 0.314 | 0.005 | 0.306 | 0.375 | 0.621 | 0.027 | −0.001 | 0.353 |

## APPENDIX
## Continued.

| | | $R^2$ (Anzeindaz data set) | | | AUC by cross-validation (Anzeindaz data set) | | | AUC with the Nant dataset (transferability) | | | Variation partitioning with GEO ($R^2$) | | | | Variation partitioning with SNOW ($R^2$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Names | Occurrences | TC | GEO | SNOW | TC | GEO | SNOW | TC | GEO | SNOW | TC | GEO | TC + GEO | Unexplained | TC | SNOW | TC + SNOW | Un-explained |
| *Globularia cordifolia* | 15 | 0.708 | 0.718 | 0.746 | 0.933 | 0.848 | 0.917 | 0.452 | 0.476 | 0.488 | 0.689 | 0.020 | 0.041 | 0.250 | 0.688 | 0.041 | 0.042 | 0.229 |
| *Gypsophila repens* | 13 | 0.439 | 0.502 | 0.424 | 0.757 | 0.807 | 0.758 | 0.707 | 0.720 | 0.707 | 0.339 | 0.077 | 0.142 | 0.442 | 0.473 | 0.000 | 0.009 | 0.518 |
| *Helianthemum nummularium* s.l. | 15 | 0.511 | 0.513 | 0.516 | 0.812 | 0.772 | 0.766 | 0.350 | 0.365 | 0.335 | 0.366 | 0.020 | 0.182 | 0.432 | 0.523 | 0.017 | 0.025 | 0.436 |
| *Helictotrichon versicolor* | 11 | 1.000 | 1.000 | 1.000 | 0.813 | 0.708 | 0.771 | NA | NA | NA | 0.486 | 0.000 | 0.514 | 0.000 | 0.973 | 0.000 | 0.027 | 0.000 |
| *Hieracium bifidum* aggr. | 15 | 0.226 | 0.279 | 0.227 | 0.745 | 0.677 | 0.723 | 0.774 | 0.833 | 0.780 | 0.161 | 0.079 | 0.083 | 0.676 | 0.231 | 0.020 | 0.014 | 0.735 |
| *Hippocrepis comosa* | 10 | 0.582 | 0.833 | 0.589 | 0.824 | 0.746 | 0.796 | 0.488 | 0.571 | 0.488 | 0.610 | 0.245 | −0.007 | 0.152 | 0.598 | 0.017 | 0.005 | 0.380 |
| *Hieracium villosum* aggr. | 12 | 0.434 | 0.423 | 0.436 | 0.793 | 0.717 | 0.781 | 0.412 | 0.412 | 0.450 | 0.372 | 0.011 | 0.090 | 0.527 | 0.466 | 0.016 | −0.004 | 0.522 |
| *Hieracium murorum* aggr. | 10 | 0.697 | 0.372 | 1.000 | 0.873 | 0.738 | 0.700 | 0.633 | 0.433 | 0.450 | −0.083 | −0.727 | 0.811 | 1.000 | 0.972 | 0.273 | −0.245 | 0.000 |
| *Homogyne alpina* | 28 | 0.693 | 0.738 | 0.719 | 0.912 | 0.894 | 0.894 | 0.833 | 0.860 | 0.833 | 0.297 | 0.053 | 0.411 | 0.239 | 0.737 | 0.032 | −0.030 | 0.260 |
| *Pritzelago alpina* s.str. | 15 | 0.516 | 0.584 | 0.512 | 0.844 | 0.859 | 0.863 | 0.785 | 0.798 | 0.819 | 0.580 | 0.079 | −0.040 | 0.380 | 0.501 | 0.008 | 0.040 | 0.451 |
| *Leontodon hispidus* s.l. | 29 | 0.641 | 0.675 | 0.634 | 0.893 | 0.897 | 0.889 | 0.702 | 0.702 | 0.685 | 0.331 | 0.044 | 0.328 | 0.297 | 0.605 | 0.002 | 0.054 | 0.339 |
| *Ligusticum mutellina* | 25 | 0.469 | 0.507 | 0.482 | 0.775 | 0.773 | 0.785 | 0.718 | 0.709 | 0.700 | 0.240 | 0.054 | 0.268 | 0.437 | 0.518 | 0.025 | −0.009 | 0.466 |
| *Lotus alpinus* | 11 | 0.479 | 0.579 | 0.467 | 0.845 | 0.832 | 0.830 | 0.592 | 0.489 | 0.595 | 0.229 | 0.113 | 0.263 | 0.395 | 0.485 | 0.001 | 0.008 | 0.506 |
| *Lotus corniculatus* | 22 | 0.408 | 0.394 | 0.435 | 0.759 | 0.730 | 0.741 | 0.824 | 0.843 | 0.861 | 0.412 | 0.010 | 0.055 | 0.523 | 0.505 | 0.038 | −0.038 | 0.495 |
| *Luzula multiflora* | 12 | 1.000 | 0.000 | 1.000 | 0.928 | 0.864 | 0.839 | 0.983 | 0.914 | 0.966 | −0.283 | −1.000 | 1.283 | 1.000 | 0.967 | 0.000 | 0.033 | 0.000 |
| *Myosotis alpestris* | 13 | 0.260 | 0.254 | 0.288 | 0.670 | 0.633 | 0.596 | 0.704 | 0.642 | 0.712 | 0.258 | 0.023 | 0.057 | 0.662 | 0.335 | 0.044 | −0.020 | 0.641 |
| *Nardus stricta* | 14 | 0.752 | 0.820 | 0.784 | 0.915 | 0.911 | 0.809 | 0.879 | 0.948 | 0.862 | 0.413 | 0.069 | 0.357 | 0.160 | 0.780 | 0.035 | −0.009 | 0.195 |
| *Pedicularis verticillata* | 11 | 0.637 | 0.677 | 0.647 | 0.806 | 0.790 | 0.747 | 0.286 | 0.304 | 0.304 | 0.330 | 0.048 | 0.343 | 0.279 | 0.657 | 0.018 | 0.017 | 0.309 |
| *Phleum alpinum* aggr. | 19 | 0.430 | 0.574 | 0.420 | 0.794 | 0.780 | 0.812 | 0.573 | 0.467 | 0.560 | 0.400 | 0.149 | 0.072 | 0.378 | 0.471 | 0.006 | 0.001 | 0.522 |
| *Phyteuma orbiculare* | 21 | 0.291 | 0.295 | 0.308 | 0.687 | 0.631 | 0.649 | 0.611 | 0.602 | 0.519 | 0.326 | 0.030 | 0.018 | 0.626 | 0.362 | 0.032 | −0.018 | 0.623 |
| *Plantago alpina* | 27 | 0.524 | 0.524 | 0.601 | 0.843 | 0.801 | 0.881 | 0.613 | 0.619 | 0.631 | 0.391 | 0.018 | 0.157 | 0.434 | 0.613 | 0.082 | −0.065 | 0.369 |
| *Plantago atrata* s.str. | 23 | 0.696 | 0.711 | 0.695 | 0.884 | 0.866 | 0.881 | 0.729 | 0.719 | 0.705 | 0.574 | 0.024 | 0.152 | 0.249 | 0.719 | 0.006 | 0.007 | 0.267 |
| *Poa alpina* | 33 | 0.545 | 0.555 | 0.538 | 0.840 | 0.819 | 0.819 | 0.696 | 0.746 | 0.692 | 0.390 | 0.025 | 0.189 | 0.395 | 0.554 | 0.005 | 0.025 | 0.416 |
| *Poa minor* | 13 | 0.495 | 0.486 | 0.491 | 0.810 | 0.743 | 0.808 | 0.793 | 0.788 | 0.808 | 0.491 | 0.011 | 0.029 | 0.469 | 0.508 | 0.009 | 0.012 | 0.471 |
| *Potentilla aurea* | 22 | 0.637 | 0.779 | 0.658 | 0.893 | 0.898 | 0.884 | 0.653 | 0.660 | 0.660 | 0.365 | 0.139 | 0.299 | 0.196 | 0.678 | 0.028 | −0.014 | 0.308 |
| *Poa cenisia* | 11 | 0.176 | 0.168 | 0.323 | 0.687 | 0.697 | 0.787 | 0.473 | 0.412 | 0.342 | 0.152 | 0.024 | 0.044 | 0.780 | 0.167 | 0.160 | 0.029 | 0.643 |
| *Potentilla crantzii* | 18 | 0.408 | 0.433 | 0.444 | 0.821 | 0.796 | 0.804 | 0.759 | 0.759 | 0.707 | 0.195 | 0.045 | 0.242 | 0.517 | 0.448 | 0.048 | −0.010 | 0.514 |
| *Polygala alpestris* | 13 | 0.569 | 0.600 | 0.559 | 0.803 | 0.761 | 0.788 | 0.900 | 0.900 | 0.933 | 0.417 | 0.044 | 0.184 | 0.355 | 0.601 | 0.002 | 0.000 | 0.397 |
| *Polygonum viviparum* | 32 | 0.667 | 0.715 | 0.686 | 0.888 | 0.895 | 0.895 | 0.704 | 0.700 | 0.752 | 0.332 | 0.056 | 0.352 | 0.260 | 0.695 | 0.026 | −0.011 | 0.290 |
| *Pulsatilla alpina* s.str. | 10 | 0.257 | 0.444 | 0.251 | 0.758 | 0.707 | 0.711 | 0.634 | 0.634 | 0.644 | 0.154 | 0.203 | 0.121 | 0.522 | 0.285 | 0.013 | −0.009 | 0.712 |
| *Ranunculus alpestris* | 14 | 0.671 | 0.712 | 0.687 | 0.836 | 0.819 | 0.813 | 0.769 | 0.712 | 0.769 | 0.518 | 0.048 | 0.178 | 0.256 | 0.686 | 0.023 | 0.010 | 0.281 |
| *Ranunculus montanus* aggr. | 34 | 0.756 | 0.771 | 0.757 | 0.932 | 0.919 | 0.884 | 0.822 | 0.814 | 0.831 | 0.421 | 0.022 | 0.353 | 0.204 | 0.766 | 0.007 | 0.008 | 0.218 |
| *Saxifraga paniculata* | 14 | 0.355 | 0.356 | 0.425 | 0.817 | 0.697 | 0.820 | 0.715 | 0.685 | 0.869 | 0.186 | 0.025 | 0.201 | 0.588 | 0.340 | 0.081 | 0.047 | 0.532 |
| *Salix retusa* | 20 | 0.713 | 0.751 | 0.750 | 0.906 | 0.821 | 0.894 | 0.613 | 0.628 | 0.622 | 0.457 | 0.044 | 0.284 | 0.215 | 0.757 | 0.040 | −0.015 | 0.218 |
| *Saxifraga oppositifolia* | 13 | 0.448 | 0.452 | 0.445 | 0.767 | 0.783 | 0.744 | 0.607 | 0.619 | 0.601 | 0.462 | 0.025 | 0.013 | 0.500 | 0.486 | 0.011 | −0.011 | 0.513 |
| *Saxifraga aizoides* | 28 | 0.250 | 0.241 | 0.241 | 0.623 | 0.613 | 0.641 | 0.513 | 0.548 | 0.526 | 0.308 | 0.021 | 0.017 | 0.654 | 0.328 | 0.011 | −0.003 | 0.664 |
| *Scabiosa lucida* | 23 | 0.362 | 0.430 | 0.346 | 0.748 | 0.772 | 0.728 | 0.634 | 0.646 | 0.634 | 0.183 | 0.086 | 0.211 | 0.520 | 0.385 | 0.001 | 0.009 | 0.605 |
| *Sedum atratum* | 11 | 0.189 | 0.306 | 0.248 | 0.683 | 0.742 | 0.713 | 0.522 | 0.625 | 0.598 | 0.144 | 0.137 | 0.086 | 0.634 | 0.229 | 0.075 | 0.000 | 0.696 |
| *Sesleria caerulea* | 31 | 0.623 | 0.645 | 0.616 | 0.877 | 0.846 | 0.841 | 0.569 | 0.621 | 0.574 | 0.368 | 0.034 | 0.283 | 0.315 | 0.623 | 0.003 | 0.028 | 0.346 |
| *Selaginella selaginoides* | 23 | 0.900 | 0.918 | 0.901 | 0.918 | 0.847 | 0.878 | 0.519 | 0.585 | 0.515 | 0.449 | 0.020 | 0.460 | 0.070 | 0.880 | 0.004 | 0.030 | 0.086 |

## APPENDIX
## Continued.

| Names | Occurrences | $R^2$ (Anzeindaz data set) | | | AUC by cross-validation (Anzeindaz data set) | | | AUC with the Nant dataset (transferability) | | | Variation partitioning with GEO ($R^2$) | | | | Variation partitioning with SNOW ($R^2$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | TC | GEO | SNOW | TC | GEO | SNOW | TC | GEO | SNOW | TC | GEO | TC + GEO | Unexplained | TC | SNOW | TC + SNOW | Unexplained |
| *Silene acaulis* | 12 | 0.746 | 0.752 | 0.811 | 0.891 | 0.841 | 0.899 | 0.593 | 0.426 | 0.505 | 0.287 | 0.016 | 0.478 | 0.220 | 0.662 | 0.065 | 0.102 | 0.170 |
| *Silene vulgaris* s.l. | 12 | 0.511 | 0.620 | 0.553 | 0.766 | 0.698 | 0.682 | 0.625 | 0.639 | 0.639 | 0.583 | 0.110 | −0.011 | 0.318 | 0.540 | 0.048 | 0.032 | 0.380 |
| *Soldanella alpina* | 31 | 0.603 | 0.650 | 0.645 | 0.871 | 0.873 | 0.872 | 0.704 | 0.688 | 0.688 | 0.313 | 0.058 | 0.309 | 0.319 | 0.656 | 0.049 | −0.033 | 0.328 |
| *Taraxacum officinale* aggr. | 12 | 0.271 | 0.259 | 0.300 | 0.734 | 0.638 | 0.745 | 0.638 | 0.603 | 0.707 | 0.267 | 0.016 | 0.022 | 0.695 | 0.294 | 0.046 | −0.005 | 0.665 |
| *Thymus praecox* subsp. *polytrichus* | 21 | 0.568 | 0.628 | 0.564 | 0.883 | 0.854 | 0.853 | 0.649 | 0.595 | 0.601 | 0.612 | 0.072 | −0.023 | 0.339 | 0.576 | 0.007 | 0.013 | 0.403 |
| *Thesium alpinum* | 14 | 0.419 | 0.448 | 0.478 | 0.744 | 0.717 | 0.784 | 0.552 | 0.517 | 0.552 | 0.311 | 0.047 | 0.152 | 0.490 | 0.463 | 0.067 | 0.000 | 0.470 |
| *Thlaspi repens* | 25 | 0.600 | 0.596 | 0.596 | 0.904 | 0.829 | 0.868 | 0.794 | 0.803 | 0.815 | 0.512 | 0.012 | 0.108 | 0.368 | 0.621 | 0.007 | −0.001 | 0.373 |
| *Trollius europaeus* | 13 | 0.570 | 0.609 | 0.562 | 0.817 | 0.903 | 0.846 | 0.889 | 0.870 | 0.889 | 0.387 | 0.050 | 0.216 | 0.347 | 0.584 | 0.003 | 0.019 | 0.394 |
| *Trifolium pratense* s.str. | 24 | 0.599 | 0.664 | 0.649 | 0.868 | 0.844 | 0.876 | 0.873 | 0.867 | 0.893 | 0.311 | 0.072 | 0.318 | 0.298 | 0.656 | 0.055 | −0.026 | 0.316 |
| *Trifolium thalii* | 14 | 0.451 | 0.475 | 0.458 | 0.805 | 0.657 | 0.823 | 0.713 | 0.759 | 0.731 | 0.272 | 0.043 | 0.207 | 0.479 | 0.498 | 0.020 | −0.020 | 0.501 |
| *Vaccinium gaultherioides* | 12 | 0.782 | 0.828 | 0.791 | 0.887 | 0.845 | 0.884 | NA | NA | NA | 0.358 | 0.047 | 0.446 | 0.149 | 0.794 | 0.013 | 0.010 | 0.183 |
| *Vaccinium myrtillus* | 15 | 0.624 | 0.825 | 0.634 | 0.767 | 0.869 | 0.811 | 0.983 | 1.000 | 0.931 | 0.388 | 0.187 | 0.274 | 0.151 | 0.648 | 0.018 | 0.014 | 0.321 |
| *Vaccinium vitis-idaea* | 10 | 0.705 | 0.751 | 0.714 | 0.861 | 0.865 | 0.826 | NA | NA | NA | 0.291 | 0.052 | 0.436 | 0.221 | 0.676 | 0.015 | 0.051 | 0.257 |
| *Veronica aphylla* | 16 | 0.486 | 0.488 | 0.501 | 0.778 | 0.766 | 0.743 | 0.633 | 0.625 | 0.647 | 0.352 | 0.021 | 0.186 | 0.442 | 0.554 | 0.026 | −0.016 | 0.437 |
| *Viola calcarata* | 14 | 0.469 | 0.501 | 0.468 | 0.846 | 0.835 | 0.803 | 0.536 | 0.607 | 0.512 | 0.178 | 0.049 | 0.317 | 0.456 | 0.436 | 0.012 | 0.059 | 0.492 |