



# Sustainability of *Artemisia umbelliformis* gathering in the wild: an integration of ecological conditions and harvesting exposure

Ninon Fontaine, Perrine Gauthier, Sophie Caillon, John D. Thompson,  
Isabelle Boulangeat

## ► To cite this version:

Ninon Fontaine, Perrine Gauthier, Sophie Caillon, John D. Thompson, Isabelle Boulangeat. Sustainability of *Artemisia umbelliformis* gathering in the wild: an integration of ecological conditions and harvesting exposure. *Global Ecology and Conservation*, 2024, 51, pp.e02886. 10.1016/j.gecco.2024.e02886 . hal-04651272

**HAL Id: hal-04651272**

**<https://hal.inrae.fr/hal-04651272v1>**

Submitted on 17 Jul 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License



Contents lists available at ScienceDirect

## Global Ecology and Conservation

journal homepage: [www.elsevier.com/locate/gecco](http://www.elsevier.com/locate/gecco)

## Original Research Article

Sustainability of *Artemisia umbelliformis* gathering in the wild: An integration of ecological conditions and harvesting exposureNinon Fontaine<sup>a,\*</sup>, Perrine Gauthier<sup>a</sup>, Sophie Caillon<sup>a</sup>, John D. Thompson<sup>a</sup>, Isabelle Boulangeat<sup>b</sup><sup>a</sup> CEF, CNRS, Univ. Montpellier, EPHE, IRD, 1919 route de Mende, Montpellier 5 34293, France<sup>b</sup> Univ. Grenoble Alpes, INRAE, LESSEM, 2 Rue de la Papeterie, Saint-Martin-d'Hères 38402, France

## ARTICLE INFO

## Keywords:

Harvesting

Integrative approach

Social-ecological system

Génépi

Wild alpine plant

High Mountain ecosystems

## ABSTRACT

Harvesting of wild plants is a traditional practice that is sustainable if the plant populations reproduce and persist. The *génépi*, *Artemisia umbelliformis*, occurs on crests and summits in the Alps, and is harvested mainly by amateurs. However, little is known about the ecology of this species and the practice of harvesting has received little scientific attention. Here we assess the sustainability of *génépi* harvesting through an integrative approach combining: (1) the quantification of spatial ecological variation across the distribution of *A. umbelliformis* in the southern Alps and (2) the examination of the social-ecological parameters that modulate the intensity of harvesting practices. We showed that topographic roughness is important for the presence of the species at a 25-m resolution, while its cover at a 1-m resolution is mainly influenced by space availability (with a fine-grained stony substrate and limited vegetal cover). Our results show how the amateur activity of harvesting depends on resource availability, sitehiking attractiveness, and to a lesser extent the accessibility of the harvesting site. More precisely, harvesting intensity is more closely correlated with resource availability at the landscape scale than at the harvesting site scale, with a stronger importance of plant density in a large zone (500 m and 1 km buffers) than local density in a given site. Finally, we map both the potential ecological sensitivity of *A. umbelliformis* and its exposure to harvesting to produce an integrated ecological risk assessment for the conservation of this species. This study illustrates how the concept of the niche can be more precisely recognised by integrating both human and ecological dimensions, particularly when dealing with the sustainability of wild plant harvesting.

## 1. Introduction

In conservation planning and resource management, “ecological risk assessment” provides a framework to evaluate the ecological effects that result from the combination of human activities and environmental parameters (Mattson and Angermeier, 2007; Suter et al., 2003), and the potential vulnerability of species, habitats and ecosystems to a diversity of ecological and social pressures (Gallagher et al., 2012; Noss, 2000). It thus provides a means to assess priorities for conservation management (Kerns and Ager, 2007), e.g. the spatial delimitation of vulnerable areas (Abbitt et al., 2000). The notion of vulnerability can be decomposed into different components that concern the exposure to risk factors, their intensity and impact, and the sensitivity of species, habitats and ecosystems

\* Corresponding author.

E-mail address: [ninon.fontaine@cefe.cnrs.fr](mailto:ninon.fontaine@cefe.cnrs.fr) (N. Fontaine).<https://doi.org/10.1016/j.gecco.2024.e02886>

Received 2 November 2023; Received in revised form 8 February 2024; Accepted 4 March 2024

Available online 6 March 2024

2351-9894/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

to different risk factors (Stelzenmüller et al., 2010; Wilson et al., 2005).

As a result of their sedentary nature, wild plant populations cannot avoid repetitive impacts. When harvested repeatedly without taking their sensitivity into account, wild plant populations are at risk, even if the effects of harvesting on populations may vary in relation to harvester practices (e.g. intensity, the part of the plant that is collected, tools that are used), the life form and demographic traits of the plant (Ghimire et al., 2005; Van der Voort and McGraw, 2006), and the ecological conditions where the plant grows (Svenning and Macía, 2002), i.e. its ecological niche. To assess the sustainability of wild plant harvesting, an integrative approach is thus necessary, combining both ecological variables and sociological features associated with the practice of harvesting (Schmidt and Ticktin, 2012; Teixidor-Toneu et al., 2022; Ticktin et al., 2023). The variation of these factors should be analysed at different spatial scales.

High mountain areas are particularly interesting for the study of plant vulnerability to harvesting and the development of a spatial interdisciplinary approach. First, in these areas, crests and summits are particularly harsh environments (Körner, 2011, 2003) where ecological conditions may change on small spatial scales in relation to micro-topography and sharp gradients in abiotic variables such as substrate granulometry (rocks, stones, bare soil) or micro-climatic conditions (Scherrer and Körner, 2011; Tovar et al., 1995). Second, harvesting is dependent on resource distribution and availability (Hawkes and O'Connell, 1981; Soldati and de Albuquerque, 2012); hence its practice may be spatially structured in relation to the heterogeneity of mountain environmental conditions. Two important elements here are the relative inaccessibility and hazardousness of reaching certain areas in mountain environments (Bourdeau, 2005). The danger and difficulties associated with mountain harvesting make this activity possible only for certain people. It is particularly true for *génépi*, a group of plants growing in high-altitude rocky habitats which stems are harvested for personal use during recreational activities as *génépi* carry a strong alpine imaginary (Delahaye, 2008).

The objective of this paper is to jointly integrate sociological and ecological parameters into a study of the potential risk of harvesting for plant populations. Our study involves a spatial identification of the main potential risk factors, including both ecological conditions and harvesting pressure for a wild plant species growing in a high mountain environment. To do so we construct an integrative approach in which we (1) describe the ecological niche of the study species at different spatial scales, (2) explore the parameters influencing the spatial distribution and intensity of harvesting practices and (3) based on these two lines of information, identify how sensitivity and exposure of plants to harvesting, combined in an ecological risk assessment framework, could improve conservation strategies.

## 2. Material & methods

### 2.1. Study species

Four *génépi* species (*Artemisia eriantha*, *A. genipi*, *A. glacialis* and *A. umbelliformis* - Asteraceae) occur in the southern Alps. Their stems are harvested mainly for the preparation of liqueurs (e.g. Delahaye, 2008; Rivière-Sestier, 2000), obtained by macerating the floral stems in alcohol for around 40 days, and then adding sugar. Although professional harvesting of *génépi* species has declined due to cultivation (Rey and Slacanin, 1997), recreational harvesting is still very common (field observations and newspapers, e.g. Dauphiné Libéré, 2021). In addition to being primarily a non-commercial product, *génépi* stems are non-essential resource, they do not enter the daily diet of harvesters and the liqueur is associated to festive moments. *Génépi* harvesting is thus a recreational activity from the harvest to the transformation and consumption. Recreational harvesting can nevertheless affect plant populations, and the multiplicity of harvester profiles made the control of the harvesting amount and sites even more difficult.

All four species primarily grow above 2000 m.a.s.l. in alpine rocky habitats (Tison and Foucault, 2014), but little is known about their precise ecology nor the impacts of human harvesting on their distribution. In the southern Alps, where this study was undertaken, *Artemisia umbelliformis* is the most frequent of the four species, more fragrant than *A. glacialis* and generally preferred by recreational harvesters. Our study thus focused on *A. umbelliformis*.

Occurrence data for *A. umbelliformis* were extracted from the SILENE database of the "Conservatoire Botanique National Méditerranéen de Porquerolles" (<http://www.silene.eu/index.php?cont=accueil>, last accessed on 10 March 2022), from the Biodiv' AURA database of the Pôle d'Information Flore-Habitats-Fonge (<https://www.biodiversite-auvergne-rhone-alpes.fr/>, last accessed on 17 March 2022), from the Ecrins National Park database ([https://geonature.ecrins-parcnational.fr/dataexport/Observations\\_Biodiversite\\_Synthese\\_PNE\\_SIG.gpkg](https://geonature.ecrins-parcnational.fr/dataexport/Observations_Biodiversite_Synthese_PNE_SIG.gpkg), last accessed on 10 March 2022), and from our own field records. Only locations posterior to 1980 were considered, to avoid occurrences collected with too much uncertainty on the localisation, and we excluded observations < 5 m apart to avoid potential redundancies. Our database contained 4042 occurrences of *A. umbelliformis* in the French Alps.

*A. umbelliformis* is subject to regulatory control of harvesting. In the core-zone of the Vanoise National Park (NP) harvesting is completely forbidden, while in the core zone of the Mercantour NP, harvesting is permitted in the month of August, for 80 flowering stems per person in sites 200 m away from a road. Outside of the core zone of the Vanoise and Mercantour NP in the southern Alps (including the Ecrins NP), harvesters are allowed to cut 100 flowering stems per person per day.

### 2.2. Study areas

The niche and spatial distribution of *A. umbelliformis* were studied in the French Alps and more detailed observations were made at a plot scale (local conditions – 1 m<sup>2</sup>, harvesting measures – around 400 m<sup>2</sup>) in the Mercantour NP. The Mercantour NP is the southernmost distribution of *A. umbelliformis* in the Alps, and is characterised by a complex geology and diverse alpine and Mediterranean climatic influences. Altitude in the core zone ranges from 490 to 3143 m.a.s.l., where 1448 occurrences of *A. umbelliformis*

occur (36% of French Alp occurrences) from 1243 to 3073 m.a.s.l.

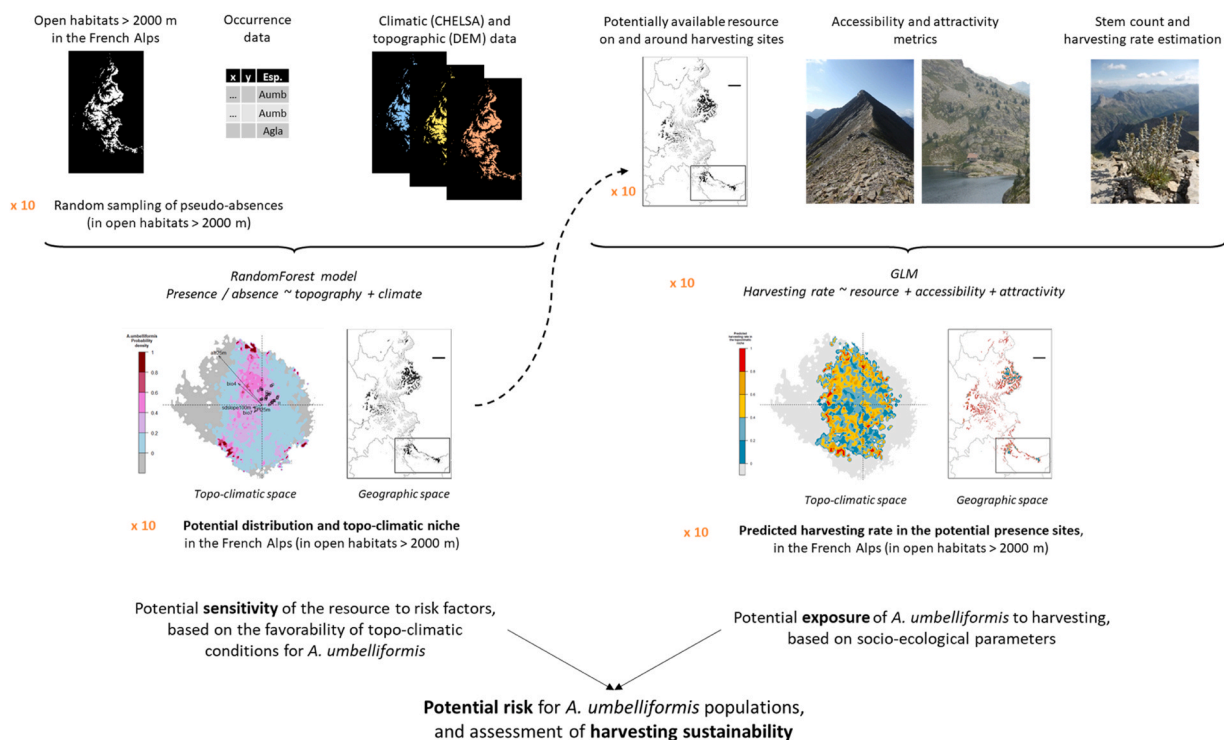
The analysis of *A. umbelliformis* distribution was restricted to open habitats above 2000 m.a.s.l., in order to focus on favourable ecological conditions where the species is the most abundant in high mountain habitats. This habitat filter concerns only 5.7% of the French Alps observations and less than 0.2% of those in the Mercantour NP. The plot scale measures were used to describe the local ecological conditions where *A. umbelliformis* plants occur and the way harvesting practices varies among sites.

### 2.3. Characteristics of the ecological niche

Topographic parameters were derived from a digital elevation model (BD Alti® version 2.0 IGN -<https://geoservices.ign.fr/documentation/diffusion/telechargement-donnees-libres.html> - accessed on 5 September 2020). Data at 25 m resolution was used, and altitude, aspect, slope, and a standardised topographic position index (*TPI*) were calculated in a raster format for the whole French Alps, using the “terrain” function in the R package Raster (Hijmans et al., 2020). *Eastness* and *northness* were calculated as  $\sin(\text{aspect})$  and  $\cos(\text{aspect})$ , respectively. To provide an index of topographic roughness, we calculated the slope angle variability around each 25 m unit, using a window of 100 m width. *Eastness* and *northness* at 100 m resolution were also calculated to describe hillside effect.

Climatic parameters were extracted from the CHELSA database (Karger et al., 2021). The resolution of this data is around 1 km, providing a broad indication of climatic variability across the French Alps. We considered that climate at lower resolution is mainly a modulation of regional climate at 1 km because of topography, so that a combination of climatic and topographic data describes fairly accurately the topo-climatic niche of *A. umbelliformis* at the scale of the French Alps. We used the 19 bioclimatic variables derived from CHELSA database, together with five climate-related variables built from products of CHELSA initiative (Brun et al., 2022): frost change frequency (*fcf*), growing degree days and number of growing days at 0°C (*gdd0* and *ngd0*), snow cover days (*scd*) and near-surface wind speed (*sfcwind*).

To refine this topo-climatic niche characterisation at a 25-m resolution, we selected 26 sites of *A. umbelliformis* covering the different geological units of the Mercantour NP, for a fine-scaled study of the ecological niche. In each site, three 1-m<sup>2</sup> quadrats were selected in high-density patches of the study species. Following previous studies of this kind (Fontaine et al., 2022; Gizaix et al., 2021; Papuga et al., 2018), topographic and edaphic characteristics were measured in each quadrat, together with substrate analysis, plant community descriptions and an estimation of *A. umbelliformis* density (Appendix D).



**Fig. 1.** Workflow of the main steps of modelling to characterise the ecological niche of *Artemisia umbelliformis* and associated potential harvesting, to assess the potential risks. The “x 10” indicates that the step was repeated 10 times.

## 2.4. Spatialisation of exposure and intensity of harvesting

### 2.4.1. Estimation of harvesting intensity

Harvesting of *génépi* is done by cutting floral stems generally just above the leaves of the rosette. It is thus possible to count the number of cut stems for each rosette and the number of remaining, entire stems or stem bases that are visible at the end of the harvesting season (in September): the harvesting rate (cut stems/total number of stems) is used to estimate the harvesting intensity. In 21 of the 26 sites characterised for their ecological niche at a 1-m resolution, we quantified stem production and harvesting rate for all flowering plants in each quadrat. We also included around 30 additional flowering rosettes situated close to the three quadrats in each site, in order to provide a more complete estimation of rates of stem harvesting for each site. Twenty-four additional sites of harvesting estimation were studied in order to cover a wider range of conditions, mainly in terms of accessibility. We thus had a total of 45 harvesting sites, and counts were done in 2020, 2021 and 2022 with some sites visited once and other visited the three years.

### 2.4.2. Variation in harvesting intensity

We hypothesised that harvesters optimise their search by avoiding sites with a long or difficult access or with low levels of resources, and by combining a pleasant hike with *génépi* harvesting. This fits with optimal foraging theory and the fact that our study primarily involves recreational harvesting. We estimated the abundance of *génépi*, accessibility to the site (travelling time from a point of motorised access), accessibility *within* the site (difficulty and danger of navigating and approaching plants within the site), and finally the interest of the site in terms of the objective of the hike. These parameters were calculated at a 100 m resolution, which we consider consistent with the scale at which harvesters prospect *génépi*.

Resource availability was estimated *in* the site, using plant and stem counts (density of *A. umbelliformis* rosettes, flowering rosettes and stems), and *around* the site, using the potential presence of *A. umbelliformis* predicted from topo-climatic conditions (Fig. 1 - modelling procedure presented in 2.5.) to avoid the spatial disequilibrium in actual observation data. We used three buffer sizes: 200 m, 500 m or 1 km radius around the site, and counted the number of 25 m pixels with predicted presence of *A. umbelliformis* within these radii.

To assess accessibility to the site we used the least-cost-path method in which we first computed a friction surface (i.e. human displacement speed in each raster unit, depending on path presence and slope angle), then cumulated the costs of moving from one raster unit to another to obtain the minimal cost, quantified as the minimal access time (Appendix A). To assess accessibility *within* the site, corresponding to the danger (risk of falling) of moving in and around the site, we used the slope at the site as a proxy of hazard, as slope increases instability and the risk of falling. We also considered that roughness is important, because a chaotic topography makes harvesting harder and requires increased attention.

To assess the interest of a site, we considered that the presence of a summit close to the site could be an added value to the hike. We thus calculated the minimal distance between the site and a summit. We used the “orographic detail” list in the BD Topo® (version 3.0 IGN - <https://geoservices.ign.fr/bdtopo>) and selected peaks and summits with more than an intercommunal importance. Lakes and refuges could also be attractors as they give an objective to the hike and the latter can be a step in trekking. We used the same indices as for summits, with lake localisation obtained from “plan d’eau” shapefile from BD Topo®, and refuge localisation from CampToCamp database (<https://www.campnocamp.org>).

Another parameter obtained from harvester interviews is the discreet and secretive aspect of the practice: harvesters prefer places where they cannot be seen. We traduced this through a discretion variable, calculated by the distance as the crow flies from known paths (extracted from BD Topo®).

## 2.5. Models and multivariate analyses

For the potential distribution of *A. umbelliformis* in the French Alps, we used occurrences and topo-climatic data at a 25 m resolution, to build a spatial distribution model using Random Forest (RF, R package *randomforest*, Liaw and Wiener, 2002) (Appendix B). This is a powerful method to detect data patterns even with noisy or sparse data, as is often the case with opportunistic occurrences. Moreover, RF are not based on assumptions about the type of relation between response variable and predictors, and are less sensitive to pseudo-absence selection (Barbet-Massin et al., 2012).

Ten random samplings of pseudo-absences allowed us to evaluate the variability of models depending on input data. We used the same ratio pseudo-absences/presences as proposed by Barbet-Massin et al. (2012), and evaluated the 10 models (corresponding to the 10 random samplings of pseudo-absences) through calibration-validation procedure with 70/30% of the data (10 times for each pseudo-absence sampling) using several quality and predictive capacity metrics (McFadden, Nagelkerke, Tjur  $R^2$ , and AUC, Kappa, TSS respectively (Allison, 2013; Thuiller et al., 2009)).

The importance of each variable in the 10 complete RF model was calculated as  $1 - \text{cor}(\text{Pred}_{\text{raw},i}, \text{Pred}_{\text{randomised},i})$ , a metric which is implemented in the R package BIOMOD (Thuiller et al., 2009), using the correlation between predictions based on the raw data ( $\text{Pred}_{\text{raw},i}$ ) and predictions based on raw data with the variable  $i$  being randomised ( $\text{Pred}_{\text{randomised},i}$ ). A strong correlation between the two predictions means that the variable  $i$  gives the same information as its randomised version, and is thus of low importance.

Using all the data concerning harvesting intensity at the site scale (accessibility, attractiveness, resource availability), we built GLM to detect which and how the variables affect the harvesting rate (selecting less correlated variables, and searching for better explanatory variables in both directions in the stepwise search - R package *stats* (R Development Core Team, 2010)). We removed correlated variables within each group of variables: distance to a lake was strongly correlated with distance to a refuge (Pearson correlation coefficient  $\text{cor}=0.76$ ,  $p<0.001$ ), as was the density of plants with the density of flowering plants ( $\text{cor}=0.93$ ,  $p<0.001$ ) and



the potential presence of *A. umbelliformis* in buffers of either 200 m or 500 m radius ( $cor=0.87$ ,  $p<0.001$ ). Although correlations were important between density of stems and density of plants ( $cor=0.73$ ,  $p<0.001$ ), and between potential presence of *A. umbelliformis* in buffer zones of 1 km and 500 m radius ( $cor=0.77$ ,  $p<0.001$ ), we chose to keep both variables in each case in order to examine their relative importance. We acknowledge the limitations associated with the correlations between these two variables in the interpretation of results. For the GLM we used a binomial function with a logistic link, as harvesting rate is a repetition of Bernoulli's experiment for each stem (cut or entire).

In the risk assessment procedure, plant distribution is a proxy for sensitivity and harvesting intensity for exposure (Fig. 1). We used the models obtained for the ecological niche and harvesting rates to predict the potential distribution of the species and its harvesting rates in the French Alps, in open habitats above 2000 m.a.s.l. For harvesting rate, extrapolation was restricted to 20% of the range of calibration, to avoid the potential threshold effects or truncated response curves. These predictions were mapped in the geographic space and plotted in the topo-climatic space (Principal Component Analysis with all combinations of topo-climatic conditions that exist in open habitats above 2000 m.a.s.l. in the French Alps, using the function *dudi.pca* - R package *ade4* (Dray et al., 2018)).

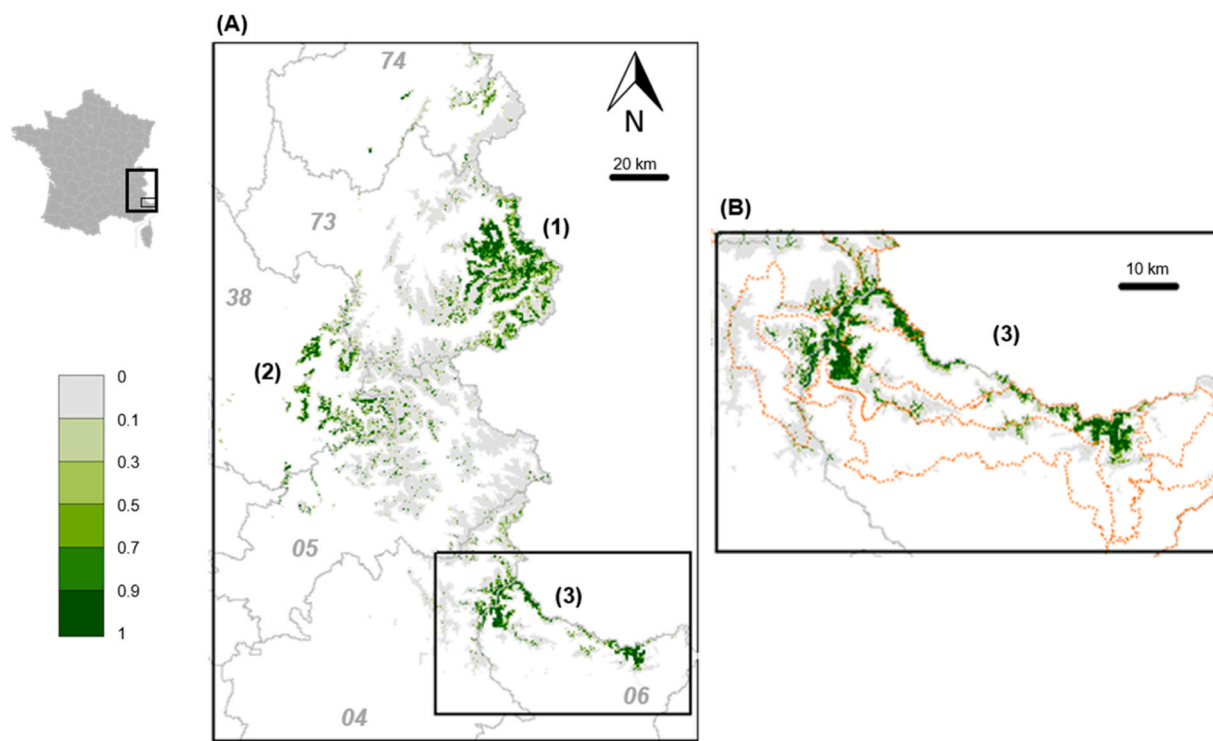
We also used data collected in the study of 1-m<sup>2</sup> quadrats to test for variation in ecological variables on a fine scale resolution and their contribution to the abundance of *A. umbelliformis* and harvesting rate (Appendix D).

### 3. Results

We focused first on the ecological niche to assess the potential *sensitivity*, and secondly on the spatial distribution of harvesting intensity to assess the *exposure* of *A. umbelliformis* to this risk factor. Finally, we combined *sensitivity* and *exposure* to assess ecological risks.

#### 3.1. Ecological niche characteristics

Using RF modelling, we were able to detect which topo-climatic variables are important in explaining the spatial distribution of *A. umbelliformis*. The mean AUC for the 100 repetitions of the model is 0.89, and the five main variables, out of thirty-five ordered by



**Fig. 2.** Predictions of *A. umbelliformis* presence in open habitats above 2000 m.a.s.l., (A) in the French Alps and (B) in the Mercantour National Park. The figure summarises ten RandomForest model predictions using topo-climatic variables as predictors and ten different random samplings of pseudo-absences. Light grey pixels correspond to the background of the model, i.e. open habitats above 2000 m.a.s.l., and coloured pixels are areas where *A. umbelliformis* is predicted to be present, the darker being the higher proportion of models (on ten predictions) predicting presence. Grey lines and numbers correspond to the French department (74 Haute-Savoie, 73 Savoie, 38 Isère, 05 Hautes-Alpes, 04 Alpes-de-Haute-Provence, 06 Alpes-Maritimes); orange lines in (B) are the Mercantour National Park perimeter (core and membership area). The three main identified areas are east of the Savoie department (1), west of the Ecrins National Park (2) and nearly everywhere in the Mercantour National Park (3).

decreasing relative importance (using the mean importance value of 100 repetitions of the model), are slope variability (*sdslope* - 20.5%), temperature annual range (*bio7* - 13.6%), topographic position index (*TPI* - 9.1%), temperature seasonality (*bio4* - 7.6%) and altitude (6.6%) (Appendix C).

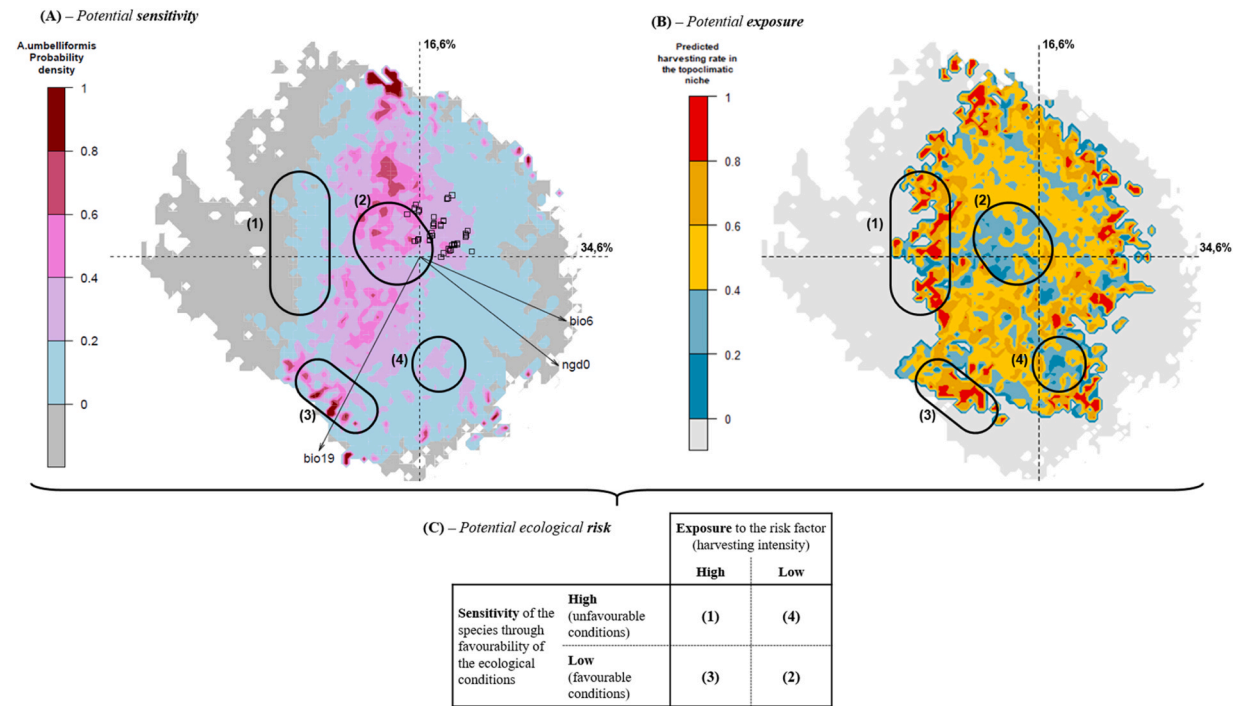
While these topo-climatic parameters are important for the presence/absence of the species, they do not significantly affect *A. umbelliformis* cover within sites. At a fine resolution, substrate and biotic components measured in the 1-m<sup>2</sup> quadrats are more important than topographic and edaphic variables for the variability of the species' cover (Appendix D).

Predictions from the RF model were plotted in geographic and topo-climatic spaces, in open habitats above 2000 m.a.s.l. In the French Alps, the model shows three main zones of favourable environmental conditions for *A. umbelliformis* (Fig. 2): (1) east of the Savoie department, (2) west of the Ecrins NP and (3) across the Mercantour NP. It is less probable to observe this species in the Mont Blanc Massif, in the east and centre of the Hautes-Alpes department (05 – Fig. 2), even though open habitats above 2000 m.a.s.l. are common in these areas. In the topo-climatic space, the density of modelled presence appears to be divided among several topo-climatic groups, as witnessed by the dark pink areas (Fig. 3A). Both limits of the main axis in this space are of low suitability for *A. umbelliformis*, this axis being positively correlated with snow cover duration (*scd*) and negatively with temperature variables (*bio6*–*5*–*11*–*10*–*1*).

3.2. Variability of harvesting intensity

Following the selection of uncorrelated variables, GLM was run and the stepwise selection of variables, based on AIC, led to the removal of the quadratic term of stem density, while all other variables had a significant effect on both quadratic and linear terms. Compared to the null model (based on the randomisation of the explanatory variables), the mean AIC gain is 34%, the likelihood ratio test is significant ( $p<0.001$ ), Nagelkerke and Cox-Snell pseudo-R<sup>2</sup> (quality statistics based on deviance of the null model (Allison, 2013)) are 0.98. As scores of the harvesting model based on variables measured in quadrats are clearly lower (Appendix D), we focused on harvesting models based on variables at the site resolution.

The models explained 65% of the deviance on average. They showed a significant effect of the year, with a harvesting rate in 2020



**Fig. 3.** Potential ecological sensitivity of *A. umbelliformis* (A) and exposure to harvesting (B) in the ecological space, with corresponding ecological risk assessment (C). Ecological space is represented through a PCA of the topo-climatic conditions in open habitats above 2000 m.a.s.l. in the French Alps: the first axis is driven by temperature variables (*ngd0*: number of growing days above 0°C, *bio6*: minimal temperature of the coldest month), the second axis is driven by precipitations (*bio19*: precipitation of coldest quarter). (A) Topo-climatic space with predictions of *A. umbelliformis* presence. In each combination of conditions, the colour scale represents the number of predicted presences (best model) relative to the availability of these conditions in the study area. Small squares correspond to the combination of topo-climatic conditions sampled for harvesting evaluation. (B) Median of the predicted harvesting rate of *A. umbelliformis* in each combination of topo-climatic conditions. The colour scale represents the median of predicted harvesting rate in each combination of topo-climatic conditions, these conditions being associated with accessibility, attractiveness and resource abundance, used as predictors in the GLM for harvesting rate. The four zones identified by numbers in (A) and (B) correspond to typical cases in (C). In (A) and (B) grey background represents the existing topo-climatic conditions that are not favourable to *A. umbelliformis* (model predictions).

significantly higher than that in 2022, and a significantly lower rate of harvesting in 2021 than in the two other years. However, this variable is of relatively low importance in the overall model (<5% - Table 1).

Resource availability had a highly significant effect on harvesting rate (41.0% of cumulative importance), with a stronger importance of plant density in a large zone (500 m and 1 km buffers) compared to local density in a given site (approximately within a 25 m radius - Table 1).

Attractiveness and the interest of the hike made an important contribution to the model (28.4% of cumulative importance), mainly because of refuges. However, refuges are not attractors as harvesting rate increases with distance to refuges that are generally situated at lower altitudes, further away from the crests where *A. umbelliformis* is more abundant.

Accessibility to and within the site had a cumulative importance of 26.0% together with distance to a path (also considered as a parameter for discretion). Sites closer to paths were less harvested than sites further away, but if access time (the calculation of this parameter includes paths) is too high, harvesting rate decreased. Concerning accessibility, the danger associated with moving in and around the site described by *sd(slope)* had a negative effect on harvesting rate (Table 1).

### 3.3. Combining ecological niche characteristics and harvesting intensity to assess ecological risk

We used variables that vary at the site scale (accessibility, discretion, attractiveness, resource availability - Table 1) to predict harvesting rates in the French Alps where *A. umbelliformis* could occur (based on RF predictions). In the absence of data on density of stems and plants in the entire French Alps, we used measured median values of these densities, considering that their importance is low (Table 1) and thus that they are not primary determinants of harvesting rate. Harvesting rate was variable across the topo-climatic niche space of *A. umbelliformis*, and was predicted to be higher in the outer part of the niche (e.g. in zones (1) and (3) - Fig. 3B), and lower in the centre of the topo-climatic space (e.g. in (2)). It was also highly variable in geographic space (Appendices E and F).







Considering the topo-climatic space for both potential presence and harvesting intensity, it appears that zone (3) of the topo-climatic space (Fig. 3) has both a high ecological favourability (probability density close to 1) and a high predicted harvesting rate (low sensitivity but high exposure to harvesting risk). On the contrary, zone (1) is less ecologically favourable (probability density close to 0) and harvesting rate is predicted to be high, meaning that both sensitivity and exposure to harvesting risk are high. Risk is the lowest in zone (2) with high ecological favourability and low exposure, while it is intermediate in zone (4) with low exposure but also less favourable ecological conditions (Fig. 3C).

The four typical cases in Fig. 3 can be represented in geographic space (Appendix F). Using the median of predicted values as a threshold for potential sensitivity and exposure indices, it appears that across the French Alps, the risk is high for 29.1% of spatial units that represent a potential presence of *A. umbelliformis* (at least one model predicting presence), with relatively unfavourable topo-climatic conditions and high predicted harvesting rate (e.g. zone (1) in Fig. 3), and the risk is low for 29.2%, with favourable conditions and low harvesting rate (zone (2)). Zones (3) and (4) correspond to 20.9% and 20.8% of spatial units respectively.

To further examine the role of regulatory control on harvesting, we quantified and compared predicted mean harvesting rate in the

**Table 1**

**Variables affecting harvesting rate**, selected in a stepwise manner in a GLM with quadratic link between variables and harvesting rate. The symbol corresponds to the shape of the response of harvesting rate to the variable (shown only if there is at least one model where the relative importance of the variable is higher than 10%), with the number of models where the relative importance of the variable is higher than 10%. The importance of the variable is calculated in the same way as RF models (see 2.5.), comparing the predictions of the model with the real variable and its randomised version.

Context variables		Effect of the variables on the harvesting rate (number of cut stems relatively to total stem number - GLM with a logistic regression)		
		Shape of response and number of models with a relative importance > 10%	Relative importance (%)	
Accessibility	Minimal access time to the site from a motorised access		2	7.7%
	Slope of the site	-	-	1.5%
	Roughness of relief on the site (danger - <i>sd(slope)</i> )		2	5.5%
Discretion	Distance to a path (as the crow flies)		6	11.2%
Attractiveness	Distance to a summit	-	-	2.0%
	Distance to a refuge		10	26.4%
Resource	Density of <i>A. umbelliformis</i> in a 500 m buffer		5	14.8%
	Density of <i>A. umbelliformis</i> in a 1 km buffer		5	23.3%
	Density of stems on the harvesting site	-	-	0.7%
	Density of plants on the harvesting site	-	-	2.2%
Date	Year of the study	20 > 22 > 21	-	4.6%



three national parks (NP) in the French Alps (Table 2). In the Vanoise NP *A. umbelliformis* is not a limited resource, whereas topographic conditions in the two other national parks are less favourable for the species. It is also in the Vanoise NP that harvesting rate is predicted to be the lowest (Table 2). However, predictions are limited by the range of conditions used for calibration: in the Ecrins NP sites with *génépi* are less accessible (time to reach sites and slope are both higher than in the Mercantour NP (Appendix A)), and resource density is also different (Fig. 2).

#### 4. Discussion and conclusion

Our ecological risk assessment approach reveals the ecological parameters of the niche that affect the sensitivity of *A. umbelliformis* and the degree of exposure in terms of variation in harvesting intensity. With our results, we are not able to determine if the study species is “in danger”: to do so data on population dynamics for several years are needed as it is a perennial species. What our results underline is the importance of conjointly taking into account sociological and ecological parameters to describe the conditions where plant populations are likely to persist, and thus inform conservation strategies related to harvesting.

##### 4.1. Potential sensitivity of *A. umbelliformis* to risk factors

Topographic parameters are important predictors of *A. umbelliformis* distribution in open habitats above 2000 m.a.s.l. While slope variability and topographic position on a 25 m resolution are closely related to the presence of *A. umbelliformis*, mean slope values and exposure at this resolution are of low importance. Hence, *A. umbelliformis* can be found on a range of slopes and aspects, as long as “roughness” creates favourable local conditions, in terms of micro-climatic variability.

The importance of temperature variables (diurnal and annual range, seasonality) for the model of *A. umbelliformis* presence is consistent with the fact that temperature is a major constraint on plant species in mountain environments with an extended period of freezing risk and a short growing season (Körner, 2003). The importance of temperature parameters in defining the potential niche of *A. umbelliformis* suggests that climate change and associated temperature evolution will probably have a strong effect on its distribution. However it is hard to project with certainty temperature changes in topographically complex high mountain environments where this species occurs (Rahbek et al., 2019). In addition, temperature changes have cascading effects on snow cover, glacier persistence, permafrost and hydrological dynamics (Gobiet et al., 2014; Pepin et al., 2022) that may affect *A. umbelliformis* presence by changing the availability of new open spaces free from ice, as observed for *Artemisia genipi* (Erschbamer, 2007). Although these complex interactions make it difficult to predict the climatic sensitivity of *A. umbelliformis* to future changes, it is well known that climate warming may significantly affect high mountain plants due to the vulnerability of cold-adapted species in alpine areas (Hoegh-Guldberg et al., 2018; White et al., 2023).

For climatic variables and their effects on *A. umbelliformis* distribution at the European scale, using Maxent modelling, de Medeiros et al. (2018) found that precipitation during the driest quarter of the year and mean temperature of the wettest quarter contribute most to a model of *A. umbelliformis* distribution. In our study, temperature variables are more important than precipitation variables, particularly temperature variability (diurnal and annual range, seasonality). The difference between our study and the approach of de Medeiros et al. (2018) reveals the importance of spatial scale and resolution for the study of species distributions and their niches, and the hierarchical effect of environmental variables.

While known occurrences of *A. umbelliformis* represent only 0.3% of 25 m grid units of open habitats above 2000 m.a.s.l., topographically favourable units represent on average 18.5% of the studied area. This difference is probably due, at least in part, to a lack of prospection (in agreement with field observations), historical and dispersal factors and local soil and biotic interactions (Boulangeat et al., 2012; Zhu et al., 2013), as observed for space availability (on and above the soil – Appendix D). The hierarchical effect of environmental variables acting as successive filters can be seen in our study of topography. This variable plays a major role for

**Table 2**

**Comparison of three national parks in the French Alps in terms of potential availability and predicted harvesting rate of *A. umbelliformis*.**

The availability of *A. umbelliformis* (i.e. favourable area) is derived from predicted presences based on topo-climatic RandomForest models (mean value of 10 models based on different pseudo-absences random sampling - data were aggregated from 100 m to 25 m resolution). Mean and standard deviation (sd) for predicted harvesting rate are also calculated from the 10 models based on different pseudo-absences random sampling. Only a subpart of this favourable area is used for predictions as the sites used to calibrate the harvesting model do not cover the whole gradient of conditions encountered in the French Alps, and extrapolation out of the range of calibration is considered to be inaccurate.

		Surface (km <sup>2</sup> )	Surface favourable to <i>A. umbelliformis</i> ... (km <sup>2</sup> and % of total area)	... where extrapolation is considered reasonable (km <sup>2</sup> and % of favourable area)	Predicted harvesting rate where extrapolation is considered reasonable (mean ± sd)
Vanoise	Core zone	533	310 (58.1%)	123 (39.6%)	0.355 ± 0.127
	Membership area	208	27 (12.8%)	9 (32.9%)	0.341 ± 0.088
Ecrins	Core zone	930	187 (20.1%)	6 (3.3%)	0.427 ± 0.180
	Membership area	1597	129 (8.1%)	7 (5.7%)	0.648 ± 0.141
Mercantour	Core zone	679	211 (31.1%)	102 (48.5%)	0.362 ± 0.074
	Membership area	1122	32 (2.8%)	1 (3.5%)	0.665 ± 0.212

the presence of the species in open habitats above 2000 m.a.s.l., but a less important role for local cover. Guisan and Thuiller (2005) also concluded that species distribution and bioclimatic range are primarily related to climatic factors and topography, while variation in abundance is driven by local resource factors.

#### 4.2. A complex of important variables influences exposure of *A. umbelliformis* to harvesting intensity

In the Mercantour NP, the variability of harvesting intensity is closely associated with resource availability and attractiveness of the site (Table 1), while accessibility is of relatively less importance. *A. umbelliformis* harvesting thus differs from optimal foraging theory which predicts that foragers optimise time and energy spent to get a maximum amount of resources (Soldati and de Albuquerque, 2012). This discrepancy is not surprising: g  n  pi gathering is a pleasant activity in which amateur harvesters combine enjoyable hikes with non-profit harvesting. They are not searching to optimise effort and time but to share enjoyable moments with friends and family or to observe wild animals.

The negative link between *A. umbelliformis* density around sites of harvesting and harvesting intensity in a given site suggests that harvesters do not adapt their harvesting modes to the amount of resource around a site. The stronger effect of large densities in the surrounding zone compared to the effect of site density alone implies that the harvesting practice is not targeted on a single specific site but rather on a large area with several patches of the plant resource. This is probably related to the relative rarity of the resource at the site level.

The time needed to reach a site and the danger associated with moving within a site are the most important accessibility variables in our models: harvesters avoid both risky and physically demanding sites. Our discussions with harvesters and people enthusiastic of high mountain environments indeed revealed a mental association between g  n  pi and accidents (or even deaths), as reported by Coll (2011) and various newspaper articles (Dauphin   Lib  r  , 2022, 2011a, 2011b). Because of the importance of danger, we only studied *A. umbelliformis* sites that are accessible without the use of specialised climbing equipment, hence the gradient of conditions is only a subset of the accessibility range. That said, extremely dangerous sites can only be visited by expert rock climbers and alpinists. It would thus be interesting to compare g  n  pi harvesting rates in our study with observations along equipped climbing routes. It is well known that climbing can reduce plant species' richness and abundance on vertical cliff faces (Boggess et al., 2021), however studies focused on species for which human impact is related to harvesting and not just a consequence of climbing, are rare.

Finally, in terms of site choice, harvesters show a preference to return to the same favourite sites (our interviews), as observed for mushroom collecting (Larr  re and de La Soudi  re, 2009). This behaviour may represent a form of appropriation of a specific area and the knowledge of best resource places (Coudard, 1982), and also the importance of particular relational values with plants growing there, i.e. a form of human-plant reciprocity (Locqueville et al., submitted manuscript). This "place attachment" (Sebastien, 2020) could affect site choice in relation to memories or past experiences. Difficult to include in our models, this kind of variables underlines the importance of an ethnological approach for our understanding of patterns of harvesting that cannot be measured in a quantitative manner.

#### 4.3. Integrating ecological and sociological parameters to assess potential risks for a wild harvested plant

##### 4.3.1. Harvesting and ecological processes

*A. umbelliformis* harvesting in the French Alps is predicted to be variable among different parts of its ecological niche, notably with more than 80% of harvested stems in topo-climatic conditions that are less favourable for the species (e.g. zone (1) in Fig. 3). Although only stems are harvested and the sustainable harvesting rate could be higher (Ticktin, 2004), this practice limits seed production and dispersal and may thus affect the demographic rates of *A. umbelliformis*' populations. Moreover, the plant is rarely strongly rooted in the rocky substrate and harvesting can destabilise or completely uproot a plant if it is not done carefully with scissors or secateurs. Indeed, uprooting was observed for 1% of plants with at least one cut stem in 2021 (unpublished data). The ecological niche of *A. umbelliformis* is also locally restricted by substrate or biotic interactions, adding further constraints on plant population dynamics and persistence.

The specific spatial distribution of harvesting suggests that if dispersal between sites is possible, populations in favourable topo-climatic conditions may act as a source, e.g. zone (2) in Fig. 3, and others as sinks, in less favourable conditions, e.g. zone (1). Such source-sink dynamics have been observed in relation to hunting (Novaro et al., 2005) and livestock herbivory (Berry et al., 2008). This inter-population relationship could also be relevant for the distribution of *A. umbelliformis* in relation to harvesting. At the same time, dispersal could also be boosted by humans because harvesters can obtain seeds or plants from the wild and transplant them to their gardens (Appendix D) and harvesters may also play a direct role in g  n  pi dissemination (Auffret et al., 2014).

However, in this study we were not able to predict precise harvesting rates in areas where resource conditions, accessibility and attractiveness are distant from the conditions of sites in the Mercantour NP where harvesting was measured for model calibration. Beyond the calibration range, if response curves show threshold effects or truncated bell shape curves, predicted harvesting rates could be far from reality. Moreover, it is possible that the reasons and practices of harvesters differ among mountain regions, a further limitation to the extrapolation of our model beyond its calibration range.

##### 4.3.2. The benefits of an integrative approach

Our study has revealed strong interactions between ecological processes and harvesting practices, and the need for an integrative approach to analyse conditions for sustainable harvesting. An integrative approach is often based on the concept of social-ecological systems (Berkes et al., 2000) and biodiversity conservation is common in research on the dynamics of socio-ecosystems (de Vos et al.,

2019), primarily because the fate of conservation actions depends on both ecological and social processes (Mascia et al., 2003). In a similar perspective, the description and analysis of the social-ecological system in which harvesting occurs is of much interest for the conservation of the plant resource. Here it is necessary to identify the ecological and sociological dimensions that determine the conditions required for harvested plants to persist, that could define the “social-ecological niche” of the harvested plant species.

In our study, if only topo-climatic niche dimensions on a coarse resolution are considered, *A. umbelliformis* would be largely distributed in the French Alps above 2000 m.a.s.l., especially in the Mercantour NP (Fig. 2, Table 2). In this respect this species does not appear to be threatened at the scale of its geographic range (Rabinowitz, 1981). Although this broad-scaled niche characterisation revealed a lack of data, the diagnostic could also change because of variation in social-ecological parameters that affect species population dynamics more locally. Hence, integrating the risk of harvesting could improve the assessment of the conservation status of plant species. Ignoring the sociological information on harvesting could in fact lead to a positive diagnosis for the conservation status of *A. umbelliformis* in some ecological conditions, e.g. zones (2) and (3), where the social conditions are potentially very different – the harvesting rate is predicted to be higher in zone (3) compared to (2). This would lead to a poorly informed and mistaken positive diagnosis for zone (3). It should also be kept in mind that a presence probability close to 1 does not mean that harvesting is less threatening because *A. umbelliformis* is more abundant: abundance and occurrence probability are not necessarily correlated (Lee-Yaw et al., 2022; Sporbert et al., 2020).

This social-ecological approach is beneficial for conservation structures. Discussions with national park managers have revealed that génépi harvesting is not a serious issue in the Vanoise NP, whereas in the Mercantour NP rangers have observed that harvesting is potentially detrimental to génépi persistence in some areas. Hence, either the plant resource is abundant and sensitivity is low, or exposure and intensity of harvesting are low in the Vanoise NP. This territory is more topo-climatically favourable to *A. umbelliformis* than the Mercantour NP with respectively 58.1% vs 31.1% of topo-climatically favourable conditions in their core zones (Table 2), although we predicted equivalent harvesting rates (ca. 36%). Hence, the first assumption appears to be the most realistic.

One of the main national park missions in France is to promote sustainable uses that contribute to natural and cultural heritage preservation (<http://www.parcsnationaux.fr/fr>). When the objective is to maintain both *A. umbelliformis* populations and the social practice of harvesting, communication of rules for best practices should insist on low resource levels in parts of the ecological niche with poor ecological conditions, and on high harvesting rates in other parts, depending on the component of risk that is identified. National park regulations can also be adapted to identify areas where génépi harvesting should be forbidden, for example in poor ecological conditions for the species, and other sites with a low amount of stems that can be harvested, where harvesting rates are high. Thus, mapping the risk and its components provides key information on what and where to harvest, for managers to define sensitivity and exposure thresholds depending on the specific context of the natural area they manage (Appendix F).

Developing a joint social-ecological approach is however challenging. First, it requires integration of processes on different spatial scales; ecological conditions and harvesting vary from the regional scale to the local plot scale (3.1., Appendix D). A hierarchical framework is thus necessary for the joint study of social-ecological parameters (hierarchical modelling framework - Guisan and Thuiller, 2005). Another challenge is that it is difficult to incorporate human behaviour into social-ecological models because of the multifactorial and socially induced decisions and choices. We are thus undertaking comprehensive interviews with harvesters to better understand their practices, and thus improve the description of the social-ecological system around a wild species that is a resource for human populations and their social activity in natural areas.

## Funding

This work is part of the programme TRANECOL Transitions écologiques et flore protégée: la gestion conservatoire à l'échelle de la niche, funded by the Office Français pour la Biodiversité & the CeMEB (Montpellier).

## CRedit authorship contribution statement

**John D. Thompson:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing. **Sophie Caillon:** Supervision, Writing – review & editing. **Perrine Gauthier:** Conceptualization, Data curation, Funding acquisition, Methodology, Writing – review & editing. **Ninon Fontaine:** Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Isabelle Boulangeat:** Conceptualization, Methodology, Supervision, Writing – review & editing.

## Declaration of Competing Interest

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.

## Data availability

Data will be made available on request.

## Acknowledgements

This study is part of the programme TRANECOL “Transitions écologiques et flore protégée: la gestion conservatoire à l'échelle de la

niche”, funded by the Office Français pour la Biodiversité & the CeMEB (Montpellier). We thank the “Conservatoire Botanique National Méditerranéen” and the “CBN Alpin” for access to data; the Mercantour National Park for authorisations and its staff for discussions, the help on the field and to identify the génépi sites, particularly Philippe A., Marion B., François B., Hervé B., Cédric B., Laurent M.D., Adèle R., Sophie R., Nathalie S., Anthony T., Laurent Z. We are also grateful for the help of the technical staff of the Plateforme d'Analyse Chimique en Ecologie du CeMEB based at the CEF, Louis Clouet for help in the field, Raphaëlle Leclerc and Virginie Pons for the technical support. We are grateful to the harvesters who accepted to talk about their practices and to Dominique C. for newspaper articles on génépi harvesting.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02886](https://doi.org/10.1016/j.gecco.2024.e02886).

## References

- Abbutt, R., Scott, J.M., Wilcove, D., 2000. The geography of vulnerability: Incorporating species geography and human development patterns into conservation planning. *Biol. Conserv.* 96, 169–175. [https://doi.org/10.1016/S0006-3207\(00\)00064-1](https://doi.org/10.1016/S0006-3207(00)00064-1).
- Allison, P., 2013. What's the Best R-Squared for Logistic Regression? [WWW Document]. URL (<https://statisticalhorizons.com/r2logistic>) (accessed 6.15.20).
- Auffret, A.G., Berg, J., Cousins, S.A.O., 2014. The geography of human-mediated dispersal. *Divers. Distrib.* 20, 1450–1456. <https://doi.org/10.1111/ddi.12251>.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol. Evol.* 3, 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>.
- Berkes, F., Folke, C., Colding, J., 2000. *Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience*. Cambridge University Press.
- Berry, E.J., Gorchov, D.L., Endress, B.A., Stevens, M.H.H., 2008. Source-sink dynamics within a plant population: the impact of substrate and herbivory on palm demography. *Popul. Ecol.* 50, 63–77. <https://doi.org/10.1007/s10144-007-0067-z>.
- Bogges, L.M., Harrison, G.R., Bishop, G., 2021. Impacts of rock climbing on cliff vegetation: A methods review and best practices. *Appl. Veg. Sci.* 24, e12583 <https://doi.org/10.1111/avsc.12583>.
- Boulangeat, I., Philippe, P., Abdulkhak, S., Douzet, R., Garraud, L., Laverne, S., Lavorel, S., Van Es, J., Vittoz, P., Thuiller, W., 2012. Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Glob. Change Biol.* 18, 3464–3475. <https://doi.org/10.1111/j.1365-2486.2012.02783.x>.
- Bourdeau, P., 2005. Les représentations de la nature dans le discours publicitaire sur le matériel et les vêtements de sports de montagne (1982–2002). À la recherche d'indicateurs géoculturels du rapport à l'ailleurs dans les sociétés urbaines contemporaines. *Loisir Société Soc. Leis.* 28, 31–48. <https://doi.org/10.1080/07053436.2005.10707669>.
- Brun, P., Zimmermann, N.E., Hari, C., Pellissier, L., Karger, D.N., 2022. Global climate-related predictors at kilometre resolution for the past and future (preprint). *ESSD – Land/Biosciences and biodiversity*. <https://doi.org/10.5194/essd-2022-212>.
- Coll, D., 2011. Le Génépi, plante ambivalente. Du plaisir à l'effroi de la mort, in: *Actes Du Séminaire d'ethnobotanique de Salagon 2011*. Presented at the Les plantes et l'effroi - Vieux fantasmes, illusions, nouvelles peurs, Musée et jardins de Salagon.
- Coujard, J.-L., 1982. La cueillette, pratique économique et pratique symbolique. *Études Rural* 87, 261–266. <https://doi.org/10.3406/rural.1982.2888>.
- Dauphiné Libéré, 2011a. Un randonneur fait une chute mortelle. Dauphiné Libéré.
- Dauphiné Libéré, 2011b. Un ramasseur de génépi fait une chute mortelle. Dauphiné Libéré.
- Dauphiné Libéré, 2021. Cueillette du génépi: ce qui est autorisé. et ce qui ne l'est pas ! Dauphiné Libéré.
- Dauphiné Libéré, 2022. Un chercheur de génépi chute et se blesse à la tête. Dauphiné Libéré.
- Delahaye, M.-C., 2008. Le génépi. Équinoxe, Saint-Rémy-de-Provence.
- de Vos, A., Biggs, R., Preiser, R., 2019. Methods for understanding social-ecological systems: a review of place-based studies. *Ecol. Soc.* 24 <https://doi.org/10.5751/ES-11236-240416>.
- Dray, S., Dufour, A.-B., Thioulouse, J., Jombart, with contributions from T., Pavoin, S., Lobry, J.R., Ollier, S., Borcard, D., Legendre, P., Chessel, S.B. and A.S.B. on earlier work by D., 2018. ade4: Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences.
- Erschbamer, B., 2007. Winners and Losers of Climate Change in a Central Alpine Glacier Foreland. *Arct. Antarct. Alp. Res.* 39, 237–244. [https://doi.org/10.1657/1523-0430\(2007\)39\[237:WALOC\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2007)39[237:WALOC]2.0.CO;2).
- Fontaine, N., Gauthier, P., Casazza, G., Thompson, J.D., 2022. Niche variation in endemic liliom pomponium on a wide altitudinal gradient in the maritime alps. *Plants Basel Switz.* 11, 833. <https://doi.org/10.3390/plants11060833>.
- Gallagher, A.J., Kyne, P.M., Hammerslag, N., 2012. Ecological risk assessment and its application to elasmobranch conservation and management. *J. Fish. Biol.* 80, 1727–1748. <https://doi.org/10.1111/j.1095-8649.2012.03235.x>.
- Gazaix, A., Grillas, P., Papuga, G., Fontes, H., Sabatier, F., Pons, V., Gauthier, P., Thompson, J.D., 2021. Ecological niche differentiation among six annual *Lythrum* species in Mediterranean temporary pools. *Oecologia*. <https://doi.org/10.1007/s00442-021-05067-7>.
- Ghimire, S.K., McKey, D., Aumeeruddy-Thomas, Y., 2005. Conservation of Himalayan medicinal plants: harvesting patterns and ecology of two threatened species, *Nardostachys grandiflora* DC. and *Neopicrorhiza scrophulariiflora* (Pennell) Hong. *Biol. Conserv.* 124, 463–475. <https://doi.org/10.1016/j.biocon.2005.02.005>.
- Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., Stoffel, M., 2014. 21st century climate change in the European Alps—A review. *Sci. Total Environ.* 493, 1138–1151. <https://doi.org/10.1016/j.scitotenv.2013.07.050>.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>.
- Hawkes, K., O'Connell, J., 1981. Alyawara Plant Use and Optimal Foraging Theory. *Hunt.- Gatherer Foraging Strateg. Ethnogr. Archaeol. Anal.*
- Hijmans, R.J., Eten, J. van, Sumner, M., Cheng, J., Bevan, A., Bivand, R., Busetto, L., Canty, M., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J.A., Hiemstra, P., Hingee, K., Geosciences, I. for M.A., Karney, C., Mattiuzzi, M., Mosher, S., Nowosad, J., Pebesma, E., Lamigueiro, O.P., Racine, E.B., Rowlingson, B., Shortridge, A., Venables, B., Wueest, R., 2020. raster: Geographic Data Analysis and Modeling.
- Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K.L., Engelbrecht, F., Guiot, J., Hijikata, Y., Mehrotra, S., Payne, A., Seneviratne, S.I., Thomas, A., Warren, R., Zhou, G., 2018. Impacts of 1.5°C of Global Warming on Natural and Human Systems, in: *Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*. pp. 175–312.
- Karger, D.N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Appleton, M.R., 2021. Climatologies at high resolution for the earth's land surface areas - CHELSA V2.1 (current). <https://doi.org/10.16904/ENVIDAT.228.V2.1>.
- Kerns, B.K., Ager, A., 2007. Risk assessment for biodiversity conservation planning in Pacific Northwest forests. *For. Ecol. Manag.* 246, 38–44. <https://doi.org/10.1016/j.foreco.2007.03.049>.

- Körner, C., 2003. *Alpine Plant Life*. Springer Berlin Heidelberg, Berlin, Heidelberg. <https://doi.org/10.1007/978-3-642-18970-8>.
- Körner, C., 2011. Coldest places on earth with angiosperm plant life. *Alp. Bot.* 121, 11–22. <https://doi.org/10.1007/s00035-011-0089-1>.
- Larrère, R., de La Soudière, M., 2009. *Cueillir la montagne: à travers landes, pâtures et sous-bois*, Ibis Press. ed.
- Lee-Yaw, J.A., McCune, J.L., Pironon, S., Sheth, S.N., 2022. Species distribution models rarely predict the biology of real populations. *Ecography* 2022, e05877. <https://doi.org/10.1111/ecog.05877>.
- Liaw, A., Wiener, M., 2002. Classification and Regression by randomForest. *R News* 2, 18–22.
- Locqueville, J., McKey, D., MacDonald, K.L., Coq, S., Caillon, S., submitted manuscript. Navigating human-plant reciprocity: commercial harvesting of a medicinal plant fosters multi-actor landscape management. *People Nat.*
- Mascia, M.B., Brosius, J.P., Dobson, T.A., Forbes, B.C., Horowitz, L., McKean, M.A., Turner, N.J., 2003. Conservation and the social sciences. *Conserv. Biol.* 17, 649–650. <https://doi.org/10.1046/j.1523-1739.2003.01738.x>.
- Mattson, K.M., Angermeier, P.L., 2007. Integrating human impacts and ecological integrity into a risk-based protocol for conservation planning. *Environ. Manag.* 39, 125–138. <https://doi.org/10.1007/s00267-005-0238-7>.
- de Medeiros, C.M., Hernández-Lambrano, R.E., Ribeiro, K.A.F., Sánchez Agudo, J.Á., 2018. Living on the edge: do central and marginal populations of plants differ in habitat suitability? *Plant Ecol.* 219, 1029–1043. <https://doi.org/10.1007/s11258-018-0855-x>.
- Noss, R.F., 2000. High-risk ecosystems as foci for considering biodiversity and ecological integrity in ecological risk assessments. *Environ. Sci. Policy* 3, 321–332. [https://doi.org/10.1016/S1462-9011\(00\)00112-X](https://doi.org/10.1016/S1462-9011(00)00112-X).
- Novaro, A.J., Funes, M.C., Walker, R.S., 2005. An empirical test of source-sink dynamics induced by hunting. *J. Appl. Ecol.* 42, 910–920. <https://doi.org/10.1111/j.1365-2664.2005.01067.x>.
- Papuga, G., Gauthier, P., Pons, V., Farris, E., Thompson, J., 2018. Ecological niche differentiation in peripheral populations: a comparative analysis of eleven Mediterranean plant species. *Ecography* 41. <https://doi.org/10.1111/ecog.03331>.
- Pepin, N.C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., Seibert, P., Serafin, S., Schöner, W., Terzagio, S., Thornton, J.M., Vuille, M., Adler, C., 2022. Climate changes and their elevational patterns in the mountains of the world. *Rev. Geophys.* 60, e2020RG000730 <https://doi.org/10.1029/2020RG000730>.
- R Development Core Team, 2010. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Rabinowitz, D., 1981. Seven forms of rarity. In: *The Biological Aspects of Rare Plants Conservation*. Wiley, pp. 205–217.
- Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J., Fjeldså, J., 2019. Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* 365, 1108–1113. <https://doi.org/10.1126/science.aax0149>.
- Rey, Ch, Slacanin, I., 1997. Domestication du gène blanc (*Artemisia umbelliformis* Lam.). *Rev. Suisse Vitic. Arboric. Hortic.* 29, I–VIII.
- Rivière-Sestier, M., 2000. *Remèdes populaires en Dauphiné*. PUG, Saint-Martin-d'Hères.
- Scherrer, D., Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J. Biogeogr.* 38, 406–416. <https://doi.org/10.1111/j.1365-2699.2010.02407.x>.
- Schmidt, I.B., Ticktin, T., 2012. When lessons from population models and local ecological knowledge coincide – effects of flower stalk harvesting in the Brazilian savanna. *Biol. Conserv.* 152, 187–195. <https://doi.org/10.1016/j.biocon.2012.03.018>.
- Sebastien, L., 2020. The power of place in understanding place attachments and meanings. *Geoforum* 108, 204–216. <https://doi.org/10.1016/j.geoforum.2019.11.001>.
- Soldati, G.T., de Albuquerque, U.P., 2012. A new application for the optimal foraging theory: the extraction of medicinal plants. *Evid. -Based Complement. Altern. Med.* ECAM 2012, 364564. <https://doi.org/10.1155/2012/364564>.
- Sporbert, M., Keil, P., Seidler, G., Bruehlheide, H., Jandt, U., Ačić, S., Biurrun, I., Campos, J.A., Čarni, A., Chytrý, M., Čusterevska, R., Dengler, J., Golub, V., Jansen, F., Kuzemko, A., Lenoir, J., Marcenò, C., Moeslund, J.E., Pérez-Haase, A., Rusa, S., Šilc, U., Tsiropidis, I., Vandvik, V., Vasilev, K., Virtanen, R., Welk, E., 2020. Testing macroecological abundance patterns: the relationship between local abundance and range size, range position and climatic suitability among European vascular plants. *J. Biogeogr.* 47, 2210–2222. <https://doi.org/10.1111/jbi.13926>.
- Stelzenmüller, V., Ellis, J.R., Rogers, S.I., 2010. Towards a spatially explicit risk assessment for marine management: assessing the vulnerability of fish to aggregate extraction. *Biol. Conserv.* 143, 230–238. <https://doi.org/10.1016/j.biocon.2009.10.007>.
- Suter, G.W., Norton, S.B., Barnhouse, L.W., 2003. The Evolution of Frameworks for Ecological Risk Assessment from the Red Book Ancestor.
- Svenning, J.-C., Macía, M., 2002. Harvesting of *Geonoma macrostachys* Mart. leaves for thatch: an exploration of sustainability. *For. Ecol. Manag.* 167, 252–262. [https://doi.org/10.1016/S0378-1127\(01\)00699-5](https://doi.org/10.1016/S0378-1127(01)00699-5).
- Teixidor-Toneu, I., Giraud, N.J., Karlsen, P., Annes, A., Kool, A., 2022. A transdisciplinary approach to define and assess wild food plant sustainable foraging in Norway. *ppp3 Plants People Planet* 10332. <https://doi.org/10.1002/ppp3.10332>.
- Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>.
- Ticktin, T., 2004. The ecological implications of harvesting non-timber forest products: ecological implications of non-timber harvesting. *J. Appl. Ecol.* 41, 11–21. <https://doi.org/10.1111/j.1365-2664.2004.00859.x>.
- Ticktin, T., Charitonidou, M., Douglas, J., Halley, J.M., Hernández-Apolinar, M., Liu, H., Mondragón, D., Pérez-García, E.A., Tremblay, R.L., Phelps, J., 2023. Wild orchids: a framework for identifying and improving sustainable harvest. *Biol. Conserv.* 277, 109816 <https://doi.org/10.1016/j.biocon.2022.109816>.
- Tison, J.-M., Foucault, B. de, 2014. *Flora Gallica: Flore de France*. Biotope Editions, Mèze.
- Tovar, J., Olmo, F.J., Alados-Arboledas, L., 1995. Local-scale variability of solar radiation in a mountainous region. *J. Appl. Meteorol.* 1988-2005 (34), 2316–2322.
- Van der Voort, M.E., McGraw, J.B., 2006. Effects of harvester behavior on population growth rate affects sustainability of ginseng trade. *Biol. Conserv.* 130, 505–516. <https://doi.org/10.1016/j.biocon.2006.01.010>.
- White, F.J., Rosbakh, S., Orsenigo, S., Mondoni, A., 2023. Fit for the future? Alpine plant responses to climatic stress over two decades of seed bank storage. *Biol. Conserv.* 286, 110267 <https://doi.org/10.1016/j.biocon.2023.110267>.
- Wilson, K., Pressey, R.L., Newton, A., Burgman, M., Possingham, H., Weston, C., 2005. Measuring and incorporating vulnerability into conservation planning. *Environ. Manag.* 35, 527–543. <https://doi.org/10.1007/s00267-004-0095-9>.
- Zhu, G., Liu, G., Bu, W., Gao, Y., 2013. Ecological niche modeling and its applications in biodiversity conservation. *Biodivers. Sci.* 21, 90. <https://doi.org/10.3724/SP.J.1003.2013.09106>.