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RESEARCH ARTICLE

Uncovering the distribution and limiting factors of Ericaceae-dominated shrublands in the French Alps

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Abstract

Mountain shrublands are widespread habitats of the European Alps. Shrub encroachment into above treeline grazed lands profoundly modifies biodiversity and ecosystem functioning. Yet, mountain shrublands remain overlooked in vegetation distribution modeling because it is difficult to distinguish them from productive grasslands. Here, we used the pigment-sensitive spectral indices based on Sentinel-2 bands within a specific phenological window, to produce a high-resolution distribution map of mountain shrublands in the French Alps. We evaluated the performance of our classification using a large dataset of vegetation plots and found that our model is highly sensitive to Ericaceous species which constitute most of the dense alpine shrublands in the French Alps. Our analysis of topoclimatic and land-use factors limiting the shrubland distribution at regional scale found that, consistent with the ecophysiology of shrubs, expansion is limited by a combination of water deficit and temperature. We discussed the past and current land-use implications in the observed distribution and put forward hypotheses combining climate and land-use trajectories. Our work provides a baseline for monitoring mountain shrub dynamics and exploring the response of shrublands to past and ongoing climate and land use changes.

Highlights

- Ericaceous-dominated mountain shrubland are key habitats in alpine ecosystems, and understanding their dynamics is limited by the difficulties of mapping them using remote sensing.

- Pigment-sensitive spectral indices based on Sentinel-2 bands used within a specific phenological window successfully allows Ericaceous-dominated mountain shrublands mapping.

- Topoclimatic factors related to water conditions are driving the distribution of Ericaceous-dominated mountain shrublands at regional scale while temperatures drives the upper elevation boundaries.

- Decline of the traditional agro-sylvo-pastoral system is suggested as a common critical juncture in the trajectory of shrublands across all mountain ranges.

- Local topoclimatic conditions is suggested to have led to contrasting growth and encroachment depending on the location within the ecological niche of the habitat identified in this analysis.

Introduction

Species distributions are expected to track climate change, with cold ecosystems at the forefront due to their inherent thermal constraints and the fact that temperatures are rising at twice the global rate (Gobiet et al. 2014, N. Pepin 2015, Wang et al. 2016). Over the past decade, a large number of studies have documented vegetation responses to accelerated warming rates, including phenological shifts (Choler 2015, Choler 2023), increases in vegetation greenness (Anderson et al. 2020, Choler et al. 2021, Bayle et al. 2023, Dentant et al. 2023), upward migration of thermophilous species (Gottfried et al. 2012, Dentant et al. 2023) or shifts in ecotones such as the treeline (Harsch et al. 2009, Hagedorn et al. 2014, BernerGoetz 2022) or the shrubline (Cannone et al. 2007, Hallinger et al. 2010, Rundqvist et al. 2011, Dial et al. 2016, Myers-Smith et al. 2018).

While the distribution and the physiological limits of the tree life form have been widely investigated (Paulsen and Körner 2014, Camarero et al. 2021), those of shrubs are less documented. This is partly due to the difficulty of mapping shrubland vegetation using aerial or satellite images in comparison to forest stands (Stow et al. 2004, Tape et al. 2006, Bayle et al. 2019). This technical limitation has hindered the accurate identification of marginal populations (i.e. shrubline) and global climate-based modeling of potential shrubline position, comparable to that provided by Paulsen and Körner (2014) for the tree line. Although local studies based on shrub ring growth and recruitment analyses have highlighted the importance of temperature and water availability as the main drivers of shrubline advance in arctic and alpine tundras (Myers-Smith et al. 2018, Francon et al. 2021, Cannone et al. 2022), the climatic drivers of shrublands distribution remain poorly constrained at the global scale.

There is growing evidence that shrub encroachment, which refers to the expansion of low-stature woody plant species into grasslands and sparsely vegetated ecosystems, is underway in European mountains (Cannone et al. 2007, Montané et al. 2007, Grau et al. 2019, Urbina et al. 2020, Cannone et al. 2022), and is favored by summer pasture abandonment (MacDonald et al. 2000, Tasser et al. 2007, Gartzia et al. 2014, Ameztegui et al. 2016) and in bio-climate changes (Gehrig-Fasel et al. 2007, Francon et al. 2020). The resulting expansion of shrublands has profound effects on many ecosystem properties and services (Myers-Smith et al. 2011), including species diversity (Anthelme et al. 2001, Freléchoux et al. 2007), nutrient cycling (McKinley and Blair 2008), water balance (Huxman et al. 2005, Alewell and Bebi 2010), carbon balance (Urbina et al. 2020, Mekonnen et al. 2021), plant resource availability for wild and domestic herbivores (Van Auken 2009, Perotti et al. 2018), or landscape aesthetics (Schirpke and Tasser 2021). For all these reasons, a comprehensive mapping of shrub cover from both a scientific and conservation management perspective is needed.

Distinguishing shrub cover from other vegetation types remains a challenge using widely available imagery (Bayle et al. 2019). Interestingly, certain shrub species, particularly those belonging to the Ericaceae family, accumulate anthocyanin pigments at fall in response to various abiotic and biotic stressors (Boldt et al. 2014, Liu et al. 2018). Autumn reddening of Ericaceae leaves provides a promising opportunity to improve shrubland mapping. In the western European Alps, shrublands are mostly composed of species belonging to the genera *Rhododendron*, *Vaccinium* or *Juniperus* (Theurillat et al. 1994, Poldini et al. 2004). In particular, shrublands dominated by *Rhododendron ferrugineum* and/or *Vaccinium* sp. (Ericaceae) are frequently a main component of the subalpine vegetation belt (Ozenda 1989). Bayle et al. (2019), as proof-of-concept, recently took advantage of the unique phenology of anthocyanin accumulation in the leaves of shrubs in late fall to discriminate Ericaceous-dominated shrublands

from surrounding grasslands at local scale using the Normalized Anthocyanin Reflectance Index (NARI) based on Sentinel-2 red-edge bands.

Here, we aimed to improve the mapping of mountain shrublands using absorption features of canopies in the red-edge bands and to analyze the factors underpinning its observed biogeographical distribution. For this, we extracted two vegetation indices as proxies of anthocyanin and chlorophyll concentrations from Sentinel-2 reflectance time series. Using a large dataset of more than 3000 vegetation plots, we analyzed the spectral signature of shrublands dominated by different species. With this method we were able to delineate the shrublands dominated by Ericaceous with high accuracy. After validating our spectral model using 3000 vegetation plots, we characterized the topoclimatic and current land-use drivers of Ericaceous-dominated dense alpine shrublands using high-resolution climatology and pastoral units datasets. In spite of their recognized importance which we discuss based on literature, we were unable to consider historical land use in this analysis, due to the lack of temporal data at a sufficient spatial resolution. Our study constitutes an unprecedented opportunity to assess shrub life-form distribution along biogeographical gradients. It provides a basis for an extended analysis of the ecology and encroachment dynamics of mountain shrublands and their implications for biodiversity and ecosystem services.

Materials & Methods

Study site, vegetation classes and selection of pixels

The study area covers the French Alps (Fig. 1) and represents about 40,600 km² of land area with an elevation ranging from sea level to 4809 m and stretching from Nice to Chamonix in the Mont-Blanc range. The southern part is characterized by Mediterranean influence (dry summer and wet autumn and winter) while the northern part is colder and more humid. The area also experiences a strong rain shadow effect, with inner valleys receiving reduced summer precipitation and high thermal amplitudes. Above forest areas of the French Alps are actively grazed by domestic herbivores with noticeable differences between the northern and southern parts (Drogue 1950). The northern Alps are characterized by a high level of cattle farming and few sheep farms, in contrast to the southern Alps, which are mainly farmed by transhumance sheep (Dobremez et al. 2016).

We limited our analysis to areas above 1400 m and focused on four land cover classes: (1) forests, (2) grasslands, (3) shrublands and (4) bare soil which were described as mutually exclusive and spatially exhaustive land cover classes for our study site (Anderson et al. 1976). For our study, we constructed a common reference grid with a 20 x 20 m spatial resolution projected in Lambert 93 (EPSG:2154) on which gridded datasets were reprojected. In case of continuous variables, it was reprojected using bilinear methods. We estimated the elevation from the 25-m resolution European Digital Elevation Model (EU-DEM, version 1.1).
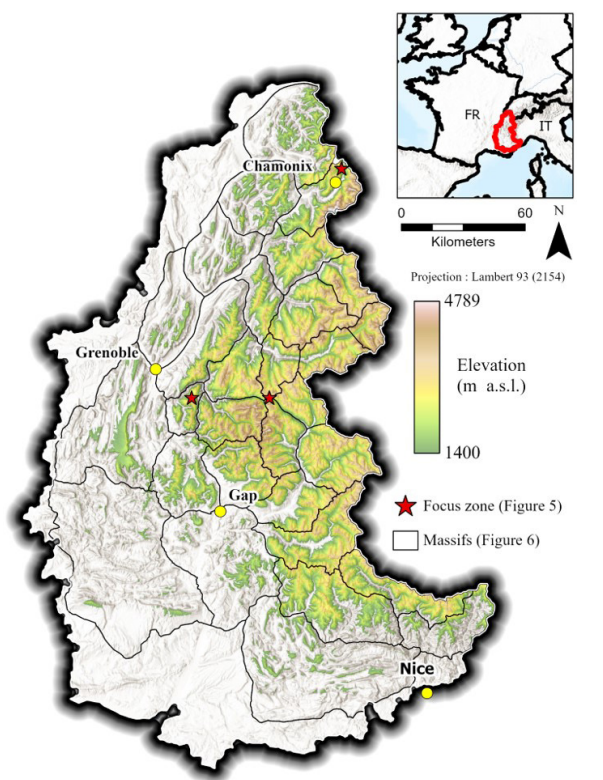
Figure 1. Study area in the French Alps. The blue contour indicates French ranges used in Fig. 6. Red stars correspond to the focus zone shown in Fig. 5.

Shrubland classification and validation

Predictive variables

Our analysis relied on the computation of two spectral indices from Sentinel-2A and 2B over the period 2017-2021. Sentinel-2 is an Earth observation mission composed of two identical satellites, Sentinel-2A and 2B, launched on 23 June 2015 and 7 March 2016, respectively. The 5-day revisit time available since March 2017 combined with high spatial resolution (10 or 20 m) enables improved capacity to detect seasonal variation in patchy and heterogeneous plant canopies distributed across topographically complex terrain such as mountain ecosystems. We used all available scenes for 2017, 2018, 2019, 2020 and 2021 in Google Earth Engine (Gorelick et al. 2017) from September 1st to November 1st (hereafter summarized as "Fall"). Spectral bands were obtained at Surface Reflectance levels (corrected from atmospheric, terrain and cirrus correction by running Sen2cor), and clouds, and cloud shadows were removed using the Sentinel-2 Cloud Probability product (with probability threshold of 0.65). We computed the Normalized Anthocyanin Reflectance Index (NARI) and the Normalized Chlorophyll Reflectance Index (NCRI), which are both normalized adaptations of the three band model from Gitelson et al. (2006). All computations were made on Google Earth Engine from which we extracted the vegetation indices. NARI and NCRI are sensitive to plant canopy anthocyanin and chlorophyll content, respectively, and were computed using the following formulas:

$$NARI_F = \frac{\frac{1}{B3} - \frac{1}{B5}}{\frac{1}{B3} + \frac{1}{B5}}$$

$$NCRI_F = \frac{\frac{1}{B5} - \frac{1}{B7}}{\frac{1}{B5} + \frac{1}{B7}}$$

where B3, B5 and B7 are the reflectances of the green (559.8 ± 36 nm), the red-edge 1 (704.1 ± 15 nm) and the red-edge 2 (782.8 ± 20 nm) channels. We computed the median of NARI and NCRI for each year, hereafter referred to as $NARI_F$ and $NCRI_F$ (Fall) and then computed the median of the five years. These two variables were used in the random forest classifier as predictive variables.

Photo-interpretation data

When classifying complex areas with multiple land cover classes, some of which have high intra-class variability, the coverage of ground reference information (training sites) should be as large as possible to represent all the variability in a category (PalMather 2003). We identified training sample points for four classes: forest, shrubland, grassland and bare soil. While generically called 'shrubland', we built our sampling scheme focusing on Ericaceous-dominated shrubland, which is the focus of this paper. We used high resolution images from ESRI World Imagery available on ArcGIS Pro for photo interpretation. For the French Alps, it is based on 0.5m Maxar (Vivid) Imagery ranging from year 2014 to 2021 and month July to October. For Ericaceous-dominated shrubland, we relied on images taken at fall as the visible reddening facilitates the photo-interpretation. This procedure resulted in 2564, 2485, 935 and 5423 samples for forests, grasslands, shrublands and bare soil respectively.

Random Forest classification workflow

We calibrated a random forest algorithm to classify the four land cover classes using the photo-interpretation data set and the two predictive variables $NARI_F$ and $NCRI_F$ described above. For each training sample, we extracted the $NARI_F$ and $NCRI_F$. We randomly sampled 935 samples (smallest sample set) in each vegetation class to balance the sample size and partitioned the data set into a model training subset (two thirds of pixels) and a model evaluation subset (one third of pixels). We repeated this procedure 1000 times, meaning that we implemented a random forest model for each data set. We relied on the out-of-bag classification accuracy to select the best random forest model. We assessed predictor importance for each land cover class separately using the mean decrease in accuracy metric, which indicates the suitability of a predictor. Predictor importance was based on a permutation-based importance measure, which measured the effect of reshuffling each predictor on model accuracy. Then, we examined how the classification probabilities depend on the values taken by each predictor by computing partial dependence plots.

We used the random forest models and evaluated their performance. For the final classification product, we constructed a random forest model using a similar approach without partitioning between training and evaluation subsets. Finally, we applied the final random forest model to all areas above 1400 m. We used the 'pdp', (Liaw 2002, Greenwell 2017, Kuhn 2023).

Floristic plots for species-specific responses

Since our classification approach relies on pigment phenology, which is known to be species-specific, we used a large data set of vegetation ground surveys to analyze the response of shrublands dominated by different species. We extracted all available vegetation plots above 1400 m a.s.l. from the regional Conservatoire Botanique National Alpin (CBNA) database, resulting in N = 16,105 unique plots across the French Alps. The surveys are botanical inventories made in plots of 100 to 500 m². The abundance of each species is evaluated semi-quantitatively with the Braun-Blanquet relative abundant coefficient ranging from very low abundance (scores : "i", "P" and "r") to higher abundance (from 1 to 5). We converted the abundance score to horizontal cover using score definition, resulting in 6 classes: 0 (i, P, r), 2.5 (1), 15 (2), 37.5 (3), 62.5 (4) and 87.5 (5) %. We focused on four shrub species that are known to be dominant in shrublands, i.e. *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Vaccinium uliginosum* and *Juniperus communis.* Other shrub species such as *Juniperus sabina*, *Empetrum nigrum*, *Arctostaphylos uva-ursi* were not considered as too few samples were available.

Since monospecific dense shrublands are of little interest in terms of plant diversity or nature conservation, they tend to be avoided in floristic surveys, resulting in few plots with shrub abundance higher than 62.5%. Also, although shrub species are common in undergrowth vegetation, our method based on satellite remote sensing does not allow them to be detected because of the trees. Thus, we removed floristic surveys with more than 25% of tree strata as informed by survey metadata. However, in most of the metadata, this information was unavailable, so we examined each individual survey in Google Earth Pro to remove those located in forest or with very high density of trees. We ultimately analyzed 1822 surveys with at least one of the four species present, resulting in 646, 344, 510 and 322 plots for *Juniperus communis, Rhododendron ferrugineum, Vaccinium myrtillus* and *Vaccinium uliginosum* respectively.

As a complementary approach, we selected three sites of the French Alps: Lautaret Pass, Taillefer near Grenoble and Loriaz near Mont-Blanc. We used available ground pictures to benchmark the classification results. For the Taillefer and Loriaz sites, the shrubland is dominated by *Rhododendron ferrugineum* with high cover of *Vaccinium uliginosum* and *Vaccinium myrtillus*. At Lautaret, the shrubland is dominated by *Vaccinium uliginosum* and *Vaccinium myrtillus* with very few individuals of *Rhododendron ferrugineum*.

Biogeographic characterization of shrublands

We computed the elevation distribution of shrublands, grasslands, forests and bare soils for each massif in the French Alps. Mountain range delineation followed the one used in Vernay et al. (2022) with modifications to produce more relevant biogeographical units.

We used the CHELSA v2.1 and CHELSA-BIOCLIM+ datasets (Karger et al. 2017, Brun et al. 2022) to retrieve the climate normals of the reference period 1981-2010. CHELSA is a high resolution climatology that provides downscaled estimates of surface with a horizontal resolution of 30 arc sec (Karger et al. 2017). The following variables were used to characterize the summer (June- August) climate in the study area: mean daily minimum air temperature (tasmin), surface downwelling shortwave radiation (rsds). In addition, we computed the Gams index (Gams 1932) that has been used as a proxy of rainfall continentality in temperate mountains (Michalet et al. 2020). The Gams index was calculated following the equation:

$$cotg(a) = 4Pw/A$$

where Pw and A represent the sum of precipitation (mm) computed over the coldest quarter (bio19) and the elevation (m a.s.l), respectively. In addition, we extracted bedrock data from the 1:1 million OneGeology pan-European harmonized surface geological maps distributed by the European Geological Data Infrastructure portal (http://www.europe-geology.eu/). Surface geological units were aggregated into two categories: (i) siliceous rocks including igneous and metamorphic rocks (granite, gneiss, etc.), and ferromagnesian rocks (serpentine, amphibolite, andesite, basalt, etc.). and (ii) hard (dolomite, limestone, etc.) and clastic sedimentary rocks (schist, mudstone, shale, flysh, etc.). We used the French alpine pastoral inventory that provides distribution of surfaces used by extensive domestic grazing as a proxy of current land-use (i.e., pastoral units). Study areas were splitted as either within or outside of pastoral units which we interpret as either being currently affected by domestic herbivory or not.

To model the relationships between biogeographic variables and mountain shrubland distribution, we implemented a feature effect method in a Random Forest classification model. More specifically, we used the Accumulated Local Effects (ALE) method (Apley and Zhu 2020). ALE is the only feature effect method that succeeds in staying on distribution and isolating feature effects in situations where predictive features are highly correlated. As some of our variables were highly correlated ($r^2 > 0.75$), we computed ALE plots for each predictive feature (rsds, tasmin, gams angle, bedrock and pastoral units) to assess the feature effect when other features are marginalized. We repeated the operation 100 times by randomly sampling half of the data set each time. We used the 'ALEPlot' (ApleyZhu 2020) and 'caret' (Kuhn 2023) R packages.

Finally, we completed our analysis by assessing the effect of local topographical factors (elevation and slope aspect) on the distribution of shrublands.

We subdivided the French Alps into two bioclimate domains using a Gams angle value of 62.5 as determined by ALE. For each domain, we computed the proportion of shrublands along elevation and diurnal anisotropic heating (DAH) classes. The DAH index approximates the anisotropic heating of land surface to radiation.

We computed DAH as cos(amax - a) * arctan(b), where a is the aspect, b is the slope and amax corresponds to the aspect with the maximum total heat surplus. We used amax = 212° as we noticed that this SSW orientation corresponds on average to the earliest first snow-free day derived from Sentinel-2 products in the southwestern Alps (unpublished results).

Results

Shrubland classification

The four land cover classes were well separated in a two-dimensional $NARI_F$ and $NCRI_F$ spectral space (Fig. 2). $NCRI_F$ values of shrublands exhibit overlapping with those of forest and grasslands and were more clearly discriminated along the NARIF gradient. The Random Forest classification performed very well with an average Kappa index of 0.87 ± 0.009, an F-score of 0.9 ± 0.011 and a balanced overall accuracy of 0.93 ± 0.008. Bare soils were classified with high accuracy while vegetation classes had lower but still high performance (Fig. 3A). The importance of the variables varied between classes, with $NARI_F$ being specifically important for discriminating shrublands while all three other classes were mostly discriminated based on $NCRI_F$ (Fig. 3A). Partial dependence plots highlighted the classification probability of each class along the variable's gradient while marginalizing the other variable (Fig. 3B). We found that pixels were mostly classified as Ericaceous-dominated shrublands when $NARI_F$ values were higher than 0.33 ± 0.01.
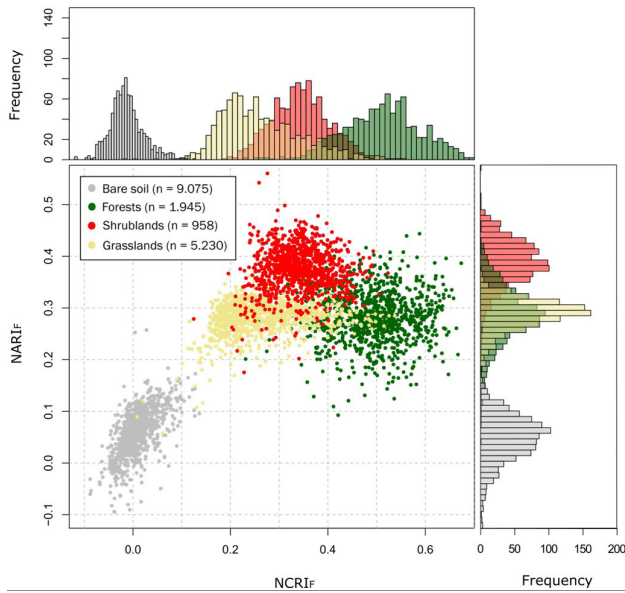

Figure 2. Distribution of training samples for the four classes within the NARIF/NCRIF two-dimensional space.
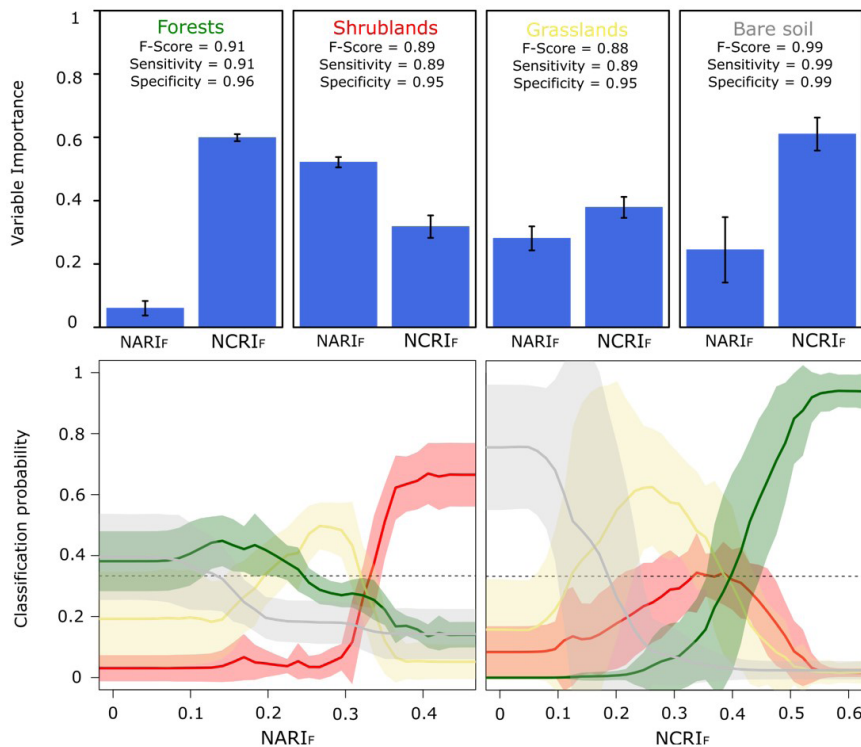

Figure 3. (A) Variables importance in the Random Forest classification for each class with respective F-score, sensitivity and specificity specified. (B) Partial Dependence Plot for NARIF and NCRIF with shown ranges corresponding to variability within the 100 random iterations.

Species-specific response to NARIF

The relative abundance of the ericaceous species had a significant influence on the NARI$_F$ as shown in Fig. 4). Increasing abundance of *R. ferrugineum*, *V. uliginosum* and *V. myrtillus* translated into an increasing NARI$_F$. In contrast, *J. communis* did not respond to NARI$_F$, which was expected as it is not part of the Ericaceae family and does not accumulate anthocyanin in the fall. Interestingly, we found that NARI$_F$ values were below the threshold used by the 20-m scale classification for species abundance lower than 62.5% (Figs. 3 and 4), highlighting the sensitivity of our classification to shrubland cover. As stated in section 2.2.4, vegetation plots with shrubland species abundance higher than 62.5% were missing from the database, hence, we were unable to directly determine the horizontal cover percentage that corresponds to the NARI$_F$ threshold. Nonetheless, through visual interpretation of the plots, shrubs species abundance higher than 70% floristic plot appears sufficient to be classified as shrubland by our classification model (Fig. 4). In addition to this analysis, we show three examples of our classification results in iconic places of the French Alps (Fig. 5). These examples illustrate the high spatial resolution of the classification, which allows a precise delineation of shrublands in highly heterogeneous slopes.

Biogeographic distribution

The proportion of ericaceous-dominated shrublands in the above treeline area of the French Alps massifs is shown in Fig. 6. Dense ericaceous-dominated shrublands are found mainly in the northern and external massifs, occupying almost 30% of the above-forest open lands in the Beaufortain massif between 2000 and 2100 m and up to 40% in the Mont-Blanc massif between 1900 and 2000 m asl. In contrast, these habitats are scarcer in the southern and inner parts of the study area. Only 5% of shrublands are located above treeline in the Queyras massif. Dense ericaceous-dominated shrublands tend
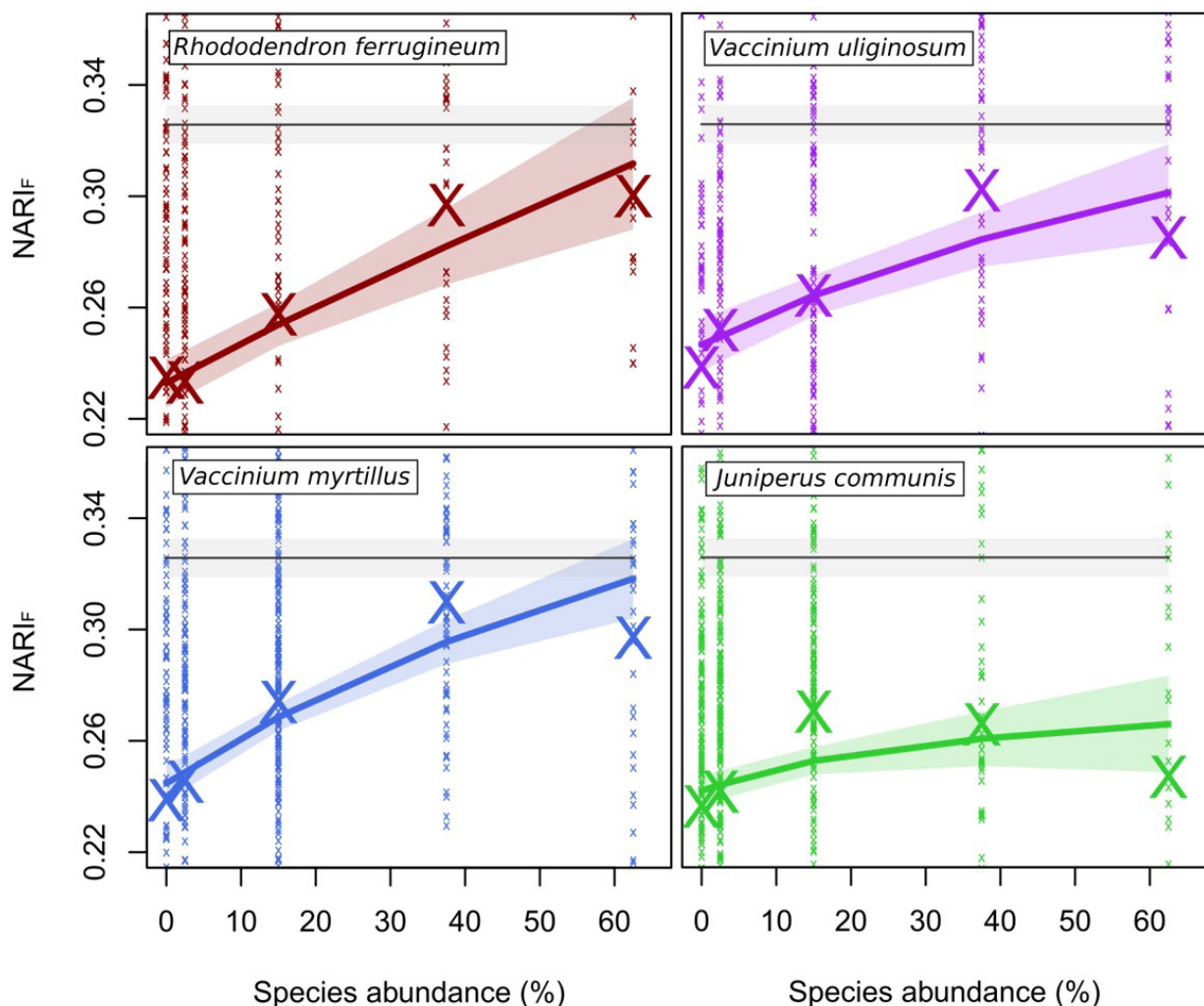

Figure 4. Relation between NARI$_F$ and species abundance for *Rhododendron ferrugineum, Vaccinium uliginosum, Vaccinium myrtillus and Juniperus communis.* Curves correspond to loess fit with span = 2. Confidence interval corresponds to 0.95. Crosses represent mean values for each abundance class. Horizontal gray bars show the NARIF threshold used by the random forest classification to classify a pixel as "shrublands".

Subalpine shrublands dominated by *Vaccinium uliginosum/myrtillus* (Lautaret pass)

Subalpine shrublands dominated by *Rhododendron ferrugineum/Vaccinium uliginosum* (Taillefer)

Subalpine shrublands dominated by *Rhododendron ferrugineum/Vaccinium uliginosum* (Loriaz)
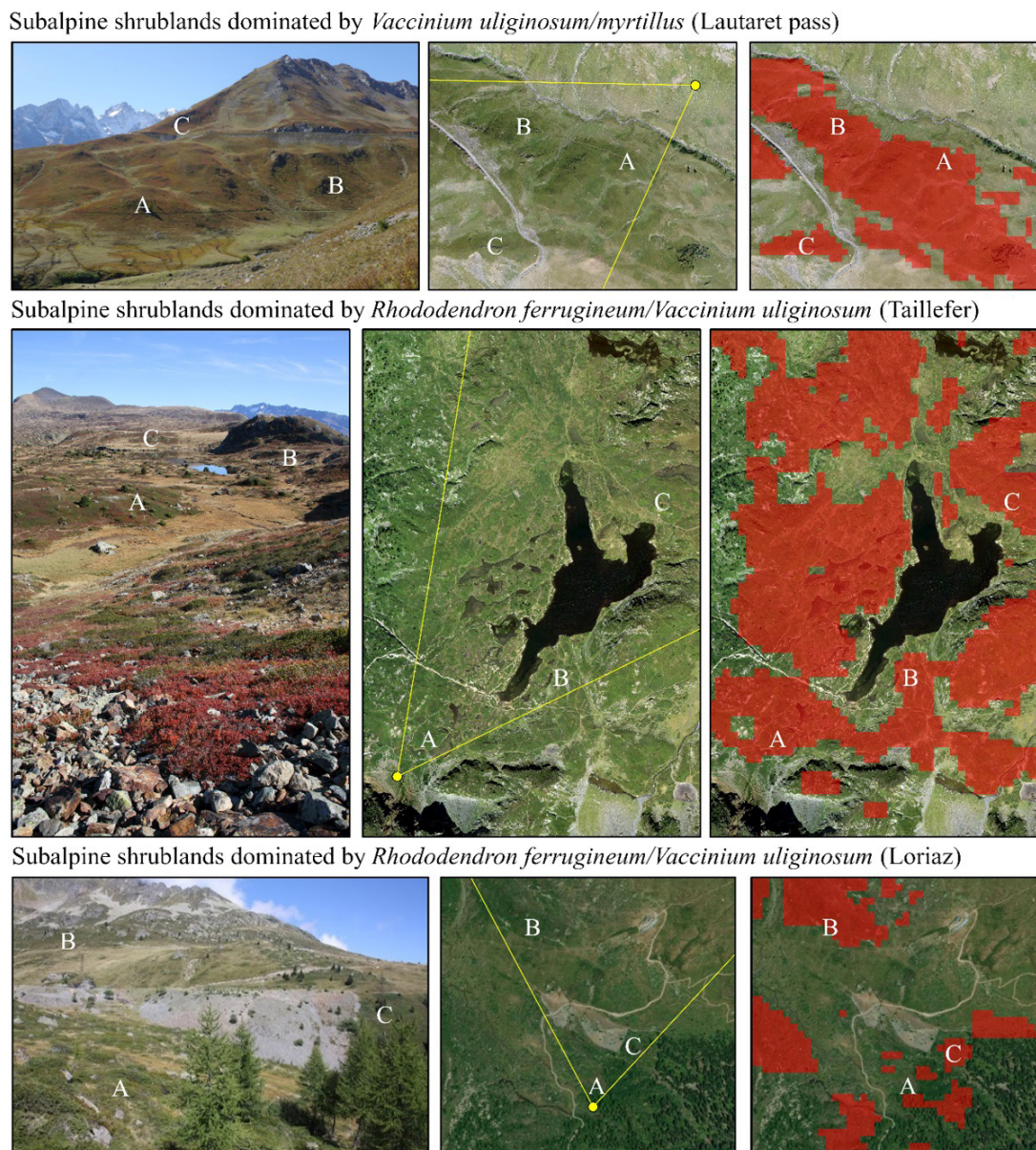

Figure 5. Shrublands classification results (right column) on three locations (top row) Lautaret pass, (middle row) Taillefer, (bottom row) Loriaz, informed with ground photography (left column) and very-high resolution aerial images (middle column).

to be mostly found in the northern (RSDS < 65.5), external (GAMS < 62.5) and at the subalpine level (3° < TASMIN < 5°) of the French Alps (Fig. 7a-c). In addition, we detected a slight effect of bedrocks and presence of pastoral units, highlighting a trend for more shrublands on siliceous bedrock and outside of pastoral units, but ALE values are low compared to the three other variables (Fig. 7d-e). Overall, climatic variables were found to be the most important to explain the distribution of dense ericaceous-dominated shrublands, with only minor effects attributable to bedrock and recent pastoral activities (Fig. 7f).

Lastly, we examined shrubland distribution along mesotopographic gradients (Fig. 8). In the moist external Alps (Low rainfall continentality, Gams angle < 62.5°), shrublands are located in both north and south-exposed slopes at an average elevation

of 2000 m asl, but with a narrower elevation range in the south-exposed slopes. In the dry inner Alps (High rainfall continentality, Gams angle > 62.5°), shrublands are almost exclusively found on north-exposed slopes, at higher average elevation (2150 m asl) and with a lower boundary at 1950 m asl (Fig. 8).

Discussion

Unprecedented high-resolution, large-scale mapping of mountain shrublands

Understanding the distribution and topoclimatic factors influencing ericaceous-dominated shrublands in mountains is crucial for comprehending shrub encroachment and its impact on biodiversity and ecosystem functioning. For the first time, building on the specific
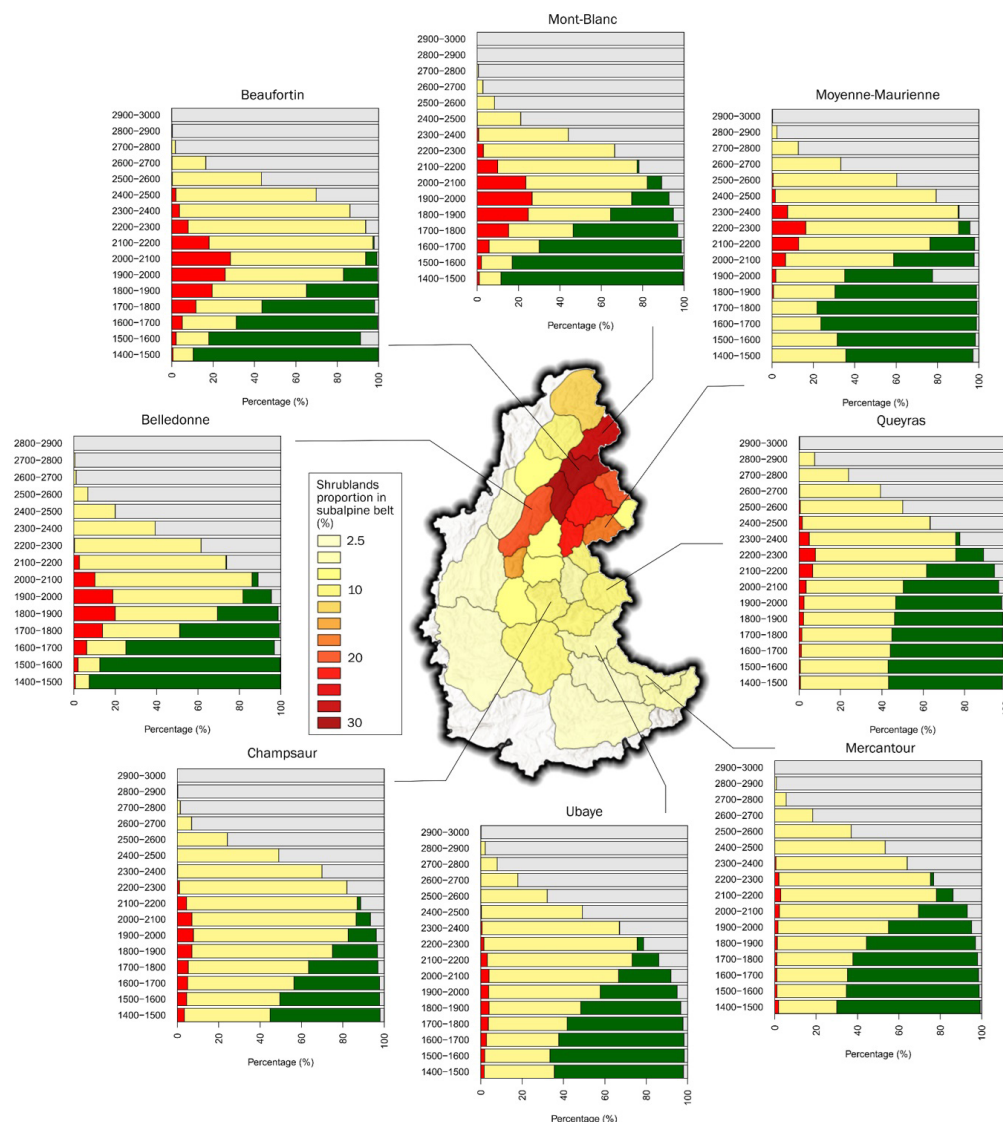
Figure 6. The central map depicts the maximum proportion occupied by shrublands in the subalpine belt (between 1800 and 2300 m a.s.l.). Stacked barplot shows the elevational distribution of vegetation life-forms for six massifs from 1400 to 3000 m a.s.l. (Beaufortain, Mont-Blanc, Belledonne, Haute-Maurienne, Queyras, Champsaur, Haut-Var, Mercantour). Colors represent the four classes with gray, yellow, red and green representing bare soil, grasslands, shrublands and forests respectively.

absorption features of Ericaceae-dominated shrublands (Fig. 2), we have overcome the challenges associated with mapping shrublands and produced a spatially exhaustive mapping at high spatial resolution (Fig. 6). This allowed us to characterize the bioclimatic niche of Ericaceous-dominated shrublands across the French Alps by identifying determinants of their distribution at both regional and local scales (Figs. 7 and 8). The reliability of our remote sensing analysis is supported by a large dataset of vegetation ground surveys from which we precisely defined the vegetation type and cover actually mapped by our method (Figs. 4 and 5). Our precise and automated mapping is an important contribution toward future monitoring efforts aimed at improving our understanding of the major changes in biodiversity and ecosystem functioning associated with shrub encroachment.

Our approach adopts a deliberately simple methodology, utilizing only two spectral indices designed to identify the occurrence of shrublands based on seasonal dynamics of pigments in plant canopies. Anthocyanins and chlorophyll contained in leaf tissues exhibit varying concentrations both over the course of the growing season and across the different species that dominate shrublands or grasslands. While our approach has demonstrated a high level of effectiveness in achieving its intended purpose, it has limitations for providing information at species level. For example, we are unable to distinguish between dense rhododendron shrubland with high canopy (up to 40 cm) compared to prostrate shrubland characterized by *Vaccinium* spp. and other Ericaceae such as *Kalmia procumbens* with lower canopy height between 10 and 20 cm. These two situations represent highly contrasting habitat
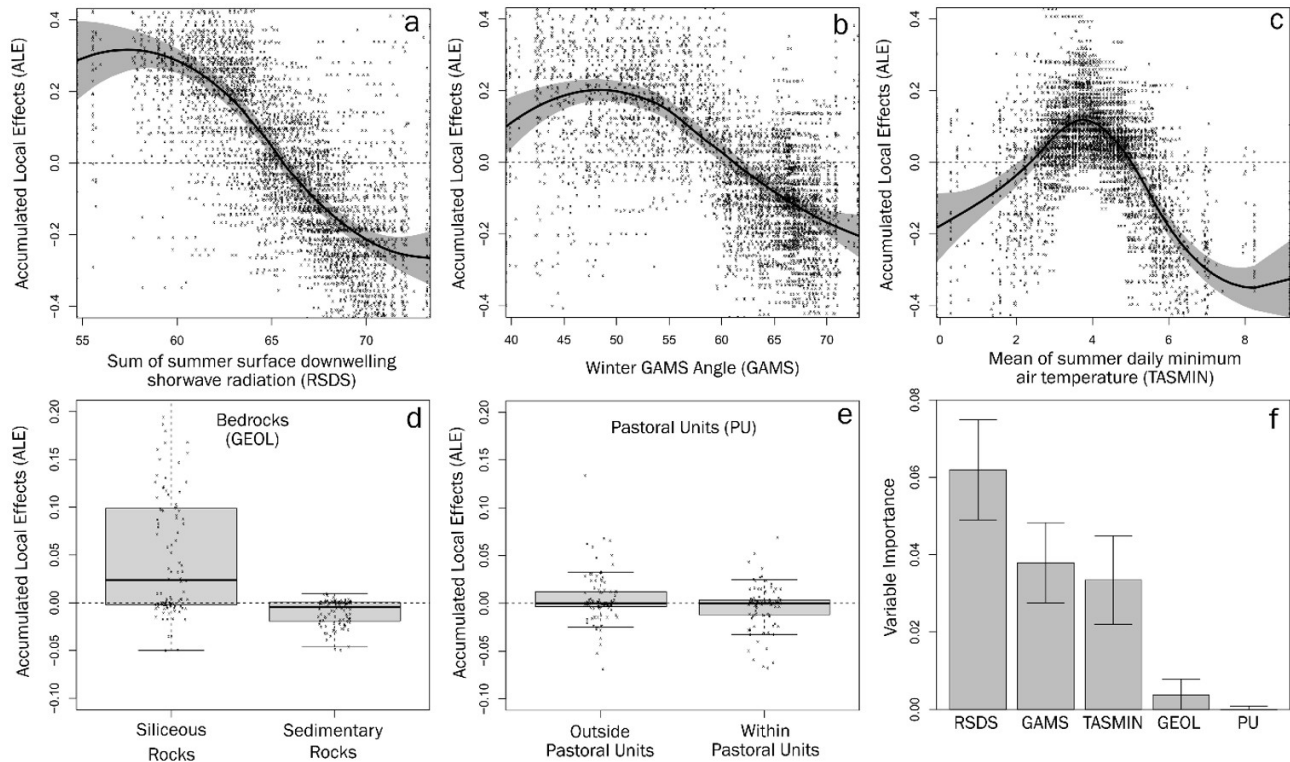
Figure 7. Accumulated Local Effects of RSDS, GAMS, TASMIN, GEOL and PU variables on the distribution of shrublands.
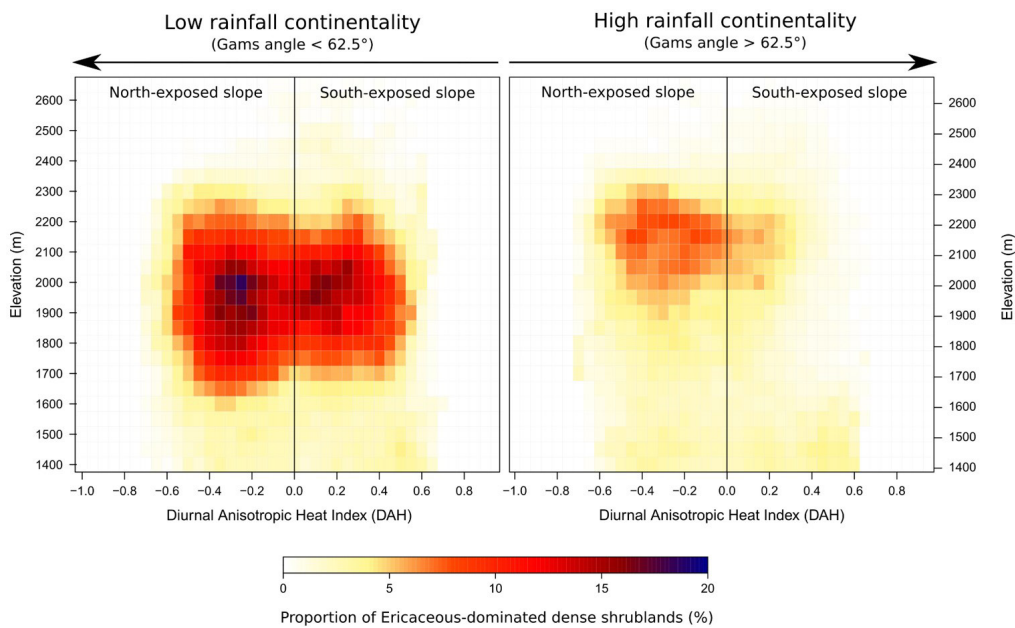

Figure 8. Mesotopographic distribution of shrublands depending on their continentality highlighting that shrublands located in internal and drier massifs tends to be at higher elevation than those in external and wetter massifs.

features, plant diversity and food resources for fauna. Furthermore, it is important to note that our method inadequately detects shrublands primarily dominated by *Juniperus communis*. This outcome is unsurprising, as juniper does not accumulate anthocyanin during the autumn season. Other mapping of mountain shrublands has been proposed using so-called big data approaches with shrublands defined as woody vegetation with height under 5 m (Inglada et al. 2017, Zanaga et al. 2021). In contrast, distribution maps at shrub species level have been obtained using species distribution modeling (Komac et al. 2016, Puchalka et al. 2023).

Overall, these approaches are complementary, as in general, definition of 'shrublands' is too broad to allow biogeographical characterization in big data approach, while shrub species mapping are generally based on coarse climatic data sets that result in limited spatial accuracy. Our approach lies somewhere in between, with high spatial and habitat accuracy achieved thanks to high resolution satellite data and specific spectral indices. Hyperspectral airborne imaging spectroscopy (AIS) could offer the opportunity to link develop our approach by building specific indices for more generalist alpine habitats (Marcinkowska-Ochtyra et al. 2018).

Delineating range limits of shrublands and shrubline

Species range limits are the expression of a species' realized ecological niche over space. Species distribution shifts (e.g. shrub encroachment) can reflect either gradual niche evolution over time or a species tracking its environmental niche in response to changing environmental conditions, including biotic interactions or land-use (Sexton et al. 2009). Edge or marginal populations, i.e. individuals located at the edge of their ecological niche, are expected to be the first to respond to environmental changes and are thus pivotal for determining species' responses to anthropogenic climate change (Rehm et al. 2015). Our mapping enables us to precisely define the realized ecological niche of the main ericaceous shrub species that form Ericaceae-dominated shrublands (e.g. *Vaccinium* sp. and *R. ferrugineum*), and thus to differentiate and compare core populations from more marginal ones. This is of particular interest because the comparison between central and marginal populations provides an understanding of determinants of species' ranges (Kawecki 2008, Kolzenburg 2022) and could allow forecasting of their future dynamics (HampePetit 2005).

Trees at their upper elevation limit are undoubtedly the most studied case of marginal populations. Because the presence of a forest is easily identifiable at large scale, it has been possible to identify the climatic limits of these life forms, so-called 'treeline' (PaulsenKörner 2014), and to project their future dynamics and relationship with their limiting factors (Camarero et al. 2021). Drawing parallels with Körner (2012) treeline definition, i.e. "the line connecting the highest patches of forest", our mapping offers insight into shrubline identification. Local disturbances affecting observed treeline position, such as grazing activity or geomorphic processes, could also locally suppress the elevation of the shrubline, although these hypotheses remain to be confirmed and applied to the shrub life form in an alpine context. By connecting the highest shrubland patches with a shrub density exceeding 70%, we can effectively delineate the shrubline for the entire French Alps. This line represents the uppermost range limit of the shrub life-form distribution at high elevations. Other studies, based on field observations and aerial photographs, have delineated the shrubline to monitor its dynamics (Dial et al. 2007, Dial et al. 2016, Myers-Smith et al. 2018). However, they are usually limited to a local scale, and the results are rarely placed in a broader climatic context.

Distribution and influencing factors of Ericaceae-dominated shrublands

In the context of the French Alps, we have shown that ericaceous-dominated shrublands are distributed in the northern and external subalpine belt (Figs. 7 and 8) corresponding to wetter conditions compared to the southern inner subalpine belt. Therefore, shrublands occurring in South-exposed slopes of the inner Alps (e.g. in the Queyras massif) can be considered as marginal populations. Interestingly, Francon et al. (2021) found that continentality and slope aspect significantly modulate the radial growth response of *R. ferrugineum* to elevated growing degree days, with populations located in the drier inner Alps responding negatively to increasing temperature during the growing season. Our results show that these populations are located at their range limit. Inversely, Francon et al. (2021) found that *R. ferrugineum* individuals in the wettest locations will benefit from the future warming without water limitation. We found that those individuals are actually located in the optimal domain of Ericaceous-dominated shrublands (Gams angle around 50°). This suggests that moisture availability shapes the range limit of Ericaceous shrubs and that the ongoing changes in water deficit due to rising temperature will have a negative impact on shrublands at their dry range limit, i.e. the southern inner Alps (Michalet et al. 2020).

We found a limited effect of bedrock on the distribution of ericaceous shrubs, yet R. ferrugineum is known to occur mainly on siliceous rocks (Theurillat et al. 1994). This is because dense shrublands dominated by V. uliginosum or V. myrtillus can be found in either siliceous or sedimentary rocks, hence marginalizing the bedrock specificity of R. ferrugineum (Fig. 7). Regarding pastoral activities, we also found limited effect compared to climatic variables. Areas not currently under domestic grazing do not appear to be more conducive to the presence of shrublands. Also, considering the time needed for shrubs to develop (PornonDoche 1995), it is likely that the slight effect detected is due more to the fact that the areas currently being farmed are located where there is less woody cover than vice versa. However, it is known that pastoral practices can locally suppress the presence of woody vegetation, notably through the use of fire-clearing, which is still used in some places (Rius et al. 2009, Bal et al. 2011, SeijoGray 2012, PausasKeeley 2014). Similarly, ski resorts have been shown to negatively affect woody vegetation cover due to mechanical damages (Wipf et al. 2005). Thus, the lack of effect can be explained by a difference in scale between our analyses and these local phenomena, suggesting a more detailed study that also includes geomorphological processes and biotic competition.

Implications for future dynamics of shrublands

Our results raise questions about the future dynamics of shrublands. While several studies show a strong link between shrub dynamics and encroachment and climatic factors (Šenfeldr et al. 2021, Yang et al.

2022, Francon et al. 2023), the role of past land use cannot be overlooked (Galop 1994, Améztegui et al. 2010, Ameztegui et al. 2016, MalfasiCannone 2020). Land abandonment during the industrial revolution has been a major driving force behind the current trajectory of alpine landscapes (Tasser et al. 2007, Rutherford et al. 2008, Pecher et al. 2011), as at that time, farmers used high mountain pastures for their cattle and eliminated shrublands by fire. Therefore, two hypothesis have to be considered: (1) The current distribution is primarily shaped by climate site conditions, (2) The current distribution is the outcome of contrasting past land-use of the mountain ranges. As an alternative hypothesis, we suggest that the decline of the traditional agro-sylvo-pastoral system that started in the mid-19th century is a common critical juncture in the trajectory of shrublands across all mountain ranges (CapocciaKelemen 2007). Starting from this period, site topoclimatic conditions have led to contrasting growth and encroachment rates with more rapid growth and expansion in the core of the niche, and thus to broader distribution, while shrublands located in marginal areas undergo slower growth and expansion, and thus limited space occupancy. This hypothesis is supported by early demographic data suggesting a relatively similar demographic decline across the French Alps, starting at the same dates and with a similar magnitude (Préau 1963). Consistent with this, PornonDoche (1995) studied the age and dynamics of *R. ferrugineum* individuals and found that in closed shrublands, the oldest ramets (individuals) were dated to the late 19th century, while Escaravage et al. (1996) estimated the age of the oldest individual in a nearby subalpine closed shrublands to be at least 300 years old. Similar age structure was found in the Italian Alps (MalfasiCannone 2020). Their results suggest that individuals aged 50-60 years spread vegetatively when grazing ceased until shrublands canopy closure (Pornon et al. 1997). These studies were all conducted at a site that we identified as being in the core range of ericaceous-dominated shrublands (Taillefer Massif, in the northwestern French Alps). Escaravage et al. (1996) compared a wet site with a drier site and explained the ability of shrubs to colonize a slope through their ability to develop vegetatively, with vegetative propagation being favored on wet sites. Further investigation into the age structure of closed shrublands in marginal populations could provide evidence on the respective role of past or current land-use and site conditions on shrublands trajectories in above forest areas.

Conclusion

Our study fills a critical knowledge gap regarding shrub ecology and dynamics in the European Alps. For the first time, using remote sensing, we successfully detected the occurrence of shrublands in the French Alps at a 20m resolution. Our findings demonstrate that the interplay of rainfall continentality and topography plays a crucial role in shaping the range limits of ericaceous-dominated shrublands. To a large extent, this confirms observations from the first biogeographers using a quantitative approach. The perspectives offered by this cartography extend to various research prospects. First, it enables the identification of sites located at the margin of species niches, where dendrochronological or ecophysiological investigations could be conducted at individual level. Secondly, it facilitates the analysis of bioclimatic factors explaining the shrubline position and dynamics. Lastly, it offers a unique opportunity to investigate the past and future dynamics of shrubs, including potential drivers such as climate, site conditions, grazing, and other past human activities. Addressing these questions is paramount for our ability to forecast future trajectories of alpine vegetation and effectively adapt to the resulting changes in ecosystem services. Ultimately, our study provides an important baseline tool for monitoring mountain shrub dynamics, which we believe can be applied in the years ahead to track and better understand ongoing shifts in the alpine shrub ecotone.

Acknowledgements

Data Availability Statement

The data that support the findings of this study are available upon reasonable request from the authors. Ericaceous-dominated mountain shrublands classification raster can be found in the following link: https://zenodo.org/records/10154518.

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