Received: 4 October 2022 | Revised: 19 May 2023 | Accepted: 6 June 2023
DOI: 10.1111/jbi.14689

RESEARCH ARTICLE

Journal of Biogeography WILEY

Snow cover persistence as a useful predictor of alpine plant distributions

Thomas Panchard[1] | Olivier Broennimann[1,2] | Mathieu Gravey[3] | Grégoire Mariethoz[2] | Antoine Guisan[1,2]

[1]Department of Ecology & Evolution, University of Lausanne, Lausanne, Switzerland
[2]Institute of Earth Surface Dynamics, University of Lausanne, Lausanne, Switzerland
[3]Institute for Interdisciplinary Mountain Research, Austrian Academy of Sciences, Innsbruck, Austria

Correspondence
Thomas Panchard, Department of Ecology & Evolution, University of Lausanne, Lausanne, Switzerland.
Email: tpanchard@gmail.com

Funding information
Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung; SNF INTEGRALP, Grant/Award Number: CR23I2_162754

Handling Editor: Gerald M. Schneeweiss

Abstract

Aim: Snow cover persistence (SCP) has significant effects on plants in high-elevation ecosystems. It determines the length of the growing season, provides insulation against low temperatures and influences water availability, thereby shaping the vegetation mosaic. Despite its importance, SCP is rarely used in plant species distribution modelling. In this study, we examine whether incorporating SCP in plant species distribution models (SDMs) improves their predictive power. We investigate the link between species' ecology and SDM improvements by the addition of various SCP predictors.

Location: Western Swiss Alps.

Taxon: 206 alpine flowering plants (angiosperms).

Methods: We produced three maps of landsat satellite-based SCP indices over an entire mountain region, one of them using an online open access platform allowing quick and easy replication and used them as a predictor in plant SDMs alongside commonly used predictors. We tested whether this improved the predictive performance of plant SDMs.

Results: All three SCP indices improved the overall SDM predictive accuracy, but the overall improvement was potentially limited by their correlation with other climatic predictors. Alpine plant species known for their dependence on snow benefited more from the additional snow information.

Main Conclusions: SCP should be used for predicting at least the distribution of alpine, snow-related plant species. Given that adding snow cover improves SDMs and that snow duration decreases as climate warms, future predictions of alpine plant distributions should account for both snow predictor and associated snow change scenarios.

KEYWORDS
plant distributions, remote sensing, snow cover persistence, species distribution models, Swiss Alps, vegetation

1 | INTRODUCTION

Global environmental changes affect biodiversity through causing species range shifts, leading to habitat losses and gains (Díaz et al., 2019). Species distribution models (SDMs; Guisan & Zimmermann, 2000; Guisan & Zimmermann, 2017) can both model the current and predict future distributions of species, making them a useful tool for conservation planning and decision-making (Algar et al., 2009; Guisan et al., 2013; Guisan & Zimmermann, 2000; Pineda & Lobo, 2009). Yet, SDMs' accuracy is key for their use in conservation (Araújo et al., 2019). In particular, it is especially important to use ecologically meaningful predictors (Austin & Niel, 2011; Mod et al., 2016; Scherrer & Guisan, 2019), as models lacking critical ecological information are potentially at risk of missing their conservation target (Guisan et al., 2013).

SDMs are based on the environmental niche concept, that is an n-dimensional hypervolume of species requirements in environmental space (Hutchinson, 1957). This implies that species distributions are shaped by multiple environmental drivers. The most common predictors in plant SDMs are climatic (Mod et al., 2016), typically various expressions of temperature and precipitations, sometimes complemented with topographic variables (e.g., slope; Truong et al., 2017). Both are easy to obtain and give predictions of decent quality (Pradervand et al., 2014), but only partly explain plant distributions (Austin & Niel, 2011; Mod et al., 2016; Scherrer & Guisan, 2019) so that additional environmental information is expected to improve SDMs.

Snow in particular is known to be a relevant parameter in alpine and arctic environments (e.g., Billings & Bliss, 1959), yet has been largely overlooked in SDMs (Guisan et al., 1998; Niittynen & Luoto, 2018). Snow is critical for vegetation distribution in high-elevation ecosystems (Evans et al., 1989; Rissanen et al., 2021; Verrall & Pickering, 2020; Walker et al., 1993) because the vegetation mosaic usually follows patterns of snow melting isoline, which defines the start of the growing season in alpine ecosystems (Friedel, 1961; Körner, 2003). The effects of snow cover persistence (SCP) on plants include protection against winter desiccation, ice blast, low temperatures and herbivory, shorter growing season and water provision (Billings & Bliss, 1959; Walker et al., 1993), selecting different plant species depending whether they can complete their life cycle under these conditions (Friedel, 1961; Galen & Stanton, 1995; Körner, 2003). In particular, species found in snowbeds, where snow accumulates during winter and lasts longer in spring and summer, benefit from the insulation and water supply provided by snow, but require shorter life cycles. Conversely, plants avoiding snowbeds usually can have longer growing periods and need higher nutrient supply (Galen & Stanton, 1995; Gjaerevoll, 1956; Odland & Munkejord, 2008).

Climate change, through the decrease in duration and thickness of snow cover (Solomon et al., 2007), affects plant phenology and ecophysiology (Bintanja & Andry, 2017; Rebetez & Reinhard, 2008; Tenenbaum, 2005). More specifically, the loss of snow insulation induces severe frost damages to plants (Wipf et al., 2009), especially to snowbed species that have lower frost resistance (Bannister et al., 2005). Future changes in snow cover patterns caused by global warming should thus have severe effects on many alpine plant species (Keller et al., 2005; Matteodo et al., 2016; Zong et al., 2022).

Existing evidence of the importance of snow distribution and duration for alpine plant species begs the question why so few SDMs in mountain regions included snow cover as predictor (Dubuis et al., 2013; Engler et al., 2011; Guisan et al., 1998; Randin, Engler, et al., 2009; Siniscalco et al., 2011). Snow parameters (e.g., onset and disappearance) are constrained by an interplay of many factors, such as wind, topography and solar radiation (Gottfried et al., 1999; Liston & Sturm, 1998), which makes it difficult to predict these parameters spatially across rugged mountain landscapes (Rango et al., 1977; Zappa, 2008).

Recent advances in geographic information systems and remote sensing technologies now allow obtaining high-quality snow cover data for the past and the present (Lievens et al., 2019; Olefs et al., 2020). This opened the way for larger-scale studies of the influence of snow cover on the distribution of plant species (Randin et al., 2020; Zimmermann et al., 2007). In a recent study, Niittynen and Luoto (2018) used a new approach to quantify SCP from a large dataset of Landsat satellite images and incorporate it as an additional predictor in plant SDMs. As introducing a snow index in SDMs for arctic plants improved drastically their performance, the same can be expected for alpine regions, yet this remained to be tested.

The goal of this study was, therefore, to assess the extent to which snow indices can improve plant SDMs in alpine landscapes, and more specifically (1) to test the importance of different SCP indices, including a newly developed approach using Google Earth Engine (GEE); (2) to assess whether the SCP indices provide complementary or redundant information with topoclimatic predictors; and, finally, (3) to test if the added snow persistence indices provide relevant information for particular species, and if so, for which species, under current climate.

2 | MATERIALS AND METHODS

2.1 | Study area

The 700 km^2 study area is located in the Western part of Switzerland (46°10′–46°30′ N, 6°50′–7°10′ E) and contains all the Alps of the Vaud state. It spans a wide elevation gradient from 375 m in the Rhone plain to 3210 m at the top of the Diablerets massif. Vegetation is largely restricted by elevation, ranging from broadleaf forests at low elevation to alpine grasslands and nival vegetation at higher elevations. Humans had a marked influence on the landscape and vegetation (Randin, Engler, et al., 2009). It is a priority area for transdisciplinary research with many biological and environmental data available (see http://rechalp.unil.ch; Figure 1, Von Daniken et al., 2014).

2.2 | Species data observations

Plant data come from a field campaign carried out from 2002 to 2009, 912 plots of 4 m^2 were sampled (Figure 1; [Buri et al., 2017; Dubuis et al., 2011]), following a random-stratified equal sampling design (Hirzel & Guisan, 2002), with 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°) as stratifying factors, and a minimal distance of 200 m between plots to minimize spatial auto-correlation (Chevalier et al., 2021; Pottier et al., 2013). The sampling was limited to open, non-forest vegetation.

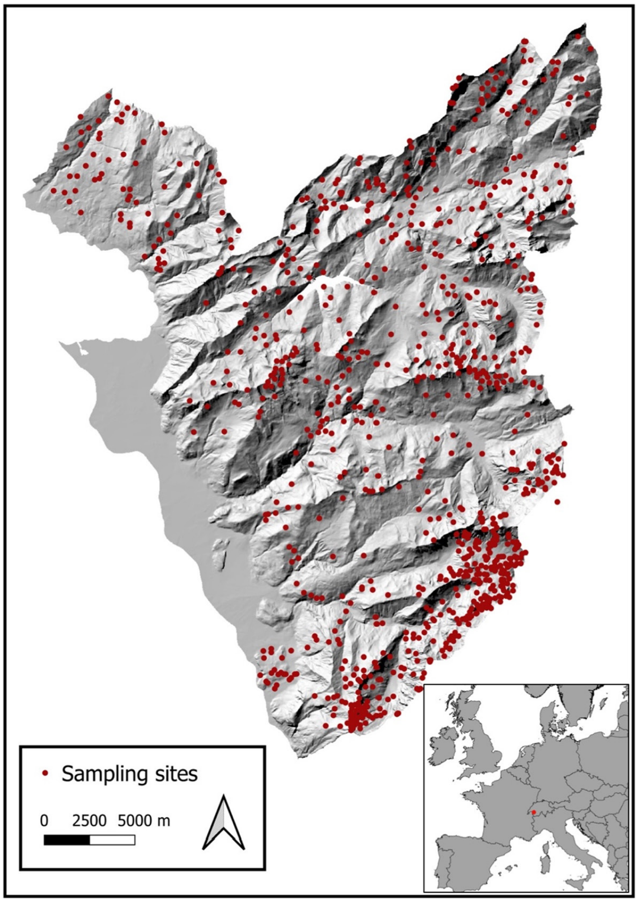

FIGURE 1 Localization of the study area in the Swiss alps. The 912 vegetation sampling plots are symbolized with points. EPSG:21781.

2.3 | General analytical workflow

The analyses followed two steps. First, we built three different SCP index maps (Figure 2). Second, we tested the increase in predictive power when adding each SCP map to plant SDMs across 206 species, when the SCP map was used alongside (i) other climatic variables, (ii) topographical variables and (iii) both previous types of variables. We used this framework to assess which of the three SCP indices best improved the predictive power of plant SDMs.

2.4 | Remote sensing data

The remote sensing data consisted of satellite images (surface reflectance Tier 1, collection 2 Landsat TM 4 & 5, ETM+ 7 and OLI 8) at a resolution of 30 m, ranging from 1984 to 2019, freely accessible from the U.S. Geological Survey (https://www.usgs.gov). The satellite images intersecting our study area were selected in GEE (earthengine.google.com). We only used images from the 50th to the 250th day of the year (DOY) to capture the start of the growing season while 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 & Woodcock, 2012) to remove all the pixels obscured by clouds in every image. Due to the roughness of the terrain, we excluded the shadows of the mountains from all the images using the ee.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 shadow value to every pixel. All shadowed pixels were removed from the data. Finally, we used the ee.Reducer.count function in GEE to export a map representing the number of values available for every pixel in the study area.

2.5 | SCP map

Different approaches were used to build three SCP indices, each determining, for every pixel in the study area, the mean 'DOY' at which the snowmelts (Figure 2). All approaches rely on the NDSI calculated on all images with different DOY. The widely used NDSI is based on the reflectance difference between the green and the 1.6 µm shortwave infrared bands (Crane & Anderson, 1984; Dozier, 1989; Hall et al., 1995; Hall et al., 2002) and ranges from −1 (no snow) to 1 (snow). The three SCP approaches differed in that the first one was entirely computed within GEE while the two others required exporting the NDSI maps to R where more advanced statistical analyses could be conducted, using two distinct NDSI thresholds to calculate the SCP indices.

Unless specified otherwise, all statistics and GIS manipulations were performed in R 3.5.3 (R Core Team 2019), using the raster package (Hijmans et al., 2019).

2.5.1 | Approach 1: GEE

Each image was reclassified using the same Fmask snow classification (Zhu et al., 2015; Zhu & Woodcock, 2012), with snow being identified above NDSI values of 0.15. Across all images, every pixel in the study area was thus attributed a collection of presences and absences of snow, each associated with a DOY. Because Landsat images are not available continuously for every day, we applied to every pixel a temporal moving window of 10 days, based on the DOY of each image, taking the mean of the binary snow presence–absence values in each window. This resulted, for every pixel, in a probability of snow occurrence for all DOY from the 50th day to the 250th day. The days of snowmelt for every pixel was defined as the first day in the year when this probability passed below 0.5. The pixels never reaching this threshold were considered as everlasting snow, and their value was set to 365.

We wanted this approach to be fully based on GEE, but with a resulting SCP map directly comparable to Macander et al. (2015) and Niittynen and Luoto (2018). As GEE did not allow fitting GLMs, as used in Niittynen and Luoto (2018), we used a mean moving window

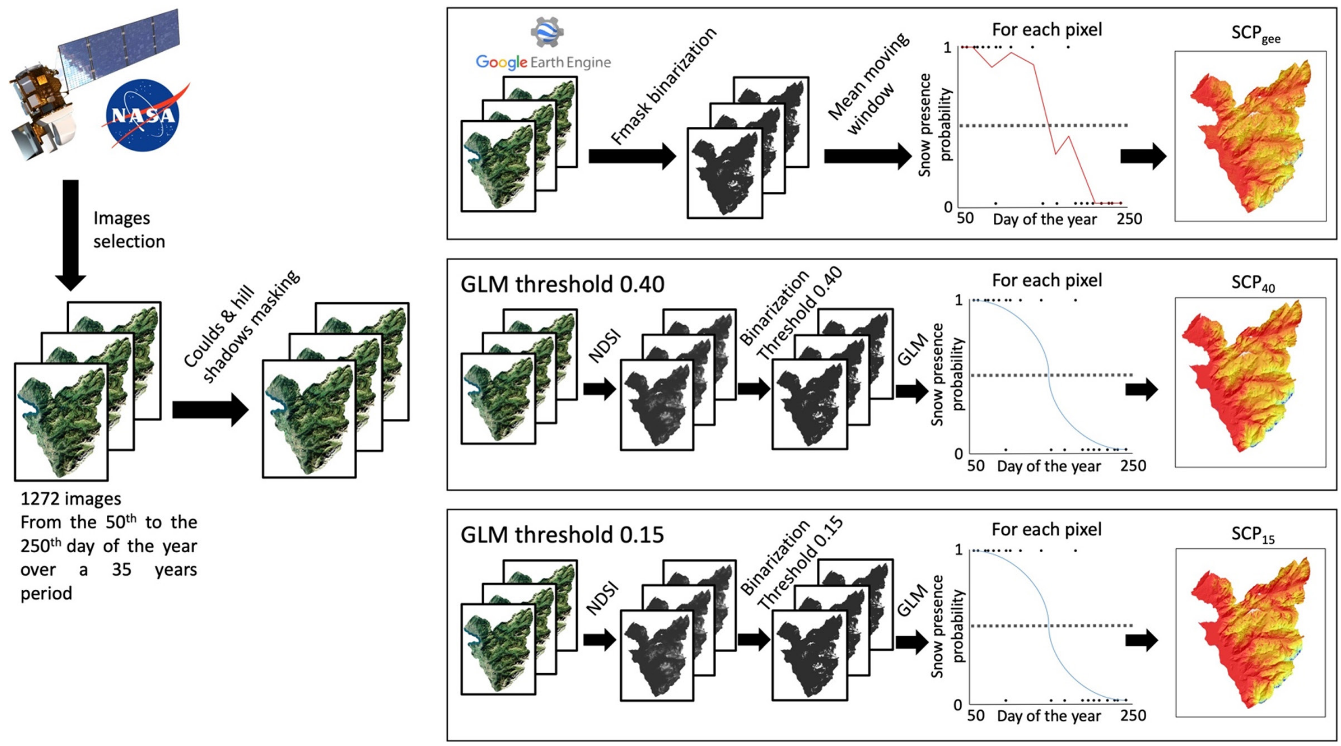

FIGURE 2 General workflow for the production of the three snow cover persistence (SCP) maps. First, the satellite images were selected and cleared from clouds and hill shadows. Then, images were treated with the three approaches to produce three SCP maps. The Google Earth Engine approach uses the Fmask classification to binarize snow presence/absence. For every pixel, a temporal moving window of 10 days, based on the day of the year (DOY) of each image and the presence or absence of snow results in the probability of snow occurrence for the 50th to the 250th DOY. The days of snowmelt for every pixel was defined as the first DOY when this probability passed below 0.5. Generalized linear model (GLM) approaches use the Normalized-Difference Snow Index (NDSI) to binarize the presence/absence of snow, based on two different thresholds (0.40 and 0.15, respectively). For every pixel, a GLM based on the DOY of each image and the presence or absence of snow results in the probability of snow occurrence for the 50th to the 250th DOY. The days of snowmelt for every pixel was defined as the first DOY when this probability passed below 0.5.

within GEE to calculate the final SCP index. Last, we rescaled the SCP map extracted from GEE to 25 m × 25 m using a bilinear interpolation to match the resolution of the other environmental variables used in the SDMs. At this stage, a few pixels had DOY values based on none or very few snow values across the year. These pixels occurred in very small patches scattered through the study area due to the presence of local hill shadow effects. We used a majority focal statistic in ARCMAP (ESRI, version 10.7) with a circle dimension of 5 cells on all pixels having less than 10 available values to replace their statistically irrelevant original value by information from surrounding pixels, thus obtaining continuous predictions. Predictions in these 'filled gaps' were rare and should therefore be considered with care. The resulting SCP map is referred to as 'SCP_{gee}'.

2.5.2 | Approach 2: GLMs with 0.40 threshold

This approach is based on the previous work of Macander et al. (2015) and Niittynen and Luoto (2018). We produced binary maps from the NDSI maps exported from GEE, rescaled to 25 m × 25 m using a bilinear interpolation to match the resolution of other predictors. We used the standard threshold value of 0.40 to reclassify all images into snow/no-snow binary maps, then used to produce the SDC map. For this, we fitted, for each pixel independently, a GLM with binomial distribution and logistic link with the binary score of every image as the dependent variable and the DOY of the image acquisition as the explanatory variable. This generated a probability of snow occurrence for every DOY from the 50th day to the 250th day. The final SCP map was produced by taking, for every pixel, the DOY where this probability of snow presence was <0.5. Finally, we applied the same method as used in the GEE approach to fill empty pixels. Hereafter, we refer to the resulting SCP map as '$SCP_{0.40}$'.

2.5.3 | Approach 3: GLMs with 0.15 threshold

The Fmask classification of snow in GEE uses many criteria to identify snow, but the main one is NDSI >0.15. Because the method of Macander et al. (2015) is based on NDSI >0.40, a difference in snow detection between both methods could simply result from the different thresholds used. To partial out this thresholding effect from the other snow detection criteria (i.e., GLM versus GEE), we produced a third map using the GLM method but with an NDSI threshold of 0.15. Hereafter, we refer to this map as '$SCP_{0.15}$'.

2.5.4 | Assessment of SCP indicators

To assess how the SCP indicators captured snow persistence in the field, we compared their values at field weather stations where snow measures were available. We computed simple correlations and tested whether SCP values obtained thought remote sensing techniques were significantly different to the ones observed in weather stations. Detailed methods and results of this analysis are presented in Methods S1 and Table S1.

2.6 | Environmental variables

2.6.1 | Current climate

In addition to the SCP maps, we used a set of 5 environmental variables commonly used in SDM studies (Buri et al., 2017; Dubuis et al., 2011; Parolo & Rossi, 2008; Randin, Vittoz, et al., 2009). Two climatic variables—mean temperature of the growing season (tmpr) and sum of precipitation of the growing season (prci)—were calculated from the daily MeteoSwiss Grid-Data Products at 1 km (Begert & Frei, 2018) for the 3 months June–August using the reference period 1981–2010, then downscaled to 25 m × 25 m throughout the study area using local elevation-based regressions (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 3 months. The precipitation index prci was also derived from daily MeteoSwiss data, downscaled with local regression with elevation heterogeneity to 25 m × 25 m. Three topographical variables—topographic position (topo), slope and daily potential incoming solar radiation (srad)—were all calculated from the Swiss DEM at a 25 m × 25 m resolution. The srad variable was computed with the ta_lighting module in SAGA GIS. Slope was calculated based on the surrounding elevation values in a neighbouring window of 3 pixels using the slope function from the spatial analyst extension in ArcGIS. The topo variable was calculated using the custom AML function in ArcGIS (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 indicate gullies and valley bottoms, values close to 0 indicate flat terrain or steady slopes and positive values indicate mountain tops and ridges.

2.6.2 | Multicollinearity analyses

To visualize the relationship between the climatic, topographic and snow predictors, we calculated the matrix of Pearson correlation coefficients between all initial predictors using all the values of the different predictors. In addition, we performed a GLM to determine whether the SCP maps could be explained by the topoclimatic predictors. For the latter, topographic and climatic predictors were used, independently and together, as the explanatory variables and SCP as the response variable.

2.7 | Species distribution models

We modelled all plant species with >30 occurrences over the set of sampled sites, resulting in models for 206 species (Table S2). We used an ensemble approach in the biomod2 R package including three different modelling techniques: (i) GLMs with a binomial family and logistic link, allowing linear and 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 with 1000 trees, an interaction depth of 7, a shrinkage factor of 0.001 and a bag fraction of 0.5.

To test the models' prediction accuracy, we used 80% of the data for model training and 20% for model evaluation and repeated this 100 times. During each repetition, we used the area under the receiver-operating characteristic curve (AUC; Swets, 1988) and the true skill statistics (TSS; Allouche et al., 2006) maximized across the whole range of thresholds between 0 and 1 (maxTSS; [Guisan & Zimmermann, 2017]) as threshold-independent predictive accuracy metrics, and calculated variable importance. For each species and SCP map, we then combined model predictions fitted with the three techniques through a mean weighted by the respective maxTSS values.

Using this procedure, five different types of models were fitted, depending on the predictors included the following: (i) snow only (Snow), (ii) topographic and snow (Topo+Snow), (iii) climatic and snow (Clim+Snow), (iv) topographic and climatic (Topo+Clim), and (v) topographic, climatic and snow (Topo+Clim+Snow) (Figure S1).

To test whether the inclusion of the snow variables (SCP) does not improve the models by chance, we compared, for each species and each model including SCP, the accuracy of models fitted with each original SCP map with models including instead the same variable with randomized values, hereafter called SCP *shuffled*. This ensures a similar size structure between the compared models (i.e., same numbers of predictors). This method has previously proven effective for testing the improvement of adding new variables in SDMs (Buri et al., 2017; Buri et al., 2020; le Roux et al., 2013; Niittynen & Luoto, 2018; Zimmermann et al., 2009).

Models based on SCP as a single predictor first allowed (i) quantifying the predictive performance of this variable alone. Next, comparing the SDMs built with (ii) Topo+Snow and (iii) Clim+Snow allowed testing whether the SCP map conveyed complementary information to the climatic or topographic variables, respectively. We also built (iv) a Topo+Clim model without any snow predictor and compared it to (v) the Topo+Clim+Snow models to assess the additional predictive power of snow when added to the more traditionally used topo-climatic models.

2.8 | SDM comparisons

To 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 SCP map (SCP_{gee}, $SCP_{0.15}$ or $SCP_{0.40}$) and with the corresponding shuffled version. We also compared the performances of the SCP maps with each other to assess which was the most suited for SDMs (le Roux et al., 2013).

We also fitted a general linear model to find out whether the model improvement was increasing with the species' elevation of occurrence (based on species occurrences' mean elevation), with the elevation as the predictor and the model improvement as the response. Finally, we tested whether the species' ecological indicator values (EIV; Landolt et al., 2010) had an influence on the models' improvements with a variance analysis, with the EIV as the explanatory variable and the model improvement as the response variable.

3 | RESULTS

3.1 | SCP map

The mean number of available images per pixel (i.e., non-cloudy or shaded) is 422±138 with a maximum of 704. Pixels without any available images represent 0.16% of the study area and 0.3% pixels have less than 10 images available.

An important difference is observed in the mean snow melting DOY between the SCP maps computed with a 0.15 threshold ($SCP_{0.15}$ and SCP_{gee}) and a 0.40 threshold ($SCP_{0.40}$) (Figure 3). The mean snow melting DOYs over the study area are 91.2, 90.5 and 86.2 for SCP_{gee}, $SCP_{0.15}$ and $SCP_{0.40}$. In all indices, the snow melting DOY ranges from 50 in the plain (the default minimum) to 365 (the default maximum) in the permanent snow patches of the Diablerets massif. The snow indices show a relatively high correlation with other climatic variables, but low correlation with topographic variables (Table 1). Accordingly, only the GLMs including climatic variables have a high deviance value (D^2=0.52 for SCP_{gee} and D^2=0.78 for both $SCP_{0.15}$ and $SCP_{0.40}$). GLMs including topographic predictors hardly explain SCP maps (D^2=0.05 for SCP_{gee}, D^2=0.14 for $SCP_{0.15}$ and D^2=0.15 for $SCP_{0.40}$). When combined, GLM with climatic and topographic variables could predict a large part of the SCP maps (D^2=0.54 for SCP_{gee}, 0.83 for $SCP_{0.15}$, 0.84 for $SCP_{0.40}$).

When compared with the other two SCP maps, SCP_{gee} shows a correlation of 0.76 with $SCP_{0.15}$ and 0.77 with $SCP_{0.40}$, whereas those two have a correlation of 0.98.

Observed and remotely sensed SCP show a high correlation (Table S1), especially when comparing the station's value to the SCP_{15} (r=0.82) or the SCP_{40} (r=0.78). The correlation is lower between the stations' observed values and the SCP_{GEE} (r=0.77). There is no significant difference between the SCP values observed in the weather stations and the remotely sensed SCP maps (W=5,097,752, p-value=0.36 for the SCP_{40}, W=4,555,327, p-value=0.16 for the SCP_{40} and W=9,561,617, p-value=0.17 for the SCP_{gee}). The mean SCP difference between weather stations and remote sensed values is 10.6 days for SCP_{gee} and SCP_{40} and 9.2 days for SCP_{15}.

3.2 | Species distribution models

3.2.1 | Topo+Clim+Snow

The Topo+Clim+Snow (v) ensemble models integrating the SCP_{gee}, $SCP_{0.15}$ and $SCP_{0.40}$ maps have always a significantly better

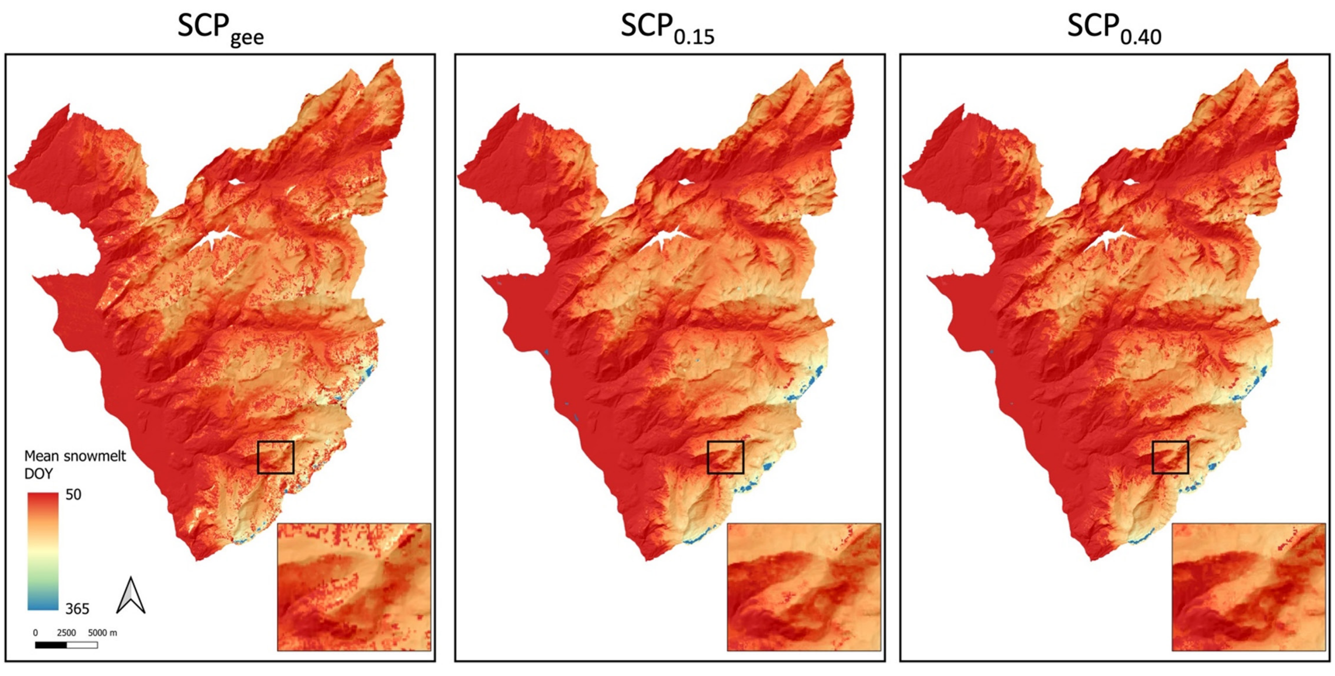

FIGURE 3 Different snow cover persistence (SCP) indices produced by the different approaches in the study area of the Swiss Alps. These indices are further used as predictors in SDMs. The colour-code represents the variation in SCP form the 50th to the 250th day of the year. EPSG:21781.

TABLE 1 Correlation between the SCP maps and other climatic variables and prediction of the generalized linear models (GLMs) computed with climatic/topographic/both predictors.

	Tmpr	Rhires	Srad	Slope	Topo	Corr_GLM_topo	Corr_GLM_clim	Corr_GLM_all
SCP_{gee}	−0.72	0.71	−0.16	0.05	0.11	0.22	0.72	0.74
SCP_{15}	−0.90	0.86	−0.31	0.09	0.21	0.37	0.88	0.91
SCP_{40}	−0.89	0.86	−0.33	0.08	0.19	0.39	0.88	0.92

evaluation, both in AUC and maxTSS, than the shuffled models (Wilcoxon signed rank test, all *p*-values and *V*-values in Tables S3 and S4). maxTSS increases by 0.01 for SCP_{gee}, and by 0.02 for both $SCP_{0.15}$ and $SCP_{0.40}$, representing an improvement of model performance of 1.4% for SCP_{gee}, 2.5% for $SCP_{0.15}$ and 2.3% for $SCP_{0.40}$ (Table S3).

$SCP_{0.15}$ and $SCP_{0.40}$ are performing significantly better than SCP_{gee} (Wilcoxon signed rank test, *V*-value = 5695.5, *p*-value <0.001 and *V*-value = 6389.5, *p*-value <0.001, respectively), but $SCP_{0.15}$ and $SCP_{0.40}$ do not differ (Wilcoxon signed rank test, *V*-value = 11,084, *p*-value = 0.32; Figure 4a). Respective maxTSS of the models are also presented in Table S3. Similar results are obtained with AUC as the evaluation metric (Table S4).

SCP map have a high importance in the models (Figure 4b), with a mean importance of 0.33 for $SCP_{0.15}$ and 0.32 for $SCP_{0.40}$, making it the second most important predictor after temperature. SCP_{gee} has lower importance (0.17), ranking fourth among the 6 variables.

3.2.2 | Additional models

Models integrating only climatic or topographic predictors with SCP maps always have a significantly higher maxTSS difference between the shuffled and the base model than the Topo+Clim models (Wilcoxon signed rank test, *p*-values and *V*-values in Table S5; Figure 4c). The Topo+Snow models have significantly higher maxTSS improvement than Clim+Snow models. The performance difference between the base and the shuffled models is always significant (Wilcoxon signed rank test, *p*-values and *V.values* in Table S3). Models with only SCP as predictor have maxTSS values of 0.44 ± 0.12, 0.52 ± 0.12 and 0.51 ± 0.12 for the SCP_{gee}, $SCP_{0.15}$ and $SCP_{0.40}$, respectively (Figure 4d). The models failed to converge for 15 species, 7.2% of the overall species' pool.

Hereafter, we use $SCP_{0.15}$ as the most relevant SCP index for plant species to develop future analyses and projections.

3.3 | Snow importance for species

The importance of adding the snow variable is variable among species, improving 77.7% of the species models, with maxTSS improvements of >5% for 43 species, and model degradation for 44 species. *Anthyllis vulneraria* shows the largest maxTSS decrease (−7.1%), and *Phleum hirsutum* the greatest increase (+14.2%) (Table S2). Snowbed species (Delarze et al., 1998), such as *Salix herbacea*, *Veronica alpina*, *Poa alpine*, have the highest improvement in maxTSS (5.5%, 5.4% and 9.2%) (Figure 5).

Species elevation occurrences slightly explain model improvements with snow as a predictor (GLM, *p*-value < 0.05, D^2 = 0.027, Figure S2), but not EIVs (Anova, DF = 6, all *p*-value > 0.05).

For future climate scenarios (Figure S3), we observe species-specific changes in suitable habitats by species between traditional projections and the one with the SCP decrease added, but there is no general trend across species. *Soldanella alpina* shows, for instance, slight decreases and gains in suitable areas, whereas *Anthyllis vulneraria* only slightly loses areas (Table S6).

4 | DISCUSSION

This study is important in three ways. First, it is among the first to assess the importance of SCP in plant SDMs in alpine ecosystems using advanced remote sensing methods involving a large number of images and within-pixel trend analyses. Overall, models improved with the addition of the SCP predictors, especially for snow-dependent species. Second, we provide a new method, allowing robust production of SCP indices anywhere in the world, quickly in GEE. It brings ecologically relevant information and improved spatial predictions for a number of alpine species. Finally, our results also suggest that knowledge on species ecology is and should always remain the most important criteria for the selection of predictors in SDMs.

4.1 | A new approach producing useful SCP maps

Our method for image selection resulted in a large pool of values available for each pixel. Ecological remote sensing studies often use a pool of images without clouds (Niittynen & Luoto, 2018; Zimmermann et al., 2007), or use a composite image made of multiple images (Wylie et al., 2003), thus throwing away potentially useful data. However, this method has drawbacks: The cloud classification, although the best available at the time, is not perfect and can result in giving away snow information, leading to an underestimation of the SCP. In addition, using images from the 50th to the 250th DOY, while trying to attenuate imprecisions in the snow index due to variation in snowfall in winter, does not exclude the rare events of snow in the spring or at the end of summer. However, the validation of remotely sensed SCP maps using weather stations shows that, although not perfect, all methods reproduce correctly the main trends in snow persistence (Table S1). Despite being limited to the small

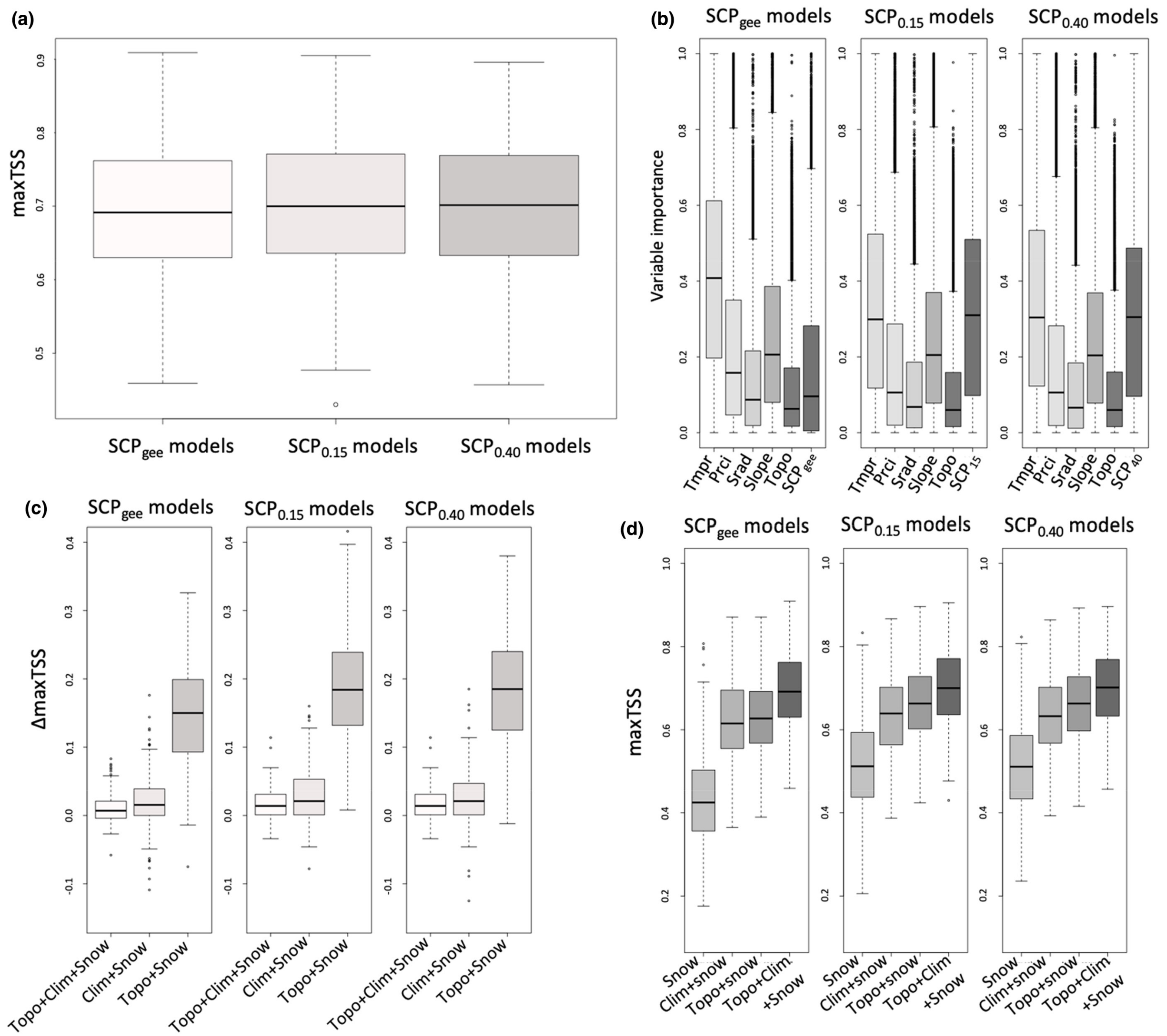

FIGURE 4 Boxplot of evaluations of the different models. (a) Overall maxTSS of the ensemble models Topo+Clim and different SCP maps. (b) Variable importance for the different models built with Topo+Clim and different SCP maps. (c) Difference in maxTSS between the original model and the shuffled one, for Topo+Clim+Snow, Clim+Snow, Topo+Snow models with different SCP maps. (d) maxTSS of the Snow, Clim+Snow, Topo+Snow and Topo+Clim+Snow models built with different SCP maps.

amount of weather stations available in our study area, the remotely sensed SCP maps produced in this article are representing a correct image of the snowmelt dynamics. They probably hold relevant information about the snowmelt dates and should therefore be suitable as a predictor for plant species distributions models. Among the SCP maps tested, the SCP_{15} map seems to better represent SCP.

The two different approaches—GEE and GLMs—gave similar SCP maps, but the GEE produced noisier results. This result, also confirmed by the validation of the SCP maps, can first be explained by the statistical methods available in GEE. Indeed, we had to use a mean moving window approach, which is more sensitive to outliers than the GLM method. In addition, the Fmask classification used to classify snow and clouds absence or presence in each image also has reported weaknesses (Richiardi et al., 2021; Stillinger et al., 2019). This imperfection can sometimes lead to snow being classified as clouds, leading to an underestimation of the SCP indices. On the other hand, 'dark' clouds (thin and transparent clouds) can be classified as snow, leading to overestimation of the SCP indices. All these factors are probably leading to a suboptimal snow index in GEE compared to the R approach.

In turn, GEE offers an easier-to-use method for the scientific community than the more tedious GLM approach in R. Despite the imperfections of this approach, this SCP index holds consistent information (Table S1), and thanks to its implementation in GEE allows quick and reproducible replication around the world. In addition, using all available images and removing residual clouds with the

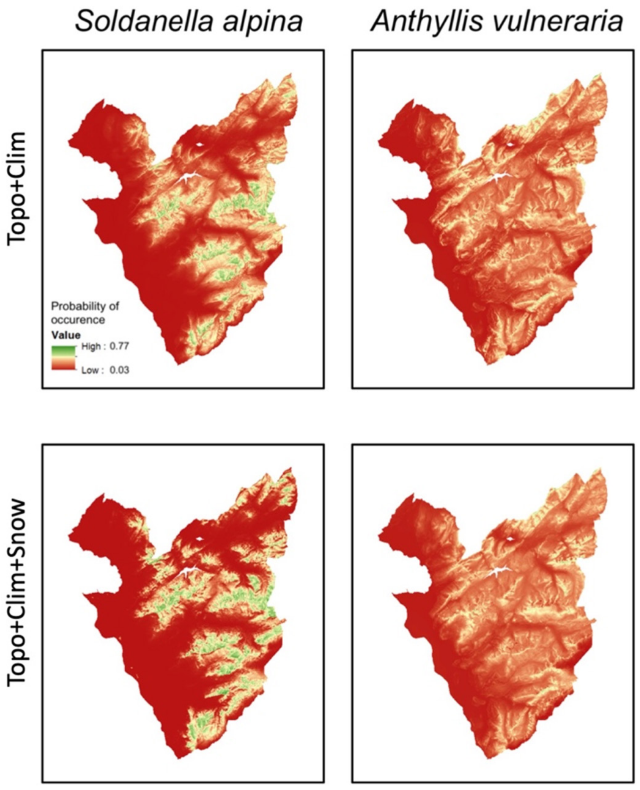

FIGURE 5 Continuous predictions for *Soldanella alpina* (maxTSS improvement of 9% with SCP predictor) and *Anthyllis vulneraria* (−7% of maxTSS) in the study area in the swiss Alps for current climate, modelled with and without SCP predictor. EPSG:21781.

Fmask classification results in a larger data set, here more than three times larger than the manual selection of images used by Niittynen and Luoto (2018). Although we did not formally compare the two approaches, the large increase in the amount of data available could constitute an improvement, but more does not necessarily mean better and the negative points discussed above may cancel out the potential ameliorations brought by the larger amount of data. Hence, further research is needed to investigate this question.

Finally, all data processing is handled by the Google Data Center Infrastructure, drastically reducing the amount of time and resources needed for computations. Our results highlight the need for more advanced statistical tools (like GLMs) in GEE.

4.2 | Snow cover improves plant species distribution predictions

We show that snow is a critical parameter for some species in alpine ecosystems. The large majority of species in our study, along the whole elevation gradient, saw marginal to good improvement in plant distribution predictions. The GEE method shows smaller model improvements than the more advanced GLM one, but all approaches improved overall SDM accuracy. The two GLM approaches with two different thresholds yielded similar results, showing that it is not better than the GEE approach because of the snow detection sensitivity 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 our study were not as high as those reported by Niittynen and Luoto (2018). First, the models we obtained can be, on average across all species, considered as yielding good predictions (Guisan & Zimmermann, 2017; Swets, 1988). Even those built with the shuffled SCP predictors have rather high evaluation scores, overall leaving little room for improvement. The fact that the other climatic variables used in our study are already of good quality at fine resolution, at least for temperature, probably hindered the ability of the additional information brought by the SCP maps to improve the plant distribution models, especially given the high correlation between the SCP and other climatic predictors. This is supported by the models built with the SCP maps and either the topographic or the climatic predictors. The climate-only models have low amelioration by SCP, whereas topographic-only models are improved by almost 30%, highlighting that SCP maps have most redundant information with the climatic variables, especially temperature, which are most often used in SDMs (Mod et al., 2016). Therefore, adding an SCP predictor could particularly help increase SDMs when good-quality temperature data are not available.

Another explanation for the smaller improvements in SDM performance is that the mountain species (i.e., not all alpine) considered here might overall interact less with snow than the strictly arctic species considered in Niittynen and Luoto (2018). Our study area shows a broad elevation gradient, from the lowland to the highest peaks, implying that low- and mid-elevation species or species occurring strictly below the tree line might not be driven by snow patterns. Moreover, even alpine plant species vary in their dependence on SCP (Randin, Vuissoz, et al., 2009). Some rely on snowbeds for insulation, while others avoid snow accumulation to extend their growing season (Galen & Stanton, 1995; Gjaerevoll, 1956; Odland & Munkejord, 2008).

Snow could also have effects on plants that cannot be easily transcribed in an SCP map. For example, at the resolution used here, snow depth or microclimatic variations are not properly considered. 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 & Sturm, 1998). Boserup (2018) showed that, for a small subset of our study area, using remote sensing images of higher resolution (Worldview2 at 1.3 m or Sentinel at 10 m resolution) can yield better results, despite a shorter time period of image availability. However, accurate images like worldview2 are not open access and their acquisition can quickly become expensive for a large study area (700 km^2 here). Finally, snow can also have indirect effects not easily captured in our maps. For example, water released by snowmelt does not only affect the place at which the snowpack is located, but also downstream.

Finally, the use of presence–absence data here could also have hindered the full potential of SCP. Fitting SDMs with abundance data in future SDM studies could make the SCP index more important, as already illustrated by Randin, Jaccard, et al. (2009) for the importance of landuse in SDMs.

4.3 | Species ecology matters

Model improvement proved highly variable among species, suggesting that species ecology remains a key aspect to consider when selecting predictors in SDMs (Austin & Niel, 2011; Mod et al., 2016; Scherrer & Guisan, 2019). Many of the species that had a reduction in model performance have little or no interaction with snow, such as low-elevation species for which the start of the growing season does not depend on snow.

Some high-elevation plant species also saw their models degraded by the addition of a snow predictor, such as *Androsaceae chamaejasme*, *Poa minor* and *Saxifraga aizoides* (all occurring above 2100 m in our dataset). Thus, being at high-elevation does not mean necessarily that snow is a relevant predictor. These species probably do not have a strong relationship with SCP thus resulting in a degradation of independent model evaluation when SCP is added as a predictor.

In addition, the taxonomic resolution used in this study can probably explain why some species have their models' evaluation degraded after the addition of the SCP predictor. Indeed, some taxonomic groups used here, mainly because of their laborious identification in the field, species complex or subspecies that have slightly different ecology. For example, *Anthoxanthum odoratum* aggr. comprises *A. alpinum* and *A. odoratum* s. str., the first occurring at higher altitude pastures with longer SCP thus may have a greater relationship with SCP than the second one. This is the same situation for the species with the strongest decrease in model's accuracy, Anthyllis *vulneraria* s. l., which comprises two subspecies, *A. vulneraria* subsp. *alpestris* and *A. vulneraria* subsp. *carpatica*.

Globally, model improvement was higher for species occurring at high elevation, showing the overall importance of snow for many alpine species. Among species for which snow largely improved model performance are snowbed species and species of snowless windy slopes. The first group of species strongly relies on snow cover for cold insulation or as a moisture source during the growing season. Species such as *Salix herbacea*, *Veronica alpina*, or *Soldanella alpina* are typical snowbed species and saw the highest improvements. Species living in windy environments, where the SCP is shorter, also see improvement by the SCP index. The position of the species along a 'snow persistence gradient' does not really explain the improvements in model's performance. Other species such as *Helictotrichon versicolor*, *Homogyne alpina*, *Vaccinium gaultherioides* and *Dryas octopetala*, which have already been the subject of studies of the importance of snow cover in SDMs (Beck et al., 2005), saw moderate to good improvements in model accuracy. This reveals the importance of SCP to also inform on areas with reduced snow cover, such as windy environments on ridges, which are also critical for some species.

4.4 | Perspectives for future projections

Alpine and Arctic ecosystems are both driven by snow cover, and should thus experience drastic changes caused by climate change in the near future (Randin, Engler, et al., 2009), already observable in the Alps (Rumpf et al., 2022). To our knowledge, there is no accurate snow cover decrease scenario available for the Swiss Alps. Therefore, for illustrative purposes, we used here a basic snow decrease scenario based on existing knowledge (Beniston, 2003) to simulate the effect of climate change-induced SCP decrease in plant distributions (Method S2, Figure S3 and Table S6). This illustrates the need for better knowledge and scenarios of the evolution of climatic variables other than temperature and precipitation in the future. Niittynen et al. (2018) already showed that taking snow cover decrease into account in future projections of plant SDMs could lead to dramatic differences compared to a temperature increase only. However, the latter study reported larger species losses than in our study, likely due to the striking topographical differences between the two areas. In the Arctic, species must migrate longer distances in latitude to reach a similar difference in temperature as a small altitudinal shift allows in the Alps, but this remains to be tested.

In our prospective future projections, results are highly variable among species. Most species are predicted to shift to higher elevation, both when predicted with and without the SCP variable. This is in agreement with the current knowledge on warming scenarios in the Alps (Engler et al., 2011; Parolo & Rossi, 2008; Randin, Engler, et al., 2009). Generally speaking, plants predicted to experience a large decrease in habitat suitability under warming have their loss attenuated when the SCP decrease map was used in the models (e.g., *Salix herbacea*, *Veronica alpina*, *Ligusticum mutellina*, *Soldanella alpina*). A cause may be the melting of medium and long-lasting snow, simulated in our SCP decrease scenario maps, which starts to be observed in the Alps (Rumpf et al., 2022) and offers new suitable habitats for alpine species at medium to high elevation.

5 | CONCLUSION

Our study shows the importance of accounting for snow in plant SDMs developed in alpine ecosystems. Our approach and findings support that SCP indices should be more systematically taken into consideration as predictors when modelling the distribution of plant species that interact with snow. We further proposed a method to calculate the necessary snow indices at any place on Earth.

AUTHOR CONTRIBUTIONS

Thomas Panchard conceived the ideas, supervised by Olivier Broennimann and Antoine Guisan. Thomas Panchard produced the snow cover persistence index supervised by Mathieu Gravey and Grégoire Mariethoz. Olivier Broennimann and Antoine Guisan provided the climatic and topographic data as well as the occurrence data. Thomas Panchard performed the models, and analysis, supervised by Olivier Broennimann. Thomas Panchard wrote the first version of the manuscript, corrected and adapted with the help of Olivier Broennimann and Antoine Guisan.

ACKNOWLEDGEMENTS

We thank the USGS for allowing open access to satellite data. Thanks to Julie Boserup and Carmen Cianfrani for early analyses. We are grateful to Mathieu Chevalier, Sabine Rumpf, Maude Baudraz, Flavien Collart and Marc Bastardot for useful comments on this manuscript. We thank reviewers Shengwei Zong and Pekka Niittynen for their comments on the manuscript, especially for their insights into the remote sensing part, and the editor Gerald Schneeweiss for his useful comments and suggestions, especially on the ecology of species. This project received support from the SNF INTEGRALP project (grant nr CR23I2_162754). We thank the rechalp project (http://rechalp.unil.ch) for providing the plant observations and environmental data. No permit was required for plant sampling. This project received support from the SNF INTEGRALP project (grant nr CR23I2_162754).

CONFLICT OF INTEREST STATEMENT

No, there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used for this project can be found at:

1. Landsat images are freely available from the U.S. Geological Survey
2. Code used to compute the snow cover persistence map via Google Earth Engine is available at: https://code.earthengine.google.com/658d2a2dd95521147171887ddbeffdb9?noload=true or https://doi.org/10.5281/zenodo.8043552
3. Code used to compute the snow cover persistence map via R is available at: https://doi.org/10.5281/zenodo.8043552
4. Topographical data can be obtained through the Swiss Federal Office of Topography
5. Climatic data can be obtained through the MeteoSwiss Grid-Data Products
6. Plant occurrence data are available at: https://doi.org/10.5281/zenodo.8043552

ORCID

Thomas Panchard https://orcid.org/0000-0001-8263-4493
Olivier Broennimann https://orcid.org/0000-0001-9913-3695
Mathieu Gravey https://orcid.org/0000-0002-0871-1507
Grégoire Mariethoz https://orcid.org/0000-0002-8820-2808
Antoine Guisan https://orcid.org/0000-0002-3998-4815

REFERENCES

Algar, A. C., Kharouba, H. M., Young, E. R., & Kerr, J. T. (2009). Predicting the future of species diversity: Macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography*, *32*(1), 22–33. https://doi.org/10.1111/j.1600-0587.2009.05832.x

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Araújo, M. B., Anderson, R. P., Barbosa, A. M., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, *5*(1), eaat4858. https://doi.org/10.1126/sciadv.aat4858

Austin, M. P., & Niel, K. P. V. (2011). Improving species distribution models for climate change studies: Variable selection and scale. *Journal of Biogeography*, *38*(1), 1–8. https://doi.org/10.1111/j.1365-2699.2010.02416.x

Bannister, P., Maegli, T., Dickinson, K. J. M., Halloy, S. R. P., Knight, A., Lord, J. M., Mark, A. F., & Spencer, K. L. (2005). Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage? *Oecologia*, *144*(2), 245–256. https://doi.org/10.1007/s00442-005-0087-3

Beck, P. S. A., Kalmbach, E., Joly, D., Stien, A., & Nilsen, L. (2005). Modelling local distribution of an Arctic dwarf shrub indicates an important role for remote sensing of snow cover. *Remote Sensing of Environment*, *98*(1), 110–121. https://doi.org/10.1016/j.rse.2005.07.002

Begert, M., & Frei, C. (2018). Long-term area-mean temperature series for Switzerland—Combining homogenized station data and high resolution grid data. *International Journal of Climatology*, *38*(6), 2792–2807. https://doi.org/10.1002/joc.5460

Beniston, M., Keller, F., Koffi, B., & Goyette, S. (2003). Estimates of snow accumulation and volume in the Swiss Alps under changing climatic conditions. *Theoretical and Applied Climatology*, *76*, 125–140. https://doi.org/10.1007/s00704-003-0016-5

Billings, W. D., & Bliss, L. C. (1959). An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology*, *40*(3), 388–397.

Bintanja, R., & Andry, O. (2017). Towards a rain-dominated Arctic. *Nature Climate Change*, *7*(4), 263–267. https://doi.org/10.1038/nclimate3240

Boserup, J. (2018). Improving alpine plants species distribution models with high resolution remote sensed snow cover. Master Thesis. https://www.unil.ch/ecospat/files/live/sites/ecospat/files/shared/PDF_site/Boserup2018_MSc.pdf

Broennimann, O. (2018). CHclim25: A high spatial and temporal resolution climate dataset for Switzerland. Ecospat Laboratory. https://www.unil.ch/ecospat/home/menuguid/ecospat-resources/data.html

Buri, A., Cianfrani, C., Pinto-Figueroa, E., Yashiro, E., Spangenberg, J. E., Adatte, T., Verrecchia, E., Guisan, A., & Pradervand, J.-N. (2017). Soil factors improve predictions of plant species distribution in a mountain environment. *Progress in Physical Geography: Earth and Environment*, *41*(6), 703–722. https://doi.org/10.1177/0309133317738162

Buri, A., Grand, S., Yashiro, E., Adatte, T., Spangenberg, J. E., Pinto-Figueroa, E., Verrecchia, E., & Guisan, A. (2020). What are the most crucial soil variables for predicting the distribution of mountain plant species? A comprehensive study in the Swiss Alps. *Journal of Biogeography*, *47*(5), 1143–1153. https://doi.org/10.1111/jbi.13803

Chevalier, M., Mod, H., Broennimann, O., Di Cola, V., Schmid, S., Niculita-Hirzel, H., Pradervand, J.-N., Schmidt, B. R., Ursenbacher, S., Pellissier, L., & Guisan, A. (2021). Low spatial autocorrelation in mountain biodiversity data and model residuals. *Ecosphere*, *12*(3), 3. https://doi.org/10.1002/ecs2.3403

Crane, R. G., & Anderson, M. R. (1984). Satellite discrimination of snow/cloud surfaces. *International Journal of Remote Sensing*, *5*(1), 213–223. https://doi.org/10.1080/01431168408948799

Delarze, R., Gonseth, Y., Eggenberg, S., & Vust, M. (2015). *Guide des milieux naturels de Suisse, nouvelle édition (Rossolis).*

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Butchart, S., Chan, K., Garibaldi, L., Ichii, K., Liu, J., Subrmanian, S., Midgley, G., Miloslavich, P., Molnár, Z., Obura, D., ... Zayas, C. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of* the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://uwe-repository.worktribe.com/output/1493508

Dozier, J. (1989). Spectral signature of alpine snow cover from the landsat thematic mapper. *Remote Sensing of Environment*, *28*, 9–22. https://doi.org/10.1016/0034-4257(89)90101-6

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P., & Guisan, A. (2013). Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science*, *24*(4), 593–606. https://doi.org/10.1111/jvs.12002

Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J. P., & Guisan, A. (2011). Predicting spatial patterns of plant species richness: A comparison of direct macroecological and species stacking modelling approaches. *Diversity and Distributions*, *17*(6), 1122–1131. https://doi.org/10.1111/j.1472-4642.2011.00792.x

Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araujo, M. B., Pearman, P. B., Le Lay, G., Piedallu, C., Albert, C. H., Choler, P., Coldea, G., De Lamo, X., Dirnbock, T., Gegout, J. C., Gomez-Garcia, D., Grytnes, J. A., Heegaard, E., Hoistad, F., … Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, *17*(7), 2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Evans, B. M., Walker, D. A., Benson, C. S., Nordstrand, E. A., & Petersen, G. W. (1989). Spatial interrelationships between terrain, snow distribution and vegetation patterns at an arctic foothills site in Alaska. *Ecography*, *12*(3), 270–278. https://doi.org/10.1111/j.1600-0587.1989.tb00846.x

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, *45*(2), RG2004. https://doi.org/10.1029/2005RG000183

Ford, K. R., Ettinger, A. K., Lundquist, J. D., Raleigh, M. S., & Lambers, J. H. R. (2013). Spatial heterogeneity in ecologically important climate variables at coarse and fine scales in a high-Snow Mountain landscape. *PLoS One*, *8*(6), e65008. https://doi.org/10.1371/journal.pone.0065008

Friedel, H. (1961). *Schneedeckendauer und Vegetationsverteilung im Gelände*. Forstl. Bundes-Versuchsanst.

Galen, C., & Stanton, M. L. (1995). Responses of snowbed plant species to changes in growing-season length. *Ecology*, *76*(5), 1546–1557.

Gjaerevoll, O. (1956). The plant communities of the Scandinavian Alpine snow-beds. *Det Kgl Norske Videnskabers Selskabs Skrifter*, *1*, 405.

Gottfried, M., Pauli, H., Reitter, K., & 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.

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: With applications in R*. Cambridge University Press.

Guisan, A., Theurillat, J. P., & Kienast, F. (1998). Predicting the potential distribution of plant species in an Alpine environment. *Journal of Vegetation Science*, *9*(1), 65–74.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., Regan, T. J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., … Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, *16*(12), 1424–1435. https://doi.org/10.1111/Ele.12189

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*(2–3), 147–186.

Hall, D. K., Riggs, G. A., Salomonson, V. V., DiGirolamo, N. E., & Bayr, K. J. (2002). MODIS snow-cover products. *Remote Sensing of Environment*, *83*(1), 181–194. https://doi.org/10.1016/S0034-4257(02)00095-0

Hall, D. O., Ojima, D. S., Parton, W. J., & Scurlock, J. M. O. (1995). Response of temperate and tropical grasslands to CO_2 and climate change. *Journal of Biogeography*, *22*(2–3), 537–547.

Hijmans, R. J., van Etten, J., Sumner, M., Cheng, J., Bevan, A., Bivand, R., Busetto, L., Canty, M., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J. A., Hiemstra, P., Geosciences, I. for M. A, Karney, C., Mattiuzzi, M., Mosher, S., Nowosad, J., … Wueest, R. (2019). *raster: Geographic Data Analysis and Modeling* (3.0-7). https://CRAN.R-project.org/package=raster

Hirzel, A., & Guisan, A. (2002). Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling*, *157*(2), 331–341. https://doi.org/10.1016/S0304-3800(02)00203-X

Hutchinson, G. E. (1957). Population studies—Animal ecology and demography—Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427.

Keller, F., Goyette, S., & Beniston, M. (2005). Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Climatic Change*, *72*(3), 299–319.

Körner, C. (2003). Limitation and stress—Always or never? *Journal of Vegetation Science*, *14*(2), 141–143.

Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Nobis, M., Rudmann-Maurer, K., Schweingruber, F. H., & Theurillat, J. P. (2010). *Flora indicativa: Ecological indicator values and biological attributes of flora of Switzerland and the Alps*. Haupt.

le Roux, P. C., Virtanen, R., & Luoto, M. (2013). Geomorphological disturbance is necessary for predicting fine-scale species distributions. *Ecography*, *36*(7), 800–808. https://doi.org/10.1111/j.1600-0587.2012.07922.x

Li, S., Sun, D., Goldberg, M. E., & Sjoberg, B. (2015). Object-based automatic terrain shadow removal from SNPP/VIIRS flood maps. *International Journal of Remote Sensing*, *36*(21), 5504–5522. https://doi.org/10.1080/01431161.2015.1103918

Lievens, H., Demuzere, M., Marshall, H.-P., Reichle, R. H., Brucker, L., Brangers, I., de Rosnay, P., Dumont, M., Girotto, M., Immerzeel, W. W., Jonas, T., Kim, E. J., Koch, I., Marty, C., Saloranta, T., Schöber, J., & De Lannoy, G. J. M. (2019). Snow depth variability in the Northern Hemisphere mountains observed from space. *Nature Communications*, *10*(1), 1. https://doi.org/10.1038/s41467-019-12566-y

Liston, G. E., & Sturm, M. (1998). A snow-transport model for complex terrain. *Journal of Glaciology*, *44*(148), 498–516. https://doi.org/10.3189/S0022143000002021

Macander, M. J., Swingley, C. S., Joly, K., & Raynolds, M. K. (2015). Landsat-based snow persistence map for Northwest Alaska. *Remote Sensing of Environment*, *163*, 23–31. https://doi.org/10.1016/j.rse.2015.02.028

Matteodo, M., Ammann, K., Verrecchia, E. P., & Vittoz, P. (2016). Snowbeds are more affected than other subalpine–alpine plant communities by climate change in the Swiss Alps. *Ecology and Evolution.*, *6*, 6969–6982.

Mod, H. K., Scherrer, D., Luoto, M., & Guisan, A. (2016). What we use is not what we know: Environmental predictors in plant distribution models. *Journal of Vegetation Science*, *27*(6), 1308–1322.

Niittynen, P., Heikkinen, R. K., & Luoto, M. (2018). Snow cover is a neglected driver of Arctic biodiversity loss. *Nature Climate Change*, *8*(11), 997–1001. https://doi.org/10.1038/s41558-018-0311-x

Niittynen, P., & Luoto, M. (2018). The importance of snow in species distribution models of arctic vegetation. *Ecography*, *41*(6), 1024–1037. https://doi.org/10.1111/ecog.03348

Odland, A., & Munkejord, H. K. (2008). Plants as indicators of snow layer duration in southern Norwegian mountains. *Ecological Indicators*, *8*(1), 57–68.

Olefs, M., Koch, R., Schöner, W., & Marke, T. (2020). Changes in snow depth, snow cover duration, and potential snowmaking conditions in Austria, 1961–2020—A model based approach. *Atmosphere*, *11*(12), 12. https://doi.org/10.3390/atmos11121330

Parolo, G., & Rossi, G. (2008). Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology*, *9*(2), 100–107.

Pineda, E., & Lobo, J. M. (2009). Assessing the accuracy of species distribution models to predict amphibian species richness patterns. *Journal of Animal Ecology*, *78*(1), 182–190. https://doi.org/10.1111/j.1365-2656.2008.01471.x

Pottier, J., Dubuis, A., Pellissier, L., Maiorano, L., Rossier, L., Randin, C. F., Vittoz, P., & Guisan, A. (2013). The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. *Global Ecology and Biogeography*, *22*(1), 52–63. https://doi.org/10.1111/j.1466-8238.2012.00790.x

Pradervand, J. N., Dubuis, A., Pellissier, L., Guisan, A., & Randin, C. (2014). Very high resolution environmental predictors in species distribution models: Moving beyond topography? *Progress in Physical Geography*, *38*(1), 79–96. https://doi.org/10.1177/0309133313512667

Randin, C. F., Ashcroft, M. B., Bolliger, J., Cavender-Bares, J., Coops, N. C., Dullinger, S., Dirnböck, T., Eckert, S., Ellis, E., Fernández, N., Giuliani, G., Guisan, A., Jetz, W., Joost, S., Karger, D., Lembrechts, J., Lenoir, J., Luoto, M., Morin, X., … Payne, D. (2020). Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. *Remote Sensing of Environment*, *239*, 111626. https://doi.org/10.1016/j.rse.2019.111626

Randin, C. F., Engler, R., Normand, S., Zappa, M., Zimmermann, N. E., Pearman, P. B., Vittoz, P., Thuiller, W., & Guisan, A. (2009). Climate change and plant distribution: Local models predict high-elevation persistence. *Global Change Biology*, *15*(6), 1557–1569. https://doi.org/10.1111/j.1365-2486.2008.01766.x

Randin, C. F., Jaccard, H., Vittoz, P., Yoccoz, N. G., & Guisan, A. (2009). Land use improves spatial predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation Science*, *20*(6), 996–1008. https://doi.org/10.1111/j.1654-1103.2009.01098.x

Randin, C. F., Vittoz, P., Jaccard, H., Yoccoz, N. G., & Guisan, A. (2009). Land use improves spatial predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation Science*, *20*(6), 996–1008.

Randin, C. F., Vuissoz, G., Liston, G. E., Vittoz, P., & Guisan, A. (2009). Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the Western Swiss Alps. *Arctic Antarctic and Alpine Research*, *41*(3), 347–361. https://doi.org/10.1657/1938-4246-41.3.347

Rango, A., Salomonson, V. V., & Foster, J. L. (1977). Seasonal streamflow estimation in the Himalayan region employing meteorological satellite snow cover observations. *Water Resources Research*, *13*(1), 109–112. https://doi.org/10.1029/WR013i001p00109

Rebetez, M., & Reinhard, M. (2008). Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theoretical and Applied Climatology*, *91*(1–4), 27–34.

Richiardi, C., Blonda, P., Rana, F. M., Santoro, M., Tarantino, C., Vicario, S., & Adamo, M. (2021). A revised snow cover algorithm to improve discrimination between snow and clouds: A case study in Gran Paradiso National Park. *Remote Sensing*, *13*(10), 10. https://doi.org/10.3390/rs13101957

Rissanen, T., Niittynen, P., Soininen, J., & Luoto, M. (2021). Snow information is required in subcontinental scale predictions of mountain plant distributions. *Global Ecology and Biogeography*, *30*(7), 1502–1513. https://doi.org/10.1111/geb.13315

Rumpf, S. B., Gravey, M., Brönnimann, O., Luoto, M., Cianfrani, C., Mariethoz, G., & Guisan, A. (2022). From white to green: Snow cover loss and increased vegetation productivity in the European Alps. *Science*, *376*(6597), 1119–1122. https://doi.org/10.1126/science.abn6697

Scherrer, D., & Guisan, A. (2019). Ecological indicator values reveal missing predictors of species distributions. *Scientific Reports*, *9*(1), 1–8. https://doi.org/10.1038/s41598-019-39133-1

Siniscalco, C., Barni, E., & Bacaro, G. (2011). Non-native species distribution along the elevation gradient in the western Italian Alps. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology*, *145*(1), 150–158. https://doi.org/10.1080/11263504.2010.540786

Solomon, S., & Intergovernmental Panel on Climate Change, & Intergovernmental Panel on Climate Change (Eds.). (2007). *Climate change 2007: The physical science basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Stillinger, T., Roberts, D. A., Collar, N. M., & Dozier, J. (2019). Cloud masking for landsat 8 and MODIS terra over snow-covered terrain: Error analysis and spectral similarity between snow and cloud. *Water Resources Research*, *55*(7), 6169–6184. https://doi.org/10.1029/2019WR024932

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, *240*(4857), 1285–1293.

Tenenbaum, D. J. (2005). Global warming: Arctic climate: The heat is on. *Environmental Health Perspectives*, *113*(2), A91–A91. https://doi.org/10.1289/ehp.113-a91a

Truong, T. T. A., Hardy, G. E. S. J., & Andrew, M. E. (2017). Contemporary remotely sensed data products refine invasive plants risk mapping in data poor regions. *Frontiers in Plant Science*, *8*, 770. https://doi.org/10.3389/fpls.2017.00770

Verrall, B., & Pickering, C. M. (2020). Alpine vegetation in the context of climate change: A global review of past research and future directions. *Science of the Total Environment*, *748*, 141344. https://doi.org/10.1016/j.scitotenv.2020.141344

Von Däniken, I., Guisan, A., & Lane, S. (2014). RechAlp.vd: Une nouvelle plateforme UNIL de support pour la recherche transdisciplinaire dans les Alpes vaudoises. *Bulletin de la Société Vaudoise des Sciences Naturelles*, *94*(2), 175–178.

Walker, D. A., Halfpenny, J. C., Walker, M. D., & Wessman, C. A. (1993). Long-term studies of snow-vegetation interactions. *Bioscience*, *43*(5), 287–301. https://doi.org/10.2307/1312061

Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, *94*(1), 105–121. https://doi.org/10.1007/s10584-009-9546-x

Wylie, B. K., Johnson, D. A., Laca, E., Saliendra, N. Z., Gilmanov, T. G., Reed, B. C., Tieszen, L. L., & Worstell, B. B. (2003). Calibration of remotely sensed, coarse resolution NDVI to CO2 fluxes in a sagebrush–steppe ecosystem. *Remote Sensing of Environment*, *85*(2), 243–255. https://doi.org/10.1016/S0034-4257(03)00004-X

Zappa, M. (2008). Objective quantitative spatial verification of distributed snow cover simulations—An experiment for the whole of Switzerland / Vérification quantitative spatiale objective de simulations distribuées de la couche de neige—Une étude pour l'ensemble de la Suisse. *Hydrological Sciences Journal*, *53*(1), 179–191. https://doi.org/10.1623/hysj.53.1.179

Zhu, Z., Wang, S., & Woodcock, C. E. (2015). Improvement and expansion of the Fmask algorithm: Cloud, cloud shadow, and snow detection for landsats 4–7, 8, and sentinel 2 images. *Remote Sensing of Environment*, *159*, 269–277. https://doi.org/10.1016/j.rse.2014.12.014

Zhu, Z., & Woodcock, C. E. (2012). Object-based cloud and cloud shadow detection in Landsat imagery. *Remote Sensing of Environment*, *118*, 83–94. https://doi.org/10.1016/j.rse.2011.10.028

Zimmermann, N. E., Edwards, T. C., Moisen, G. G., Frescino, T. S., & 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*(5), 1057–1067. https://doi.org/10.1111/j.1365-2664.2007.01348.x

Zimmermann, N. E., Yoccoz, N. G., Edwards, T. C., Meier, E. S., Thuiller, W., Guisan, A., Schmatz, D. R., & Pearman, P. B. (2009). Climatic extremes improve predictions of spatial patterns of tree species.

Proceedings of the National Academy of Sciences, *106*(Supplement_2), 19723–19728. https://doi.org/10.1073/pnas.0901643106

Zong, S., Lembrechts, J. J., Du, H., He, H. S., Wu, Z., Li, M., & Rixen, C. (2022). Upward range shift of a dominant alpine shrub related to 50 years of snow cover change. *Remote Sensing of Environment*, *268*, 112773. https://doi.org/10.1016/j.rse.2021.112773

BIOSKETCH

Thomas Panchard is a wildlife biologist who dedicates his research to understanding the major drivers of plant and animals distributions. Trought his work at the ECOSPAT lab he seeks to integrate novel methods and tools for biodiversity monitoringand conservation planning.

Olivier Broennimann is a biogeographer who is interested in developing tools to assess and understand the impacts of global change on biodiversity from regional to global scale.

Mathieu Gravey leads the Digital Landscape Group at the Institute for Interdisciplinary Mountain Research, where as a geostatistician, machine learning and remote sensing researcher, he applies remote sensing technologies and cloud computing to pioneer advancements in geoscience.

Gregoire Mariethoz, leader of the GAIA lab, researches the integration of remote sensing data in models to gain a better understanding of earth systems processes.

Antoine Guisan is a spatial modeler and biogeographer, especially interested in species ecologiacal niches and distributions, with a specific interest in global change studies and mountain ecosystems. He is leading the ECOSPAT lab at the University of Lausanne.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Panchard, T., Broennimann, O., Gravey, M., Mariethoz, G., & Guisan, A. (2023). Snow cover persistence as a useful predictor of alpine plant distributions. *Journal of Biogeography*, *00*, 1–14. https://doi.org/10.1111/jbi.14689