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Testing the power of remotely sensed snow cover duration to predict plant species distributions in alpine ecosystems

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Abstract

The impact of snow on plant distributions in arctic and alpine ecosystems has been known for decades. However, as major progress was made in the development of alpine plant species distribution models, snow cover was recurrently disregarded as predictor. Here we filled this gap by using a large set of satellite images to produce three snow cover duration indexes. One of them is using an online platform, allowing quick and easy replication anywhere in the world. We examined the increase in predictive power brought by addition of the snow predictor in species distribution models of 206 alpine plants, alongside other commonly used topoclimatic predictors. Despite the snow indexes containing redundant information with other climatic predictors, addition of each of the three indexes resulted in an overall increased accuracy of the models. Species being known for their interaction with snow seem to benefit especially from the additional information carried by the snow indexes. In the context of global warming, our findings suggest that scenarios of snow cover decrease should be considered when assessing the future distribution of snow-sensitive alpine plant species.

Résumé

L'impact de la neige sur la répartition des plantes dans les écosystèmes arctiques et alpins est connu depuis des décennies. Cependant, à mesure que des progrès importants ont été réalisés dans l'élaboration de modèles de distribution des espèces végétales alpines, la couverture neigeuse a été de façon récurrente négligée comme prédicteur. Dans cette étude, nous avons comblé cette lacune en utilisant un vaste ensemble d'images satellitaires pour produire trois indices de durée de la couverture de neige. L'un d'eux utilise une plateforme en ligne, permettant une reproduction rapide et facile partout dans le monde. Nous avons examiné l'augmentation de la puissance prédictive apportée par l'ajout du prédicteur de neige dans les modèles de distribution des espèces de 206 plantes alpines, aux côtés d'autres prédicteurs topoclimatiques couramment utilisés. Malgré le fait que les indices de neige contiennent des informations redondantes avec d'autres prédicteurs climatiques, l'ajout de chacun des trois indices a entraîné une augmentation globale de la précision des modèles. Les espèces connues pour leur interaction avec la neige semblent bénéficier tout particulièrement de l'information supplémentaire apportée par les indices de neige. Dans le contexte du réchauffement climatique, nos résultats suggèrent que les scénarios de diminution de la couverture neigeuse devraient être pris en compte lors de l'évaluation de la distribution future des espèces végétales alpines sensibles à la neige.

Keywords

Climate change; Remote sensing; Snow cover duration; Species distribution models; Swiss Alps; Vegetation

Abbreviations

DOY= day of year; GEE = Google earth engine; GLM = generalized linear models; NDSI = normalized-difference snow index; prci = sum of precipitation for the growing season; SCD = snow cover duration; SDM = species distribution model; srad= solar radiation, calculated with DEM; tmpr= mean temperature of the growing season; topo= topographical position

Introduction

The world is undergoing critical environmental changes that can have major effects on biodiversity (Díaz et al., 2019). Species are experiencing shifts in distribution, colonizing new environments or suffering from local extinction due to the disappearance of suitable habitats. Species distribution models (SDM; Guisan and Zimmermann, 2000; Guisan et al., 2017) can both predict the current and future distribution of species, making it a useful tool for conservation planning and decision making (Pineda and Lobo, 2009; Algar et al., 2009; Guisan et al., 2013). Nonetheless, SDMs need to reach a certain quality in order to be relevant for conservation (Araújo et al., 2019). In this regard, Scherrer & Guisan (2019) showed the importance of using predictors relevant to the ecology of the studied species. Unfortunately, in plants SDMs, ecological knowledge about the species is not necessarily what is being used as predictors, usually because of a lack data availability (Mod et al., 2016). Models built in such a way are ignoring critical ecological information, resulting in reduced accuracy and usefulness.

SDMs are based on the environmental niche concept, defined as a n-dimensional hypervolume in environmental space (Hutchinson, 1957). That implies that species distributions are driven by multiple environmental variables, depending on the specific needs and physiological limitations of each species. Predictors used in SDMs are usually at least including climatic maps, typically various expressions of temperature and precipitations, and topographic maps, e.g. slope (Truong et al., 2017). Both are easy to obtain and give predictions of decent quality (e.g. Pradervand et al., 2014). However, it was suggested that using only those predictors may not explain all the variation in plants distributions (Mod et al., 2016; Scherrer and Guisan, 2019). Additional environmental information might hence help improve SDMs accuracy.

Snow in particular has been overlooked so far in SDMs (Niittynen and Luoto, 2018), although knowledge from theoretical plant ecology indicates that it might be a relevant parameter in alpine and arctic environments. Snow is critical for vegetation distribution in high elevation ecosystems (Evans et al., 1989; Walker et al., 1993). Vegetation mosaics usually follow the snow melting isoline, which defines the start of the growing season in alpine ecosystems (Friedel, 1961; Körner, 2003), strongly supporting the role of snow cover as a key driver of

plant distributions in these landscapes. Its effects, benefic or detrimental, on plants have been known for decades, including among others, protection against winter desiccation, ice blast, low temperatures and herbivory, shorter growing season and humidity released by the melting snow (Billings and Bliss, 1959; Walker et al., 1993). Some plant species directly rely or avoid those conditions in order to complete their life cycle (Friedel, 1961; Galen and Stanton, 1995). Some plants are known to rely heavily on snow cover (Körner, 2003). Such plants need the insulation and the reliable water supply provided by the snow layer. They are usually found in snowbeds, areas where snow accumulates during the winter and lasts longer in spring and summer. Other species tend to avoid snowbeds. The latter plants usually need a long growing period to reproduce early in the season and higher nutrients supply (Gjaerevoll, 1956; Galen and Stanton, 1995; Odland and Munkejord, 2008).

Global changes have been shown to affect alpine and arctic ecosystems more than the rest of the world (Tenenbaum, 2005; Rebetez and Reinhard, 2008; Bintanja and Andry, 2017), subsequently decreasing the duration and the thickness of the snow cover dramatically (IPCC, 2017). Those changes can have dramatic effects on plants phenology and physiology. In particular, the loss of insulation due to snow cover has been shown to induce frost damages to plants (Wipf et al., 2009), especially for snowbed species that are known to have lower frost resistance than other plants (Bannister et al., 2005). The future perturbation in snow cover due to temperature rise in the Alps will certainly have a drastic effect on future habitat availability for many alpine and arctic species (Keller et al., 2005; Matteodo et al., 2016).

These evidences of the importance of snow for alpine and arctic plant species, under current and future climate, rises interrogations on why so little usage of this predictor is made in many SDMs in mountain regions (Engler et al., 2011; Siniscalco et al., 2011; Dubuis et al., 2013, p. 201; but see Randin et al., 2009c). Unlike usual climatic predictors, which can be mapped relatively easily by interpolation of meteorological stations data corrected by elevation, snow is harder to predict across a landscape. Indeed, snow distribution at the start of the growing season is dictated by many factors, such as wind, topography and solar radiation (Gottfried et al., 1999; Liston and Sturm, 1998, 1998), which makes it difficult to map (Rango et al., 1977).

Recent advances in geographic information systems (GIS) and remote sensing technologies now allow obtaining high quality mapped data for the past and the present, which can be used

to build snow distribution maps. This opens the way for larger scale studies of the influence of snow cover on the distribution of plant species (Zimmermann et al., 2007). At the turn of the new millennium, few studies included snow cover in plant SDMs (Guisan et al., 1998; Guisan and Theurillat, 2000; Dirnbock et al., 2003; Beck et al., 2005). However, those existing mainly used simple snow indexes, with limited remote sensing data (e.g. local aerial photographs). Still, those papers found that snow was a relevant predictor, making later disappearance from SDMs surprising (Niittynen and Luoto, 2018).

In a recent study, Niittynen and Luoto (2018) used a newly developed technique to quantify snow cover duration from a large dataset of Landsat satellite images and incorporate it as additional predictor in plant SDMs. Unlike precedent studies, the authors focused on snow cover duration, this parameter being pointed out as the most obvious impact of snow on plants (Körner, 2003). In the study of Niittynen and Luoto (2018), the introduction of this index in SDMs for arctic species in northern landscapes resulted in a large improvement of their accuracy. This suggests that plant SMDs in alpine regions might similarly benefit from the addition of accurate snow indexes.

The goals of this study is to assess the extent to which snow indexes can improve spatial modelling of plants in alpine landscapes, and more specifically to: (1) test the importance of different snow cover duration indexes, including a newly developed approach using Google earth engine (GEE); (2) assess whether the snow cover duration indexes provide complementary or redundant information with topo-climatic predictors; and finally (3) test if the new snow indexes bring relevant information for particular species, and if so which ones, under current climate and in the context of climate change projections.

To achieve this, we first produced three different snow duration indexes: one based on a newly developed method implemented within the online platform Google Earth Engine (GEE); and two based on the same approach used by Niittynen et al. (2018), but using different thresholds for snow identification. All approaches are using NASA's Landsat images (https://www.usgs.gov) and estimate the average snow melting date across the study area. This way to express the snow cover duration was chosen because snowmelt defines the start of the growing season (Friedel, 1961; Körner, 2003), hence having the most obvious effect on plants. In addition, the spatial patterns of snowmelt were shown to remain similar from one

year to the other (Anderton et al., 2004; Schirmer et al., 2011). We expect that the GEE approach, although more efficient by being entirely embedded in the single online GEE platform and thus easily adaptable to any study area, might result in an index of lesser importance in SDMs due to the limited built-in statistical tools. It is also expected that snow indexes might bring new relevant information for SDMs (Niittynen and Luoto, 2018) but also contain redundant information with topoclimatic predictors (Horsch, 2003). Finally, due to the altitudinal gradient in the Alps, it can be expected that interaction with snow might differ a lot from species to species (Randin et al., 2009c). Therefore, the amelioration in the SDMs predictions using snow index should be intimately linked with species ecology.

Material and Methods

Study area

The study area, also known as RechAlp (http://rechalp.unil.ch) (figure 1) is located in the Western Swiss Alps (Canton de Vaud, 46°10' to 46°30' N, 6°50' to 7°10' E). It is an area of 700 km^2 located within a temperate climate type. It spans a wide elevation gradient, from 375 m a.s.l. in the Rhone plain to 3210 m a.s.l. at the top of the Diablerets massif. Vegetation is thus largely controlled by the altitudinal gradient, ranging from broadleaf forests at low elevation to alpine grasslands and nival vegetation at the highest areas. Humans had and still have a marked influence, e.g. pasturing, forest logging and water capitation, on the landscape and therefore on the vegetation (Randin et al., 2009b).

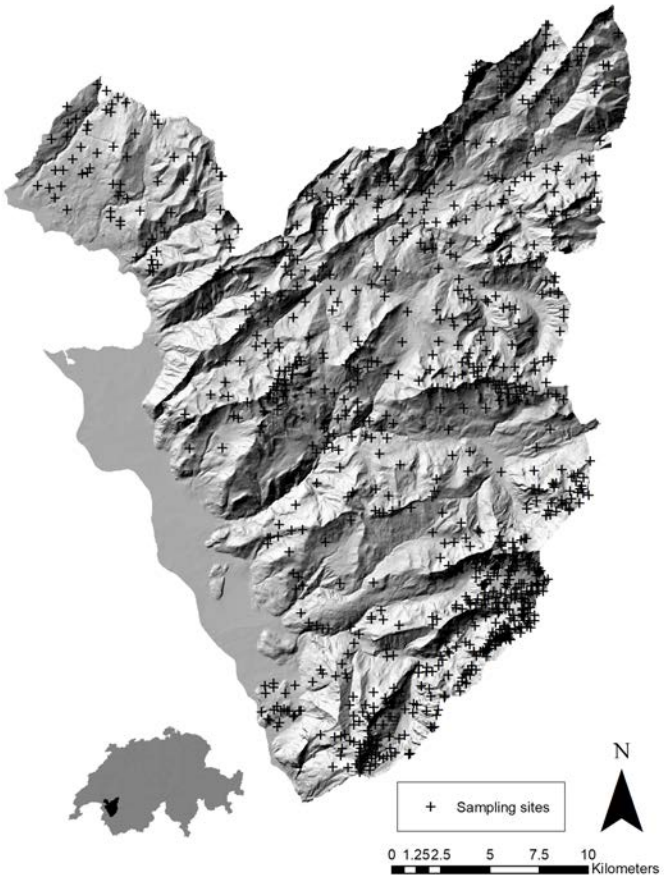

Figure 1: Localization of the study area in the Swiss alps. The 912 sampling plots are symbolized with cross

Species data collection

During the summers 2002 to 2009, a total of 912 4 m^2 plots were sampled (Dubuis et al., 2011; Buri et al., 2017), following a random-stratified equal sampling design (Hirzel and Guisan, 2002). The stratifying factors were elevation (10 classes, from 375 m to 3201 m a.s.l.), slope (three classes, 0-5°,5-25° and >25°) and aspect (five classes, North, East, South, West and no aspect if slope <5°) and the minimal distance between plot was set to 200 m in order to minimize spatial auto-correlation (Chevalier et al. in review). The sampling was limited to open, non-forest vegetation.

General analytical workflow

This study was structured in two steps. First, we built three different snow cover duration index (SCD) maps, based on three distinct approaches (Figure 2). Second, we tested across 206 species the increase in predictive power of plant species distribution models (SDM) when adding the SCD variables. We tested independently the increase in predictive power when the SCD map was used alongside (i) other climatic variables, (ii) topographical variable and (iii) both previous types of variables. Finally, we assessed which of the three SCD methods best improved the predictive power of plant SDMs.

Remote sensing data

The remote sensing data consisted of satellite images - Landsat TM 4 & 5, ETM+ 7 and OLI 8 - ranging from 1984 to 2019, freely accessible from the U.S. Geological Survey (https://www.usgs.gov). The satellite images were filtered in Google Earth Engine (GEE; https://code.earthengine.google.com), selecting those with at least one pixel covering our study area. Since we were only interested in snowmelt, coinciding with the start of the growing season, we only used images that ranged from the 50^{th} to the 250^{th} day of the year. That way, we captured the start of the growing season, ignoring potential local variation of snow cover during the cold season. A total of 1272 images were extracted. We used the Fmask classification (Zhu et al., 2015; Zhu and Woodcock, 2012) to remove all the pixels obscured by clouds in every image. Fmask is a classification algorithm developed to detect clouds and snow in Landsat images. Due to the roughness of the terrain, we excluded the shadows of the mountains from all the images using the terrain.hillshadow function available in GEE (Li et al., 2015). This function uses the azimuth and zenith of the sun together with a Digital Elevation Model (DEM), here the Shuttle Radar Topography Mission (SRTM) (Farr et al., 2007), to

attribute a shadowed or un-shadowed value to every pixel. All shadowed pixels were removed from the data. Finally, we used the reduce.count function in GEE to export a map representing the number of value available for every pixel in the study area.

Snow duration map

Three approaches were used to build snow indexes, that will further be compared for their potential to improve SDMs. We quantified snow persistence, since it has been shown that it best represents the impact that snow has on vegetation (Körner, 2003). All approaches determine, for every place across the study area, the mean day of the year at which the snow melts. The first approach is based on the Fmask classification, and was completely computed in GEE. The second and third approaches are based on a method that was recently used to produce snow cover duration index for SDMs (Macander et al., 2015; Niittynen and Luoto, 2018). The three methods are as follow.

Approach 1: Google Earth Engine

Here, each image was reclassified using the Fmask snow classification. Its algorithm works in a similar manner as the one previously used for the clouds mask. This algorithm is described in Zhu and Woodcock, (2012). Among others, it is based on a normalized difference between the green and the short wave infra-red bands (NDSI, defined in the next section) above a threshold value of 0.15. From this classification resulted a binary map of snow presence and absence for each image taken a different day of the year (DOY). Across all images, every pixel in the study area thus was attributed a collection of presences and absences of snow, each associated with a DOY. For each pixel, we applied a temporal moving window of 10 days, based on the DOY at which the image was taken, taking the mean of the binary snow presence/absence values in each window. This resulted, for every pixel in the study area, in a probability of snow occurrence for all DOY from the 50^{th} to the 250^{th} day. The days of snowmelt for every pixel was defined as the day when this value reached a 0.5 or lower probability of snow presence threshold. The pixels never reaching this threshold were considered as everlasting snow, and their value were set to 365.

We wanted this approach to be fully based on GEE, with a resulting SCD map that could be directly used and compared to the Macander et al. (2015) and Niittynen et al. (2018) ones. However, at the time of this study, GEE did not offer advanced statistical tools, such as generalized linear models (GLMs) used in Niittynen et al. (2018). Therefore, we made use of a mean moving window to calculate a snow index in GEE.

In order to match with the other environmental data used in the SDMs, we exported the resulting SDC map from GEE, and rescaled it to 25 m x 25 m using a bilinear interpolation, in order for them to match the resolution of the other environmental variables used in the SDMs.

At the end of the process, a few pixels had no or very few snow values across the year. Those pixels were distributed in very small patches scattered through the study area and were due to the presence of local hill shadows effects. We filled them in to obtain continuous predictions over our study area. We used a majority focal statistic in ARCMAP (ESRI, version 10.7) with a circle dimension of 5 cells, on all pixel having less than 10 available values. Predictions in these 'filled gaps' should be considered with great care. The resulting SCD map produced with this approach is further referred as "SCD_{gee}".

Unless specified differently, all the statistics and GIS manipulations were performed in GEE.

Approach 2: Generalized Linear Models with 0.40 threshold

This approach is based on the previous work of Macander et al. (2015) and Niittynen et al. (2018). We calculated the Normalized-Difference Snow Index (NDSI) on every image in R. The NDSI uses the difference between reflectance of the green and the shortwave infrared (SWIR) bands to produce a widely used index (Crane and Anderson, 1984; Dozier, 1989; Hall et al., 2002, 1995). This NDSI is defined as follows:

$$NDSI = \frac{(Green - SWIR)}{(Green + SWIR)}$$

This index ranges from -1 (no snow) to 1 (snow). We then produced binary maps from the NDSI maps, using the standard threshold value of 0.40 (Macander et al., 2015; Niittynen and Luoto, 2018) for all images. All pixels above this threshold were interpreted as covered by snow and those below as free of snow. Next, we used these binary maps to produce the snow

cover duration (SDC) map. For this, we fitted, for each pixel independently, a Generalized Linear Model (GLM) with binomial distribution and logistic link with the binary score of every image as the dependent variable and the DOY at which the picture was taken as the explanatory variable. This generated a probability of snow occurrence for every DOY from the 50th to the 250th. The final SCD map was produced by taking, for every pixel, the DOY where this probability of snow presence passed below the 0.5 threshold. Finally, the same filling technique as applied for the GEE approach was used. Hereafter, the resulting SCD map will be called "$SCD_{0.40}$".

All the statistics and GIS manipulations were performed in R 3.5.3 (R Core Team 2019), using the raster package (Hijmans et al., 2019) (except for analyses specified on other software).

Approach 3: Generalized Linear Models with 0.15 threshold

The Fmask classification of snow, used in the GEE approach, is an algorithm that uses many criteria to identify snow. But the main criteria that decides for the classification as snow is that the NDSI should be above 0.15. Since the method of Macander et al. (2015) is based on a

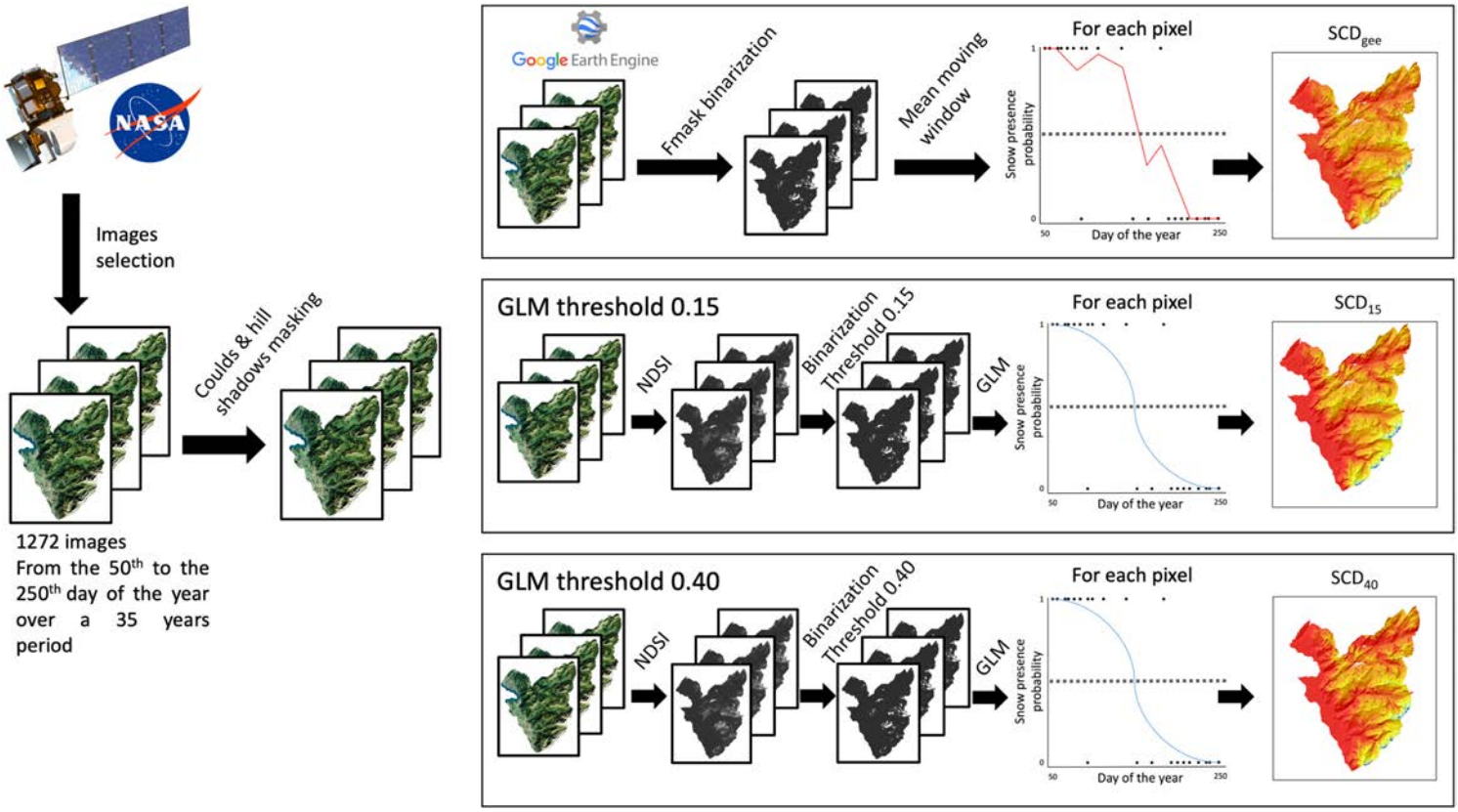

Figure 2: General workflow for the production of the three snow cover duration maps. First the satellite images were selected and cleared from clouds and hill shadows. Then images were treated with the three approaches to produce three snow cover duration map

different threshold of 0.40, a difference in snow detection between the two methods could thus simply result from using a different threshold. In order to differentiate the effect of the method of snow detection from the effect of the threshold, we produced a third map using the GLM method (previous section) but with a lower NDSI threshold of 0.15. This map will further be referred to as "$SCD_{0.15}$".

Environmental variables

Current climate

In addition to the three SCD map produced above, we used a set of 5 environmental variables commonly used in SDM studies (e.g. Parolo and Rossi, 2008; Randin et al., 2009b; Dubuis et al., 2011; Buri et al., 2017). Two climatic variables: mean temperature of the growing season (tmpr) and sum of precipitation for the growing season (prci). The reference period for the predictors was 1981 to 2010. We added three topographical variables: the topographical position (topo), the slope (slope) and solar radiation (srad), calculated from a digital elevation model (DEM) at a 25 m resolution. The tmpr variable was derived from the daily MeteoSwiss Grid-Data Products at 1km (Beniston et al., 2003), then downscaled with local regression with elevation to 25 m x 25 m for the study area (Broennimann, 2018). We only kept the mean for the months of the growing season (June, July and August) as reference period, and computed the mean temperature for these three months. The precipitation index prci was also derived from daily MeteoSwiss data, downscaled with local regression with elevation heterogeneity to 25 m x 25 m. We selected the same months as before, and the final index was computed as the sum of the means of the 3 months. The srad variable was computed with module ta_lighting in SAGA GIS and accounts for daily potential incoming solar radiation. The topo and slope variables were derived from the Swiss digital elevation model at 25 m resolution (https://www.swisstopo.admin.ch). The slope was calculated as the angle of the slope based on the surrounding elevation values in a neighboring window of 3 pixels using the slope function from the spatial analyst extension for ArcGIS. The topo variable was calculated using the AML function for ArcGIS written by Niklaus E. Zimmermann at WSL (https://www.wsl.ch/staff/niklaus.zimmermann/programs). It expresses the difference in elevation in meters of a given location compared to the surrounding terrain at various scales. Negative values thus indicate gullies and valley bottoms, values close to 0 indicate flat terrain or steady slopes and positive values indicate mountain tops and ridges. In order to visualize

the relationship between the climatic, topographic and snow predictors, we calculated the matrix of Pearson correlation coefficient between all initial predictors. In addition, we performed a generalized linear model to check if the SCD maps could be explained by the topoclimatic predictors. Topographic and climatic predictors were used, independently and together, as the explanatory variable and the SCD values as dependent variable.

Future climate

For projections in future climate, we used data provided by the CH2011 initiative (Zubler et al., 2014) for temperature and precipitation variables, downscaled with bilinear interpolation at 25 m x 25 m to match the resolution of the present climate (previous section). We used the A2 climate change scenario (IPCC, 2000) for the time period of 2070-2099. We computed the final variable in the same manner as for the current climate, resulting in the future mean temperature of the growing season ($tmpr_F$) and future sum of precipitations of the growing season ($prci_F$). Regarding the decrease in snow cover, although many studies were published on snow cover changes in the Alps (e.g. Whetton et al., 1996; Dye and Tucker, 2003; Hantel and Hirtl-Wielke, 2007; Klein et al., 2016), no method was easily applicable to derive snow change scenario for our study area, due to the wide elevation range. Therefore, we used the work of Beniston et al., (2003), predicting a decrease in SCD of 120 days at 1000 m a.s.l. and 55 days at 2250 m a.s.l. for the A2 climate change scenario. We simply used a linear interpolation based on those two points on the altitudinal gradient to subtract the numbers of days corresponding to each altitude to the current SCD map, resulting in the future SCD_F map.

Species distribution models

For this study, we modelled all species with more than 30 occurrences over the set of sampled sites, resulting in models for 206 plant species (listed in supp. mat. 1). We used an ensemble approach implemented in the biomod2 package in R including three different modeling techniques: (i) generalized linear models (GLM) with a binomial family and logistic link, allowing quadratic terms but no interaction; (ii) generalized additive models (GAM) with a binomial family, logistic link and smothers with 4 degrees-of-freedom; and (iii) gradient boosting machine (GBM) with 1000 trees, an interaction depth of 7, a shrinkage factor of 0.001 and a bag fraction of 0.5.

To test the model's prediction accuracy, we used 80% of the species data for calibration and held 20% out for their evaluation. Each model was replicated 100 times. During each replication, we used the area under the receiver-operating characteristic curve (AUC; Swets, 1988) and the true skill statistics (Allouche et al., 2006) maximized across the whole range of thresholds between 0 and 1 (maxTSS; (Guisan et al., 2017) as the evaluation metrics for the accuracy of the models. Variable importance was also recorded from each replication. From the models fitted with the three techniques, we built an ensemble model for each species and SCD map, by applying a weighted sum of probabilities, with weight based on the maxTSS. All the previous models were used, regardless to their accuracy, and the same evaluation metrics as before were used: AUC and maxTSS. All the models were fitted using the R package biomod2 (Thuiller et al., 2019).

Four different sets of models, using different predictors, were fitted: (a) a set using all the topographic, climatic and SCD predictors; (b) a set of climatic + SCD and topographic + SCD independently; (c) a set with only the SCD; (d) a set using all topoclimatic predictors, but not the SCD one. In addition to the following descriptions, a summary of the different models, projections and their comparisons is provided in figure 3.

Topoclimatic + SCD (a)

In order to test if the inclusion of the SCD variables improved the models, we examined for each species the accuracy of models fitted with each original SCD map and compared it to models including instead the same variable randomized, hereafter called SCD shuffled. This ensure a similar structure between all compared models (i.e. same numbers of predictors). This method has proven sound for testing the improvement of adding new variables in SDMs (Zimmermann et al., 2009; le Roux et al., 2013; Buri et al., 2017; Niittynen and Luoto, 2018; Buri et al., in press), by ensuring that the added variable does not increase predictive power by chance (i.e. if the added variable explains a part of the variance by chance). This resulted in the following three base models:

$$Base\ model\ GEE: tmpr + prci + srad + topo + slope + SCD_{gee}$$

$$Base\ model\ GLM\ treshold\ 0.15: tmpr + prci + srad + topo + slope + SCD_{0.15}$$

$$Base\ model\ GLM\ treshold\ 0.40: tmpr + prci + srad + topo + slope + SCD_{0.40}$$

And for each of these models, a corresponding model was fitted with the shuffled SCD variable:

$$Shuffled\ model: tmpr + prci + srad + topo + slope + SCD_{shuffled}$$

Climatic + SCD and topographic + SCD independently (b)

We compared SDMs built with SCD and either the climatic, or the topographic variables independently. These models allowed testing whether the SCD map conveyed complementary information to the climatic or topographic variables. The two resulting models for each SCD map (including shuffled maps) were defined as follows:

$$Clim + SCD\ model: tmpr + prci + SCD$$

$$Topo + SCD\ model: srad + topo + slope + SCD$$

SCD only (c)

We also build models using only the SCD as predictor, to test the accuracy of models with only this variable.

$$SCD\ only\ model: SCD$$

Without SCD (d)

And a topo-climatic model without SCD as a predictor, in order see the difference in predictions with and without this variable.

$$Model\ without\ SCD: tmpr + prci + srad + topo + slope$$

SDM predictons

Finally, for each species, we applied models under current and future climate, using the model computed for the topoclimatic + SCD models (a), using the SCD index that performs best, and models without SCD. We used maxTSS as the binarisation method to produce presence-absence maps from the probabilistic predictions.

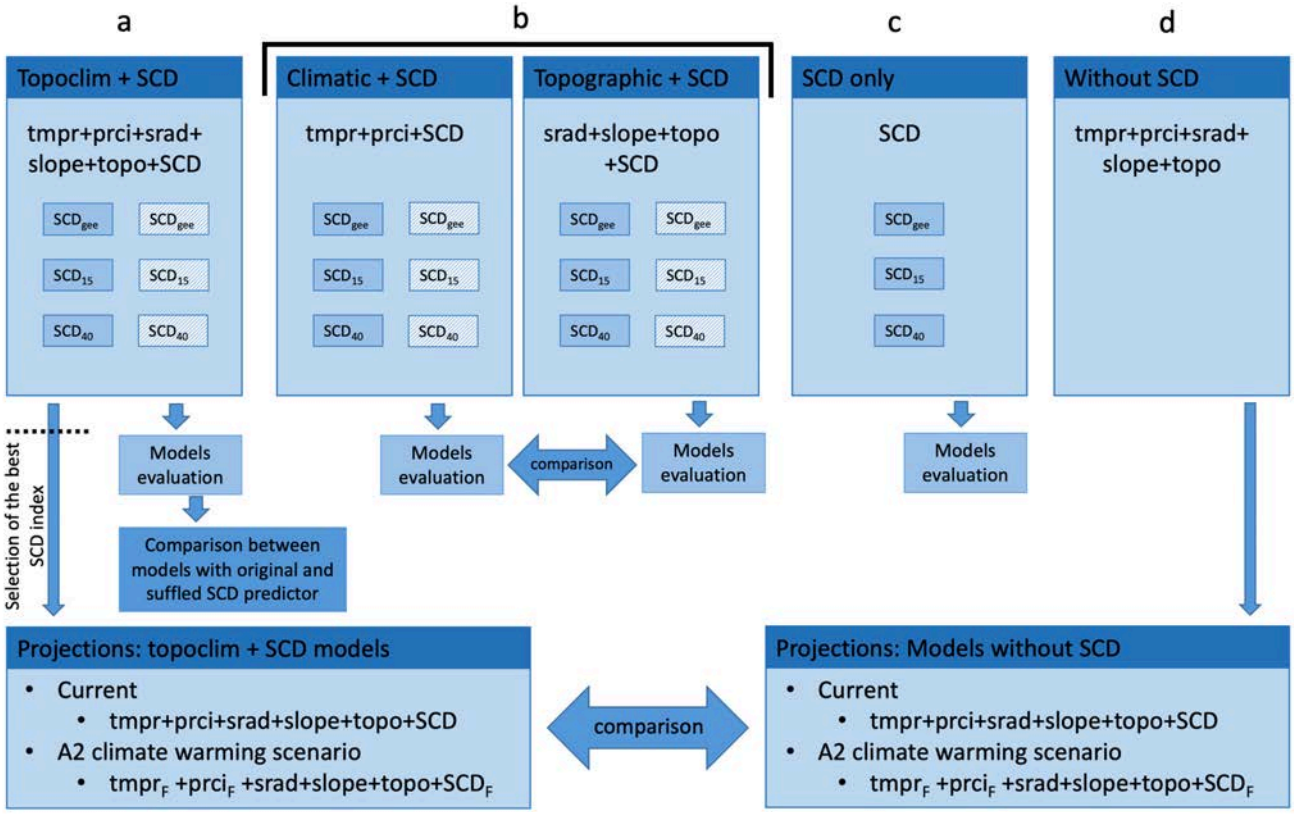

Figure 3: Summary of the different models build for this study with their respective predictors. SCD indexes in hatched symbolize the shuffled map.

SDMs comparisons

To effectively examine the improvement in model performances, we compared AUC and maxTSS values of the ensemble models. We ran a Wilcoxon signed rank test between the evaluation metric of models with the SCD map (SCD_{gee}, $SCD_{0.15}$ or $SCD_{0.40}$) and with their shuffled relative. We also compared the performances of the SCD maps with each other to assess which was the most suited for SDMs.

We also fitted a general linear model in order to find out whether the model improvement was increasing with the altitude of occurrence of the species (based on the species' mean elevation of the occurrences for our dataset), with the altitude as the predictor and the model improvement as the response. Finally we tested if the species' ecological Landolt values (Landolt et al., 2010) had an influence on the improvement due to snow with an analysis of variance, with the Landolt value as the explanatory variable and the model improvement as the response variable.

Results

Snow cover duration map

The mean number of non-cloudy or shaded Landsat images available and thus of values per pixel was 422±138 and reaching a maximum of 704 over the study area. There were pixels with 0 values (places always under cloud cover or affected by shadows). However, those pixels represented only 0.158% of the study area.

An important difference was observed in the mean snow melting DOY between the SCD maps computed with a 0.15 threshold ($SCD_{0.15}$ and SCD_{gee}) and a 0.40 threshold ($SCD_{0.40}$). The mean snow melting days over the study area were respectively 91.2, 90.5 and 86.2 respectively. In all indexes, the snow melt date ranged from 50 in the plain (the default minimum), to 365 (the default maximum) in the permanent snows patches of the Diablerets massif.

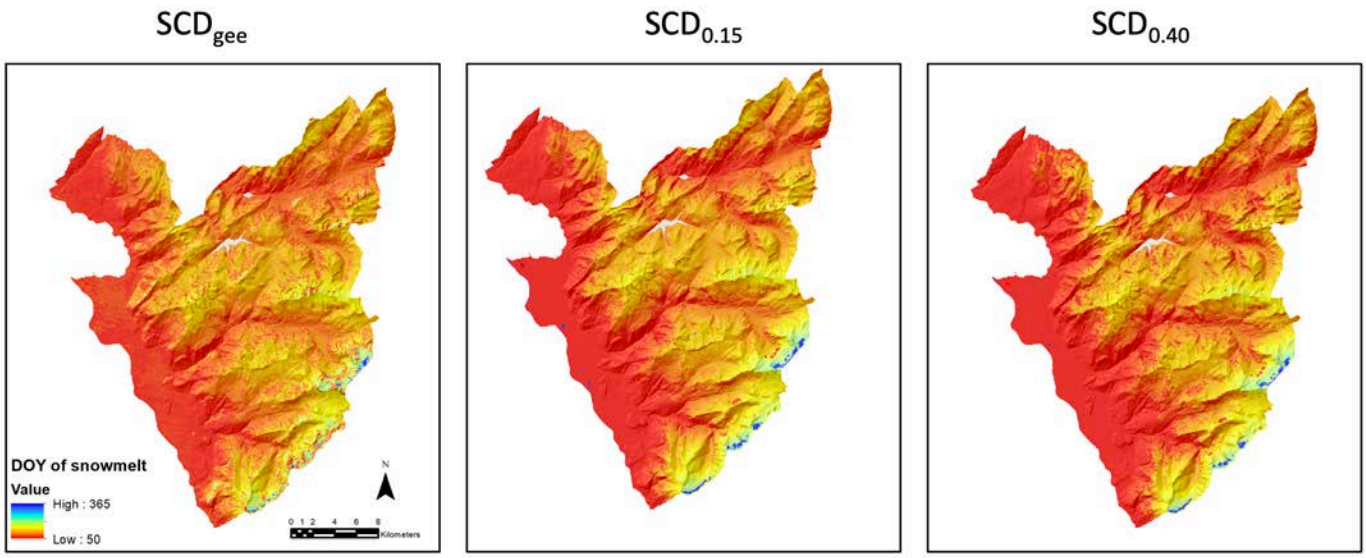

Figure 4: Different Snow cover duration indexes further used in SDMs.

The snow indexes showed a relatively high correlation with others climatic variables, but low correlation with topographic variables (table 1). In addition, the GLMs with the climatic variables only had a high deviance value (D^2), showing that they can partly explain the SCD

maps (0.52 for SCDgee and 0.78 for both SCD15 and SCD40). The D^2 values for the GLMs using the topographic predictors were lower (0.05 for SCDgee, 0.14 for SCD15 and 0.15 for SCD40). When combined, climatic and topographic variables could predict a large part of the SCD maps (GLM, D^2= 0.54 for SCDgee, 0.83 for SCD15, 0.84 for SCD40).

When compared to the other two SCD maps, SCDgee showed a correlation of 0.76 with SCD15 and 0.77 with SCD40, whereas those two had a correlation of 0.98.

Table 1: Correlation between the SCD maps and others climatic variables and prediction of the GLMs computed with climatic/topographic/both predictors

	tmpr	rhires	srad	slope	topo	corr_GLM_topo	corr_GLM_clim	corr_GLM_all
SCDgee	-0.72	0.71	-0.16	0.05	0.11	0.22	0.72	0.74
SCD15	-0.90	0.86	-0.31	0.09	0.21	0.37	0.88	0.91
SCD40	-0.89	0.86	-0.33	0.08	0.19	0.39	0.88	0.92

Species distribution models

Topoclimatic + SCD models

The topoclimatic + SCD ensemble models integrating the SCD_{gee}, $SCD_{0.15}$ and $SCD_{0.40}$ maps had always a significantly better evaluation, both in AUC and maxTSS, than the shuffled models (Wilcoxon signed rank test, all *p-values* and *V-values* in table 2). However, the increase in maxTSS was of 0.01 for the SCD_{gee}, 0.02 for both $SCD_{0.15}$ and $SCD_{0.40}$, representing an improvement of model performance of 1.4% for SCD_{gee}, 2.5% for $SCD_{0.15}$ and 2.3% for $SCD_{0.40}$(table 2).

Both $SCD_{0.15}$ and $SCD_{0.40}$ were performing significantly better than SCD_{gee} (Wilcoxon signed rank test, respectively *V-value* = 5695.5, *p-value* < 0.001 and *V-value* = 6389.5, *p-value* < 0.001), but no significant difference in maxTSS was noted between the $SCD_{0.15}$ and $SCD_{0.40}$ (Wilcoxon signed rank test, *V-value* = 11084, *p-value* = 0.32) (figure 5.a). The respective maxTSS of the models are also presented in table 2. Similar results were obtained when using the AUC as the evaluation metric (supp. mat. 2).

Despite this slight improvement in the model, the SCD map had a high importance in the models (figure 5.b). The mean importance across all the individual models were of 0.33 for the $SCD_{0.15}$ and 0.32 for $SCD_{0.40}$ making it the second most important predictor, right after temperature (tmpr). For SCD_{gee}, the importance of the SCD map was not as good, ranking it at the fourth position among the 6 variables, with a variable importance of 0.17.

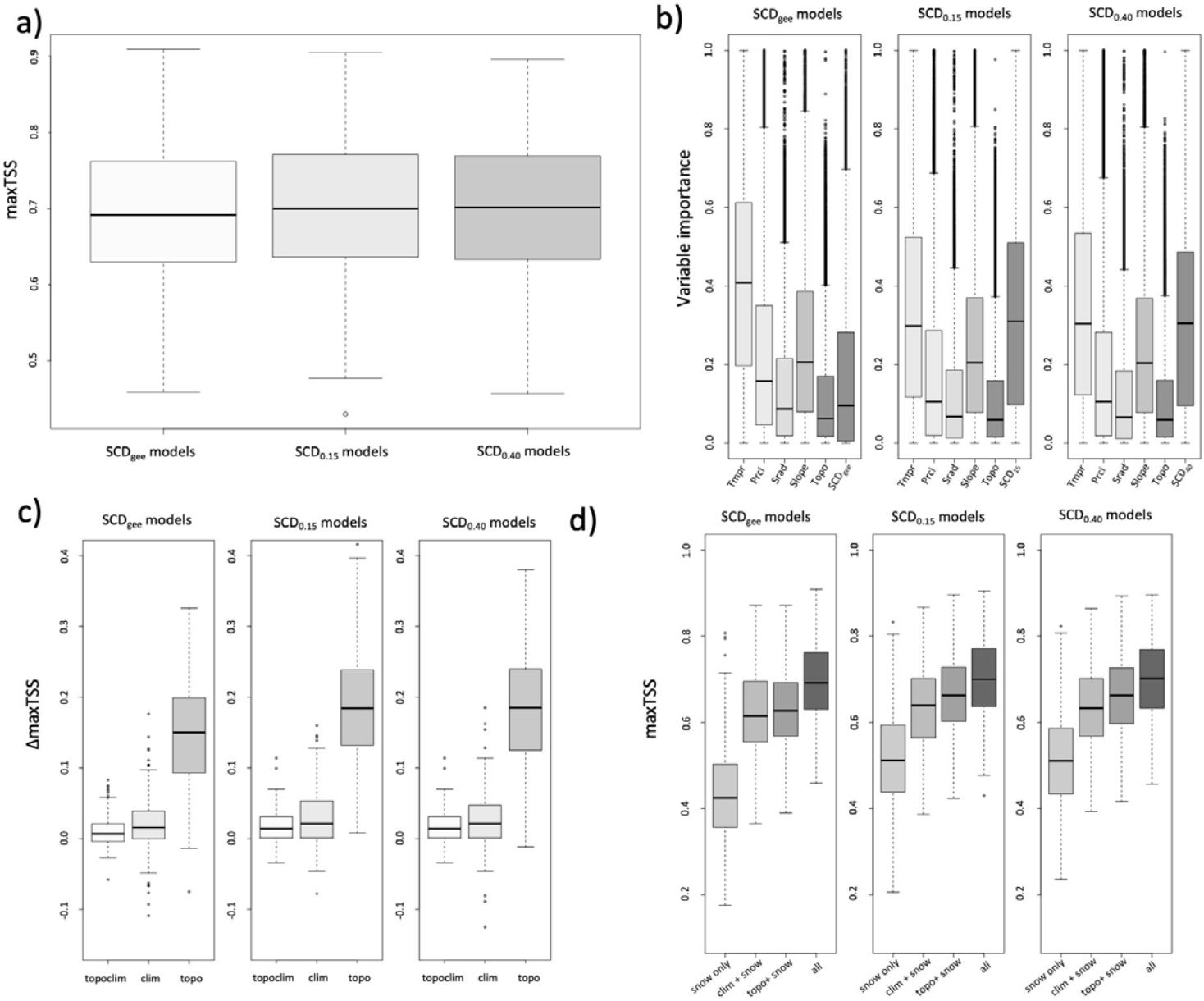

Figure 5: Boxplot of evaluations of the different models. a) Overall maxTSS of the ensemble models build with topoclimatic and different SCD maps. b) Variable importance for the different models build with topoclimatic and different SCD maps. c) Difference in maxTSS between the original model and the shuffled one, for topo-clim-snow, clim-snow, topo-snow models with different SCD maps. d) maxTSS of the snow only, clim-snow, topo-snow and topo-clim-snow models build with different SCD maps.

Additional models

Models integrating only climatic or topographic predictors with SCD maps both always had a significantly higher difference in maxTSS between the shuffled and the base model than the topoclimatic models (Wilcoxon signed rank test, *p-values* and *V-values* in supp. mat. 3) (figure 5.c). In addition, the topographic models had a significantly higher improvement in maxTSS than climatic models. The difference between the base model and the shuffled one was also always significant (Wilcoxon signed rank test, *p-values* and *V.values* table 2). The maxTSS

values of the respective models are provided in table 2. Regarding the models using the SCD as the only predictor, their maxTSS was of 0.44±0.12, 0.52±0.12 and 0.51±0.12 for the SCD_{gee}, $SCD_{0.15}$ and $SCD_{0.40}$ respectively (figure 5.d). However, the models failed to converge for 15 species, 7.2% of the overall species' pool.

From now on, we assume that SCD_{15} is the SCD index that is the most relevant for plant species. Therefore, future analysis and projections will be based on models built with SCD_{15}.

Snow importance at the species level

When looking at individual species, the addition of the snow variable was different from case to case. Overall, the integration of the SCD variable improved the models for 77,7% of the species. However, this added predictor degraded the models for 44 species. The model for *Anthyllis vulneraria* saw the largest decrease in maxTSS (-7.1%), whereas *Phleum hirsutum* was the model with the greatest maxTSS increase (+14.2%)(see supp. mat. 1 for all maxTSS changes). Plants described as snowbed species (Delarze et al., 1998) such as *Salix herbacea*, *Veronica alpina*, *Poa alpina* had among the highest improvement in maxTSS, respectively of 5.5%, 5.4%, and 9.2%.

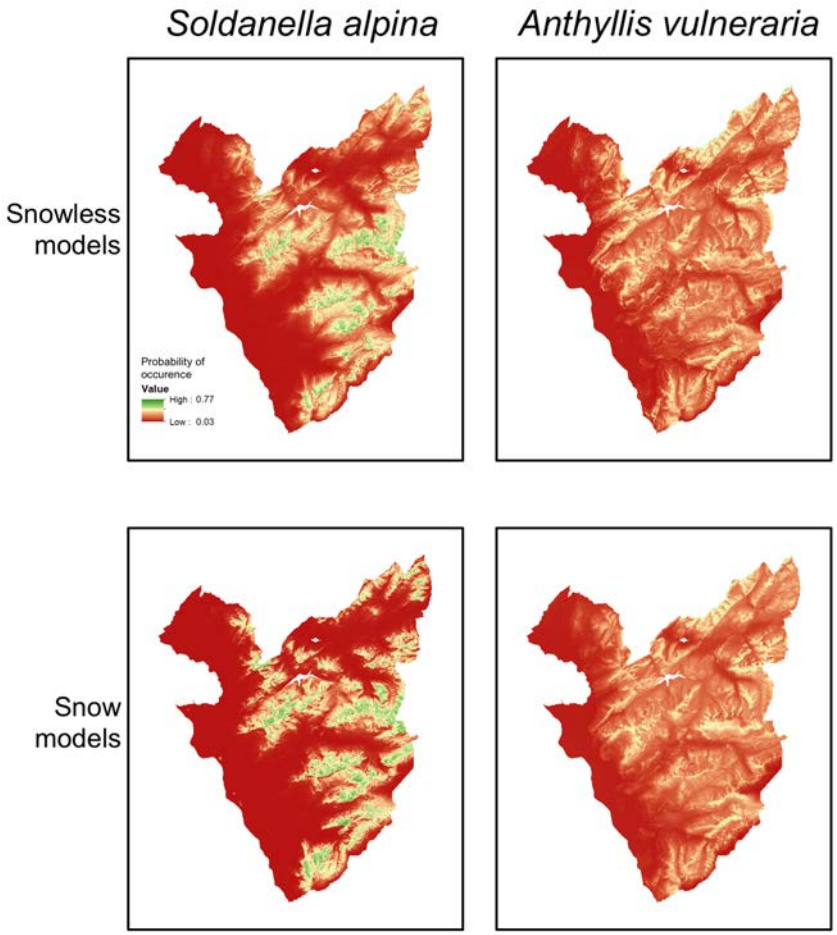

Figure 6: Continuous predictions for Soldanella alpina (maxTSS improvement of 9% with SCD predictor) and Anthyllis vulneraria (-7% of maxTSS) for current climate, for models with and without SCD predictor.

Finally, the altitude of the species occurrences can explain the differences in maxTSS between the two models (GLM, *p-value* < 0.05, $D^2 = 0.027$), but there was no link between the species'

ecological Landolt values and the improvement of the models by adding SCD (Anova, DF=6, all *p-value*>0.05).

Predictions under current and future climates

Projections using the SCD_{15} snow map had different results depending on the species. For species that had a good improvement in maxTSS, the projections were sharper (less pixels with intermediate probabilities) and suitable areas showed higher probabilities (e.g. *Soldanella alpina*, figure 7) when compared to projections made without the SCD index. For species with maxTSS degradation, the introduction of the SCD map as a predictor induced noise in the predictions (e.g. *Anthyllis vulneraria*, figure 7).

For future climate, there was no overall trend in loss of suitable habitat by species between the projections simulating temperature and precipitations change and the one with the SCD decrease added. The results were species-specific. Taking the same examples as before, *Soldanella alpina*, had, for projection with the future scenario SCD, a little decrease in his loss of area and gained a few new ones. *Anthyllis vulneraria* saw a slight increase in its lost area of distribution when taking the SCD decrease into account.

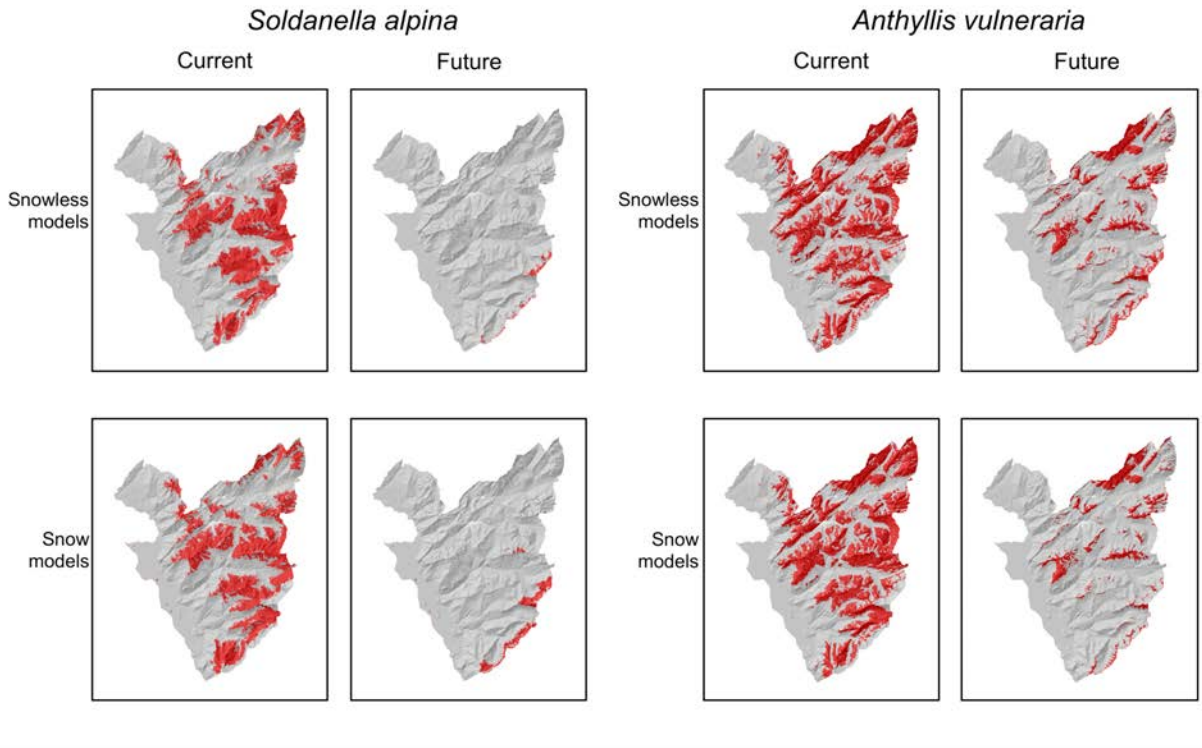

Figure 7: Binary projections for Soldanella alpina and Anthyllis vulneraria for current and future climate, with and without the SCD predictor. The binarisation was produced by a maxTSS threshold.

Table 2: Analysis of the different models (topoclimatic + SCD, climatic + SCD, topographic + SCD, snow + SCD), for each SCD map. Two first rows are the mean and the standard deviation for the TSS of the ensemble models. DiffShuf is the difference in mean TSS between the base model and the one with the shuffled SCD map. Improv is the overall improvement in mean TSS. WilcoxPVal and WilcoxVval are the results for the Wilcoxon signed rank test. Diff meanGLM/GBM/GAM are the TSS difference between the base and shuffled individual models. Diff meanIndiv are the mean of this difference for all individual models. Since snow only models are computed with only one predictor there is no comparison with a shuffled model.

	Topoclimatic + SCD			Climatic + SCD			Topographic +SCD			SCD		
	SCDgee	SCD15	SCD40	SCDgee	SCD15	SCD40	SCDgee	SCD15	SCD40	SCDgee	SCD15	SCD40
Mean TSS	0.695	0.703	0.702	0.625	0.632	0.631	0.627	0.662	0.660	0.436	0.515	0.512
SD TSS	0.093	0.092	0.092	0.098	0.096	0.093	0.096	0.089	0.091	0.117	0.117	0.115
DiffShuf	0.010	0.017	0.016	0.021	0.029	0.025	0.147	0.186	0.183			
Improv	0.014	0.025	0.023	0.033	0.045	0.039	0.234	0.281	0.277			
WilcoxPVal	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001			
WilcoxVval	15384	17743	17536	16792	17914	17176	21273	21321	21313			
Diff meanGLM	0.006	0.019	0.018	0.015	0.033	0.032	0.135	0.194	0.193			
Diff meanGBM	0.011	0.026	0.022	0.023	0.039	0.037	0.161	0.220	0.214			
Diff meanGAM	0.013	0.022	0.022	0.023	0.040	0.040	0.167	0.212	0.213			
Diff meanIndiv	0.010	0.023	0.021	0.020	0.038	0.037	0.154	0.209	0.207			

Discussion

This study was among the first to assess the importance of snow cover duration (SCD) in plant species distribution models (SDMs) in alpine ecosystems using advanced remote sensing methods involving a large number of images. Overall, the models were improved with the addition of the SCD predictor. Species that have special interactions with snow were the ones to benefit the most from the addition of this variable. We provided a new method, allowing quick production of SCD indexes anywhere in the world (where snow is important), using the Google Earth Engine (GEE) platform. This index, despite being less useful for SDMs than the two other methods developed outside GEE, showed that it could nevertheless bring relevant information for snow-dependent species. In our dataset, the SCD maps had redundant information with the others predictors, especially temperature. However, for places in the world where high quality and resolutions temperature data are not available, the introduction of remote-sensing-based SCD parameter could help increase the accuracy of SDMs. We also showed that, in the context of climate change, the snow parameter should be considered when assessing species' future habitat suitability, especially for species having strong interaction with snow. However, our results also suggest that the knowledge on species ecology is and should always remain the most important criteria for the selection of predictors in SDMs.

Three approaches produced useful SCD maps

Our method for images selection produced very good results in term of data availability, resulting in a big pool of value available for each pixel. Ecological remote sensing studies often use a pool of images available without cloud in order to use 100% of the image (Niittynen and Luoto, 2018; Zimmermann et al., 2007), or use a composite image (i.e. made of multiple images; Wylie et al., 2003). However, both options result in throwing away potentially useful data. Using all available images and removing the residual clouds with the Fmask classification resulted in a much larger data set. Here, the mean number of value per pixel was more than 3 times bigger than the number of images used by Niittynen and Luoto (2018). We did not formally compare the two methods (masking clouds for all images or use only cloudless images), so the relative improvement could not be quantified here. Yet, this dramatic increase

in the amount of data used to produce the indexes should result in an improvement of the latter.

The two different methods – Google Earth Engine (GEE) and Generalized Linear Models (GLM) – gave similar results, but the GEE produced noisier results. This is possibly due to the statistical methods available in GEE. Indeed, we had to use a mean moving window approach, which is more sensible to outliers than the GLM we could implement in the R. In turn, GEE offers wider open access use perspectives to the scientific communities than the more tedious custom GLM approaches. In addition, all data processing is handled by the Google Data Center Infrastructure, drastically reducing the amount of time and resources needed for computations. Yet our results highlight that there is a need for the implementation of more advanced statistical tools into the GEE platform. Although GEE can currently be used in any part of the world easily, quickly, inexpensively, and with consistent results, it lacks some key statistical options – such as to allow the fitting of GLMs – that would need to be integrated in future versions of the platform.

Snow cover improves plant species distribution predictions

In accordance with the work by Niittynen and colleagues (2018) in the Arctic, we showed that snow is a critical parameter to take into account when building SDMs in alpine ecosystems. The GEE method showed weaker improvements of the models than the one using the GLMs. Yet, all approaches helped increase the accuracy of the models. There was no difference between the two GLM approaches, using the two different thresholds. This shows that this method is better than the GEE approach not because of the sensitivity of the detection of snow, but because either the snow classification methods or the statistical method for assessing the day of snowmelt were better with GLMs.

However, the improvements found in this particular study do not match those reported by Niittynen and Luoto (2018). First of all, we note that the models we obtained can be, on average across all species, considered as yielding good predictions (Swets, 1988; Guisan et al., 2017). Even those built with the shuffled SCD predictors had rather high evaluation metrics, overall leaving little room for improvement. The fact that the others climatic variables used in our study are of good quality and good resolutions, at least for temperature, probably hindered the quality of the information brought by the SCD maps. In addition, the SCD indexes

had a relatively high correlation with some other predictors, especially with temperature. This was further illustrated by the models built with the added SCD maps and either the topographic or the climatic predictors. The climate only models had only a low amelioration by SCD whereas the latter improved the topographic-only model by almost 30%. This highlights that the SCD maps have most redundant information with the climatic variables, especially with temperature, which is usually the most used predictor in SDMs (Mod et al., 2016). Therefore, adding the SCD predictor could particularly help increase SDM's predictive accuracy when high quality and high resolution temperature data is not available.

Another explanation for the limited improvements in model performance is that the vegetation in the Alps – or at least the majority of species considered in this study - might overall interact less with snow than Arctic species. Our study area shows a broad elevation gradient, representative of the situation in the Alps. This implies that medium elevation species might have very little or even no interaction with snow. It is known that alpine species vary a lot in their relationship with snow (Randin et al., 2009c). For species that have little to no interaction with snow, because of their ecology or altitude of occurrence, adding this predictor with little meaning resulted in noise that degraded the models (see next subsection).

It can also be argued that snow can have effects on vegetation that, by nature, cannot be currently transcribed in SDMs by a SCD map, at least with the species and environmental data used in this study. For example, at the resolution used here, microclimate is not properly taken into account. Some effects of snow on species act at a very fine scale (Ford et al., 2013), microtopography having a prominent role on snow distribution (Liston and Sturm, 1998). As already shown by Boserup (2019) for a small subset of our study area, using remote sensing images of higher resolution can yield better results. Using satellite data from Worldview2 (1.3 m resolution) or Sentinel (10 m resolution) instead of the Landsat (30 m resolution) images used here, and despite a shorter time period of images availability, resulted in better model improvement. Yet, image sources like worldview2, unlike Landsat, are not open access and their acquisition can become quickly overly expensive for a large study area (i.e. 700 km^2 here). In addition, snow can have indirect effects. As an example, the water released by snow melting does not only affect the place at which the snowpack is located, but also all the downstream vegetation. Such effects cannot be represented in SDMs.

Finally, the inherent nature of our data could also hide part of the power of SCD introduction in SDMs. Indeed, we used species' presence-absence data, but species' abundance data might further increase the relevance of the SCD index in SDMs. This has already been illustrated by Randin et al. (2009b), for the importance of land use in SDMs. Future studies could therefore assess the importance of SCD in SDMs based on abundance data.

Varying ameliorations in performances can be explained by species ecology

Improvement in model predictions was highly variable from species to species. This shows that the ecology of the species is a critical criteria to consider when selecting predictors for plants SDMs. As mentioned before, many plants that had a reduction in model performance could be described as species having little interaction with snow. We have shown that species occurring at lower altitude had a lower improvement in model performances. For plants that experience no snow cover at the start of the growing season, adding this parameter resulted in noise decreasing the SDM accuracy.

Still, there were plant species occurring at high altitude and having their model degraded by adding a snow predictor. For instance, *Androsaceae chamaejasme* and *Saxifraga aizoides* have high mean altitude of occurrence, both above 2100 m a.s.l. in our dataset, and saw degradation of their model performance with a snow predictor added. Thus, being at high elevation does not automatically mean that snow is a relevant predictor for species. The first species is known for occurring in rocky habitats, and the second in humid and sloppy ones, two types of habitat with little snow accumulation (Lauber and Wagner, 2001).

However, a large majority of species saw marginal to good improvement in model predictions. The amelioration was better for species occurring at high altitude, showing the overall importance of snow for many alpine species. Among species for which snow largely improves model performance are found both snowbed species and species of snowless windy slopes. The first group of species strongly relies on snow cover for cold insulation or as source of moisture during the growing season. Such species as *Salix herbacea, Veronica alpina, Ligusticum mutellina* or *Poa alpina,* typical snowbed species, benefitted of the highest improvements. Species that tend to live in windy environments, where the snow cover duration is shorter than normal, also saw improvement when modeled with the SCD index. Such species as *Helictotrichon versicolor, Homogyne alpina, Vaccinium gaulhterioides* and

most importantly *Dryas octopetala,* which has already been the subject of studies of the importance of snow cover in SDMs (Beck et al., 2005), saw marginal to good improvements in model accuracy. This illustrates that it is not only the extended SCD due to snow accumulation that matters. The decreased SCD in windy environments is also critical for species distribution. Species known as windy ridge plants can also benefit from a SCD predictor in SDMs.

Future predictions should take SCD decrease into account

Alpine and arctic ecosystems are the most threatened by climate change, and snow cover is among the environmental factors that should see drastic changes in the near future (IPCC 2017). However, there is to our knowledge no precise snow cover decrease scenario available for the Swiss Alps. Therefore, we used a basic snow decrease scenario, based on existing knowledge (Beniston et al., 2003), to simulate the effect of climate change-induced SCD decrease on plants distribution. This illustrates the need for better knowledge and scenarios of the evolution of other climatic variables than temperature or precipitation in the future. Niittynen et al. (2018) already showed that taking the snow cover decrease into account in future projections of plants SDM could lead to dramatic differences compared to a temperature increase only. However, the latter study reported large losses of species' habitat suitability that we did not observe in our study. It has already been shown that the breadth of the elevation gradient is critical for species persistence (Randin et al., 2009a). In the Arctic, species have to migrate longer distances, in latitude, to reach a similar difference in temperature that a small shift in elevation can bring in the Alps. Therefore, this difference between studies can be explained by the fact that, due to its inherent characteristics, our study area still provides habitat suitability for all species in future scenarios.

In our study, the results for the future projections changed considerably from species to species. Most of the species saw a shift to higher elevation of occurrence both when predicted with and without the SCD variable. This is in agreement with the current knowledge on global warming scenarios in the Alps (Parolo and Rossi, 2008; Randin et al., 2009a; Engler et al., 2011). Generally speaking, plant having a big decrease in habitat suitability in the climate change scenario saw their loss attenuated when the SCD decrease scenario map was used in the models (i.e. *Salix herbacea, Veronica alpina, Ligusticum mutellina, Soldanella alpina…*). A cause may be the melting of medium and long lasting snow, simulated in our SCD decrease scenario maps. Indeed, the decrease in SCD offer new suitable habitats for alpine species at

medium to high elevation. This could represent some hope for high altitude species to persist in the Alps.

Conclusion

Our study showed the importance of accounting for snow in plant species distribution models developed in alpine ecosystems. Our findings support that snow cover duration indexes should be more systematically taken into consideration as predictors when modelling the distribution of plant species that interact with snow. This is especially true when projecting species in future climates, where snow cover will most likely see dramatic changes, therefore impacting future distribution of many alpine species' suitable habitats.

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Supplementary material

Supplementary material 1: Table with the name of all the species used in this study. Joined is the mean altitude of occurrence in our dataset and the improvement of the maxTSS for the topoclimatic + SCD model

Species name	Mean altitude of occurrence (m a.s.l.)	Model improvement
Acer pseudoplatanus	1276	0.031
Achillea millefolium	1245	-0.048
Acinos alpinus	1792	0.003
Adenostyles glabra	1899	0.016
Agrostis capillaris	1527	0.029
Agrostis rupestris	2118	0.022
Agrostis stolonifera	1374	0.041
Ajuga reptans	1213	0.013
Alchemilla conjuncta	1924	-0.003
Alchemilla coriacea	1684	-0.027
Alchemilla vulgaris	1521	-0.011
Alchemilla xanthochlora	1536	0.018
Androsace chamaejasme	2143	-0.010
Anthoxanthum odoratum	1489	0.048
Anthyllis vulneraria	1850	-0.071
Aposeris foetida	1632	0.069
Arabis alpina	2344	0.084
Arnica montana	1905	0.071
Arrhenatherum elatius	862	0.038
Aster bellidiastrum	1895	0.040
Astrantia major	1409	0.088
Bartsia alpina	2065	-0.003
Bellis perennis	936	0.021
Brachypodium pinnatum	1182	0.016
Briza media	1427	0.021

Bromus erectus.	974	0.019
Calamagrostis varia	1742	0.003
Campanula barbata	1965	-0.009
Campanula cochleariifolia	2106	0.030
Campanula rhomboidalis	1331	0.065
Campanula rotundifolia	1335	-0.044
Campanula scheuchzeri	2032	0.014
Cardamine pratensis	934	0.035
Carduus defloratus	1863	0.056
Carex caryophyllea	1103	-0.040
Carex ferruginea	1796	0.039
Carex flacca	1462	0.046
Carex montana	1331	0.064
Carex nigra	1661	0.017
Carex pallescens	1487	0.033
Carex sempervirens	1985	0.036
Carex sylvatica	1213	0.044
Carlina acaulis caulescens	1767	0.035
Carum carvi	1437	0.019
Centaurea jacea.	1207	0.082
Centaurea montana	1694	0.068
Cerastium fontanum	1204	0.017
Cerastium latifolium	2447	0.002
Chaerophyllum hirsutum	1499	0.042
Cirsium acaule	1659	-0.034
Cirsium palustre	1208	-0.040
Cirsium spinosissimum	2136	0.045
Clinopodium vulgare	1165	0.055
Crepis aurea	1862	0.072
Crepis biennis	1006	0.020
Crepis pyrenaica	1603	0.139
Crocus albiflorus	1630	0.035
Cruciata laevipes	1119	0.024
Cynosurus cristatus	1213	0.020
Dactylis glomerata	1208	0.001
Dactylorhiza fuchsii	1500	0.012
Daucus carota	1068	-0.031
Deschampsia cespitosa	1726	0.029
Dryas octopetala	2019	0.024
Euphorbia cyparissias	1673	0.011
Euphrasia minima	2109	0.007
Euphrasia salisburgensis	2008	-0.027
Festuca ovina	1837	0.051

Festuca pratensis	1163	-0.004
Festuca quadriflora	2215	0.006
Festuca rubra	1518	0.020
Festuca violacea	2199	0.016
Fraxinus excelsior	925	-0.016
Galium album	1026	-0.040
Galium anisophyllon	1925	-0.004
Galium megalospermum	2348	0.036
Galium pumilum	1450	0.048
Gentiana acaulis	1919	0.047
Gentiana campestris.	2082	0.028
Gentiana lutea	1555	0.038
Gentiana purpurea	1968	0.010
Gentiana verna	2060	0.002
Geranium sylvaticum	1418	0.012
Geum montanum	2064	0.033
Geum rivale	1242	-0.008
Glechoma hederacea.	736	0.021
Gypsophila repens	2027	0.035
Hedysarum hedysaroides	2114	0.009
Helianthemum nummularium	1796	0.080
Helictotrichon pubescens	1102	0.002
Helictotrichon versicolor	2079	0.037
Heracleum sphondylium	1173	0.027
Hieracium bifidum	1838	0.084
Hieracium lactucella	1576	0.018
Hieracium murorum	1627	0.039
Hieracium villosum	1960	-0.008
Hippocrepis comosa	1691	-0.040
Holcus lanatus	917	0.026
Homogyne alpina	1971	0.019
Hypericum maculatum	1582	0.063
Hypochaeris radicata	1202	0.061
Knautia arvensis	1022	-0.024
Knautia dipsacifolia.	1545	0.021
Laserpitium latifolium	1667	0.007
Lathyrus pratensis	1137	-0.008
Leontodon autumnalis	1541	-0.048
Leontodon helveticus	2053	0.017
Leontodon hispidus	1632	0.030
Leucanthemum vulgare	1564	0.054
Ligusticum mutellina	2034	0.064
Linaria alpina.	2349	0.013

Linum catharticum	1474	0.008
Lolium perenne	892	0.005
Lotus corniculatus	1579	0.032
Luzula campestris	1261	0.019
Luzula multiflora	1835	0.041
Luzula sylvatica	1688	0.083
Medicago lupulina	1039	0.021
Myosotis alpestris	2161	0.040
Nardus stricta	1865	0.053
Parnassia palustris	1835	-0.022
Pedicularis foliosa	1848	-0.009
Phleum hirsutum	1809	0.142
Phleum pratense	1261	0.010
Phleum rhaeticum	1887	0.023
Phyteuma orbiculare	1795	0.111
Phyteuma spicatum	1658	-0.007
Picea abies	1447	0.007
Pimpinella major	1450	0.099
Pimpinella saxifraga	1199	-0.015
Plantago alpina	1915	0.013
Plantago atrata.	1911	0.047
Plantago lanceolata	1171	0.041
Plantago major	1137	0.013
Plantago media	1266	0.001
Poa alpina	2044	0.092
Poa minor	2392	-0.042
Poa pratensis	1015	0.009
Poa trivialis	980	0.001
Polygala alpestris	1897	0.085
Polygala chamaebuxus	1645	0.052
Polygala vulgaris	1330	0.042
Polygonum bistorta	1364	-0.003
Polygonum viviparum	2013	-0.009
Potentilla aurea	1931	0.073
Potentilla crantzii	2007	-0.003
Potentilla erecta	1459	-0.009
Primula elatior.	1488	-0.024
Primula veris	1091	-0.001
Pritzelago alpina.	2353	0.081
Prunella grandiflora	1599	0.028
Prunella vulgaris	1319	0.021
Pulsatilla alpina	1922	-0.001
Ranunculus aconitifolius	1682	-0.028

Ranunculus acris	1226	0.012
Ranunculus alpestris	2200	0.072
Ranunculus bulbosus	875	-0.004
Ranunculus montanus	1914	0.027
Ranunculus nemorosus	1601	-0.020
Ranunculus repens	1200	-0.010
Rhinanthus alectorolophus	1315	0.086
Rumex acetosa	1081	0.028
Rumex alpestris	1589	0.031
Salix herbacea	2175	0.055
Salix retusa	2118	0.031
Sanguisorba minor	1132	0.001
Saxifraga aizoides	2196	-0.007
Saxifraga moschata	2321	0.087
Saxifraga oppositifolia	2483	0.011
Saxifraga paniculata	2220	0.006
Scabiosa lucida	1907	0.039
Sedum atratum	2289	0.040
Selaginella selaginoides	2039	0.050
Senecio doronicum	2055	0.000
Seria caerulea	2012	0.000
Silene acaulis	2309	-0.038
Silene vulgaris	1676	0.029
Soldanella alpina	1942	0.091
Stellaria graminea	1221	0.045
Taraxacum officinale	1205	0.012
Thesium alpinum	1860	0.056
Thlaspi repens	2346	0.062
Thymus praecox polytrichus	1913	0.078
Thymus pulegioides.	1400	0.002
Tragopogon pratensis	1121	0.066
Trifolium badium	1944	0.073
Trifolium medium	1351	0.013
Trifolium pratense	1395	0.020
Trifolium repens.	1272	-0.021
Trifolium thalii	2063	0.038
Trisetum flavescens	1154	0.045
Trollius europaeus	1749	0.081
Vaccinium gaultherioides	2054	0.015
Vaccinium myrtillus	1877	0.007
Vaccinium vitis.idaea	2058	0.069
Valeriana montana	1892	0.007
Veratrum album lobelianum	1594	0.054

Veronica alpina	2277	0.054
Veronica aphylla	2257	0.039
Veronica arvensis	712	0.011
Veronica chamaedrys	1204	0.037
Veronica serpyllifolia	1195	0.003
Vicia cracca.	1055	0.018
Vicia sepium	1170	0.010
Viola biflora	1781	-0.006
Viola hirta	1168	0.002

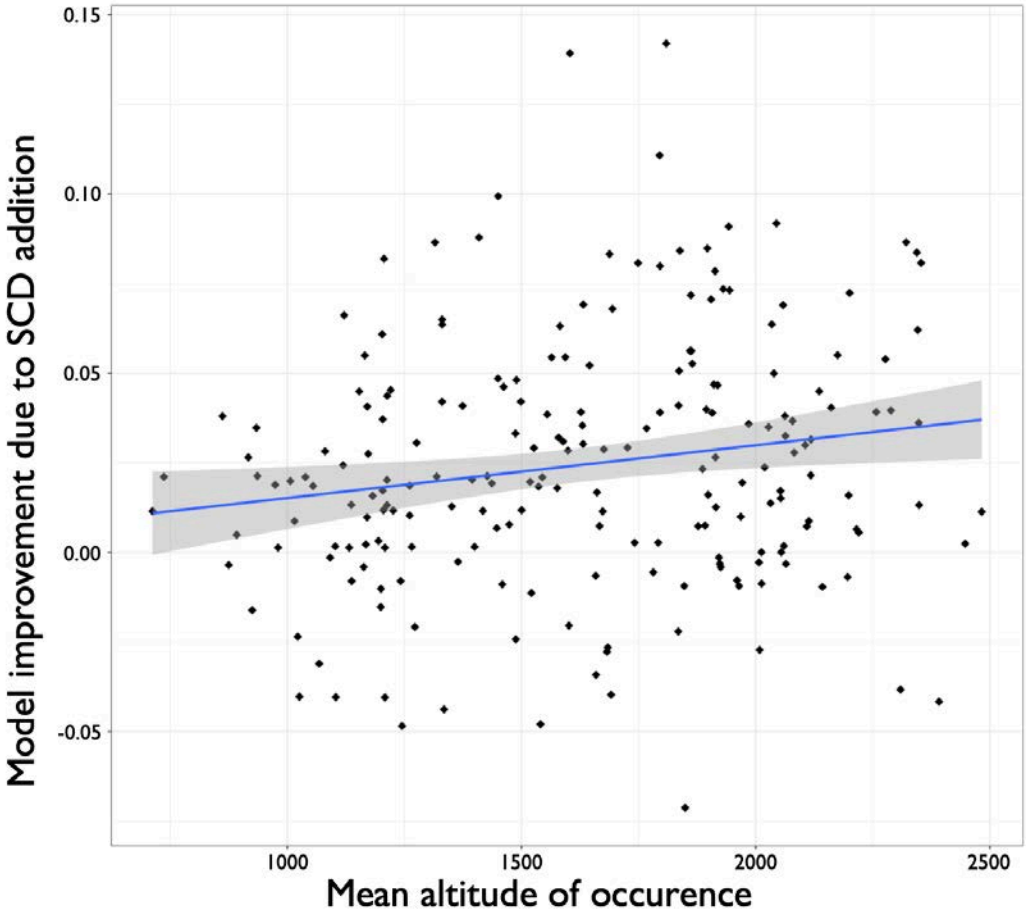
ıpplementary material 2: Table with the AUC value. Labels are the same as for table 2

		All			clim			topo			snow		
		SCDgee	SCD15	SCD40	SCDgee	SCD15	SCD40	SCDgee	SCD15	SCD40	SCDgee	SCD15	SCD40
AUC	mean	0.913	0.916	0.915	0.882	0.884	0.884	0.879	0.896	0.895	0.758	0.800	0.799
	SD	0.038	0.037	0.037	0.044	0.044	0.043	0.044	0.040	0.040	0.066	0.062	0.061
	DiffShuf	0.004	0.007	0.006	0.010	0.013	0.011	0.078	0.097	0.095			
	Improv	0.004	0.007	0.007	0.011	0.015	0.012	0.089	0.108	0.106			
	wilcoxPVal	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001			
	WilcoxVval	15028	18817	17042	17182	18357	17844	21110	21321	21318			

Supplementary material 3: P-value and v-value for the Wilcox test of the difference of ΔmaxTSS between topoclimatic + SCD, climatic + SCD and topographic + SCD models

Pval	SCDgee			SCD15			SCD40		
	Topoclimatic	Climatic	Topographic	Topoclimatic	Climatic	Topographic	Topoclimatic	Climatic	Topographic
Topoclimatic									
Climatic	<0.001			<0.001			<0.001		
Topographic	<0.001	<0.001		<0.001	<0.001		<0.001	<0.001	

Vval	SCDgee			SCD15			SCD40		
	Topoclimatic	Climatic	Topographic	Topoclimatic	Climatic	Topographic	Topoclimatic	Climatic	Topographic
Topoclimatic									
Climatic	14375			21316			21285		
Topographic	21206	20675		13838	21191		13445	21087	



Supplementary material 4: Each species plotted with as the x axis their mean altitude of occurrence in our dataset and y axis the improvement in model accuracy due to the addition of the SCD predictor. The trend line is based on the GLM described in the material and methods.in the models comparison subsection (p-value < 0.05, $D^2 = 0.027$)