How prevalent were nunataks as glacial refugia in the Alps? Insights from range hindcasting of the nival flora

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How prevalent were nunataks as glacial refugia in the Alps ? Insights from range hindcasting of the nival flora

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Abstract

The European Alps were heavily glaciated during the Pleistocene, prompting debates about plants' glacial refugia. While most alpine vegetation likely survived in lower mountain ranges, adjacent or disconnected from the Alps, or elsewhere in European lowlands, a century-old hypothesis suggests that some plants persisted on rocky peaks protruding from ice-covered areas. However, this so-called *"nunatak"* hypothesis has received relatively limited attention and support from phylogeographic studies. We modeled the potential distribution of 69 nival plant species during the Last Glacial Maximum (LGM, *circa* 20 to 25 ky ago) using species distribution models based on paleo-climatic conditions, paleo-ice extent, topographic metrics and bedrock lithologies. Two thirds of studied species and the majority of silicicolous species were predicted to have predominantly occurred on nunataks during the LGM in comparison to peripheral mountains or lowlands. Bedrock affinity, alongside topographic and climatic preferences, profoundly influenced predictions of species' refugia locations and range contractions. Silicicolous species relied heavily on nunataks, where lithology and topographic ruggedness jointly favored their survival. Calcicolous species, in contrast, primarily found refugia in peripheral and extra-alpine massifs, the inner Alps being largely uninhabitable — either due to the extensive ice cover on calcareous massifs, often located at lower elevations, or because unglaciated ones were too unsuitable for their persistence. Generalist species, with broader ecological flexibility, persisted across more diverse refugia, favoring mainly the less harsh peripheral regions. Multivariate analyses identified seven cooccurring species groups associated with distinct potential refugia. Our findings challenge the view that nunatak refugia were undervalued during glacial periods, highlighting their significance for siliceous rock-specialist nival species. This work provides a well-delimited framework for further research on alpine paleobiogeography.

Keywords: Alpine flora, Last glacial maximum, Species distribution models, Nunataks, Glacial Refugia, Pleistocene biogeography

Introduction

The spectacularly rapid climatic fluctuations of the Quaternary era (Dansgaard et al., 1993) are well known to have profoundly impacted the distribution of organisms across the arctic, boreal, and temperate biomes (Comes & Kadereit, 1998; G. Hewitt, 2000). During the Pleistocene (*circa* 2.5My to 11.7ky ago), repeated climatic fluctuations led to massive species range shifts, the formation and dissolution of dispersal routes, and community reshuffling across vegetation belts (Blytt, 1876; Van Andel & Tzedakis, 1996). Because the European Alps (Alps, hereafter) were so heavily glaciated, it was long considered that most alpine flora migrated out of this region during glacial periods and recolonized it during interglacials (so called "tabula rasa hypothesis" ; see Dahl (1987)). This theory posits that refugia were primarily located in lower peripheral massifs of the Alps (*i.e.*, peripheral refugia hereafter, Mercantour or Bergamasque Alps), in mountain ranges apart from the Alps (extra-alpine massifs hereafter, *e.g.*, Vosges, Jura, Apennines or Balkan Mountains), or in adjacent lowlands (Chodat & Pampanini, 1902). (Refer to Fig.S1 for a geographic representation of locations that will be discussed here.)

At the turn of the 20th century, the pioneering work from the Swiss botanist and geologist Marie Brockmann-Jerosch (1926) suggested an alternative hypothesis: some alpine plant species may have survived glacial periods on ice-free mountain peaks, or *"*nunataks*"* (from the Inuktituk word *nunataq*) within the permanently glaciated regions of the Alps (Holderegger et al., 2011). Although the hypothesis of nunatak survival within the Alps has received some empirical support from patterns of species diversity, such as the higher-than-expected species diversity in areas that should have been migration sinks, such as the Visp-Zermatt valley (Becherer, 1972; Brockmann-Jerosch and Brockmann-Jerosch, 1926; Stehlik, 2000; Welten and Sutter, 1982); from endemism patterns (Merxmüller, 1952); and from phylogeographic studies (*e.g.*, Parisod and Besnard, 2007; Schönswetter and Schneeweiss, 2019 ; Stehlik et al., 2002), it remains contentious and discussed for over a century. In the case of *Saxifraga oppositifolia*, for example, Gabrielsen et al. (1997) dismissed those kind of refugia that they considered superfluous. The relevance of nunatak refugia has thus long been questioned and doubted (*e.g.*, Nordal, 1987; Tollefsrud et al., 1998) to the point that, after a century of scientific inquiry, this issue was still considered "not yet settled" (Holderegger and Thiel-Egenter, 2009) or "very difficult to prove or disprove" (G. M. Hewitt, 2004). Some recent studies have reemphasized the importance of nunatak survival through phylogeographic reconstructions (*e.g.*, Larsson et al., 2021; Pan et al., 2020; Rota et al., 2024). Though it remains to be evaluated whether nunatak refugia concern only a handful of species or rather an important proportion of species inhabiting nival environments.

The nunatak refugia hypothesis implies that high-elevation bedrock surfaces remained ice-free and geographically isolated throughout the Pleistocene, providing isolated habitats for nival vegetation and fostering genetic divergence. This scenario points out fundamentally different population dynamics

compared to a peripheral refugia scenario, because these areas were occasionally connected with outer regions even during glacial periods. Paleogeomorphological evidence indeed suggests that some extensive high-elevation bedrock remained ice-free well inside the Alps during the Last Glacial Maximum (*ca*. 25-20 ky ago; LGM hereafter), as demonstrated by the continental-scale synthesis of paleo-glacier reconstruction and glacial landforms from Ehlers and Gibbard (2004). Geochronological analyses further confirmed that some Mont-Blanc rock surfaces have remained stable for most of the last glacial cycle, up to *ca*. 90ky ago (Gallach et al., 2020), long enough for substantial inter-population genetic divergences to occur.

But how can potential Pleistocene nunataks be geographically delimited within the Alps? As envisioned by Schönswetter et al. (2005), summits that were permanently isolated by Pleistocene glaciers occur within the permanent snowline. Also called "equilibrium-line altitude", this line is the average elevation that separates the accumulation zone from the ablation zone of glaciers. In the accumulation zone, glacier cover was permanent, whereas in the ablation zone, it fluctuated in thickness and extent due to inter-annual climatic variations (Braithwaite and Raper, 2009). Therefore, the geographic area of potential nunatak refugia, strictly defined as ice-free bedrock features that remained isolated throughout Pleistocene glacial periods, can be delimited by the elevation of LGM permanent snowline, since ice caps persisted longer (at least until the younger Dryas, *ca*. 12ka) above the permanent snowline. As a result, other rocky summits located below this snowline must then be defined as potential peripheral refugia. This second category also includes areas that, while possibly surrounded by persistent valley glaciers during glacial maxima, were more susceptible to dynamic reconnection with surrounding lowlands due to the temporal variability in ice coverage, as clearly demonstrated by recent paleogeomorphology modeling (Leger et al., 2025) (refer to Fig.1 for a geographic representation of classes of potential refugia).

Species' ecological preferences are key to resolving the question of Pleistocene alpine refugia. First, the thermal niche may be a major determinant of whether plant species survived on nunataks or peripheral refugia, as noted earlier by Dahl (1987) and recently demonstrated by Rota et al. (2024) on three South-Eastern alpine endemics. Indeed, species population dynamics may be differently affected by glacial-interglacial cycles according to their thermal tolerance because of paleo-glacier coverage decreasing towards higher elevations. Also, Brockmann-Jerosch and Brockmann-Jerosch (1926) clearly stated that the nunatak hypothesis might only concern "high-alpine specialists and not just any alpine plant" (as translated in Holderegger et al., 2011). Second, species' lithological affinities are a well-known driver of spatial ranges and genetic structure of alpine plants (Alvarez et al., 2009), and thus a potentially important driver of their distribution during glacial periods. Siliceous substrates indeed account for most of the potential nunatak refugia of the Alps (*e.g.*, Mont Blanc and Pennine Alps) while calcareous substrates are dominant in peripheral alpine massifs (*e.g.*, Chartreuse, Devoluy, Bernese and

Carnic Alps) — though some notable exceptions exist. Third, topography plays a key role in shaping refugia by creating microclimates that can shelter species during glacial periods (Niskanen et al., 2017). Most of the high-alpine flora is specialized in environments with a rugged topography because this corresponds to particular ecological conditions (shallow soil, microclimatic effects, steep faces, exposed rocky surface). Species like *Androsace alpina*, *A. argentea*, *Silene exscapa* or *Eritrichium nanum* seem to be highly dependent on rugged topography, as their local abundance sharply decreases as soon as topography flattens out (*personal observations*).

We may thus expect that siliceous-specialists of the nival vegetation belt are top candidates for nunatak survival in the Alps. This prediction has received partial support from past phylogeographic studies with for example *Androsace alpina* (Schönswetter and Schneeweiss, 2019), *Ranunculus glacialis* (Schönswetter et al., 2004), but also for some marginally limestone tolerant species as *Eritrichium nanum* (Stehlik, 2003; Stehlik et al., 2002). On the other hand, species with warmer thermal optima or greater tolerance to calcareous substrates may have found refugia in massifs at the periphery or outside the Alps. Empirical studies support this scenario for *Primula farinosa* (Theodoridis et al., 2016), *Campanula morettiana*, *Primula tyrolensis* (Rota et al., 2024) and some diploid population of *Biscutella laevigata* (Grünig et al., 2024). However, some silicicolous species such as *Phyteuma globulariifolium* show phylogeographic patterns consistent with peripheral rather than nunatak refugia, suggesting that substrate preference alone cannot fully predict glacial survival scenarios (Schönswetter et al., 2002). However, it remains to be tested whether nunatak survival can be considered a prevalent scenario for glacial plant refugia in the Alps.

We propose that using an approach of species distribution modeling and geographic range hindcasting into the LGM period could help to quantify the relative prevalence of alternative glacial refugia (Fig.1) for a large sample of species that are typical of nival vegetation in the Alps. Species Distribution Models (SDMs) indeed provide a powerful approach to reconstruct and analyze past species distributions by establishing statistical relationships between species' presence-absence data and environmental variables (Thuiller, 2024). By inferring the environmental conditions required for species distributions, SDMs offer an opportunity to test the suitability of nunataks as potential refugia for nival plants during the glacial periods, by modeling their distribution as function of climate, topography, bedrock and glacial coverage. Previous studies have successfully validated reconstructions based on SDMs, using fossil records and phylogeographic data, demonstrating their potential for studying past biogeographical scenarios (Alsos et al., 2009; Gavin et al., 2014). However, this approach relies on a core assumption that species' ecological niches have remained stable over time. In applying SDMs to past climates, we implicitly assume that the environmental conditions favoring a species' presence today were similarly favorable during the LGM.

In this study, we focused exclusively on the nival flora, which thrives in the coldest terrestrial environments (Dentant, 2018; Körner, 2011) and is thus most likely to have survived the highly adverse LGM-climate on nunataks. The nival flora is also highly diverse, with a high endemism rate and species of high patrimonial values (Boucher et al., 2021; Smyčka et al., 2017). For 69 nival plant species (see Methods section for species selection criteria), we constructed SDMs under contemporary conditions and projected them back to the LGM. We then compared predicted distributions, relative range contractions, and the suitability of the different refugia during the LGM and analyzed these results in relation to species' bedrock affinities. Finally, we identified major potential refugia regions for the nival flora of the Alps based on groups of species that were predicted to co-occur at the LGM.

Methods

Species selection, occurrence data and quality filtering

Our procedure of species selection was based on the exhaustive list of 4500 plant species occurring in the European Alps, as listed in *Flora Alpina* (Aeschimann et al., 2004). In order to select study species that are strictly associated with the nival vegetation belt, we used the codification provided by *Flora Alpina* to depict species abundances within each vegetation belt– 0 for absent, 1 for scarce, 2 for abundant. Although somewhat arbitrary and potentially debatable for some particular species, the use of this abundance code as a selection criterion remains convenient and homogeneous across the alpine flora, and also less prone to sampling biases than any other selection procedure. We thus selected species that are coded '0' for foothills and montane belts, '1' or '0' in the subalpine belt and '1' or '2' for the alpine and nival belt. This resulted in 80 candidate species. As an illustration of this procedure, we provide the abundance score distribution of the number of species from our selected pool as they are references in *Flora Alpina* for each vegetation belt (see Fig.S2).

We assigned each species to a class of lithological preference (*i.e.*, silicicolous, calcicolous or generalist) based on the data provided by *Flora Alpina* (Aeschimann et al., 2004), which describes whether species grow on siliceous soil, calcareous soil or both (*i.e.*, generalist).

However, since this source of information dates back to 2004, we made two modifications based on more recent findings. *Androsace pubescens* is calcicolous but was previously described as a substrate generalist, likely due to confusion with the then-unknown *A. delphinensis*, a silicicolous species. Similarly, *Eritrichium nanum*, although considered silicicolous in the Alps, grows predominantly on limestone in the Carpathians and in a small area of the south-eastern Alps, suggesting a broader substrate tolerance. (See Table S1 for a summary of all changes, see below for other changes.)

Ideally, species' lithological preferences would have been characterized using more detailed categories than those available here. However, to our knowledge, such fine-scale information does not exist for a dataset as extensive as the entire high-alpine flora. To ensure consistency across species and to avoid discrepancies in data quality, we opted to rely on a single, comprehensive literature source.

That said, lithological specificity was not entirely overlooked and is incorporated into species distribution models (see details below).

Most of the occurrence data were acquired through GBIF (Global Biodiversity Information Facility, (GBIF, 2024)), with additional occurrence data in the French Alps provided by the French Alpine National Botanical Conservatory (CBNA, see Thuiller et al. (2014)). As selected species were supposed to be specialists of high-elevation environments, we filtered out occurrence points that were located outside the so-called "alpine climatic zone", as defined by Paulsen and Körner (2014): minimum air temperature under 0.9 °C, growing season under 94 days and mean annual temperature under 6.4°C. All points falling outside this climatic zone were indeed considered erroneous, probably due to recorded occurrences in botanical gardens, misidentification or misplaced GPS points. We removed occurrence points recorded before 1990 to avoid those with a poor location accuracy, and to exclude populations that were in disequilibrium with their climatic environment or even potentially extinct. Finally, in order to retain sufficient modeling power, we discarded species for which we obtained fewer than 200 occurrence points.

We thus retained 69 study species with adequate data to build reliable SDMs (Table S2), and whose occurrence probability shows a steady increase towards higher elevations in the Alps. Due to our selection criteria, all study species are typical of high alpine nival environments, in particular rocky faces, scree slopes, moraines, and peri-glacial areas, where their ecological optimum is found, although some may occasionally occur in more vegetated environments. We used the reference taxonomy of Flora Alpina (Aeschimann et al., 2004) but have modified some species names according to more recent taxonomic revisions (see Table S1).

Geographic delimitation of potential glacial refugia

We represented and differentiated potential alpine refugia as defined by Holderegger and Thiel-Egenter (2009) using four layers of spatial data : (i) the reconstructed extent of LGM Alpine paleo-glaciers and ice-free summits Ehlers and Gibbard (2004); (ii) the LGM snowline (the same geographical delimitation as the one provided by Schönswetter et al. (2005)) which delimits Alpine massifs with longest ice coverage during Pleistocene glacial and lateglacial periods (except nunataks) within the Alps ; (iii) the biogeographical border of the Alps, as defined by the Alpine Convention (Permanent Secretariat of the Alpine Convention, 2009); and (iv) the climatic limits of the alpine zone (see above). Using these data, we mapped different potential refugia on a map with a 1km resolution, based on the following criteria (Fig.1):

- "nunataks": ice-free pixels within permanent glacier extent, *i.e.*, inside the reconstructed LGM glacier extent and the LGM snowline (*e.g.*, Écrins, Northern Pennines Alps, Hohe Tauern)
- "peripheral massifs": ice-free pixels outside the LGM snowline but within the biogeographical limits of the Alps (*e.g.*, Vercors, Monte-Viso range, Bergamasque Alps)

- "extra-alpine massif": ice-free pixels located outside the biogeographical limits of the Alps, but still matching the alpine zone climatic criterion (*e.g.*, Apennines, Vosges)
- "lowlands": all other ice-free pixels

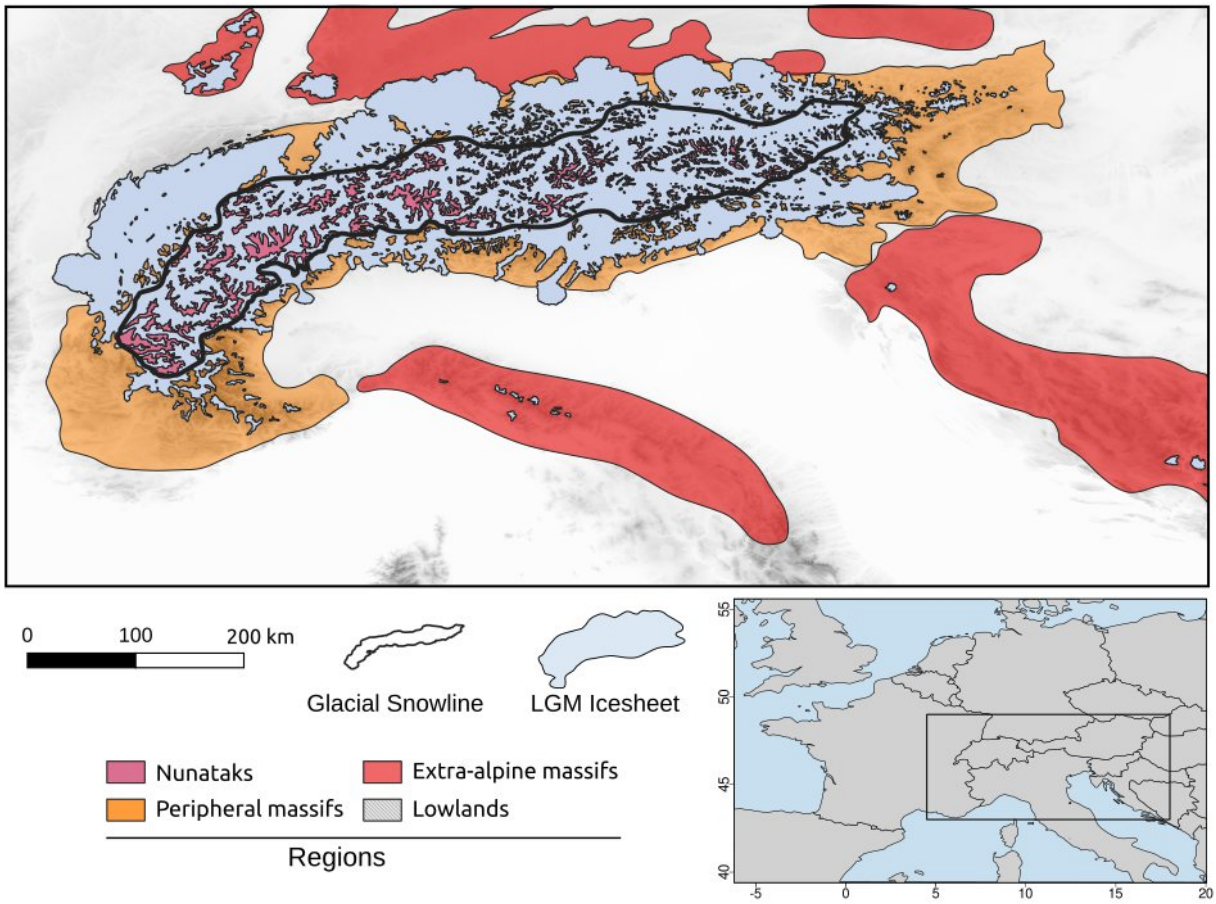

Fig.1 : Map of glaciated Alps during the LGM and location of potential glacial refugia in the modeling extent. Nunataks are high-elevation bedrock features that occur above the glacial snowline and thus remained ice-free and isolated during the LGM. Peripheral refugia are bedrock summits laying at the border of the Alps, and occurring below the snowline, thus with fluctuating glacier coverage affecting their degree of isolation throughout Pleistocene glacials. Extra-alpine refugia are mountainous areas which experienced an alpine climate during the LGM, but which are disconnected from the Alps. Lowland refugia are all other places around the Alps, that thus did not experience alpine climatic conditions during the LGM.
Background : DEM from Copernicus (2016) ; Coordinate reference system : WGS84

Species distribution models

Variable selection

Species niches were modeled as a function of three main components : climate, bedrock and topography. We used nineteen bioclimatic variables representing the current and LGM climates, which we downloaded from the CHELSA project (Karger et al., 2017), with a resolution of 30 arc seconds (≈ 1km). Bedrock types were integrated using spatial data provided by Hartmann and Moosdorf (2012), categorized into twelve classes based on the intersection of sedimentary, plutonic, metamorphic, and volcanic rocks with their mineralogical nature (carbonate or siliceous) and pH characteristics (this

variable is also referred to hereafter as "lithology"). Finally, we computed five topographic characteristics using a digital elevation model at 25m resolution (from Copernicus, 2016) : topographic roughness (topographic heterogeneity from the elevational range among a cell and its neighbors), terrain ruggedness index (absolute value of the average elevation difference between a cell and its neighbors), topographic position index (difference between a cell's elevation and the mean elevation of its neighbors, showing its position on a ridge or in a valley), slope, and aspect.

We reduced the dimension of this dataset by removing one of each pair of highly correlated variables (> 0.7), which resulted in a final set of eight variables: BIO1 (annual mean temperature), BIO3 (isothermality, *i.e.*, how large the day-to-night temperature oscillation is in comparison to the summer-to-winter oscillation), BIO4 (temperature Seasonality), BIO12 (annual precipitation), BIO15 (precipitation seasonality), topographic position index, terrain roughness, and lithology. All these variables were aggregated at a resolution of 1km for the following models.

We also used the LGM paleo-glacier reconstruction from (Ehlers and Gibbard, 2004) to filter out predicted occurrences at LGM (see below), as plant are unable to establish where ice dwells.

Modeling framework

We used the biomod2 R package (Thuiller et al., 2024) to model the distribution of each study species separately, and project their LGM potential distributions. Since different algorithms can lead to different species projections (Thuiller et al., 2019), we used an ensemble of seven state-of-the-art algorithms, namely: Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy (MAXENT), Random Forest (RF), and eXtreme Gradient Boosting Training (XGBOOST).

All these methods require presence and absence or pseudo-absence (a random subset of the available environmental conditions in the Alps) to be fitted against environmental data. For each species, we thus generated 10 sets of 1000 pseudo-absences, with an additional constrain that the pseudo-absence points were selected beyond a 1km radius around each occupied cell, as we considered they were likely other presences within the buffer. To balance presence and pseudo-absence, we added a specific weight to the model to obtain a weighted prevalence of 0.5 (*i.e.*, absences have the same weight as presences). Having 10 sets of pseudo-absence allows to account for the variation in model's fit that could happen from the random selection of pseudo-absence.

To assess the predictive accuracy of the models, we used a spatial block cross-validation procedure (Roberts et al., 2017), dividing the study area into five latitudinal bands of equal area. At each iteration, four of these blocks were used to train models, while the remaining block was used to evaluate their performances. The choice of such a spatial cross-validation aimed to account for the heavy bias of GBIF occurrence data toward the western Alps. By forcing a geographical separation between the training and

validation phases, the training and test datasets thus systematically include regions with contrasting occurrence densities, ensuring a more robust and generalizable evaluation of the models.

We used the Boyce index (Hirzel et al., 2006) as the evaluation metric, which ranges between-1 (systematic mismatch between predictions and presences) to 1 (perfect prediction). This index is particularly adapted to measure the performance of SDMs based on presence-only data. To account for the variation resulting from the cross-validation procedure, we repeated it 5 times for each algorithm and for each set of presence-pseudo-absence data. This finally led to 350 single predictions per species. These predictions were then filtered with the Boyce index to compute ensemble models.

Only models with a Boyce index score above 0.5 were combined using weighted mean and committee averaging (see below) to create ensemble models and hindcasts to the LGM. This large ensemble of predictions allows for a more comprehensive assessment of species distribution, accounting for both algorithmic diversity and sampling variability.

Models output analysis

Analysis of predicted patterns of LGM refugia

In order to evaluate species range predictions during the LGM, we reduced the dimension of prediction ensemble with two methods.

First, in order to keep the information on the uncertainty across the predictions, we used the committee averaging outputs from biomod2. The committee averaging works as follows: each continuous prediction between 0-1 from a given algorithm, set of pseudo-absence and cross-validation run, was transformed into a binary absence-presence using the threshold that maximized the Boyce index for the evaluation set of the cross-validation run. This threshold was determined individually for each combination of algorithm, pseudo-absence and cross-validation set, ensuring that the predicted presences closely match the observed occurrences (*i.e.*, the highest Boyce index possible). Then, all predictions were summed and divided by the number of retained predictions (the maximum being 350). The committee averaging score per pixel thus ranged from 0 to 1, with 0 reflecting that all predictions agree for species absence (highly certain), 1 that all predictions agree for species' presence (highly certain), 0.5 being half-half (highly uncertain). We then transformed these prediction values into binary values using a fixed threshold of 0.8 for every species. Hence, pixels with a value of 1 represent very high certainty of species presence (*i.e.*, at least 80% of predictions concur on this result). To further understand patterns of distributions and preferences of each species in previously delimited areas of potential refugia (Fig.1), we used these binary outputs to compute the relative percentages of predicted presence of each species into different refugia areas. To characterize the predicted dynamics of range contraction or expansion, we computed the size of the modeled geographic ranges of each species by summing the number of pixels (1km² size) of predicted occurrence, for both the current and LGM climates.

Second, as another way to summarize single projections, we applied the weighted mean method across all model predictions, for each species during the LGM according to their Boyce index score on the test set. This procedure assigns more weight to projections from best performing models under current conditions and ensures that final results are not influenced by under-performing models with erroneous predictions. This resulted in a suitability value for each pixel, reflecting the weighted average prediction of habitat suitability for each species within each pixel. We then calculated the mean suitability for each species within each potential refugium based on these weighted mean outputs, averaged across all pixels within each refugium type. To examine whether the mean LGM habitat suitability estimated across models for each pixel varied based on species' bedrock affinities (calcicolous, siliceous, generalists), refugia types (nunatak, peripheral, extra-alpine, and lowland refugia), and their interaction, we used a mixed-effect model and a Tukey post-hoc test. Species were included as random effects, while bedrock affinities and refugia types were treated as fixed effects.

Environmental influence on species range predictions

Quantifying the relative importance of environmental factors from SDMs is not a straightforward task. The common framework consists in permuting a selected variable X and comparing predictions with original variables with predictions made with original variables but the permuted X variable. The larger the difference, the more important the variable is to explain the prediction. However, this approach will be based on whole sets of presence and pseudo-absence data, which may exaggerate the importance of large-scale environmental factors which, in our case, include very large lowland areas in which no species were predicted. Therefore, results will only have highlighted bioclimatic variables that separate lowland areas from mountain areas (notably mean annual temperature) and outweighed all the others.

To avoid that issue, we instead re-trained a Random-Forest algorithm on the same data and used the Increase in Mean Squared Error (IncMSE) associated with randomizing each predictor. We restricted this analysis to pixels where at least one species was present, enabling us to identify precisely environmental factors that determine differences in distribution between species and not factors that cause all studied species to be predicted in mountainous regions.

Biogeographical patterns of species range predictions during the LGM

To identify groups of species that are predicted to have found refugia in the same areas during the LGM, we computed a dissimilarity matrix between all pairs of 69 study species, based on their predicted occurrences across the study grid cells, using Bray-Curtis dissimilarity index (Bray and Curtis, 1957). Then, we applied the Ward's minimum variance hierarchical clustering method (Ward Jr, 1963) to identify emerging groups of species that were predicted to co-occur at LGM, following the selection method proposed by Pang et al. (2023). The optimal number of clusters was identified using the Within-Cluster-Sum-of-Squares method. We visualized those dissimilarities and clusters using a Non-metric Multi-Dimensional Scaling (NMDS).

Because our aim was to identify main refugia areas for co-distributed groups of species during the LGM, we deliberately chose not to focus on analyzing overall species richness patterns. Instead, we focused on the computed clusters to better highlight zones where species shared refugia, which guided the following steps in our analysis.

To identify main refugia areas in and around the Alps, we calculated kernels ranges that contain 75% of the pixels in which 50%, 75% and 90% of the species in each cluster were predicted to be present at LGM. These kernel ranges thus represent areas of high species co-occurrence within each cluster (Fig.S3a and Fig.S3b) For each percentage threshold, we then computed the union of the kernel ranges across all clusters, allowing us to identify broader regions where a significant proportion of species are likely to have persisted during the LGM (see example in Fig.S3c). Each continuous area resulting from these unions was then classified into one of four categories of potential refugia: nunatak, peripheral, extra-alpine, or lowland (see example in Fig.S3d).

All data analyses were conducted using *R* (R Core Team, 2024) and R packages *biomod2* (v4.2-5) (Thuiller et al., 2024), *terra* (v1.8-5) (Hijmans, 2024), *vegan* (v2.6-8) (Oksanen et al., 2024), *randomForest* (v4.7-1.2) (Liaw and Wiener, 2002) and *adehabitatHR* (v0.4.22) (Calenge, 2024).

Results

SDMs evaluation

All individual combinations of algorithm, pseudo-absence set and cross-validation run revealed good performances under current environmental conditions, with Boyce index values ranging from 0.152 to 1. The evaluation of the ensemble predictions ranged between 0.117 and 1 for the committee averaging algorithm and between 0.593 and 1 for the weighted mean algorithm (Fig.S4 and S5). Predictions into LGM climate showed suitable regions for each species that mainly overlap with areas included in current distributions.

Predicted patterns of species LGM refugia

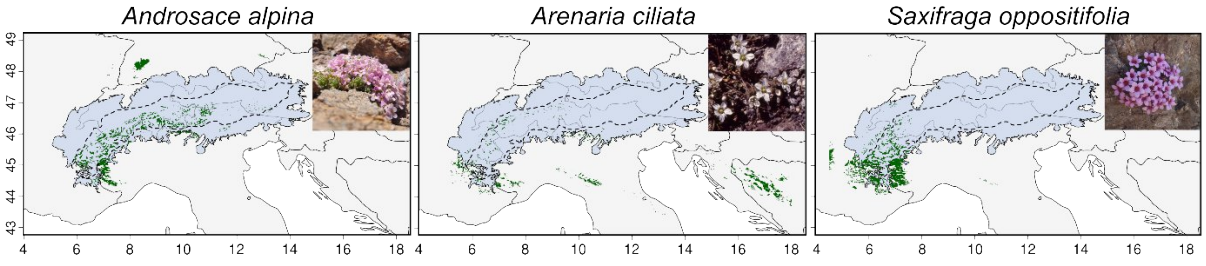

Fig.2: Examples of the projected distribution of *Androsace alpina* (silicicolous), *Arenaria ciliata* (calcicolous) and *Saxifraga oppositifolia* (generalist) during the LGM (green pixels). Solid black lines represent the countries' current administrative borders, light blue polygon represents the extent of the LGM ice extent, and the dashed line represents the delimitation of LGM snowline. Picture credits: *Androsace alpina* and *Saxifraga oppositifolia*: personal database ; *Arenaria ciliata*: TelaBotanica (see https://www.tela-botanica.org/bdtfx-nn-6166-synthese). *C*oordinate reference system *: WGS84*

SDMs predicted that all modeled species were able to occupy nunataks during the LGM, at least marginally (Fig.2 and Fig.3a). Out of the 69 studied species, nunataks could have represented more than 25% of the predicted LGM range for 59 species during the LGM, and more than 50% of their predicted LGM range for 48 of them. The remaining species were mainly predicted to be in peripheral massifs, extra-alpine massifs (especially the Vosges and the Apennines) or northern lowlands.

We found a significant association between species' bedrock affinities and the main location of their predicted LGM refugia. Indeed, silicicolous plants were predicted to survive mainly on nunataks during the LGM (mixed-effect model and Tukey post-hoc : p.value<<0.001), whereas calcicolous and generalist species were predicted to be mainly present on peripheral massifs, and with a more balanced distribution between the different types of refugia (mixed-effect model and Tukey post-hoc, calcicolous : p.value<<0.001, generalists : p.value<<0.001).

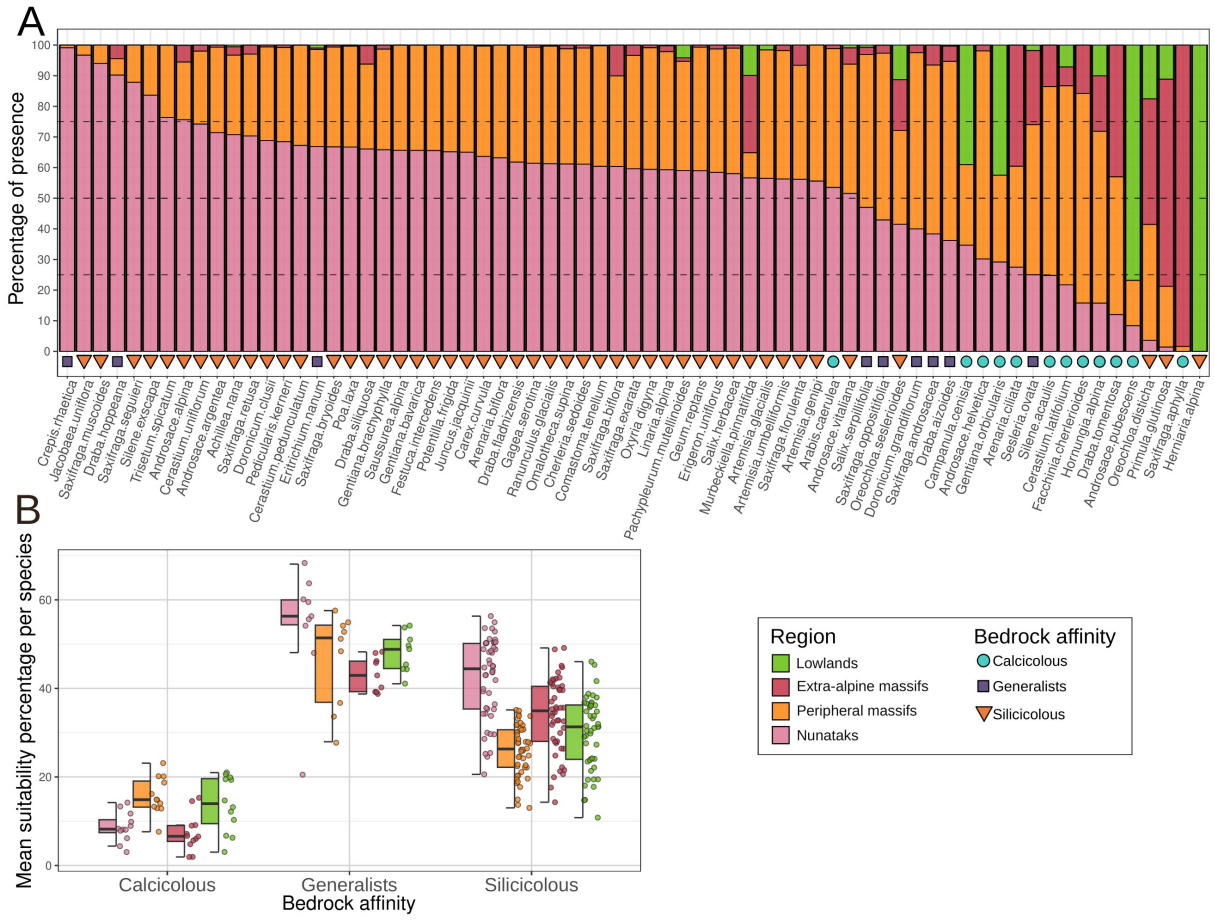

Fig.3: Relative prevalence of predicted types of refugia during the LGM for the 69 study species : **a** Percentage of presence of modeled species in different potential types of refugia during the LGM ; **b** Mean suitability of each modeled species in different potential types of refugia, grouped by bedrock affinity

In addition to a predicted distribution predominantly centered on nunataks, silicicolous species also showed a significantly higher probability of occurrence on nunataks compared to lowlands, peripheral and extra-alpine massifs (mixed-effect model and Tukey post-hoc : p.values<<0.001).

Conversely, calcicolous species appear to have a slightly significantly lower probability of occurrence on nunataks than in peripheral massifs or lowlands (mixed-effect model and Tukey post-hoc : respectively p.value= 0.0064 and p.value=0.0726) but similar with extra-alpine massifs (mixed-effect model and Tukey post-hoc : p.value=0.9328) (Fig.3b).

Predicted range contractions during the LGM were compared for calcicolous, generalist and silicicolous species (Fig.4). The largest range contractions during the LGM were observed for calcicolous and generalist species (respectively with a mean decrease of -71.6% ± 14.8 and -61.3% ± 17.8). Conversely, silicicolous species were predicted to have much more stable range sizes between the current and LGM climate (with a mean decrease of -46.2% ± 70.5).

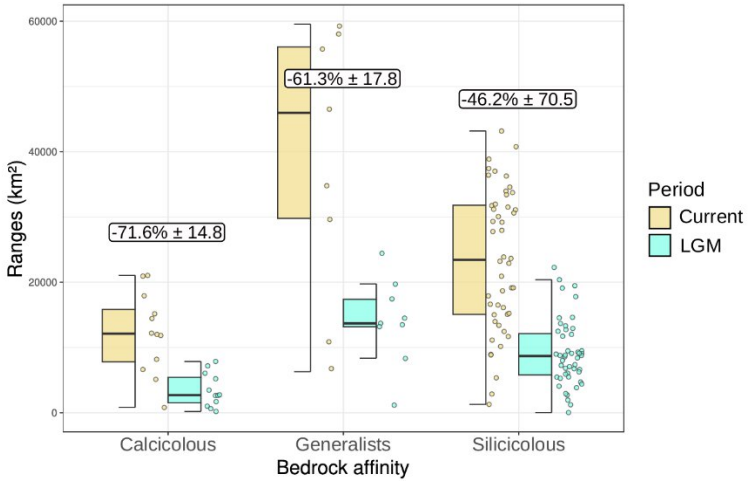

Fig.4: Comparison of predicted range sizes under current and LGM conditions for calcicolous, generalist, and silicicolous species. Numbers indicate the mean change in range size across all species within each bedrock affinity.

Environmental influence on species range predictions

The variable importance analysis showed how different environmental factors influenced the predicted distributions of species at the LGM in relation to their bedrock affinities (Fig.5). For silicicolous species, the most influential factors were lithology and the topographic roughness, followed by annual mean temperature. For calcicolous plants, environmental variables were less important overall, and the most influential factors were annual mean temperature and isothermality. For generalist species, the two most influential factors were also annual mean temperature and isothermality, and variables are more important overall.

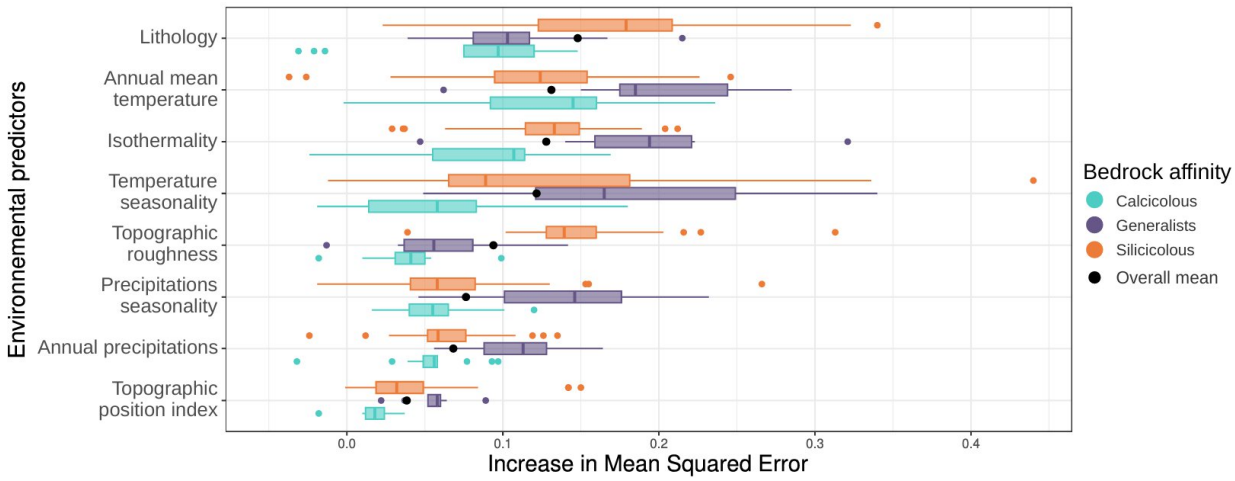

Fig.5: Relative importance of predictors in species distribution models during the LGM, computed using Random Forest and assessed by the increase in mean squared error (IncMSE) after permuting each variable, for each bedrock affinity group. Higher values indicate greater importance.

Biogeographical patterns of species range predictions at the LGM

Seven distinct clusters of species were identified (Fig.6) representing unique groups of species predicted to have had similar distributions during the LGM. Species were clustered together mainly as a function of their bedrock affinity and, to a lesser extent, depending on their ecological preferences, as shown above (see Fig.S6 for the predicted distributions of each cluster).

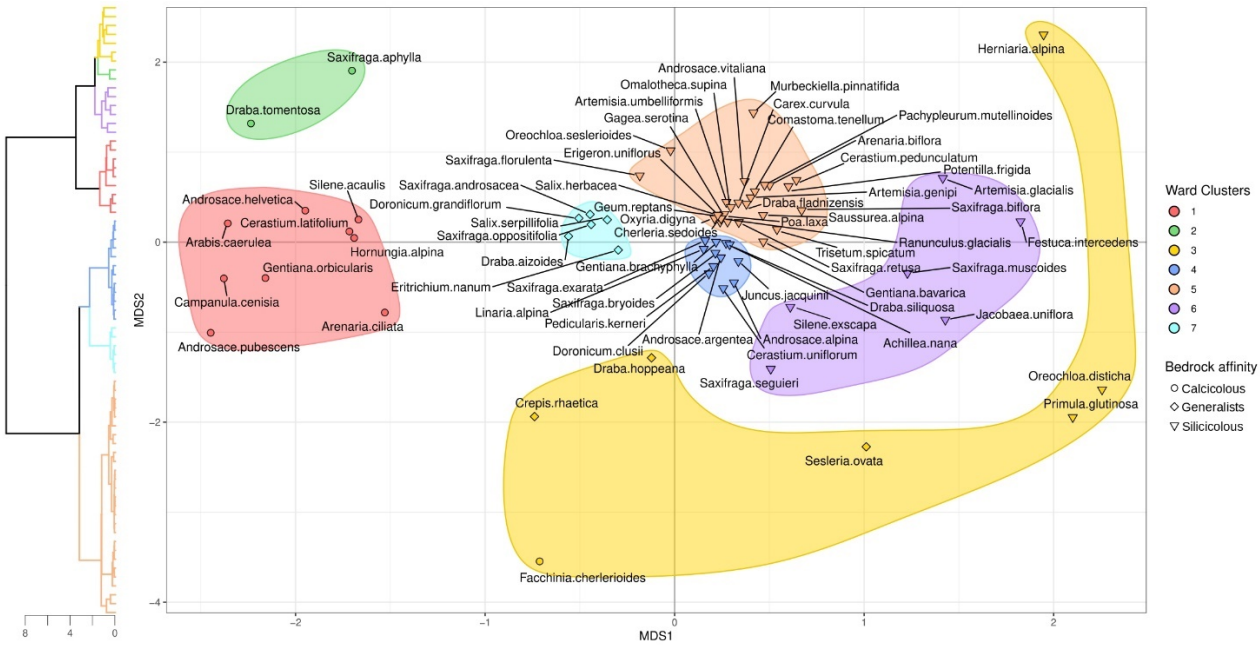

Fig.6: Non-metric multidimensional scaling of modeled species co-occurrences during the LGM, based on Bray-Curtis distance. Clusters were identified using Ward's minimum variance hierarchical clustering method, with the optimal number determined with the "within sum of squares" analysis.

Clusters 1 and 2 were composed exclusively of calcicolous species. The first cluster (with *Androsace helvetica*, *Arenaria ciliata*, or *Silene acaulis*) is predicted to be located in peripheral massifs

and nunataks of south-western Alps, but also marginally in the Carpathians and north-western extra-alpine massifs. The second cluster (with *Draba tomentosa* and *Saxifraga aphylla*) is almost exclusively predicted to be located in northern Apennines.

Cluster 3 groups mainly silicicolous species (like *Primula glutinosa* or *Herniaria alpina*) but not exclusively (like the calcicolous *Facchinia cherlerioides* or the generalist *Crepis rhaetica*). Some of these species are predicted to be scattered around nunataks, but the core of their distribution is predicted to be concentrated around eastern peripheral massifs, as well as in the north-eastern extra-alpine massifs.

Clusters 4, 5, and 6 consisted exclusively of silicicolous species and seem to have occupied the Nunataks to a greater or lesser extent, particularly in the western Alps. The fourth cluster (with species such as *Achillea nana*, *Saxifraga bryoides* or *Androsace argentea*) was especially found in nunataks of western Alps and central Switzerland, but also in peripheral massifs in the south of Piemont. The fifth cluster (with *Androsace vitaliana*, *Poa laxa*, *Saussurea alpina* or *Saxifraga biflora*) is predicted to have a quite similar distribution to the fourth, but very densely clustered and centered solely on the western Alps and restricted to the Aosta Valley and the Mont Blanc massif in the north. Cluster six (with *Artemisia glacialis* or *Silene exscapa*) is way less densely distributed and centered only on Nunataks, from the Western Alps to mideastern Switzerland.

Finally, the seventh cluster (with *Salix serpyllifolia*, *Eritrichium nanum* and *Saxifraga oppositifolia*) brought together, in a single group, almost all generalist species which are predicted to be concentrated in the Western Alps, in peripheral massifs on both side of the Alpine chain and in nunataks, but also marginally in northern Apennines and northeastern peripheral massifs.

Map of potential LGM refugia

The seven clusters of species predicted to co-occur during the LGM (Fig.6) were used to define and map potential refugia areas across the Alps. We used locations of clusters and the distribution of their species richness to define a map providing an overview of potential alpine refugia for the nival flora during the LGM (Fig.7). This map highlights 9 distinct refugia areas, each characterized by a somehow distinct community, influenced by the abiotic conditions. Table 1 details the identified regions and their associated massifs, as well as the corresponding species clusters described in Fig.6.

The western nunataks (region I) and the central nunataks (region II) proved to be significant refugia for many species. On the other hand, the eastern nunataks (region III) emerged less clearly, as only a really restricted area within this region was predicted to contain more than 90% of the species from its respective cluster. Peripheral massifs also emerged to be refugia areas, with extensive favorable zone for nival plants from western to eastern peripheral massifs (region IV, V & VII). We found evidence for some probable extra-alpine refugia for nival flora on small regions in northern Apennines, in the Vosgian and Black Forest regions and South Bohemian massifs.

ID	Refugia	Massifs	Associated clusters	Literature support
I	Western nunataks	Écrins, Belledonne, Vanoise, Gran Paradisio and Mt-Blanc	4,5,6,7	Bettin et al., (2007); Schönswetter et al., (2003)
II	Central nunataks	Valais, Bernese, Northern Lepontine, Uri and Glarus Alps	4,6	(Escobar García et al., 2012; Kosinski et al., 2019; Parisod and Besnard, 2007; Schönswetter et al., 2003; Schönswetter and Schneeweiss, 2019; Stehlik et al., 2002)
III	Eastern nunataks	Hohe Tauern and Radstadt Tauern	3	Pan et al., (2019); Schönswetter and Schneeweiss, (2019)
IV	Southern Alps, Western peripheral massifs	Chartreuse, Vercors, Devoluy, Diois and Baronnies	1,7, (2)	Parisod and Besnard, (2007); Schönswetter et al., (2005)
V	Southern Alps, eastern peripheral massifs	Mercantour, Argentera, Monte-Viso range, Val Troncea, external Gran Paradisio	4,5,6,7	Kosinski et al., (2019); Schönswetter et al., (2005)
VI	Eastern Alps peripheral massifs	Radstadt Tauern, Gurktal, Lavanttal, Ennstal and Styrian Alps	3	Pan et al., (2020); Schönswetter et al., (2005)
VII	Northwestern extra-alpine massifs	Vosgian and Black Forest regions	1,4	Grünig et al., (2024)
VIII	Northeastern extra-alpine massifs	South Bohemian massif	3	Záveská et al., (2021); Voisin et al. (in prep)
IX	Southern extra-alpine massif	Northern Apennines	2	None

Table 1: Description of potential refugia illustrated in Fig.7 with massifs included in these potential refugia, associated clusters and phylogeographical support from the literature. Cluster number in brackets indicates that the species cluster in question was only present in this area during the first 50% species-richness filter.

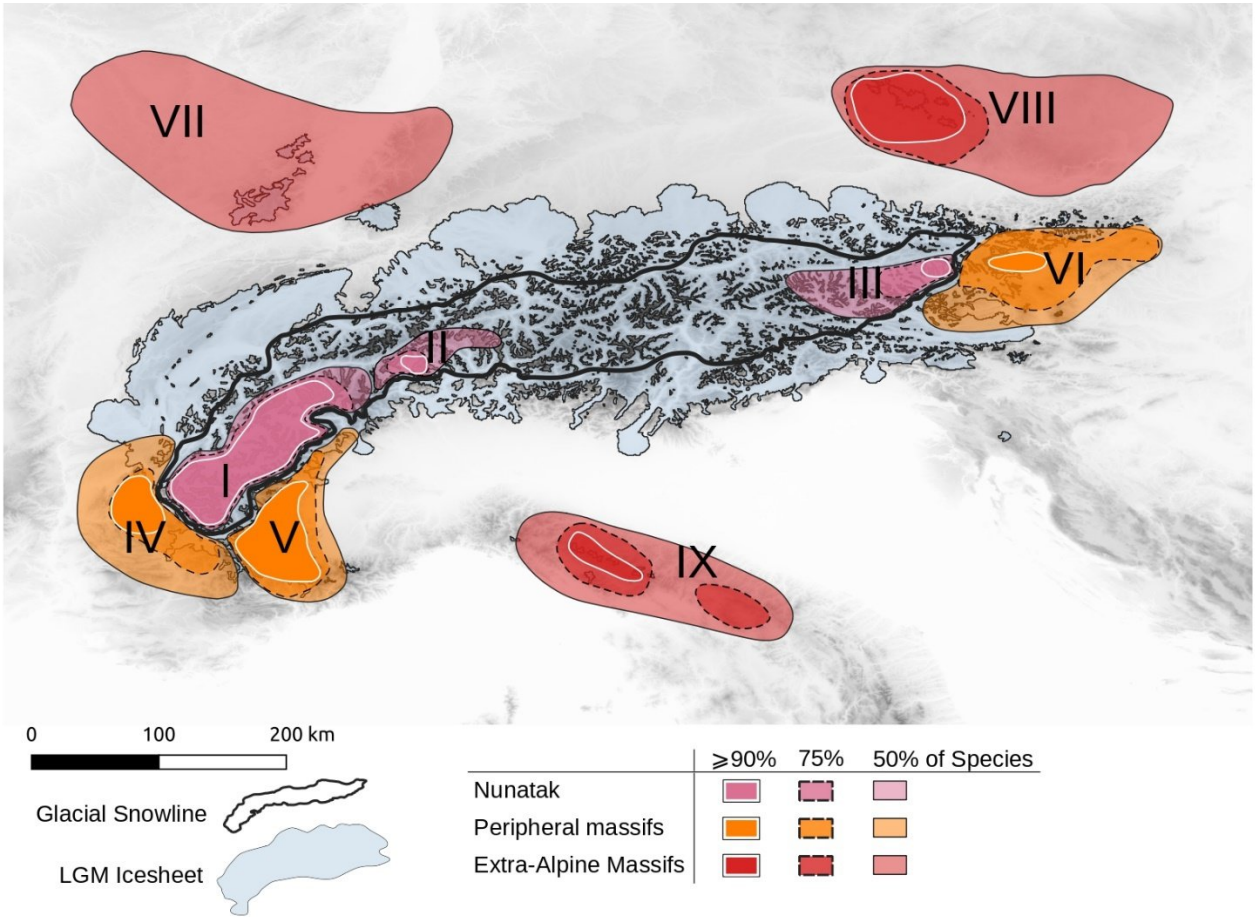

Fig.7: Spatial delineation of different potential refugia for the nival flora of the Alps during the LGM. These areas were calculated as unions of the core areas containing 50%, 75% and 90% of the species identified in the respective clusters of species predicted to co-occur during the LGM. The white lines thus delimit geographical areas that are the most likely to be refugia, according to a 90% majority rule within clusters of co-occurring species.
Background : DEM from Copernicus (2016) ; Coordinate reference system : WGS84

Discussion

In this study, we applied species distribution models to 69 nival plant species to predict their potential spatial distribution during the LGM and assess whether nunatak refugia can reasonably be considered a prevalent scenario of glacial survival for the nival flora in the Alps. The retrieved spatial patterns of high-alpine plants pinpoint contrasted glacial histories, largely influenced by each species' ecological preferences.

Our findings indicate that nunataks likely served as main refugia for two thirds of the cold-adapted species of the nival belt and for almost all of the silicicolous species thriving in these environments. Additionally, our results highlight a clear differentiation in potential LGM-refugia, with distinct predicted species assemblages during the LGM, shaped by species' climatic, lithological, and topographical preferences. This study further underscores the potential influence of these refugia on the structure of alpine biodiversity, emphasizing the glacial legacy that has shaped the present-day nival flora.

Species' niche requirements and patterns of glacial refugia

While 69% of study species are mainly predicted to have found refugia on alpine nunataks (*i.e.*, more than 50% of their predicted range), 15% were likely located in peripheral massifs, and the remaining species are predicted to have mostly passed the last glacial period predominantly outside the Alps, at least for a significant proportion of their populations. Ecological preferences played a central role in shaping the glacial histories and distribution patterns of different species groups. Bedrock lithologies, a key factor structuring genetic landscapes, as previously described by Alvarez et al. (2009), emerges as a pivotal determinant of species' histories and responses to glacial periods (Parisod, 2022).

For silicicolous species, nunataks played a predominant role in survival during the LGM. These habitats were not only places where silicicolous species were most frequently predicted to persist (Fig.3a), but they also provided significantly more favorable conditions for their survival compared to other refugia type (*i.e.*, a consistently greater probability of occurrence) (Fig.3b). Additionally, the extent of suitable habitats for silicicolous species has declined much less than for other species over time (Fig.4). This stability is closely linked to their ecological preferences for high-elevation environments (*e.g.*, rugged environments, as shown in Fig.5), which nunataks uniquely provide. The importance of terrain roughness for silicicolous species (Fig.5) also suggests that their reliance on nunataks was not solely due to the availability of siliceous bedrock. Instead, the overall environment, including the steep and topographically rugged nature of nunataks at high elevations, more precisely defines the spatial contours of the niche of these cliff-dwelling plants, as also shown by Chauvier et al. (2021). Hence, even if the availability of siliceous rocks may lead to the expectation of the prevalence of nunataks as refugia for silicicolous plants, our findings indicate that both lithology and topographical features jointly shaped their glacial survival patterns.

In contrast, calcicolous species exhibited distinct patterns of potential refugia. During the LGM, these species were predominantly predicted to have found refugia outside the inner Alps, because nunataks were mainly siliceous and, thus, not suitable for calcicolous species. Instead, they likely persisted in peripherals massifs, lowlands or extra-alpine massifs, depending on their ecological preferences (Fig.3a). This pattern aligns with the extensive glacial coverage of calcareous massifs, often located at lower elevations and with a less rugged topography (Van Der Beek & Bourbon, 2008), which favors snow accumulation and glacier development (Ehlers and Gibbard, 2008; Ivy-Ochs, 2015) resulting in a reduction of over 70% in the suitable area available for calcicolous species during the LGM (Fig.4). These species displayed lower sensitivity to environmental variables, with annual mean temperature and isothermality emerging as the most influential ones (Fig.5). These findings emphasize the diversity of environments represented by peripheral refugia and the climatic differences, particularly the contrast in isothermality patterns between the eastern and western Alps (temperature differences are

greater in the western Alps), further highlights the role of these regions in sheltering a distinctive diversity of calcicolous species during glacial periods (Fig.S7).

Generalist species show a pattern similar to what is seen with calcicolous ones. Their suitable range is predicted to have drastically decreased during the LGM but remain relatively high, because of their ability to thrive in siliceous areas of the inner Alps (*i.e.*, nunataks). Their distribution patterns are somehow diverse (Fig.3a), with some being predicted to be exclusively on nunataks (*e.g.*, *Eritrichium nanum*), and others mainly in peripheral massifs (*e.g.*, *Sesleria ovata*) which provided less extreme conditions than nunataks. This suggests that only plants with highly specific ecological requirements were compelled to find refugia on nunataks. While nunataks may have acted as last-resort refugia for most of silicicolous species, generalists benefited from a broader range of refugia in peripheral regions, facilitating persistence during ice ages. For these species, the most important environmental factors were the ones related to temperatures and precipitations, rather than bedrock types of topography. This highlights their dependence on "alpine" climatic conditions rather than a specific location, lithological or geographical constraints (Körner, 2021). Similar ecological variables have been identified as segregating factors for the paleo-demography and past distributions of alpine plants (Kropf et al., 2003; Rota et al., 2024).

Locating major glacial refugia across the Alps

The map produced by our analyses reflects a consensus of predicted species ranges during the LGM, built upon the diversity of methodological choices and the diversity of species range dynamics, mitigating methodological biases through two key strategies. First, we employed an ensemble hindcasting approach, integrating predictions from different algorithms, pseudo-absence sets and spatial split-sampling runs to account for varying algorithmic sensitivities, stochastic effects, spatial heterogeneity and, therefore, ensure robustness. Indeed, it has been repeatedly shown that when projected into future or past environmental conditions, models with similar predictive ability under current conditions could strongly diverge (Thuiller, 2004; Thuiller et al., 2019), and this could depend in the used algorithm, sampling strategy or data inputs (Araujo and New, 2006). To adopt a highly conservative approach, we combined individual predictions using committee averaging. A presence was considered valid only if at least 80% of the 350 initial predictions agreed on it at a given location (*i.e.*, scores above 0.8); otherwise, it was classified as a predicted absence. Second, to delineate geographic areas that acted as potential glacial refugia, we identified clusters of co-occurring species during the LGM. This led to the delineation of nine potential refugia regions that show how the nival flora was potentially distributed across the Alps and its surroundings during the LGM.

Beyond broad distinctions among calcicolous, silicicolous and generalist species, responses to glacial conditions were not uniform within these three categories (Fig.6). Our results reveal varying co-occurrence patterns in peripheral and extra-alpine massifs and three distinct distribution responses for

nunatak-centered species: one group occupying alpine nunataks from south-western to mid-eastern Switzerland, one centered on western Nunataks, and a third primarily distributed in eastern nunataks and peripheral massif (respectively clusters 4, 6 and 3, see Fig.7 & Table 1). These differences likely stem from environmental segregation, historical isolation and dispersal barriers, highlighting group-specific responses to Alpine glaciations.

Our results bring complementary findings to those of Schönswetter et al. (2005). First, Schönswetter et al. (2005) demonstrated the importance of southeastern, southern central and southwestern peripheral massifs refugia for species such as *Androsace alpina*, *A. wulfeniana*, *Ranunculus glaci*alis, *Phyteuma globulariifolium* or *Eritrichium nanum*, which aligns with parts of our results (region V in Fig.7). Moreover, we detected an additional potential refugium in the South Bohemian massifs (VIII). A little further north, Záveská et al. (2021) and Voisin et al. (in prep) uncovered refugia for species like *Helleborus niger*, *Aposeris foetida*, and *Cardamine trifolia* in the major beech limestone forest refugia. Although these habitats differ from those we focus on in our study, their findings echo our own in suggesting that this broader region may have played a significant role in glacial persistence and post-LGM exchanges with the Alps. Second, Schönswetter et al. (2005) provided little evidence for nunataks survival, and proposed only two nunataks areas, which correspond to what we described as the LGM biodiversity hotspot on central nunataks refugia (region II). In addition, we provide strong support for the presence of a newly recognized, extensive nunataks refugia area in the western Alps, spanning from the Mont-Blanc massif, down to the Écrins range.

The observed divergence in community compositions between western and eastern refugia, even under similar lithological settings, can be attributed to climatic differences. Despite some variability, climatic variables consistently emerged as the most important predictors of LGM plant distributions, following lithology (Fig.5). The western Alps were generally drier and colder than the eastern Alps, a contrast that was even more pronounced in nunatak refugia. Indeed, western nunataks, situated at higher elevations, experienced colder temperatures than their eastern counterparts during the LGM. Conversely, peripheral massifs exhibited the opposite trend: colder conditions were predominantly found in the eastern Alps (see Fig.S7). In addition, the steep elevation gradients of this region constrained the availability of suitable habitats between glaciated zones and lower-elevation regions lacking “high alpine” climatic and topographic conditions, thus shaping rather restricted and climatically different refugia. These findings underscore the combined influence of topography, lithology, and climate (particularly the latter two) in shaping the spatial and ecological characteristics of Pleistocene refugia in the Alps.

Schönswetter et al. (2005) identified northern peripheral refugia in eastern and central Switzerland and southern Germany for *Erinus alpinus* and *Rumex nivalis*. However, as these refugia were described for lower-elevation species, we found no evidence of glacial refugia in these regions for the nival flora.

Rota et al. (2024), using advanced molecular and computational techniques, confirmed the existence of nunatak refugia in the Dolomites, where we did not detect any major convergent patterns. Differences in communities found in refugia between the northern and southern edges of the Alps can be attributed to climatic variations and the availability of ice-free areas (Kadereit, 2024). The southern Alps, being considerably warmer (Karger et al., 2017), provided more favorable refugia conditions, whereas ice-free areas were almost absent in the mountainous part of the northern Alps.

Two extra-alpine massifs (Vosges and Apennines) were predicted to have harbored a few high-alpine species during the LGM, such as *Achillea nana* and *Androsace pubescens* in the Vosges and *Salix serpyllifolia*, *Saxifraga aphylla* or *Silene acaulis* in the Apennines. The Vosges massifs might have serve as glacial refugia for alpine species such as *Biscutella laevigata* (Grünig et al., 2024) and the presence of animal glacial relicts, such as the *Trichoptera Rhyacophila aquitanica* has already underlined the seemingly close biogeographical relationships with the Alps (Schmitt, 2009). Few studies have examined the relationship between the Alps and the Apennines during glaciations, but the presence of *Jacobaea incana*, *Ranunculus kuepferi*, *Carex foetida* and *Rhododendron ferrugineum* or the Common frog *Rana temporaria* in the Italian Peninsula supports our modeling outputs, albeit without explicit phylogeographic scenarios (Gentili et al., 2015; Stefani et al., 2012).

Limitations and perspectives

One of the key challenges in this study lies in the constraints imposed by the scale of the available data. The reconstructed LGM alpine paleo-glaciers and ice-free summits (Ehlers and Gibbard, 2004), which were essential for identifying potential refugia, were only available at a 1km resolution. While appropriate for large-scale analyses, this resolution may have been insufficient to capture finer-scale refugia relevant to species or group-specific niches. However, this resolution is certainly enough to capture rather large, contiguous refugia area that are the most likely to have allowed long-term population persistence over the course of the Quaternary period.

Another limitation applies to the attribution of bedrock affinity to species. We used the scale available in *Flora Alpina* which only describes whether a species grows on siliceous, calcareous bedrocks, or both. While certainly improvable for some species, *Flora Alpina* represents a consensual and unbiased source of data. Though, we were unable to investigate species responses at finer lithological scales but only at those three coarse levels of distinction. It is also important to mention that assigning lithological affinity to species is not always a trivial task, so we had to make compromises. For example, *Eritrichium nanum* is almost exclusively silicicolous in the Alps but grows mainly on limestone in the Carpathians and in a rather restricted region of the south-eastern Alps. We therefore classified it as generalist. Moreover, *Androsace helvetica*, though typically calcicolous, has been observed a few times on siliceous rocks in the Aiguilles Rouges massif.

Due to the large taxonomic focus of our study, we were not able to account for recently discovered or suspected edaphic vicariants but our study thus provides an interesting complement to phylogeographic studies focused on single species that examine how intraspecific lineages may have undergone contrasting quaternary histories, due to different bedrock affinities — a question that should for instance be investigated on Alpine and Carpathians populations of *Eritrichium nanum*.

Some concerns may be raised regarding the occurrence data we used in this study. First, the exclusion of occurrence data predating 1990 was primarily driven by the need to use occurrence data with sufficient location accuracy. While we are aware of the potential inertia of alpine flora in the face of climate change (Vitasse et al., 2021), we felt it necessary to minimize spatial uncertainties and focus on populations that are likely in equilibrium with recent climate conditions. Second, those same occurrence data from GBIF come with a significant spatial bias, particularly the over-representation of the western Alps compared to central and eastern regions. To account for this bias — including potential inflation of model performance due to sampling bias and spatial autocorrelation — we adjusted our modeling strategy. We implemented a spatial block cross-validation procedure (as described by Roberts et al. (2017)), dividing the study area into five latitudinal bands of equal area. This approach ensures a clearer spatial separation between training and testing datasets, thus improving the robustness and generalizable model evaluations, despite the uneven data distribution.

The Alps may offer a limited possibility for disentangling the geographic position of nunataks from their geological composition, as inner massifs are predominantly siliceous. As stated in the introduction, we indeed expected that species predominantly growing on siliceous bedrocks should be top candidates for nunatak survival. However, our analyses showed that this expectation was, by no means, straightforward. Nunataks, when defined as mountain peaks that have been permanently surrounded by glaciers during the Pleistocene, are indeed predominantly siliceous (*e.g.*, Mont-Blanc massif, Bernina range) but some notable exceptions of sedimentary nunataks do exist (*e.g.*, Northern Dolomites and parts of the Engadine). Conversely, peripheral massifs tend to generally be sedimentary, though some peripheral massifs such as in Northern Italy are siliceous (*e.g.*, Bergamasque Alps). Interestingly, none of these sedimentary nunataks and peripheral siliceous massifs were predicted as important LGM refugia. The reason for these results is that bedrock was not only the important landscape feature to determine refugia locations, but topographic roughness was also a decisive factor, as demonstrated by our sensitivity analyses. It is possible that areas of low topographic roughness were in fact impacted by glaciers that were not captured by the LGM glacier reconstruction used in this study. This calls for finer reconstructions of quaternary glacier activity using geochronological analyses, particularly on sedimentary and siliceous peripheral massifs.

Conclusion : insights into the legacy of glacial survival

Multiple ice ages, including the LGM, profoundly shaped the distribution and the micro and macroevolutionary trajectory of high-elevation plants. We found that high-alpine silicicolous species occupy a niche that has remained relatively stable over time, which might explain why most silicicolous nival-belt endemics are widespread across the Alps (*e.g.*, *Androsace alpina*). Conversely, many endemic calcicolous species are quite range-restricted and exhibit isolated evolutionary lineages, particularly at both western, eastern and along the southern edge of the Alps (*e.g.*, *Facchinia cherlerioides* subsp. *aretioides*, *Noccaea minima*, *Androsace hausmanii*, *Potentilla nitida*, *Phyteuma villarsii*, *Physoplexis comosa*) (Kadereit, 2024; Parisod, 2022; Smyčka et al., 2017).

These contrasting patterns underscore how bedrock affinity is deeply intertwined with evolutionary history (*e.g.*, Alvarez et al., 2009). Here, it is both a cause and consequence of glacial refugia.

Indeed, nunataks might also have been trigger-elements for genetic divergence, fostering allopatric speciation. Functioning as island-like systems (Marx et al., 2017), some cliff-dwelling populations became isolated during glacial cycles, leading to the emergence of isolated evolutionary lineage that became new endemic species (*i.e.*, refugial endemics according to Kadereit (2024)). Early studies have highlighted the role of nunataks in preserving glacial relict species and driving speciation, where isolated populations gave rise to distinct endemic taxa. Merxmüller (1952), for example, suggested that many species pairs (*e.g.*, *Achillea clavennae* and *A. nana*, *Androsace chamaejasme* and *A. villosa*, etc...), likely originated through allopatric divergence on nunataks. Several floristically rich regions, including ranges of Monte Rosa and the valleys of Visp, the upper Engadine, or the Bernina range were also earlier identified as potential nunatak refugia areas by Brockmann-Jerosch & Brockmann-Jerosch (1926) and summarised by Stehlik (2000) — a hypothesis later confirmed by more recent research.

For instance, the late Pleistocene divergence of the two cryptic silicicolous sister-species *Androsace saussurei* (endemic to Mont-Blanc, Valais, and Gran-Paradiso) and *A. delphinensis* (endemic to the Écrins) indeed provides support for the nunatak hypothesis. It suggests that divergence and speciation of populations occurred on the scale of the last interglacial and is supported by the fact that these species (i) frequently grow on cliffs at high altitudes above glaciers today, and that (ii) these locations may have been favorable to their existence during the coldest periods of the Pleistocene. Additionally, these species originated from a split with the calcicolous *A. pubescens*, widespread in the western Alps, suggesting a shift in bedrock affinity as a consequence of glacial isolation and a potential driver of speciation during these periods (Boucher et al., 2021).

By shedding light on how speciation may have unfolded in glacial refugia, this case study emerges as a valuable model for interpreting evolutionary dynamics in alpine environments. More broadly, it offers a compelling perspective on how the legacy of Pleistocene glaciations continues to shape the evolutionary and biogeographical patterns of mountain floras.

Thus, nunataks have served as both biodiversity museums, preserving ancient lineages, and cradles for newly emerging high-alpine-adapted biodiversity. These dynamics explain how ice ages shaped the high alpine environment as one of Europe's most biologically rich and unique regions (Aeschimann et al., 2011; Parisod, 2022).

Supplementary materials

Supplementary data associated with this article can be found, in the online version, at https://link.springer.com/article/10.1007/s00035-025-00334-2.

Declarations

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contribution

ZR, SL and WT conceived the theoretical framework of this study. HB and MG helped set up and improve models. JR provided species occurrence data. BF, PGV and SI took part in the reflection and interpretation of results. ZR carried out the modeling, statistical analysis and wrote the manuscript. SL obtained the funding. All authors read and commented on the preliminary versions, contributed to and approved the final version of the manuscript.

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Data availability statement

Open-source data used in this paper are available online on GBIF and CHELSA websites.

Research involving human and/or animals and informed consent

Not applicable

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Supplementary materials

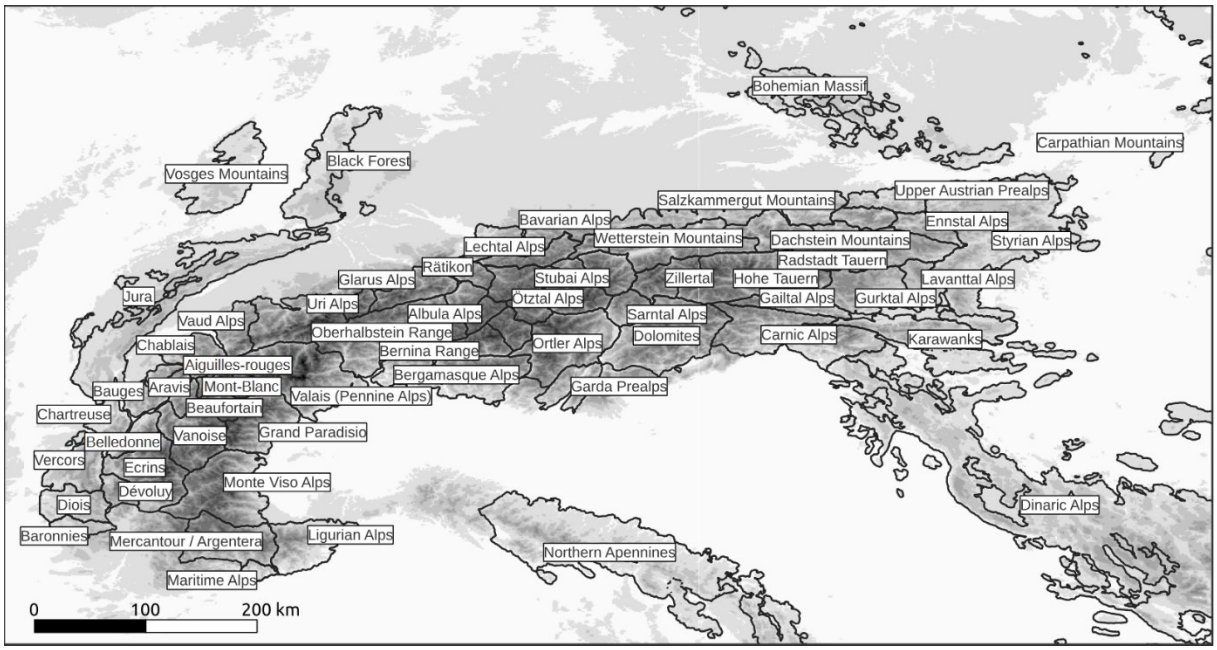

Fig.S1: Location of Alpine and extra-Alpine massifs and main localities discussed in the text. Massif boundaries are from the GMBA Mountain Inventory from Snethlage et al. (2022).
Background : DEM from Copernicus (2016) ; Coordinate reference system : WGS84

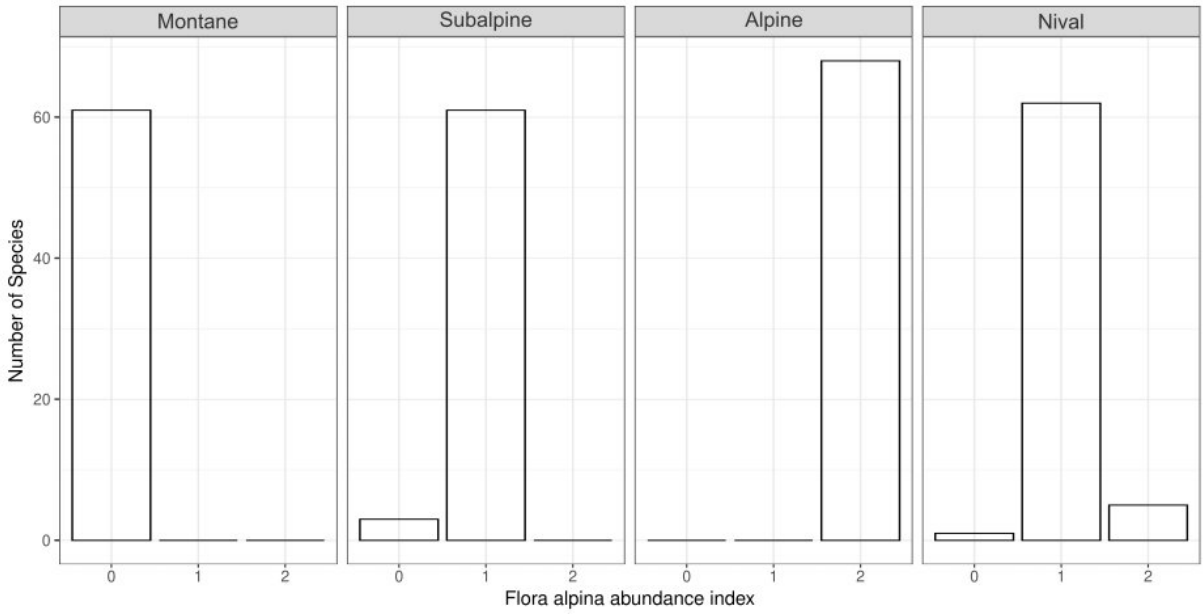

Fig.S2: Number of species from the selected pool that are referenced in Flora Alpina with an abundance score of 0, 1, or 2 across the montane, subalpine, alpine, and nival belts.

Type of Change	Species concerned (as described in *Flora Alpina*)	Change	Reference or data source
Ecological reassignment	*Androsace pubescens*	Reclassified as calcicolous (formerly generalist)	Boucher et al. (2021) /10.1038/s41598-021-90612-w
Ecological reassignment	*Eritrichium nanum*	Reclassified as substrate generalist (formerly silicicolous)	Field observations
Taxonomic revision	*Minuartia cherlerioide*	Renamed to *Facchinia cherlerioides* subsp. *aretioides*	Dillenberger & Kadereit (2015) /10.1017/S0960428615000153
Taxonomic revision	*Androsace pubescens*	Split into *A. delphinensis* and *A. pubescens* (sensu stricto)	Boucher et al. (2021) /10.1038/s41598-021-90612-w
Taxonomic revision	*Androsace alpina*	Split into *A. alpina* (sensu stricto) and *A. saussurei*	Boucher et al. (2021) /10.1038/s41598-021-90612-w
Taxonomic revision	*Androsace vandellii*	Renamed to *A. argentea*	Dentant et al. (2018) /10.1080/23818107.2018.1450784
Taxonomic revision	*Pritzelago alpina*	Renamed to *Hornungia alpina* subsp. *alpina*	Taxref, INPN (2025) https://inpn.mnhn.fr/telechargement/referentielEspece/taxref/18.0/menu
Taxonomic revision	*Gnaphalium supinum*	Renamed to *Omalotheca supina*	Taxref, INPN (2025) https://inpn.mnhn.fr/telechargement/referentielEspece/taxref/18.0/menu
Taxonomic revision	*Senecio halleri*	Renamed to *Jacobea uniflora*	Taxref, INPN (2025) https://inpn.mnhn.fr/telechargement/referentielEspece/taxref/18.0/menu
Taxonomic revision	*Lloydia serotina*	Renamed to *Gagea serotina*	Peterson et al. (2008) /10.1016/j.ympev.2007.11.016
Taxonomic revision	*Ligusticum mutellinoides*	Renamed to *Pachypleurum mutellinoides*	Taxref, INPN (2025) https://inpn.mnhn.fr/telechargement/referentielEspece/taxref/18.0/menu
Taxonomic	*Gentiana tenella*	Renamed to	Taxref, INPN (2025)

revision		*Comastoma tenellum*	https://inpn.mnhn.fr/telechargement/referentielEspece/taxref/18.0/menu

950

951 **Table S1:** Table summarizing taxonomic revisions and ecological reassignments made to species data from Flora
952 Alpina according to more recent publications or observations.
953

Family	**Species**
Asteraceae	*Achillea nana*, *Artemisia genipi*, *Artemisia glacialis*, *Artemisia umbelliformis*, *Doronicum clusii*, *Erigeron uniflorus*,*Jacobaea uniflora*, *Omalotheca supina*, *Saussurea alpina*, *Crepis rhaetica*, *Doronicum grandiflorum*
Caryophyllaceae	*Arenaria ciliata* s. str., *Arenaria biflora*, *Cerastium latifolium*, *Cerastium uniflorum*, *Cerastium pedunculatum*,*Cherleria sedoides*, *Facchinia cherlerioides* subsp. *aretioides*, *Herniaria alpina*, *Silene acaulis* s. str., *Silene exscapa*
Saxifragaceae	*Saxifraga aphylla*, *Saxifraga biflora*, *Saxifraga bryoides*, *Saxifraga exarata*, *Saxifraga florulenta*,*Saxifraga muscoides*, *Saxifraga retusa*, *Saxifraga seguieri*, *Saxifraga androsacea*, *Saxifraga oppositifolia* s. str.
Brassicaceae	*Arabis caerulea*, *Draba tomentosa*, *Hornungia alpina* s. str., *Draba fladnizensis*, *Draba siliquosa*,*Murbeckiella pinnatifida*, *Draba aizoides*, *Draba hoppeana*
Primulaceae	*Androsace helvetica*, *Androsace pubescens*, *Androsace alpina*, *Androsace argentea*, *Androsace vitaliana*,*Primula glutinosa*
Poaceae	*Festuca intercedens*, *Oreochloa disticha*, *Oreochloa seslerioides*, *Poa laxa*, *Trisetum spicatum*, *Sesleria ovata*
Gentianaceae	*Gentiana orbicularis*, *Comastoma tenellum*, *Gentiana bavarica*, *Gentiana brachyphylla*
Rosaceae	*Geum reptans*, *Potentilla frigida*
Salicaceae	*Salix herbacea*, *Salix serpillifolia*
Apiaceae	*Pachypleurum mutellinoides*
Boraginaceae	*Eritrichium nanum*
Campanulaceae	*Campanula cenisia*
Cyperaceae	*Carex curvula* subsp. *curvula*

Juncaceae	*Juncus jacquinii*
Liliaceae	*Gagea serotina*
Orobanchaceae	*Pedicularis kerneri*
Polygonaceae	*Oxyria digyna*
Ranunculaceae	*Ranunculus glacialis*
Scrophulariaceae	*Linaria alpina*

954 **Table S2**: List of species selected for modeling, grouped by family

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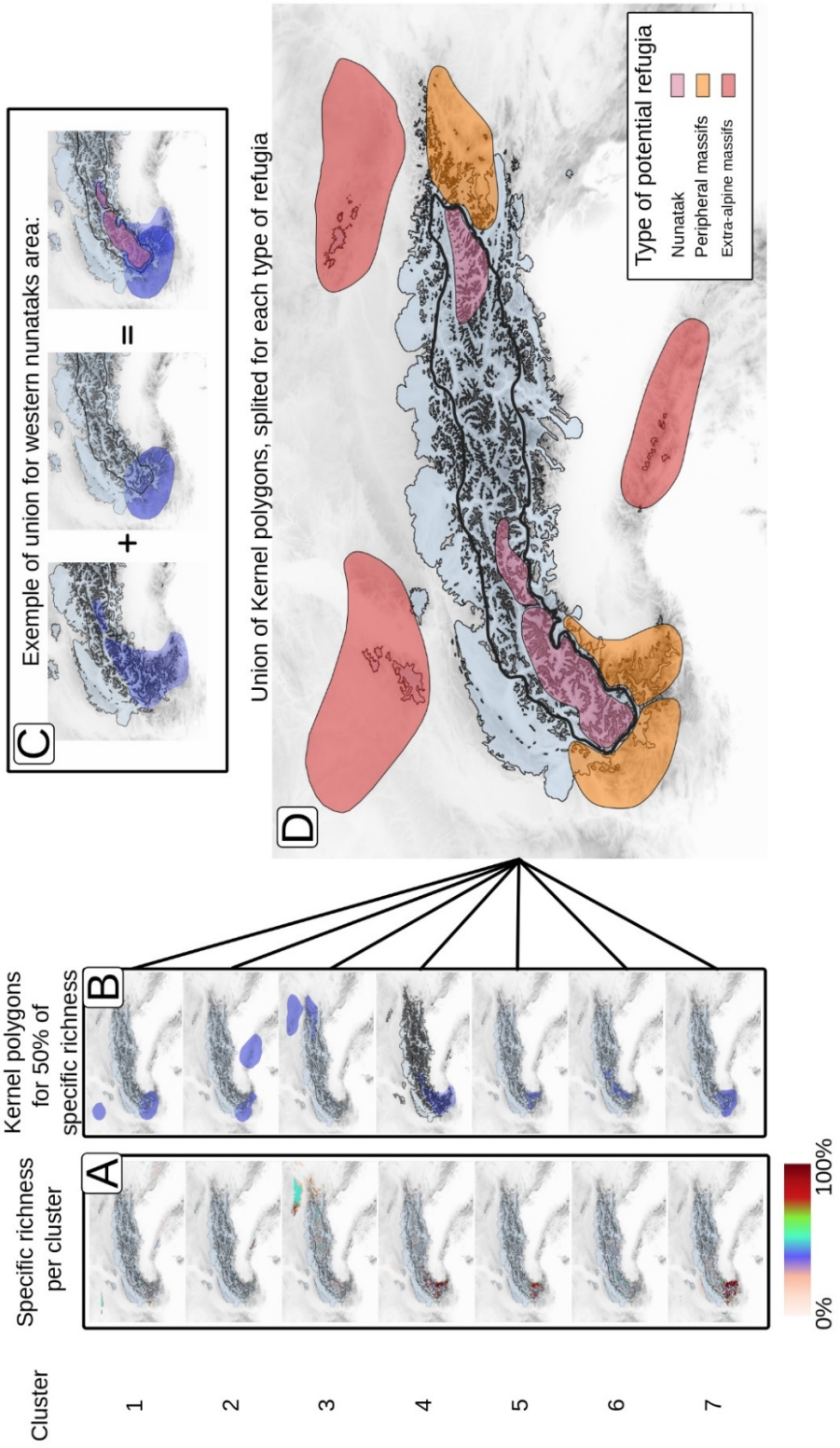
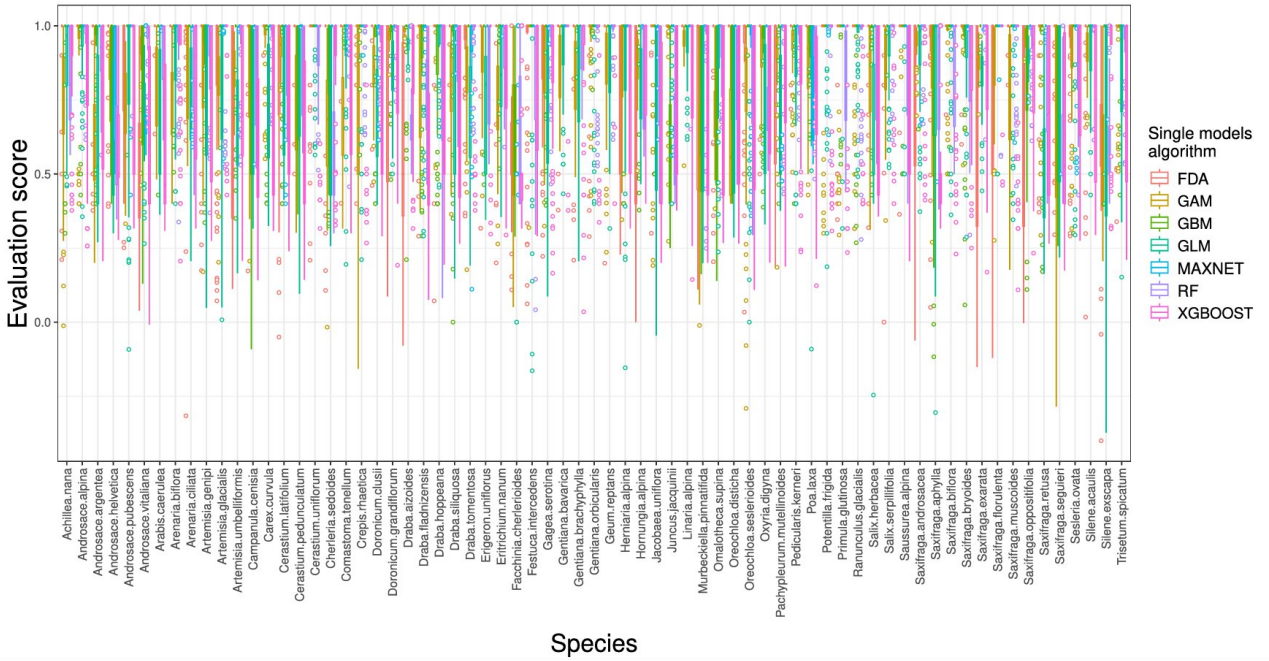


Fig.S3: Detailed procedure employed for mapping potential refugia using the example of areas containing 50% of the species present in each locality. Maps **a** depict the predicted species richness for each of the seven species clusters identified by the classification analysis. Maps **b** depict kernel ranges that contain at least 50% of species for each cluster. Panel **c** shows an illustrated example of a union procedure. The map **d** shows of union of all kernel ranges depicted in **b** with color according to type of potential refugia.

Background : DEM from Copernicus (2016) ; Coordinate reference system : WGS84



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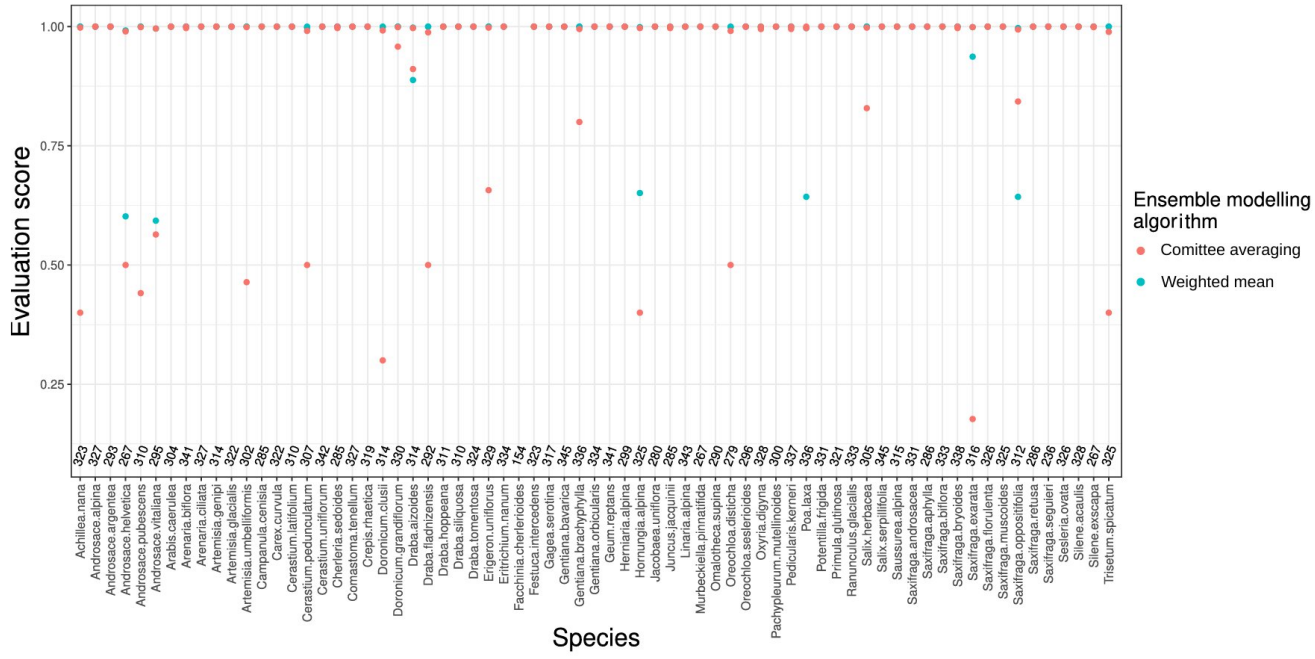
965 **Fig.S4**: Boyce index evaluation scores for single model algorithms for each modeled species.



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967 **Fig.S5**: Boyce index evaluation scores for ensemble model algorithms for each modeled species. Numbers indicate
968 the number of single projections retained for ensemble modeling after the application of the Boyce index threshold
969 of 0.5.

970

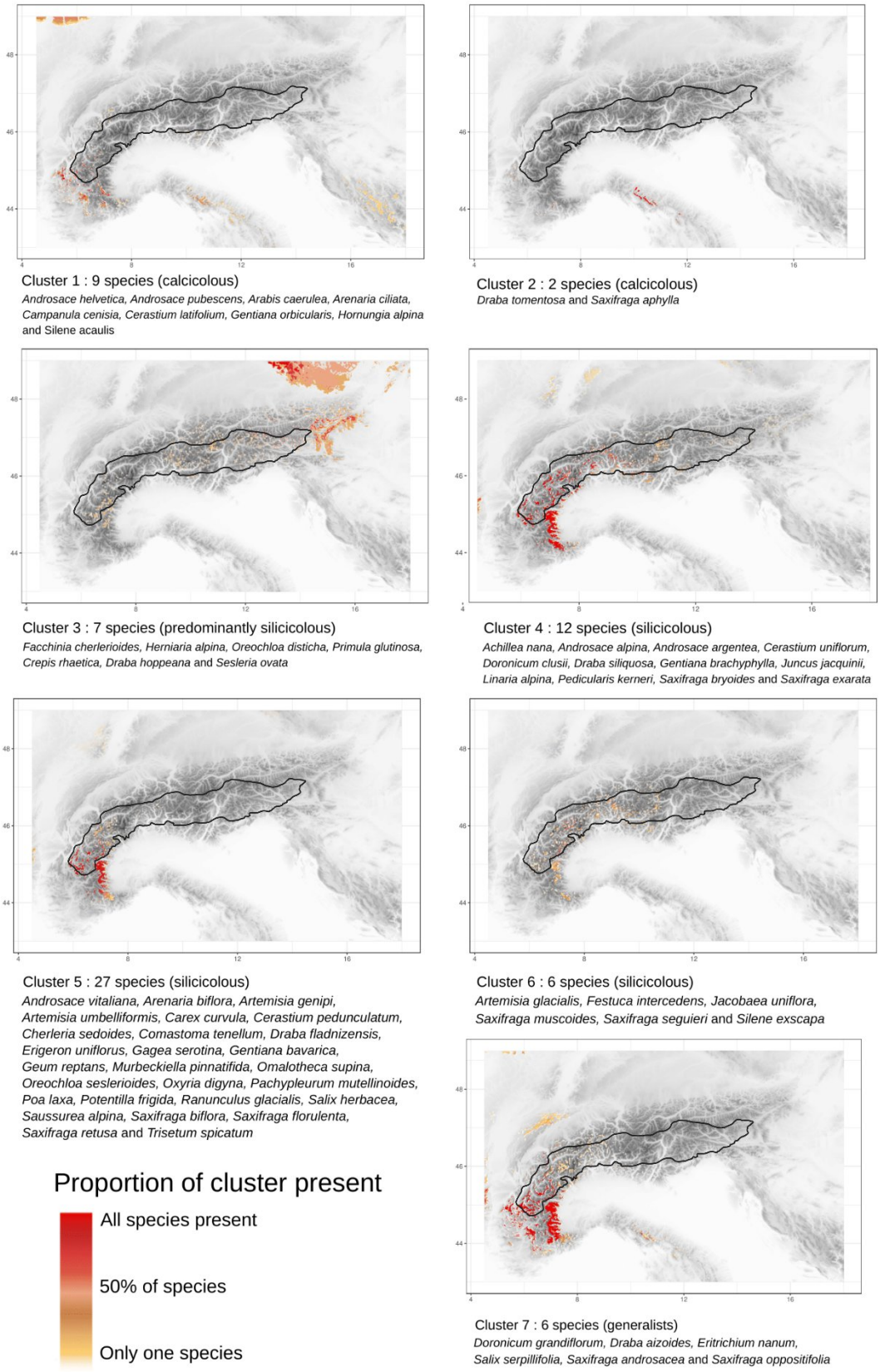
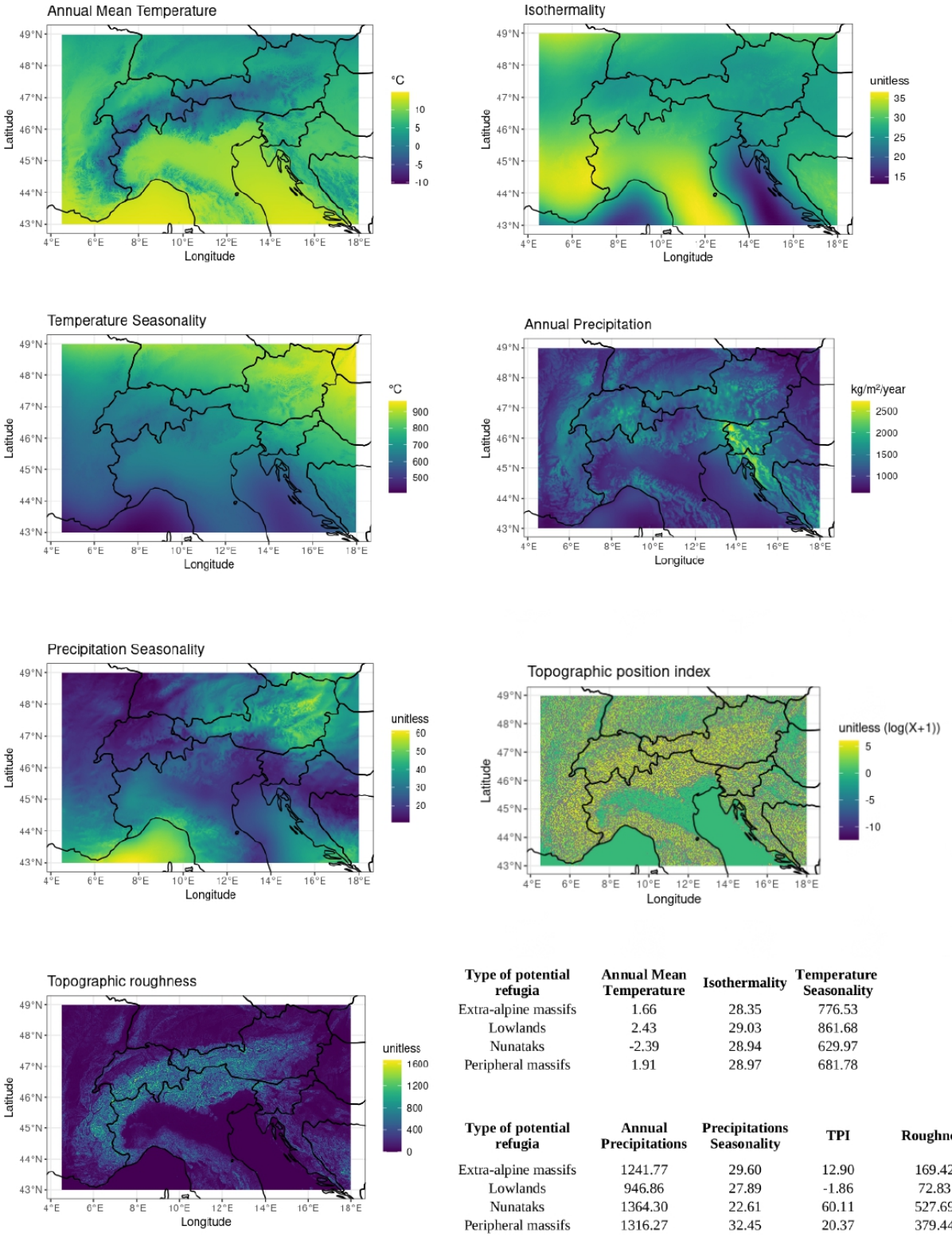


Fig.S6: Distribution of species richness for each cluster across the study area. Solid black lines represent the delimitation of LGM snowline.
Background : DEM from Copernicus (2016) ; Coordinate reference system : WGS84



Type of potential refugia	Annual Mean Temperature	Isothermality	Temperature Seasonality
Extra-alpine massifs	1.66	28.35	776.53
Lowlands	2.43	29.03	861.68
Nunataks	-2.39	28.94	629.97
Peripheral massifs	1.91	28.97	681.78

Type of potential refugia	Annual Precipitations	Precipitations Seasonality	TPI	Roughness
Extra-alpine massifs	1241.77	29.60	12.90	169.42
Lowlands	946.86	27.89	-1.86	72.83
Nunataks	1364.30	22.61	60.11	527.69
Peripheral massifs	1316.27	32.45	20.37	379.44

Fig.S7: Distribution of environmental variables during the LGM used for hindcasting species distributions across the study area. The topographical position index is shown here on a logarithmic scale to better highlight spatial variation. The table indicates average values for each environmental variable in each type of potential refugia. Coordinate reference system : WGS84