

# Harvesting of two alpine *Artemisia*: Effects of an amateur practice on wild plant dynamics

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## Societal Impact Statement

Wild plants are consumed all over the world, and knowledge of the effects of harvesting is necessary to ensure the sustainability of this activity. Our 3-year study of two closely related alpine *Artemisia* species in the Southern Alps revealed a positive impact of harvesting at the plant scale and on the short term. The response of plants to harvesting interacts with ecological conditions of the site and differs between the two species. A long-term understanding of plant dynamics at the plant and population scales is now required to fully assess the impact of harvesting practices and propose adapted conservation measures.

## Summary

- Characterizing the dynamics of wild harvested plants is essential to assess the sustainability of such practices. In extreme environments offered by high mountains, both ecological (e.g., vegetation cover and climate) and sociological (e.g., frequentation and harvesting practices) conditions show marked variation in space and time. Little is known however about how variation in harvesting and ecological conditions affects the dynamics of high-mountain plants, due to practical difficulties of monitoring (e.g., low accessibility) and the need to conduct multi-site studies. Here, we assess the effect of variation in social-ecological conditions on the dynamics of two alpine *Artemisia* species, whose stems are harvested to flavour tea, wine or liqueur.
- We monitored plants of *Artemisia glacialis* and *Artemisia umbelliformis* in 39 sites of the Southern Alps during three consecutive years (2021–2023).
- Mortality is low in the 3 years of study. Harvesting has a positive effect on plant stem production from year to year for both species, but for *A. glacialis*, both the effects of harvesting and the transition from vegetative to flowering status are mediated by variation in ecological conditions.
- The effect of harvesting on plant dynamics at the plant scale and on the short-term is positive. Further studies are needed to assess whether this result is repeated at the population scale and for long-term dynamics. Variation between

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the two closely related species illustrates that it is not possible to conclude on the sustainability of harvesting for one species based on the dynamics of a closely related species.

#### KEYWORDS

conservation, high-mountain environments, plant dynamics, social-ecological variation, sustainability, wild plant harvesting

## 1 | INTRODUCTION

The harvesting of wild plants contributes to local livelihoods, and they are consumed as natural products across the world (Pironon et al., 2024). In recent years and in many areas, harvesting practices have increased in intensity and have been modified as a result of social and economic changes (Aziz et al., 2024; Cambecèdes & Garreta, 2018). The literature on harvesting in the wild reveals a large diversity of practices, depending on the sites that are chosen for harvesting, its frequency, the part of the plant that is collected and its uses, as well as the type of transformation of the plant or the organization of the market chain after harvesting (Schmidt et al., 2019). Indeed, this system of harvesting, transformation, consumption and commercialisation not only determines the ways plants are harvested but also the sustainability of harvesting (Ticktin, 2004), a fundamental issue in biodiversity conservation, as exemplified in a recent thematic assessment on the sustainable use of wild species by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2022).

The effects of the activity of direct consumption on resource availability or on the dynamics of species' populations that are harvested have however only rarely been studied. The few studies that exist on the effects of harvesting provide contrasting results (e.g., Anderson & Rowney, 1999; Ghimire et al., 2005; Ticktin & Shackleton, 2011, for nontimber forest species). Some clearly indicate overharvesting, for example, American ginseng, *Panax quinquefolius* L. (Schmidt et al., 2019; Van der Voort & McGraw, 2006), some show that harvesting has only small effects on natural populations (Endress et al., 2004) while others illustrate that initial impacts may be followed by recovery (Rock et al., 2004). Assessing the ecological sustainability of harvesting practices is thus complicated (Aziz et al., 2024; Teixidor-Toneu et al., 2022; Ticktin, 2004).

In addition, few studies have considered the impacts on multiple sites or in different conditions, while the effects of harvesting depend on ecological conditions (Gaoue et al., 2011). Then, dealing with wild plant harvesting and its impact is complicated—ecological conditions in the wild are not controlled and social contexts are highly variable. Taking this social-ecological variability into account is necessary if we are to correctly inform the structures that define the regulations that can be crucial for the long-term conservation of harvested plants (de Souza & Prevedello, 2020).

In this study, we quantify rates of harvesting in the wild for two alpine *Artemisia* species, *A. glacialis* L. and *Artemisia umbelliformis* Lam.

(Asteraceae) whose stems are harvested today mainly to prepare teas and to flavour wine or liqueur (Delahaye, 2008). This harvesting mainly concerns independent amateur harvesters who harvest for their own consumption and much more rarely professional harvesters. Indeed, commercial harvesting in the wild has strongly decreased because of regulations defined to protect the species and the development of cultivation since the 1980s (François, 1987; Rey et al., 2002). The latter—through selected varieties and more controlled conditions—has made the supply to distilleries more regular, with a better predictability of quantities, traceability and chemical composition that guarantees a low level of thujone, a neurotoxic compound (Rey & Slacanin, 1997). Cultivation also provides information on the requirements of these species and the dynamics of stem production (Rey et al., 2002), although the conditions in cultivation (below 2000 m.a.s.l. because of practical constraints such as accessibility and available surface for a cost-effective production in the wild) are very different from those in natural habitats of the species (>2000 m).

Very little is known however on the dynamics of the two species in the wild. A monitoring programme conducted by agents of the Mercantour National Park between 2015 and 2019 showed that harvesting could affect the dynamics of *A. umbelliformis* populations (Diadema & Papuga, 2019). However, the study was restricted to three sites on a single massif and did not take into account the potential effect of the specific context of the site. The conditions of different sites can vary markedly, both in ecological and sociological terms, for example, differences in the favourability of topo-climatic conditions for the species, or as a result of variation in accessibility and attractivity for harvesters (Fontaine et al., 2024).

The precise objective of this paper is to assess the effect of harvesting on the dynamics of the two *Artemisia* species at the scale of individual plants. To capture the effect of harvesting on plants across variability of stem production from year to year and in different ecological contexts, it is necessary to take into account both harvesting intensity and environmental conditions of harvested plants. The two studied species can occur in parapatry or sympatry (they occasionally grow in the same sites) and thus have comparable local contexts. We address four specific questions: (1) How can stem harvesting be efficiently monitored? (2) Does harvesting have an effect on plant and stem dynamics? (3) Is variation in these dynamics related to variability in the ecological context of different sites? (4) Is the response to harvesting similar for these two closely related species, in terms of stem production?

## 2 | MATERIAL AND METHODS

### 2.1 | Study species

*Artemisia glacialis* L. and *A. umbelliformis* Lam. are Asteraceae growing in rocky habitats, in general above 2000 m.a.s.l. They are hemicryptophyte species with a rosette of basal leaves and erect flowering stems of 10 to 25 cm (Tison et al., 2014; Tison & de Foucault, 2014). For *A. glacialis*, all capitula are grouped at the end of the floral stems, whereas for *A. umbelliformis*, capitula are disposed along the stems, on short stalks. Their perennial lifeform means that they can be monitored over several years: they can live for 10 years or more in nature (4 to 5 years in low-altitude cultivations—François, 1987; Binet et al., 2011).

In the southern Alps, plants of the two species can produce a large number of floral stems: we counted a maximum of 290 stems for one plant of *A. glacialis* and 395 stems for one plant of *A. umbelliformis*. These characteristics make monitoring practicable in different sites. For both species, the flowering stems can be harvested to flavour tea, wine or liqueur. It is not clear if stems can be grazed by ungulates because of their repulsive odour, but some people—harvesters and agents of protected areas—state that the species are grazed (N. Fontaine, personal communication). Here, we consider grazing negligible compared with human harvesting.

### 2.2 | Study area

To widen an initial monitoring study of *A. umbelliformis* dynamics conducted by agents of the Mercantour National Park around the Côte de l'Âne summit (close to the sites AN\_Aumb<sub>i</sub> we monitored—Table 1, Figure S1) and to include different social-ecological contexts, we selected 39 study sites in and around the Mercantour National Park. These sites include 26 sites with *A. umbelliformis*, six sites with *A. glacialis*, and seven sites with both species. The greater emphasis placed on *A. umbelliformis* (thus the larger number of sites) is justified by the fact that this species is more common than *A. glacialis* in the study area (Fontaine et al., unpublished), and is preferred by harvesters because it is more aromatic (N. Fontaine, personal communication).

In the study area, *A. umbelliformis* and *A. glacialis* grow in diverse ecological conditions (Fontaine et al., unpublished), on bedrock (cliff or slab), scree slopes (with different block sizes), and sparsely vegetated grasslands (Figure 1a). In a previous study of *A. umbelliformis*, harvesting intensity was found to vary significantly across the study area (Figure 1b), in relation to historical factors, the behaviour of harvesters (reputation of sites, attractivity, accessibility), and the amount of available resources (Fontaine et al., 2024).

Ecological conditions in each site were classified into two broad categories: sites with almost no vegetation dominated by bedrock (slab and cliff) and/or scree slopes, compared with sparsely vegetated rocky grasslands. In a subset of the study sites, three 1 m<sup>2</sup>-quadrats were used to characterise local ecological conditions (Fontaine et al., unpublished) in each of the two categories. This showed that the cover of unfragmented bedrock is significantly different between

the two categories, with a mean cover of 45% for sites with almost no vegetation and 25% for sparsely vegetated rocky grasslands. The mean cover of aerial vegetation in the two types of habitat is 18% and 30%, respectively (Methods S2).

### 2.3 | Monitoring

Plants were mapped in two ways. In the majority of sites ( $n = 32$ ), plants were mapped along transects between 4.6 and 17.4 m long and 1.0 to 6.6 m wide. In a small number of sites where transects were not possible ( $n = 7$  sites), plants were mapped in relation to easily recognisable permanent reference points. Transect length was limited to a maximum of 20 m for conditions to be relatively homogeneous, and the variability of transect dimensions is linked to plant density: five plants with flowering stems was considered a minimum necessary to implement monitoring in a given site, and we limited the count to a maximum of 60 plants per site. All sites were monitored in 3 years: 2021, 2022 and 2023 (apart from two that we monitored only in 2022 and 2023: AL\_Aumb4 and AL\_Aumb5).

Monitoring was done by counting the number of flowering stems produced by individual plants, at the end of the growing season (in September). As harvesting generally occurs in August (or in July if stems are mature and if it is allowed<sup>1</sup>), at the peak of flowering, when the plants are most fragrant, flowering stems can still be entire or have been harvested. In September, stem bases are still visible after harvesting if it is done carefully with a knife or scissors, which allowed us to assess harvesting intensity on plants, that is, the number of cut stems in relation to the total number of stems for each plant. This protocol is further referred to as 'one-shot count'.

In the first year of the study when transects were installed, stems were also counted in July (to make a 'before and after count'), that is, prior to the main harvesting period. This 'before-and-after count' protocol is used to assess a potential bias of the 'one-shot count' protocol (realized in September), which may underestimate stem production and harvesting intensity because some stems and plants may be uprooted during harvesting. This 'before-and-after count' is supposed to be more accurate but it presents other problems because sites have to be visited twice a year. As *A. umbelliformis* and *A. glacialis* grow in high altitude rocky sites, fieldwork is highly time demanding (primarily because of the time needed to access study sites) and can also be a source of disturbance for sensitive habitats where species such as *Lagopus muta* live and reproduce. Indeed, for the latter, disturbing females taking care of chicks can lead to their abandonment and reproduction failure. Despite the potential biases of a simplified protocol, the 'one-shot count' was employed.

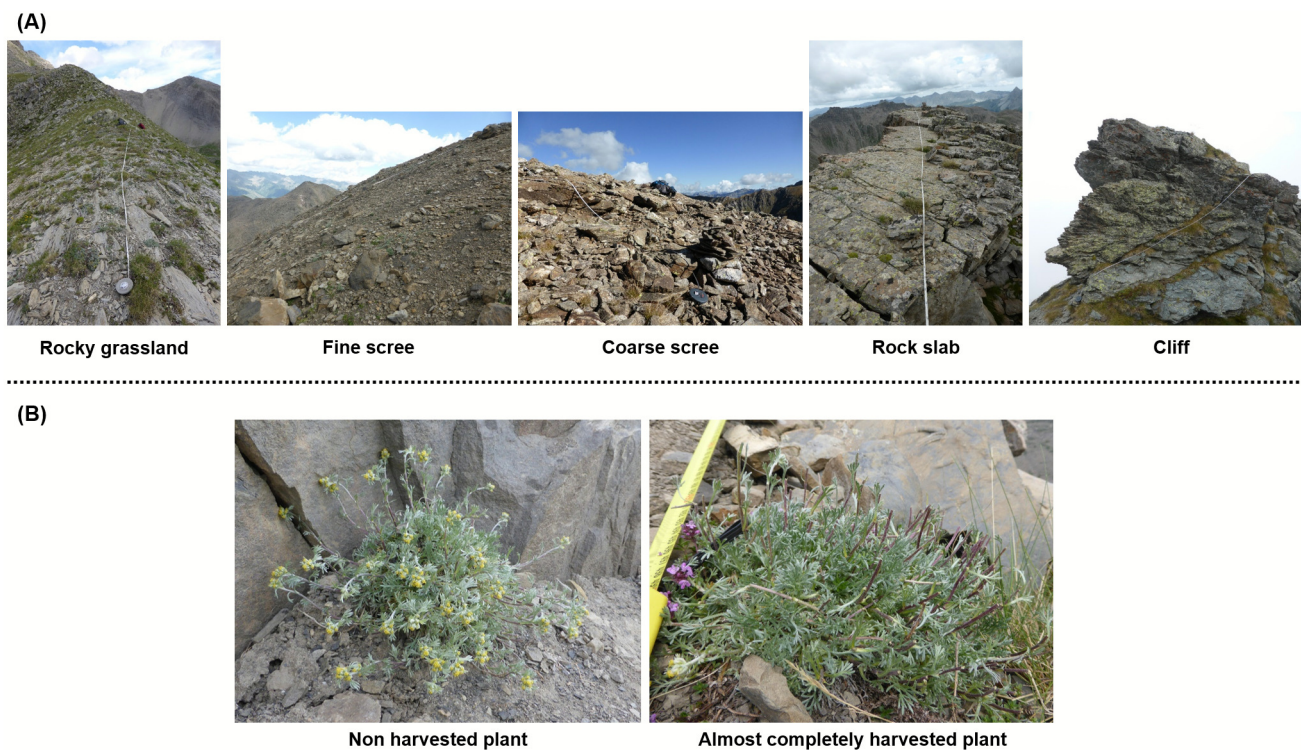
We classified each plant mapped during the study into one of four life-history stages: nonflowering rosettes, hereafter simply called

<sup>1</sup>Harvesting of the two species is allowed only during August in the core zone of the Mercantour National Park (Résolution n° 12-2014 réglementant la cueillette des baies, champignons, g n p s et Camomille du Pi mont dans le c ur du Parc national du Mercantour). All the study sites are located in the core zone apart from PC\_Aumb, PC\_Agla and PC\_AumbAgla.

**TABLE 1** List of sites where plants of *Artemisia umbelliformis* (Aumb) and *Artemisia glacialis* (Agla) were monitored in 2021–2023. Number (Nb) of plants does not take into account the number of rosettes (plants that did not flower in any of the three studied years).

ID site	Species	Nb of plants	x (lambert 93)	y (lambert 93)	Broad habitat type
AN_Aumb3	Aumb	45	1002866	6357051	Cliff
MO_AumbAgla	Agla	20	1013661	6366810	Cliff
	Aumb	7			
Q13_Aumb6Agla1	Agla	4	1014239	6366327	Cliff
	Aumb	32			
Q16_Agla	Agla	39	1000916	6354627	Cliff
Q5_Aumb	Aumb	24	1014109	6364381	Cliff
Q6_Aumb	Aumb	5	1014068	6364284	Cliff
AN_Aumb1	Aumb	54	1003173	6356725	Rock slab
CB_Aumb	Aumb	20	1013824	6365778	Rock slab
GI_Aumb	Aumb	17	1002958	6354604	Rock slab
GI_AumbAgla	Agla	12	1003913	6355407	Coarse scree
	Aumb	17			
Q1_Aumb	Aumb	14	1014166	6364412	Coarse scree
Q11_Aumb	Aumb	15	1013581	6365306	Coarse scree
Q12_Aumb	Aumb	19	1013615	6365241	Coarse scree
RG_Aumb	Aumb	48	1001520	6353980	Coarse scree
TC_Aumb	Aumb	34	1002760	6362872	Coarse scree
AL_Aumb1	Aumb	42	996059	6353625	Fine scree
AL_Aumb3	Aumb	31	996042	6353645	Fine scree
AL_Aumb4 <sup>a</sup>	Aumb	46	996764	6353652	Fine scree
BO_Aumb	Aumb	38	1003442	6367227	Fine scree
CB_Agla	Agla	39	1014146	6365800	Fine scree
PC_AumbAgla	Agla	22	1006997	6357933	Fine scree
	Aumb	33			
RG_Agla	Agla	36	1001314	6353253	Fine scree
SA_Aumb2	Aumb	48	1002599	6359761	Fine scree
AL_Aumb2	Aumb	14	996104	6353633	Rocky grassland
AL_Aumb5 <sup>a</sup>	Aumb	56	996640	6353550	Rocky grassland
AN_Aumb2	Aumb	51	1003770	6356797	Rocky grassland
AN_Aumb4	Aumb	38	1003008	6356313	Rocky grassland
CB_AumbAgla	Agla	7	1014719	6365787	Rocky grassland
	Aumb	4			
CY_Aumb	Aumb	44	997140	6356138	Rocky grassland
GI_Agla	Agla	37	1004216	6354558	Rocky grassland
MO_Agla	Agla	41	1013823	6366677	Rocky grassland
MO_Aumb	Aumb	30	1013504	6366838	Rocky grassland
PC_Agla	Agla	52	1006109	6357253	Rocky grassland
PC_Aumb	Aumb	14	1006746	6357786	Rocky grassland
Q3_Aumb	Aumb	38	1014117	6364389	Rocky grassland
Q7_AumbAgla	Agla	9	1014046	6364198	Rocky grassland
	Aumb	11			
Q8_Aumb	Aumb	7	1014016	6364181	Rocky grassland
RG_AumbAgla	Agla	8	1001665	6353359	Rocky grassland
	Aumb	4			
SA_Aumb	Aumb	36	1002438	6359862	Rocky grassland

<sup>a</sup>Two sites were monitored only in 2022 and 2023 (AL\_Aumb4 and AL\_Aumb5).



**FIGURE 1** The major habitat types where the two génépi species can be found (a), and typical harvesting situations for *Artemisia umbelliformis* (b). The two photographs in (b) were taken on the same day (26th July 2021), around 100 m apart (close to sites AL\_Aumb1 and AL\_Aumb3). Stem bases of the harvested plant are clearly visible. © N. Fontaine.

rosettes (small plants without stems of that year nor stems of a previous year), vegetative plants (plants without stems of that year but that had flowered during previous years), flowering plants, and dead plants (mortality).

The three monitoring years differ in terms of meteorological conditions. These differences were characterized from reanalyses of the outputs of the meteorological model SAFRAN for mountain climate in the Southern Alps (<https://www.umr-cnrm.fr/spip.php?article788>, Durand et al., 1993), linearly interpolated to the local conditions of altitude of the sites (details on the reanalyses are given in [Methods S1](#)).

## 2.4 | Statistical analyses

We compared the two protocols of harvesting rate estimation in 2021—‘one-shot count’ and ‘before-and-after count’—using the Wilcoxon test with paired samples (nonparametric test as the distribution of differences between estimations is not normal).

The dynamics of stem production were modelled with a generalized linear mixed-effect model (*glmer* function from the R package *lme4*; Bates et al., 2015) using a Poisson distribution (the majority of plants had a small number of stems and only a few plants had a large number of stems). Stem numbers (a proxy for plant size) were log-transformed because of this excess of small plants relative to large plants. We tested for any effect of ecological and annual climatic conditions, harvesting, and the interactions between conditions and

harvesting, between conditions and plant size and between harvesting and plant size (Table S1). A random effect of site was included in the models to account for any spatial structure of measurements. To account for overdispersion, we added an ‘observation level random effect’ (OLRE), a method that avoids making implicit and potentially erroneous assumptions about the processes that generated the overdispersion (Harrison, 2014).

As 57.0% of *A. umbelliformis* plants and 60.8% of *A. glacialis* did not have any cut stems, models were computed in two steps. First, we analysed the number of plants with at least one cut stem relative to the number of plants with no cut stems, and second, we analysed the number of cut stems compared with the total number of stems for plants that had at least one cut stem. This allowed us to assess the effect of harvesting both in terms of presence/absence (i.e., plant cut or not cut) and in terms of intensity (proportion of cut stems per plant).

## 3 | RESULTS

### 3.1 | Protocol testing

For the plants monitored in 2021 before and after the harvesting season, we observed 149 stems already cut in July (3.2% of all stems). In September, we counted 221 additional stems that were not observed in July (i.e., 4.8% of stems that developed later in the summer), while



removed from the dataset to avoid potential cartography mismatches). Mortality is very low, and lower for *A. umbelliformis* compared with *A. glacialis* with values that range from 0.4% of *A. umbelliformis* flowering plants in 2023 (three plants) to 3.8% of *A. glacialis* nonflowering plants in 2023 (four plants) (Figure 3). Such small numbers preclude statistical analyses.

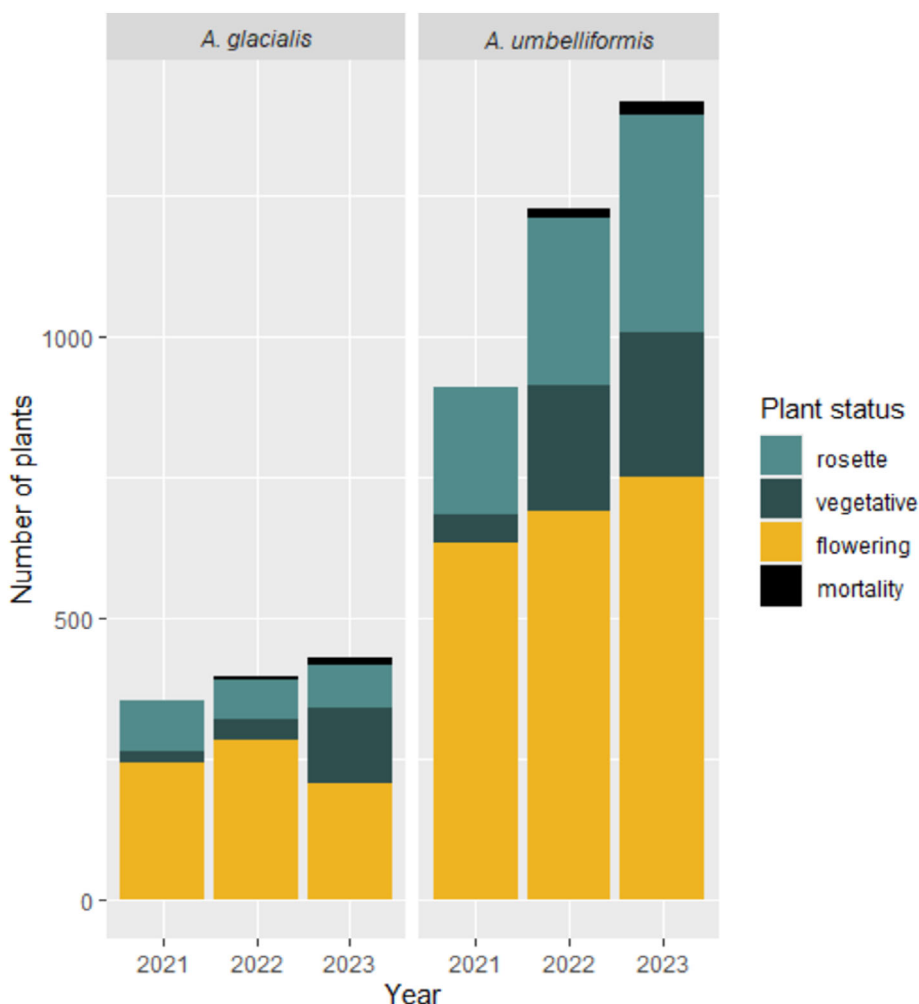
For *A. umbelliformis*, 92 (12.7%) plants that were rosettes or vegetative plants in 2021 flowered in 2022, and 117 (19.9%) of the rosettes or vegetative plants in 2022 flowered in 2023. For *A. glacialis*, 52 (29.3%) and 9 (8.5%) plants respectively showed this trend. The transition from vegetation status to flowering is significantly less probable for *A. umbelliformis* compared with *A. glacialis* ( $p$  value = .003 in the full model). While the transition does not depend on either year or habitat type for *A. umbelliformis*, both factors significantly affect the flowering transition for *A. glacialis*: the transition is less probable in 2023 compared with 2022 ( $p$  value < .001), and in sparsely vegetated rocky grasslands compared with sites with bedrock or scree slopes and almost no vegetation ( $p$  value = .009) (Table 3). The difference between the 2 years is correlated with a warmer growing season (positive anomaly of temperatures from April to July—Methods S1), and the two habitats mainly differ in species diversity (higher for grasslands) and bedrock cover (lower for grasslands—Methods S2).

The trends in transition from flowering to vegetative plants are different between the two species: the transition is more probable for *A. umbelliformis* and concerns mainly plants in sparsely vegetated rocky grassland ( $p$  value = .010). For *A. glacialis*, the probability of shifting to a vegetative state after a flowering year is higher in 2023 than in 2022 ( $p$  value < .001) (Table 3).

### 3.4 | Dynamics of stem production

Over the 3-year period of monitoring (2021–2023), stem production for *A. glacialis* was significantly lower in 2023 than in 2022 (Table 4). This interannual difference is more pronounced for plants with a small number of stems (significant interaction between year and stem number on year  $n$ —Table 4). The effect of habitat (rocky grassland vs. bedrock and scree) on stem production shows a significant interaction effect with harvesting: There is a positive effect of stem harvesting on *A. glacialis* stem production in the bedrock and scree habitat with almost no vegetation but not in rocky grassland with sparse vegetation.

For *A. umbelliformis*, the effect of ecological conditions on stem production is relatively higher and the interannual difference of stem production is relatively lower than for *A. glacialis*. In addition, the



**FIGURE 3** Number of monitored plants per species (*Artemisia glacialis* [left] and *Artemisia umbelliformis* [right]) and per status. Number of rosettes printed on the figure corresponds to groups of rosettes, thus exact rosette number is underestimated.

**TABLE 3** Interannual variability and effect of habitat conditions on transition from rosettes/vegetative to flowering for the two *Artemisia* species.

	Transition from rosette to flowering plant		Transition from flowering to vegetative			
	<i>A. glacialis</i>	>	<i>A. umbelliformis</i>	<i>A. glacialis</i>	<	<i>A. umbelliformis</i>
Year	2023 < 2022 ( $p < .001$ )		Not significant	2023 > 2022 ( $p < .001$ )		Not significant
Veget.	Sparse < almost no veget. ( $p = .009$ )		Not significant	Not significant		Sparse > almost no veget. ( $p = .010$ )

Note:  $p$  values are given for *glmer* models computed independently for each species.

**TABLE 4** Estimates of the significant terms of the Poisson mixed models of stem production from year to year for *Artemisia glacialis* and *Artemisia umbelliformis*. Nb stems: stem number; Veget: vegetation; n.s. not significant.

Nb stems <sub>n+1</sub> ~ ...	<i>A. glacialis</i>		<i>A. umbelliformis</i>	
	All plants	Cut plants only	All plants	Cut plants only
Nb stems <sub>n</sub>	0.37	0.55	0.53	0.45
year <sub>n+1</sub> ('2023' relatively to '2022')	-2.06	-3.42	0.18	n.s.
Veget ('sparse' relatively to 'almost absent')	-0.47	n.s.	0.13	-0.69
cut <sub>n</sub> ('not cut' relatively to 'cut' plants)	-0.70		-0.40	
cut rate <sub>n</sub>		n.s.		n.s.
Veget × year <sub>n+1</sub>	n.s.	n.s.	n.s.	0.73
Veget × Nb stems <sub>n</sub>	n.s.	n.s.	-0.21	n.s.
year <sub>n+1</sub> × Nb stems <sub>n</sub>	0.33	0.56	n.s.	n.s.
Nb stems <sub>n</sub> × cut <sub>n</sub>	n.s.		n.s.	
Nb stems <sub>n</sub> × cut rate <sub>n</sub>		n.s.		n.s.
year <sub>n+1</sub> × cut <sub>n</sub>	n.s.		n.s.	
year <sub>n+1</sub> × cut rate <sub>n</sub>		2.15		n.s.
Veget × cut <sub>n</sub>	0.55		n.s.	
Veget × cut rate <sub>n</sub>		n.s.		n.s.

response of stem production to warmer temperatures (*year* effect) and habitat type (*Vegetation* effect) is the opposite to that observed for *A. glacialis*: plants of *A. umbelliformis* growing in sparsely vegetated rocky grassland produce more stems than those growing in habitats with bedrock and screes. The effect of harvesting is also significant for *A. umbelliformis*, but does not depend on climatic or ecological conditions. *A. umbelliformis* plants whose stems were cut in a given year generally produce more flowering stems in the following year than plants that were not harvested. For plants with cut stems, the intensity of cutting in year  $n$  does not affect stem number in year  $n + 1$  for *A. umbelliformis*, while it has a positive effect on *A. glacialis* stem production in 2023.

## 4 | DISCUSSION AND CONCLUSION

### 4.1 | How to efficiently monitor harvesting?

The comparison of stem counts before and after harvesting allowed us to quantify specific harvesting practices and a bias of only counting

stems at the end of the harvesting period (due to late stem development). The before-and-after procedure allowed us to quantify early harvesting (i.e., before the month of August) and low cutting height (i.e., stems cut below the level of the leaves or completely ripped off). The former reveals illegal practices for plants located in the core zone of the Mercantour National Park, where *Artemisia* harvesting is only allowed in August. The reasons for this early harvesting may lie in the drier springs, earlier snowmelt, and higher temperatures that may have caused a shift in the start of the flowering period and thus stem maturation. Indeed, such a phenological shift in the flowering of alpine plants has been observed in studies of several other species (Inouye, 2008; Rammig et al., 2010; Sedlacek et al., 2015) and has also been observed by the agents of the Mercantour National Park (Fontaine, Boulangeat, et al., 2025). This may have tempted some harvesters to adapt to the temporal shift in flowering phenology. At the same time, earlier harvesting could simply be a 'first-come first-served' effect, where harvesters begin early in order to be sure to get stems before other harvesters, as observed in a *Primula* species (AFC, 2022, p. 60).

The comparison of the two protocols also underlined biases in stem dynamics and harvesting rate estimations. If the latter are made

using the difference in entire stem number in September and July, a late development of stems can lead to an underestimation of stem production and harvesting rate, because stems that develop late in the growing season ‘replace’ cut stems in the counts. If they are estimated using stem bases and entire stem numbers, stem production and harvesting rate are underestimated due to missed stems (ripped-off or cut at the collar level). Thus, neither of the two methods is perfect and unbiased, and the choice of one rather than another requires taking into account their implementation in the field. Given the instability of the rocky habitats where these *Artemisia* species grow, it is easier to monitor plants on an annual basis in order to find them despite changes in the aspect of a given site. This annual basis is also needed because harvesting can have a year-to-year effect. Moreover, it is important monitoring to be done by national park agents, in order to directly inform their decisions about harvesting regulations. For them, July and August are months with a lot of work to do, mainly because of peak visitor numbers (N. Fontaine, personal communication). The method ‘before-and-after’ required two (3-week) periods of fieldwork in July and September and thus requires a large investment in the time spent in the field—access on foot to high-altitude habitats where *génépis* grow is relatively long. The method ‘one-shot counts’, with a reasonable bias of one to two missed stems per plant on average, seems to be a good compromise and the most convenient method for park agents to take charge of monitoring.

#### 4.2 | Variation in the dynamics of plant status and stem production among species

An important result of this study is that the two *Artemisia* species show different stem production dynamics. Stem production of *A. glacialis* depends more on annual climatic conditions and less on the ecological conditions (substrate availability) when compared with *A. umbelliformis*, which shows a completely opposite pattern (Table 3, Table 4). This result is an important element of the ecological requirements of the two species that we detected in a parallel study (Fontaine et al., unpublished): the presence of *A. glacialis* is more temperature dependent than the presence of *A. umbelliformis* on a range-wide scale. In the present study, *A. glacialis* is positively affected by harvesting only in specific ecological conditions (areas with bedrock or scree and almost no vegetation), while the positive effect on *A. umbelliformis* stem production does not depend on ecological conditions. This could reflect different ecological optima for sympatric species (Giraldo-Kalil et al., 2023), with additional ecological limiting factors for *A. glacialis* that affect the recovery of the species after harvesting or some form of overcompensation dynamics (Ramula et al., 2019). Increased stem production the year following harvesting may be due to the possibility that cut stems do not use up plant resources during seed production after the harvesting period. It can also be a reaction to a signal of lower probability of surviving when stems are harvested, with plants switching to a high reproductive strategy.

The differences between the two species may also be correlated to their morphology (spreading rosettes that cover the ground for

*A. glacialis*, smaller rosettes for *A. umbelliformis*) that could correspond to different strategies: *A. glacialis* has a more clonal spreading habit than *A. umbelliformis*, which has a more clumped growth strategy. This could affect resource use, biotic interactions (Doust, 1981; Humphrey & Pyke, 1998), but also the sensitivity of species to harvesting and uprooting (the larger surface occupied by *A. glacialis* rosettes gives them more contacts to the substrate, and that could lower its sensitivity to uprooting).

Even though the two species are phylogenetically close (<http://phyloalps.org/>—sequencing from chloroplastic genome) and often occur in sympatry (thus in similar ecological conditions), they respond differently to harvesting. It is thus difficult to generalise on the effects of harvesting across species.

#### 4.3 | Conservation implications

Our study illustrates four main issues or perspectives for future work on the conservation of alpine *Artemisia* in relation to harvesting practices.

First, our 3-year monitoring study revealed that harvesting had a positive effect on stem production by *A. umbelliformis*. It is however important to limit the interpretation of this result because it may only be a short-term effect; repeated harvesting may negatively affect a plant through a cumulative impact if harvesting occurs over several years (Gaoue et al., 2011). Indeed, harvesting could have an ‘exhaustion’ effect on regrowth of individual plants (e.g., through carbohydrate storage—Jameson, 1963). Moreover, the ‘before-and-after count’ revealed that around 18% of stems were cut at the collar level or completely ripped off. This can destabilize plants that grow in rupicolous habitats. Using a knife or scissors to harvest the stems and keeping the rosette grounded should limit this destabilization.

Transient dynamics are also important in long-term behaviour of ecosystems (Hastings, 2004), and can affect grazed or harvested plant populations (e.g., Endress et al., 2004; Ghimire et al., 2007). The detection of such long-term cumulative or transient effects is limited in our study by the duration of monitoring (3 years) compared with the individual lifespan of the study species (>10 years). This underlines the need for long-term monitoring to avoid extrapolations when short-term effects are opposed to long-term dynamics (positive reactivity—Boulangeat et al., 2018). Nonetheless, the sites with high harvesting levels across the 3 years, and perhaps those for two of 3 years of the study, are clearly those where the Mercantour National Park should be the most vigilant. For sustainable harvesting, harvesters should also limit their activity on these sites.

Second, it is important to limit the interpretation of our results to the scale of individual plants. Stems bear seeds and harvesting them affects the reproduction of the plant (Medicinal Plant Specialist Group, 2007; Ticktin, 2004). Hence, although harvesting has positive effects on plant stem production in a following year, it may negatively affect the overall population dynamics due to a limitation of sexual reproduction: seed output at the end of the growing season might be reduced and less genetically diverse. This could limit both the renewal

of plant population and its dispersal ability. Concerning population renewal, Baltzer et al. (2002) showed a decrease of seedling emergence following stem harvesting for *Limonium carolinianum*. For dispersal, in the context of climate change, species may have to migrate to more north-facing slopes or latitudes and higher altitudes to track favourable climatic conditions (Parmesan & Yohe, 2003; Root et al., 2003). As plants migrate through their seeds, limiting seed development and dispersion through harvesting could have a strong effect on the population dynamics of these alpine species and their ability to track climate change. Based on stem and seedling counts on 1m<sup>2</sup>-quadrats of *A. umbelliformis*, we observed a significant positive effect of the remaining stem number in September 2021 on seedling number in September 2022. Monitoring by agents of the Mercantour National Park between 2015 and 2019 in the Côte de l'Âne site showed a decrease in seedling number (Diadema & Papuga, 2019) in relation to a high harvesting intensity. Even though it is difficult to generalize these results, these two trends suggest that harvesting could have important effects on the population demography of the study species. In terms of both long-term and population scales, our 3-year study cannot take into account long-term dynamics of *Artemisia* populations, for example, colonization-extinction processes. It is thus key to consider also seedlings in the next monitoring projects.

Third, harvesting may vary across the entire range of the two species. Our study was focused on the southern Alps, where it is well known that the overall social-ecological context differs to that in the northern part of the French Alps. In the study area, *A. glacialis* and *A. umbelliformis* are the most common g n pi species. The presence of two other species (*Artemisia eriantha* and *Artemisia genipi*) is anecdotal. Our monitoring shows that *A. umbelliformis* is preferred to *A. glacialis*, with higher proportions of harvested stems, and that the two species have different ways of harvesting (taking more stems from fewer plants for *A. umbelliformis* vs. spreading out harvesting on more plants for *A. glacialis*). Harvesting habits might be different in other parts of the Alps, possibly with other consequences on the plants. For example, a sister species, *A. genipi*, is more abundant in the northern Alps while it is at its southern distribution limit in our study area (Fontaine et al., unpublished), and this species is preferred by harvesters (N. Fontaine, personal communication). The harvesting intensity of the study species may thus be lower in areas where *A. genipi* is more present, that is, further north in the Alps, than in our study area.

Finally, harvesters play a major role in the study system, through their practices and also through their observations that could be used to cover a larger time frame, and taken together allow for a wider spatial study (Dickinson et al., 2010). This is particularly relevant given the remote location and low accessibility of the alpine habitats where the two *Artemisia* species grow (McDonough MacKenzie et al., 2017). In a parallel study where we interviewed harvesters, several of them evoked observations of particularly big plants in terms of stem number, for example, by taking photos yearly of the same plant (see Figure S3), or experiments they have performed, for example, the application of different harvesting rates on neighbouring plants, to improve the sustainability of their practices (Fontaine, Thompson,

et al., 2025). These tests and observations are particularly interesting, but are generally made in specific places and it is not possible to define general patterns from them. Interactions between scientists, harvesters and managers of natural areas represent nevertheless a potentially rich perspective for further knowledge coproduction in this study system, as shown elsewhere (e.g., Asse, 2018; Mucioki et al., 2022; P darras et al., 2020).

## AUTHOR CONTRIBUTIONS

**Conceptualization:** Ninon Fontaine, Perrine Gauthier, John D. Thompson and Isabelle Boulangeat. **Data curation:** Ninon Fontaine and Perrine Gauthier. **Funding acquisition:** Perrine Gauthier and John D. Thompson. **Methodology:** Ninon Fontaine, Perrine Gauthier and Isabelle Boulangeat. **Supervision:** John D. Thompson and Isabelle Boulangeat. **Writing—original draft:** Ninon Fontaine. **Writing—review and editing:** Ninon Fontaine, Perrine Gauthier, John D. Thompson and Isabelle Boulangeat. All authors have read and agreed to the published version of the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Datasets from field measurements are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

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