

Ecology / Écologie

# A new, isolated and endangered relict population of dwarf pine (*Pinus mugo* Turra) in the northwestern Alps

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## Abstract

Dwarf pines were discovered in 2004 during a paleoecological survey in the Mont Cenis massif (Savoie, France). These dwarf pines are the sole natural and spontaneous population in the NW French Alps of *Pinus mugo* Turra, ssp. *mughus* (Scop.) O. Schwarz. The population, fragile in light of the individual numbers, is currently isolated, but likely results from populations that would have covered larger areas during the Lateglacial or the early-Holocene, from the SW Alps (France) toward the Mont Cenis, throughout the Susa valley (Italy). With a fragmented distribution area of dwarf pine, the future of the Mont Cenis population seems altered due to important necroses observed on the topmost part of pine crowns, except for individuals that do not grow in the local ski station area. We stress the need for a conservation program to preserve this natural population, the sole known in the NW French Alps. **To cite this article:** C. Carcaillet et al., C. R. Biologies 332 (2009).

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## Résumé

**Une nouvelle population relicte isolée de pins nains (*Pinus mugo* Turra) en danger dans les Alpes du Nord-Ouest.** Des pins prostrés ont été découverts en 2004 lors de prospections paléocéologiques sur le versant nord du massif du Mont Cenis (Savoie, France). Ces pins prostrés constituent une population naturelle et spontanée dans les Alpes françaises du Nord de *Pinus mugo* Turra, ssp. *mughus* (Scop.) O. Schwarz. Cette population, fragile au regard des effectifs recensés, est actuellement isolée, mais résulterait de populations qui, durant le Tardiglaciaire voire le début de l'Holocène, ont dû couvrir de plus vastes territoires des vallées duranciennes à la vallée de la Maurienne, via la vallée de Suse en Italie. Sur une aire de distribution actuellement fragmentée, le devenir de la population de pin mugho du Mont Cenis semble compromis au regard des nécroses importantes observées sur les parties sommitales des houppiers, à l'exception des individus qui ne croissent pas dans le domaine skiable du Mont Cenis. Une procédure conservatoire semble nécessaire pour préserver cette population naturelle, la seule connue à ce jour dans les Alpes françaises du Nord. **Pour citer cet article :** C. Carcaillet et al., C. R. Biologies 332 (2009).

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**Mots-clés:** Biogéographie; Populations fragmentées; *Pinus mugo*; Alpes; Étage subalpin; Limite des arbres

## 1. Introduction

In the western Alps, the dwarf pine *Pinus mugo* Turra, considered by many authors as a subspecies *mughus* (Scop.) O. Schwarz (Christensen [1]; Farjon [2]; Monteleone et al. [3]), is known from few stands on both parts of the southern French and Italian boundary from 2000 to 2500 m a.s.l. (Gausson [4]; Montacchini [5]; Ozenda [6]; Chas [7]). The western dwarf pine populations constitute with stands from the Abruzzi massifs (Boratynska et al. [8]) disjointed and marginal patches of a fragmented and complex distribution area (Hamerník and Musil [9]). This *Pinus mugo* subspecies displays a broader distribution in the eastern Alps and far-east in the Carpathes, where dwarf pine-dominated communities constitute dense and large bushes (Ozenda [10]; Richardson [11]; Lauber and Wagner [12]). The main *Pinus mugo* phenotype in the western Alps and the Pyrenees is a tall tree, considered by a few as a distinct taxon namely *Pinus uncinata* Ramond or mountain pine (Hamerník and Musil [9]) although most authors consider it as a subspecies, i.e. *P. mugo* subsp. *uncinata* (DC.) Domin (Christensen [1]; Farjon [2]; Monteleone et al. [3]). Whatever the real taxonomic classification, these two phenotypes seems to belong to a same complex gathering several taxa (Monteleone et al. [3]; Hamerník and Musil [9]). Dwarf or mountain pines constitute mixed woodlands from the mountain to the subalpine belt, up to the upper tree-line in the inner dry and continental valleys of the Alps, generally including European larch [*Larix decidua* (Mill.)], cembra pine (*Pinus cembra* L.) and European spruce [*Picea abies* (L.) Karst]. Both *Pinus mugo* phenotype are morphologically distinct throughout their architecture and their cone morphology. However, the differences correspond to general types, because all intermediate forms can be observed, without taking into account the breed with Scots pine, *P. sylvestris* L. (Christensen [1]; Hamerník and Musil [9]). Whatever the systematic debate, the dwarf pine is hereafter named *P. mugo*, whereas the erected mountain pine is *P. uncinata*.

In June and October 2004, during paleoecological surveys, dwarf pines corresponding to the phenotype of *Pinus mugo* were discovered on the north facing slopes of the Mont Cenis massif, Savoy, France. This observation is surprising because this area is devoted to the

erected phenotype *P. uncinata*. This finding questions the presence of dwarf pines outside the known distribution area of *P. mugo*, and because such a presence has never been reported in flora books dedicated to this region in the north French Alps (e.g. Bartoli [13]; Gensac [14]; Parc National de la Vanoise [15]). Furthermore, this finding is almost synchronous with the discovery of travertines in the Susa valley (Italy) on the south-facing slopes of the Mont Cenis. One travertine, dated from 11 500 to 9500 cal. years BP, contains cone imprints whose morphologies correspond to *P. mugo* (Ali et al. [16]).

The present Note aims to describe the dwarf pine population discovered on the slopes of the Mont Cenis, to provide key information on its likely natural status, and to consider its conservation status in light of current land-use.

## 2. Material and methods

### 2.1. Study area

The study area is situated in the high Maurienne valley, south of the Vanoise massif in the northwestern Alps (Savoy, France). Climatic data are obtained from weather stations located at 1715 m a.s.l. (Bessans) and at 2000 m a.s.l. (Lanslebourg), both within the investigated area. The mean temperature for the warmest (JJA) and the coldest seasons (DJF) are  $12.5 \pm 0.7$  and  $-5.6 \pm 1.2$  °C at Bessans, and  $12.7 \pm 5.1$  and  $-4.2 \pm 1.8$  °C at Lanslebourg, respectively. Snow covers the ground for ca. 5.5 months per year at 2000 m on southern exposures, from mid-November to late April. Mean annual precipitation is  $884 \pm 167$  and  $925 \pm 233$  mm at Bessans and Lanslebourg, respectively. The high Maurienne valley is one of the driest in the Alps; the intra-annual variability and mean annual precipitation and temperature are similar to the central European continental climate.

Soils are cambisol (Bartoli [13]) settled on glacial deposit laying on a bed-rock composed of Cretaceous calcschists and marbles (Fudral et al. [17]). The average age of trees that compose the forest cover is generally younger than 50 years, although >300-years growing stands were recorded on the Lanslevillard commune (Beilhe et al., [18]). Surrounding subalpine forests are composed of larch, cembro pine and spruce, with scat-

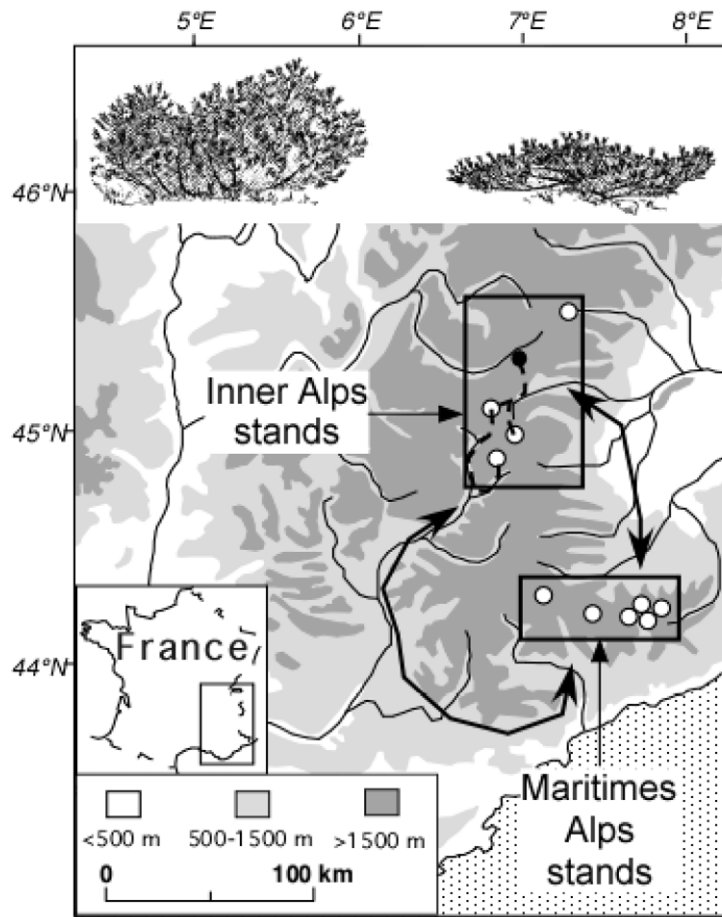


Fig. 1. Distribution map of dwarf pine *Pinus mugo* in the western Alps. The black dot corresponds to the Mont Cenis population. The open dots are the other stands. The dashed black line depicts the likely past virtual corridor of populations in the inner Alps. The black arrows display the possible glacial connections among populations from the Maritime Alps and those from the inner Alps.

tered deciduous broadleaf trees, particularly in snow-avalanche tracks: *Salix* sp., *Alnus viridis* (Chaix) DC., *Sorbus aucuparia* L. or *Betula pendula* Roth. The understorey contains Ericaceae (*Rhododendron ferrugineum* L., *Vaccinium myrtillus* L., *V. uliginosum* L., *V. vitis-idaea* L.), *Juniperus nana* L., *Sorbus chamaemespilus* (L.) Crantz and *Lonicera caerulea* L.

## 2.2. Textual archives

The documents on performed forestry works and management are archived within the French national forest service (*Office national des forêts*) at Chambéry. All textual archives concerning national and communal lands of the upper Maurienne valley were investigated in November 2005. A particular focus was consecrated on archives from communes of Bessans, Lanslebourg and Lanslevillard. The aim was to verify censuses of planta-

tion and reforestation to prove that dwarf pine were not seeded or planted, under the following possible French or Latin designations: “pin mugo, p. de(s) montagne(s), p. à crochet, p. couché”, *Pinus pumilio*, *P. mugo*, *P. montana*, *P. uncinata*, *P. mughus*.

## 2.3. Land survey and individual censuses

The prospected area is situated on the north- and west-facing slopes of Mont Cenis (Fig. 1) at elevations between 1900 and 2500 m a.s.l., in the subalpine and the lower-alpine belts. The surveyed communes are Lanslebourg, Lanslevillard and the western part of Bessans, between 06°59'N–45°18'E and 06°51'N–45°16'E. The systematic exploration was achieved during one week by a team of six persons with the aim to record all individuals, if possible.

Table 1

Geographic coordinates and vegetation context of discovered *Pinus mugo* on the north- and west-facing slopes of the Mont Cenis massif.

No	Altitude (m)	Latitude	Longitude	Vegetation
1	2250	45°17,400'	6°56,983'	<i>Larix decidua</i> and <i>Pinus cembra</i> woodland
2	2265	45°17,183'	6°56,995'	Pastured grassland
3	2300	45°17,118'	6°57,214'	Grassland with dense <i>Pinus cembra</i> seedlings
4	2382	45°17,092'	6°57,416'	Pastured grassland
5	2395	45°15,941'	6°57,452'	Pastured grassland
6	2280	45°15,870'	6°54,611'	Pastured grassland with dense cover of <i>Arctostaphylos uva-ursi</i>
7	2311	45°15,863'	6°54,695'	Grassland with <i>Dryas octopetala</i>
8	2300	45°15,855'	6°54,630'	Pastured grassland
9	2295	45°15,855'	6°54,622'	Pastured grassland
10	2295	45°15,823'	6°54,622'	Scorched grassland nearby a chair lift
11	2391	45°15,774'	6°54,797'	Grassland with <i>Dryas octopetala</i>
12	2367	45°15,643'	6°54,791'	Grassland rich in <i>Festuca paniculata</i>
13	2373	45°15,480'	6°54,868'	Grassland with <i>Arctostaphylos uva-ursii</i>
14	2230	45°15,561'	6°54,361'	Pastured grassland
15	2203	45°15,717'	6°54,626'	Pastured grassland
20	2261	45°15,816'	6°54,485'	Grassland with <i>Festuca paniculata</i> , along a ski pist
21	2250	45°15,788'	6°54,443'	Grassland with <i>Festuca paniculata</i> , along a ski pist
22	2239	45°15,795'	6°54,415'	Pastured grassland
23	2240	45°15,796'	6°54,402'	Pastured grassland
24	2239	45°15,796'	6°54,304'	Pastured grassland
25	2202	45°15,739'	6°54,365'	Grassland with <i>Festuca paniculata</i>
26	2212	45°15,859'	6°54,292'	Grassland with <i>Juniperus nana</i> , saplings of <i>Larix decidua</i> and <i>Picea abies</i>
27	2184	45°15,895'	6°54,264'	Grassland with <i>Arctostaphylos uva-ursii</i> and <i>Juniperus nana</i>

### 3. Results

The survey revealed 23 pines showing *Pinus mugo* characteristics, i.e. pines prostrated with perfectly symmetrical cones (Table 1). Uncertainties of identification could occur for a few pines that lacked cones, and the small height could result from confusion with young *Pinus uncinata*. However, it was noticeable that, in the explored area, no mountain (erected) pine was observed, although *Pinus uncinata* forests exist lower in the same valley between 10 and 30 km apart, especially on dry and calcareous soil.

The discovered dwarf pines are distributed between 2180 and 2400 m a.s.l. (Table 1). Most individuals are in pastured grassland, rich in ericoides species such as *Arctostaphylos uva-ursi*, *Vaccinium uliginosum*, *V. myrtillus*, *V. vitis-idaea*, *Rhododendron ferrugineum*, *Empetrum hermaphroditum*, but also *Juniperus nana* and *Cotoneaster integerrimus*. Near a large *Pinus mugo* individual in the commune of Lanslevillard, we observed carpets of *Arctostaphylos alpinus*, Alpine bearberry, a species rare enough to be mentioned here. A few dwarf pine are situated at the upper treeline of subalpine

forests, near 2250–2300 m a.s.l., mainly composed of cembra pine, larch, and very few spruce.

Dwarf pines are distributed on two different sectors of the investigated area, first in the eastern part into the Crozats pasture localised northward from the peak called Signal du Grand Mont Cenis (06°57'N–45°17'E), Lanslevillard (5 ind.) and, second in the Femaz pasture on the west-facing slopes of the peak called Ouillon des Arcellins (06°54'N–45°15'E), localised at the Mont Cenis Pass, Lanslebourg (18 ind.). No altitudinal pattern is observed, both in crown height and circumference. Individuals covering the largest area are not at the highest, nor at the lowest altitude (Fig. 2a, b). Four of the five individuals from the eastern sector, Crozats pasture (nos 1–4), display a large crown (max. circumference: 31 m, Fig. 2c), with dense needles and carrying cones (Fig. 3). The last individual (no. 5) is smaller with needles partly necrosed (Fig. 3). Individuals from the Femaz pasture show small crowns (circumference <7 m; max. height 1.5 m). The crown upper part of these pines is partially necrosed (Fig. 3, ind. nos 6–27).

The analysis of the archives of the forest administration shows that no tree plantation was performed on the

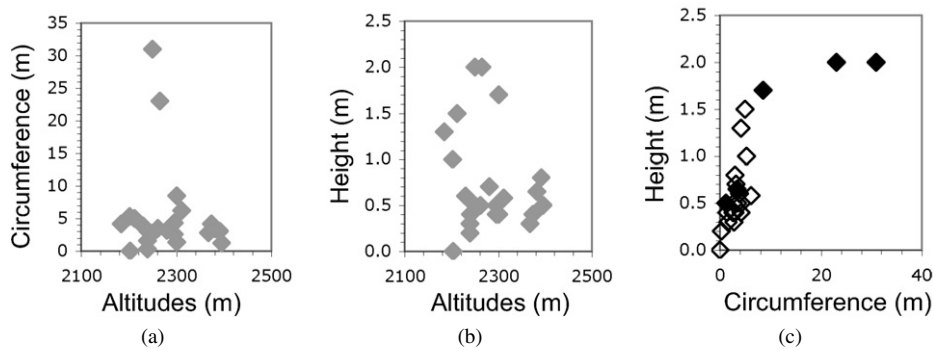


Fig. 2. Dendrometric structure of dwarf pine of the Mont Cenis massif plotted against altitude for crown circumferences (a) and for crown heights (b), and crown heights plotted *versus* circumferences (c). The open diamonds correspond to individuals of the western pasture (Femaz, Lanslebourg) and the black diamonds to those from the eastern pasture (Crozats, Lanslevillard). See text for geographic coordinates.

communes of Lanslebourg and Lanslevillard (Table 2). From all archives consulted, from Sollières-Sardières to Bessans, none indicates the plantation of dwarf pine, whatever the forest status, i.e. communal or national. The sole reported plantations were in 1975 in the valley bottom at Bessans, nearby the main road, then in 1982 and 1987 with cembro pine and spruce in the communal forest, composed of larch on the north-facing slopes of the valley, in the aim to “diversified tree resources”. Some plantations were made in national land of other communes located lower in the valley, i.e. Termignon and Sollières-Sardières. However, the species used are not indicated.

#### 4. Discussion

The lack of pine plantation, and any other tree species on the communes of Lanslebourg and Lanslevillard suggest that the discovered population of *Pinus mugo* is spontaneous and natural. The sole recorded plantations do not concern the surveyed area. The forest species used by foresters were larches, spruces, and cembra pines and no dwarf or mountain pine.

The biogeographical situation of *Pinus mugo* within the Mont Cenis area is remarkable. The dwarf pine is a centro-European species with dense and wide cover. In the western Alps, the Mont Cenis population is the first recorded in the northern French Alps. The sole known stands are in the south, in the Durance valley (Queyras massif, Étroite valley), in Italy in the Susa and Orco valleys and, far south in the valleys of the Maritime and Ligurian Alps (Bono et al. [19]; Montacchini [5]; Montacchini and Caramiello [20]; Ozenda [6]; Chas [7]; Fig. 1). Northward, the western populations are localised in the SW Wallis county, Switzerland (WSL [21]) and in the Aosta and Ossola valleys, NW

Italy (Montacchini [5]). Although in terms of distances, dwarf pines of Mont Cenis appear rather isolated, an ecological and biogeographical corridor allows the connecting of all stands within the inner Alps, from the Queyras massif to the Mont Cenis through several passes, e.g. those of Mont Genève, of Thures and of the Étroite valley between France and Italy. All these passes are under 2200 m a.s.l., and are within the natural altitudinal range of *Pinus mugo*. Although these stands along the Italian–French boundary are generally extremely isolated, they seem distributed along a virtual axis that would illustrate a wider and better connected distribution within the inner western Alps in the past, from the Savoy to the Durance valleys in France, through the Susa valley in Italy (Fig. 1). The southern and northern stands of dwarf pine within the Maritime and Ligurian Alps and the western Wallis appear totally unconnected from the inner Alps stands due to too elevated altitudes of massifs and passes. A possible connection appears at lower altitudes. However, this is not possible for dwarf pine during an interglacial environment (e.g. the current Holocene), because of the competition with erected trees of the mountain and plain belts that is unfavourable to *Pinus mugo*. The lower altitude connexion is possible only during a glacial geological period, either by the Po plain in Italy, or by hills of the Mediterranean coast in France (Fig. 1).

Palaeo-biogeographic data suggest an older broader extension of the dwarf pine phenotype of *Pinus mugo* in the inner alpine valleys (Montacchini [5]). Indeed, fossil imprints of *Pinus mugo* cones were discovered in one travertine of the Susa valley, dating from the Lateglacial-Holocene transition (Ali et al. [22]). However, these data must be considered with caution, due to the identification method involved, based on the qualitative morphology of imprints. A more systematic in-

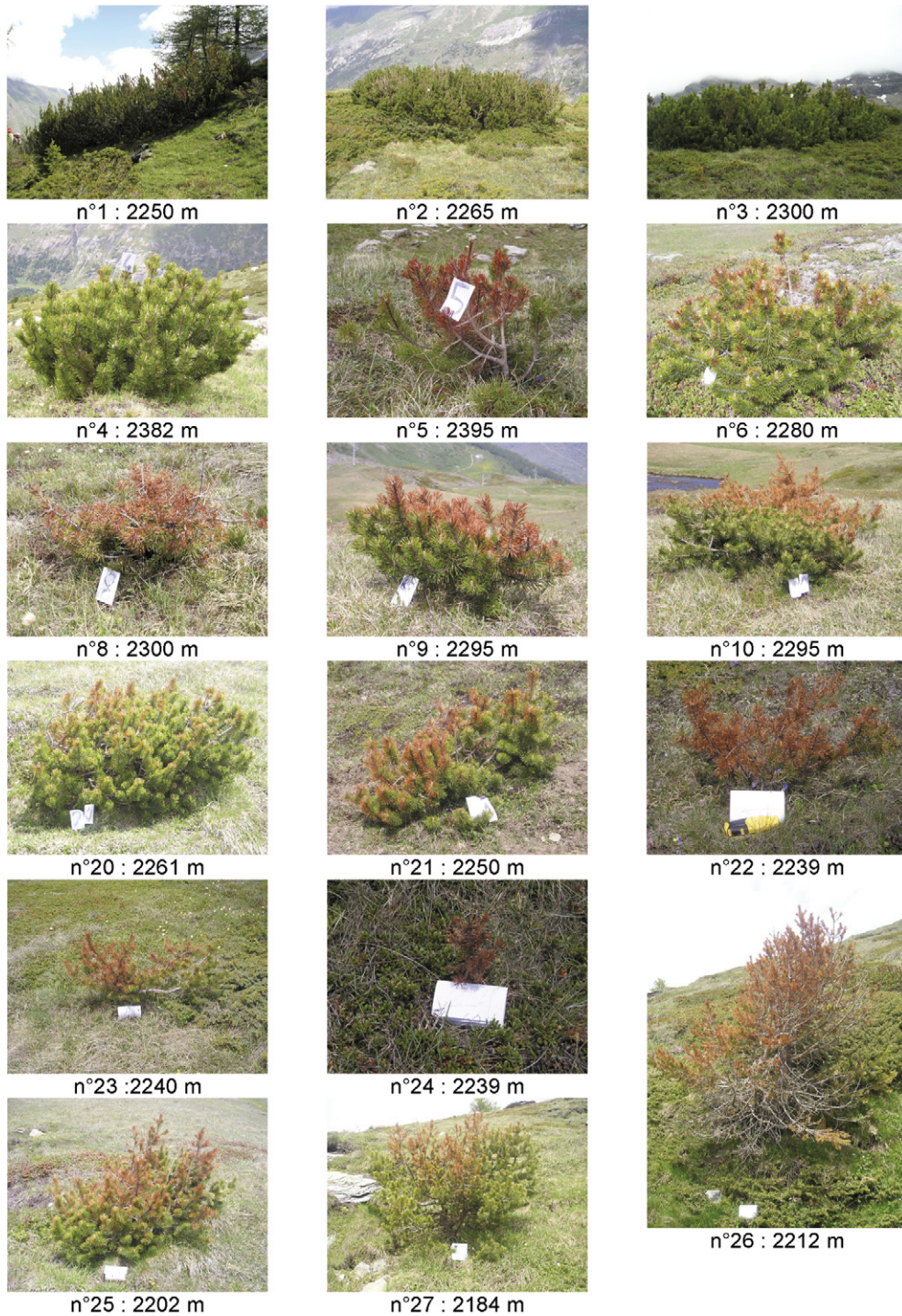


Fig. 3. Pictures and altitudes of selected specimens of dwarf pines of the Mont Cenis massif (June 2005).

investigation of travertine archives is stressed, involving a quantitative analysis of morphological structure of cone scale imprints. Hence, our investigations would better depict the past distribution of this dwarf pine, and would

analyse the ecological forcings and processes that fragmented its western geographic area. Among the fragmentation causes, the intensification of cultural land-uses in subalpine territories appears a likely explana-

Table 2

Archives from the French forest service (Office National des Forêts) at Chambéry for the high Maurienne communes of Termignon, Lanslebourg, Lanslevillard and Bessans.

Archive no	Archives title
28	ONF – Forêt communale de Bessans (1992), Révision d'aménagement forestier (1991–2015), Rapport de M. Collas, Direction régionale de Rhône-Alpes, Service départemental de la Savoie, Division de Modane, 52 p. + annexes
123	ONF – Forêt communale de Lanslebourg, Révision d'aménagement forestier (1979–2000), Direction régionale de Rhône-Alpes, Service départemental de la Savoie, Division de haute Maurienne
124	ONF – Forêt communale de Lanslevillard, Révision d'aménagement forestier, Direction régionale de Rhône-Alpes, Service départemental de la Savoie, Division de haute Maurienne
206	ONF – Forêt domaniale RTM de Sollières-Sardières, Révision d'aménagement forestier (1999–2018), Direction régionale de Rhône-Alpes, Service départemental de la Savoie, Division de Haute-Maurienne, 47 p.
207	ONF – Forêt domaniale RTM de Termignon, Révision d'aménagement forestier, Direction régionale de Rhône-Alpes, Service départemental de la Savoie, Division de Haute-Maurienne

tion, knowing that *Pinus mugo* stands are very dynamic in eastern areas under a severe land-use abandonment (Dullinger et al. [23]). However, biotic factors such as interspecific competition seem realistic, particularly during the early Holocene expansion of *Pinus cembra*, the dominant and naturally frequent subalpine species (Ali et al. [16]). Pollen approaches are not efficient to reconstruct the history of *Pinus mugo* that is mixed with those other diploxylon pines of the surroundings of SW Italian–French Alps (*Pinus sylvestris*, *P. uncinata*, *P. nigra*, *P. halepensis*, *P. pinaster*, *P. pinea*), except with the sole haploxylon species *Pinus cembra*. Only the fossil cones appear able to decipher the postglacial history of *Pinus mugo*.

The Mont Cenis population of dwarf pine is not homogeneous, nor concentrated into a single pasture, although the effectives are very low ( $N = 23$ ). It is remarkable to report that there is no altitudinal pattern. For instance, we could expect smaller and eventually prostrated individuals at higher altitudes. However, according to the situation of individuals, their physiognomy are different. Obviously, individuals from Lanslevillard (eastern pasture) display a better fitness than those of Lanslebourg (western pasture) that are almost all necrosed (Fig. 3) and of smaller size, both in crown height and circumference (Fig. 2c). Individuals from Lanslebourg are all situated in an area dedicated to winter sport and particularly to skiing. It is possible that ski activities could explain this observed pathological status on dwarf pines, i.e. the necroses of top crown needles (Fig. 3). The repeated passages of skis, eventually of devices to manage ski-trails, contribute to densify and reduce the snow layer thickness, exposing artificially needles to weathering, particularly to strong winds containing ice particles. Indeed, the Mont Cenis pass is known for its strong, glacial wind. The current status of *Pinus mugo* individuals seems critical, and

their presence could be rapidly altered if a conservation program were not started to protect them. Furthermore, dwarf pine *Pinus mugo* is on the French red list of protected species (“annexe 1, arrêté du 20 janvier 1982 relatif aux espèces végétales protégées sur l'ensemble du territoire national français”). This law indicates that species cannot be destroyed, cut, mutilated and broken-off, except in the framework of rural exploitation of lands that are traditionally cultivated, which is not the case of the dwarf pine of Mont Cenis, that are situated in former subalpine pastures that are currently used for winter sports.

## 5. Conclusion

Dwarf pines of the Mont Cenis compose a spontaneous and natural population of *Pinus mugo* Turra. This population appears fragile in light of effective numbers. It is currently isolated, but would result from populations that probably covered wider territories during the early Holocene, from the Durance valleys to the Maurienne valley, through the Susa valley. The dwarf pine population of the Mont Cenis appears altered, except the individuals that do not grow in the ski station area. A conservation program is urgent to preserve this population, the sole known in the northern French Alps.

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## References

- [1] K.I. Christensen, Taxonomic revision of the *Pinus mugo* complex and *P. × rhaetica* (*P. mugo* × *sylvestris*) (Pinaceae), *Nordic Journal of Botany* 7 (1987) 383–408.
- [2] A. Farjon, *World Checklist and Bibliography of Conifers*, Royal Botanical Gardens at Kew, Richmond, U.K., 1998.
- [3] I. Monteleone, D. Ferrazzini, P. Belletti, Effectiveness of neutral RAPD markers to detect genetic divergence between the subspecies *uncinata* and *mugo* of *Pinus mugo* Turra, *Silva Fennica* 40 (2006) 391–406.
- [4] H. Gaussen, A propos du pin mugho, *Revue Forestière Française* (1937) 695–697.
- [5] F. Montacchini, Il “*Pinus mugo*” Turra ed il “*Pinus uncinata*” Miller in Piemonte – La vegetazione, *Allionia* 14 (1968) 123–151.
- [6] P. Ozenda, Sur la valeur biogéographique des groupements à pin mugo dans les Alpes occidentales, *Compte Rendu des Séances de la Société de Biogéographie* 405 (1971) 190–194.
- [7] E. Chas, Atlas de la flore des Hautes-Alpes, Conservatoire botanique national de Gap-Charance, Conservatoire des espaces naturels de Provence et des Alpes du Sud, Parc National des Ecrins, Gap, 1994.
- [8] K. Boratynska, K. Marcysiak, A. Boratynski, *Pinus mugo* (Pinaceae) in the Abruzzi Mountains: high morphological variation in isolated populations, *Botanical Journal of the Linnean Society* 147 (2005) 309–316.
- [9] J. Hamerník, I. Musil, The *Pinus mugo* complex – its structuring and general overview of the used nomenclature, *Journal of Forest Science* 53 (2007) 253–266.
- [10] P. Ozenda, La végétation de la chaîne alpine dans l’espace montagnard européen, Editions Masson, Paris, France, 1985.
- [11] D.M. Richardson, *Ecology and Biogeography of Pinus*, Cambridge University Press, Cambridge, 1998.
- [12] K. Lauber, G. Wagner, *Flora Helvetica, Flore illustrée de Suisse*, Deuxième édition, Paul Haupt, Bern, Suisse, 2001.
- [13] C. Bartoli, Etude écologique sur les associations végétales forestières de la Haute Maurienne, *Annales des Sciences Forestières* 23 (1966) 432–761.
- [14] P. Gensac, Catalogue écologique des plantes vasculaires du Parc national de la Vanoise et des régions limitrophes, *Travaux scientifiques du Parc national de la Vanoise* 4 (1974) 1–232.
- [15] Parc National de la Vanoise, *Fleurs de Vanoise*, Edisud, Aix-en-Provence, 1993.
- [16] A.A. Ali, C. Carcaillet, B. Talon, P. Roiron, J.F. Terral, *Pinus cembra* (arolla), a common tree in the inner French Alps since the early Holocene and once extended above the present treeline: a synthesis based on charcoal data from soils and travertines, *Journal of Biogeography* 32 (2005) 1659–1669.
- [17] S. Fudral, E. Deville, U. Pognante, M. Gay, G. Fregolent, S. Lorenzoni, D. Roberd, G. Nicoud, C. Blake, A. Jayko, E. Jailard, J.M. Bertrand, M.G. Forno, G. Massazza, Carte géologique France (1/50 000), feuille Lanslebourg-Mont d’Ambin (776). BRGM, Orléans, 1994.
- [18] F. Beihle, C. Carcaillet, S. Chauchard, Élévation de la limite supérieure du sapin pectiné (*Abies alba*) depuis 1950 en Maurienne, Savoie. *Travaux Scientifique du Parc National de la Vanoise*, in press.
- [19] G. Bono, M. Barbero, L. Poirion, Groupements de “*Pinus mugo*” Turra (“*Pinus mughus*” Scop.) dans les Alpes Maritimes et Ligures, *Allionia* 13 (1967) 55–80.
- [20] F. Montacchini, R. Caramiello, Il *Pinus mugo* Turra ed il *Pinus uncinata* Miller in Piemonte. Note critiche e distribuzione, *Giornale Botanico Italiano* 102 (1968) 529–535.
- [21] WSL (2007) Wald, Schnee und Landschaft, Swiss Federal Institute for Forest, Snow and Landscape, <http://www.wsl.ch/land/products/biomod/cscfmaps/ecscf666.html>.
- [22] A.A. Ali, M. Martinez, N. Fauvart, P. Roiron, G. Fioraso, J.L. Guendon, J.F. Terral, C. Carcaillet, Incendies et peuplements à *Pinus mugo* Turra dans les Alpes occidentales (Val de Suse, Italie) durant la transition Tardiglaciaire-Holocène : une zone refuge évidente, *C. R. Biologies* 329 (2006) 494–501.
- [23] S. Dullinger, T. Dirnbock, G. Grabherr, Pattern of shrub invasion into high mountain grasslands of the Northern Calcareous Alps, Austria, Arctic, Antarctic and Alpine Research 35 (2003) 434–441.