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Research paper

Holocene upper tree-limits of *Pinus* section *sylvestris* in the Western Alps as evidenced from travertine archives

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ABSTRACT

The postglacial dynamics of *Pinus sylvestris*, *Pinus mugo* and *Pinus uncinata* are poorly documented in the Alps due to a lack of precise taxonomic resolution. We present past altitudinal distribution of these pine species, at a local scale, based on morphometric and taxonomic analyses of fossil cone imprints preserved in travertine deposits from the mountain and subalpine belt in the Western Alps. We found that *P. sylvestris* and *P. uncinata* have been present in the study area since at least 11,500 calibrated yr BP. Until 8500 cal yr BP, these conifers occupied likely a wide altitudinal range, favoured by the establishment of drier and warmer climate conditions compared to present-day. After this period, the dynamics and spatial distribution patterns of *P. sylvestris* and *P. uncinata* were strongly shaped by the expansion of more competitively superior conifers that had contributed to their local extinction from several sites and the fragmentation of their population.

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1. Introduction

In the Alps and other European mountain ranges, the *Pinus* species belonging to the section *sylvestris*, including *Pinus sylvestris* L., *Pinus mugo* Turra, and *Pinus uncinata* Mill, cover large overlapping areas and have sympatric populations (Jalas and Suominen, 1973; Richardson, 1998). The extent of their modern distribution patterns underlines the fact that they play a key role in the functioning of European forests, produce high biomass, and have contributed to carbon sequestration for several millennia. Their temporal and spatial distribution patterns are the result of long-term processes controlled by glacial refugia, climate variation, and cultural activities (Burga, 1988; Cheddadi et al., 2006). However, very little is known about the ecological mechanisms that have controlled their specific pattern of distribution since the last full glacial period, in particular at their respective upper altitudinal limits. This lack of data is because it's difficult to discriminate pine species belonging to the section *sylvestris* from pollen proxy (Reille, 1992; Schmidt et al., 2002) and impossible by wood anatomy features (Schweingruber, 1990). Although *P. sylvestris* can be distinguished from *P. mugo* and *P. uncinata* from

stomata and cuticle characteristics of their needles (Boratyńska and Bobowicz, 2001; García Álvarez et al., 2009b), there have been doubtful taxonomic identifications in previous palaeoecological investigations in locations where these pine species are sympatric. Most previous attempts to trace the past distribution of *P.* section *sylvestris* have most relied on the analysis of pollen data; however, the findings have rarely been supported by records of plant macroremains (e.g. Ponel et al., 1992; Gobet et al., 2005; Tinner and Kaltenrieder, 2005; Stähli et al., 2006). Moreover, *Pinus* pollen usually travels over distances of many kilometres (≫ 10 km) from source populations, which can potentially cause palaeovegetation reconstructions to be erroneous (Birks and Birks, 2000). Adding the fact that landscape heterogeneity and environment parameters such as soil property or exposure induce an important variability in species distribution (Ozenda, 1985; Körner, 1999), multi-proxy approaches at different spatial scales are a requirement to improve our understanding of past and future distribution of these pine species in response of climate change and land-use modifications (Botkin et al., 2007).

The present study aimed to reconstruct the past distribution of *P.* section *sylvestris* in the western Alps, based on cone imprints and needles enclosed in travertine archives. These calcareous deposits allow to discuss at local scale about past distribution of ligneous species (Ali et al., 2003a, 2003b). However discontinuity in carbonate deposition prevents any high temporal resolution approaches. To improve the fossil cone identification, we developed a morphometric method based on modern specimens, then applied this method to fossil cones. We discuss

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Table 1
Localization of modern collections.

| Taxon	Population	Localisation	Lat. long.	Alt. (m a.s.l.)
Pinus sylvestris	Ilirska Bistrika	Slovenia	45°34′10″ N 14°17′56″ E	650
	Termignon	Savoy, France	45°16′64″ N 06°50′10″ E	1600
Pinus mugo	Ilirska Bistrika	Slovenia	45°33′55″ N 14°19′02″ E	2250
	Mont Cenis	Savoy, France	45°17′40″ N 06°56′98″ E	2200
Pinus uncinata	Parco delle Alpi marittime	Piedmont, Italy	44°12′12″ N 07°29′27″ E	1600
	Termignon	Savoy, France	45°16′39″ N 06°50′53″ E	1990
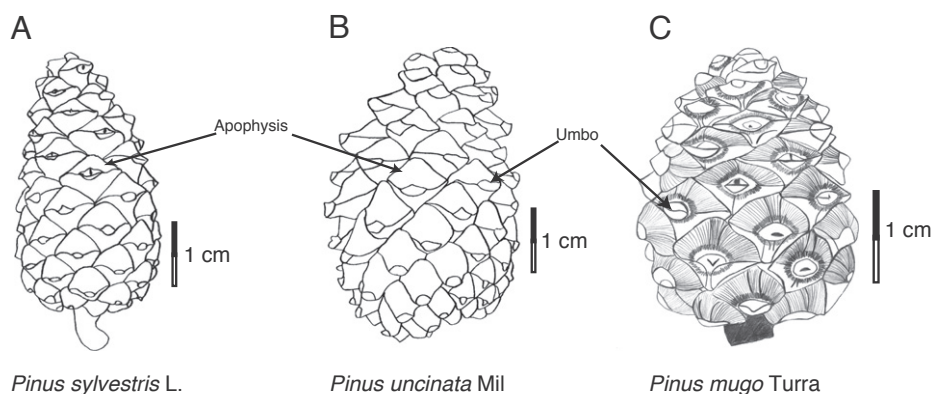
Fig. 1. Cones of *Pinus sylvestris* (A), *Pinus uncinata* (B) and *Pinus mugo* (C) showing their principal morphological features.

the spatial distribution of these pines with respect to the dynamics of other coniferous species currently found in the region at the upper forest limit; this was inferred from terrestrial macroremain studies in sub-alpine sediments.

2. Materials and methods

2.1. Modern cone sample characteristics

Modern reference material consisted of 140 cones collected from distinct populations of *P. sylvestris*, *P. uncinata* and *P. mugo*, in Slovenia, Italy and France (Table 1). The identification of modern specimens was based on tree and cone morphology (Rameau et al., 1993; Lauber and Wagner, 2001). Two populations were sampled per species and five trees were sampled from each population, except for *P. mugo* from the Col du Mont-Cenis on the French/Italian border, where only three individuals with mature cones were found (Carcaillet et al., 2009). Five cones were collected from each tree.

Female *P. sylvestris* cones are symmetrical with an umbo centred on a thin apophysis or scale (Fig. 1a). Female *P. uncinata* cones are asymmetrical with a hook-shaped umbo at the apophysis apex (Fig. 1b). However, the concave face of the cones (right side of the design) generally presents an umbo centred on a thin apophysis. The female *P. mugo* cones are symmetrical, also with an umbo centred on a thin apophysis (Fig. 1c), but the cones are smaller and rounder than those of *P. sylvestris* (Christensen, 1987).

2.2. Identification of cones and needles

In the western inner Alps, valleys contain travertine archives rich in plant-imprints (e.g. Ali et al., 2005a). Cone and needle remains of *Pinus* are very common within these calcareous accumulations that result from the bicarbonate saturation of water streams and springs (Brotto, 1986). The accumulation of these natural deposits requires stable environmental conditions (high temperature and precipitation) and is optimal within forest areas (Magnin et al., 1991; Ali et al., 2003b).

Travertine deposits were sampled both in France and Italy, between 1340 m and 2200 m a.s.l. (Fig. 2; Table 2). Fossil specimens were extracted from travertine blocks using a hammer and chisel. Cone moulds were made of the collected specimens using silicon liquid (Silastic —
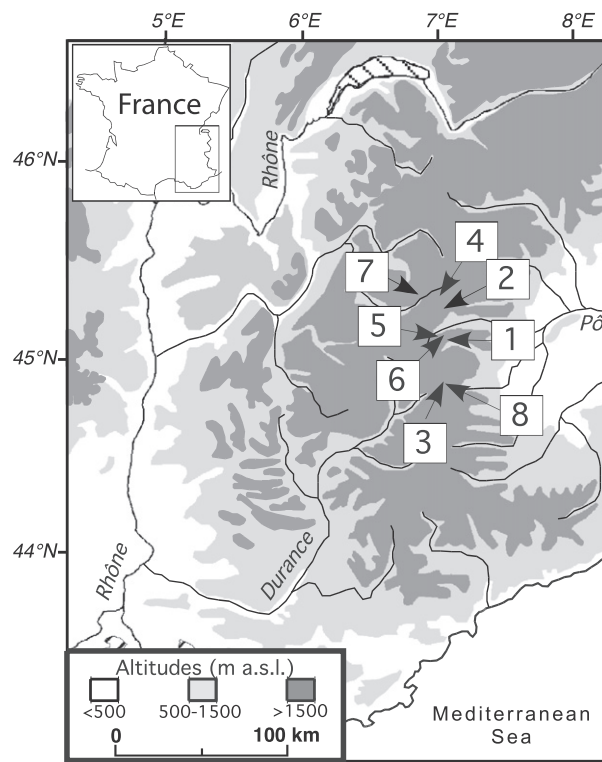

Fig. 2. Localization of the travertine sequences in the Western Alps. 7: Termignon (Maurienne valley, France); 4: Saint-Genix (Maurienne valley, France); 2: Mont-Cenis (Savoy, France), 1 4: Grand Puy (Val di Susa, Italy) 5: San Dominico (Val di Susa, Italy); 6: Selle (Val di Susa, Italy); 3: Prafarnas (Queyras massif, France); 8: Tioures (Queyras massif, France).

Table 2
Localization and main features of the study sites.

Site no.	Site name	Lat. long.	Altitude (m a.s.l.)	Present-day local vegetation[a]
1	Grand Puy	45°02′N 06°57′E	1815	Forest: *Larix decidua, Hippophae rhamoïdes, Populus tremula.*
2	Mont-Cenis	45°13′N 06°57′E	1815	Treed grassland: *Pinus uncinata, Pinus sylvestris, Betula pubescens.*
3	Prafarnas	44°45′N 06°53′E	2000	Forest: *Pinus cembra, Larix decidua, Pinus uncinata.*
4	Saint-Genix	45°17′N 06°55′E	1715	Forest: *Abies alba, Picea abies, Pinus cembra.*
5	San Dominico	45°03′N 06°52′E	1340	Forest: *Pinus sylvestris, Larix decidua.*
6	Selle	45°03′N 06°55′E	2000	Forest: *Larix decidua, Pinus cembra, Picea abies* and *Populus tremula.*
7	Termignon	45°18′N 06°49′E	1535	Forest: *Abies alba, Picea abies, Pinus sylvestris* and *Pinus uncinata.*
8	Tioures	44°42′N 06°53′E	2200	Grassland: *Fetuca ovina.*

[a] The understoreys around the travertine deposits are mostly composed of dwarf shrubs such as, *Rhododendron ferrugineum, Vaccinium myrtillus, Vaccinium vitis-idaea., Vaccinium uliginosum, Juniperus sibirica, Juniperus communis.*
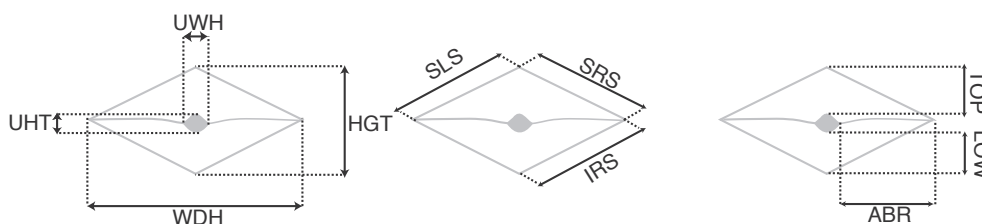
Table 3
Morphological traits measured on cone scales.

Traits	Codes
Apophysis height	HGT
Apophysis width	WDH
Superior left side of apophysis	SLS
Superior right side of apophysis	SRS
Inferior right side of apophysis	IRS
Distance between apophysis top and umbo top	TOP
Distance between apophysis low and umbo low	LOW
Apophysis beard right	ABR
Umbo height	UHT
Umbo width	UWH

3483). This technique allows cone morphology and traits to be determined with high accuracy. We used cross section of needles as a criterion to identify pines belonging to the *sylvestris* section from the other pine species. *Pinus* section *sylvestris* present needles with a semi-circular cross section while *Pinus cembra* needles, another common subalpine pine species, have a triangular cross section.

2.3. Morphometric analysis

Cones are easily identifiable between species from their general shape. Nevertheless, cone imprints are always incomplete. As a result, morphometric analysis is based on the apophyses, which are abundant and readily measurable on moulds of fossil cones. Ten measurements were taken of the apophysis of the modern reference specimens (Table 3; Fig. 3) with a digital slide calliper (precision: 0.01 mm). Measurements were performed on the upper widest part of the cones. This procedure was based on our previous morphometric investigations that showed that the bottom parts of cones were not useful for discriminating between species. In each cone, five randomly selected apophyses were measured, which allowed a convincing characterisation of the cone traits. It was determinate by the stabilisation of the mean. In total, 7000 measurements were made, 2500 for *P. sylvestris*, 2500 for *P. uncinata* and 2000 for *P. mugo.* The same trait measurements were performed on the fossil cone moulds that did not show hook-shaped apophyses, i.e. they were unidentifiable from direct morphological comparison with modern specimens.

2.4. Statistical analysis

In a first time, descriptive statistics (means, standard deviations) were obtained and one-way analysis of variance (ANOVA) using GLM procedure in SAS (v. 9.2, SAS Institute, Cary, NC) was performed to determine if there was any statically significant difference among pine species for each one of apophysis traits.

In a second time, the ten measurements taken on the apophyses of modern cones were run in a discriminant analysis (DA) with the PROC DISCRIM procedure in SAS. This procedure estimates the probabilities of affiliation of each observation (apophysis features) into each group of pine species. Then, all fossil cones, which are describe by the mean value of each apophysis traits, were included in the DA as additional individual that could be assigned to a distinct group. The affiliation probability (p) of each fossil cone to the three pine groups is calculated using Mahalanobis distances between the fossil cone and the centroids of the three pine groups. If $p \geq 0.80$, we considered the allocation as reliable. If $0.70 < p < 0.80$, the allocation was considered with caution (e.g. *P.* cf. *sylvestris*). Fossil specimens with a p-value < 0.70 were not classified.

2.5. Isotopic dating

Thirteen ^{230}Th/^{234}U and one ^{14}C AMS radiometric datings were performed on the different travertine sequences enclosing pine macroremains (Table 4). Th/U measurements performed on calcareous facies were required to confirm that there was no contamination by Thorium of different ages by elemental migration through the travertine layers (Quinif, 1989; Eikenberg et al., 2001). Possible contamination is revealed by values of the ^{230}Th/^{232}Th ratio. Values up to 17 (Bischoff et al., 1988) or 20 (Ivanovich and Harmon, 1992) indicate that detrital contamination by Thorium is negligible, thus allowing the use of the Th/U dating securely. It is important to note that all dates obtained in the present study were corrected to minimise dating errors by taking into account any potential contamination (Fietzke et al., 2005). Th/U measurements can be directly compared to the calendar chronology because there is no reservoir effect.

The unique AMS ^{14}C was obtained from charcoal fragments of *P.* type *sylvestris*, calibrated against dendrochronological years by the CALIB program version 6.0 (Stuiver and Reimer, 1993) based on the

Fig. 3. Diagram of the 10 parameters measured on the apophysis.

Table 4
Th/U and ^{14}C dating performed on the different travertine sequences.

Site	Method	Reference	^{232}Th/^{230}Th	^{14}C Age (BP)	Age (yr BP)
Tioures	Th/U	Ali et al. (2003a)	17.00		9800 ± 100
Mont Cenis	Th/U	IFM_GEOMAR,	5. 48		5460 ± 240
Mont Cenis	Th/U	IFM_GEOMAR,	12.18		6130 ± 120
Mont Cenis	Th/U	IFM_GEOMAR,	7.19		5000 ± 160
Termignon	Th/U	IFM_GEOMAR,	1.81		1610 ± 120
Termignon	Th/U	IFM_GEOMAR,	2.52		1420 ± 150
Saint Génix	Th/U	IFM_GEOMAR,	9.94		7908 ± 195
Saint Génix	Th/U	IFM_GEOMAR,	9.93		5300 ± 133
Saint Génix	Th/U	IFM_GEOMAR,	4.88		3025 ± 149
San Dominico	Th/U	Ali et al. (2006)	67.59		11506 ± 66
Selle	Th/U	Ali et al. (2006)	11.25		10145 ± 225
Selle	Th/U	Ali et al. (2006)	3.83		9475 ± 670
Grand Puy	Th/U	IFM_GEOMAR,	1.068		7800 ± 2500
Prafarnas	^{14}C	Poz-16036		8020 ± 40	$8730–9020^{a}$

[a] Calendar years are corrected for ^{14}C measurements based on the CALIB program version 6.0 (Stuiver and Reimer, 1993) based on the IntCal09 dataset (Reimer et al., 2009); 2 δ, 100% probability.

IntCal09 dataset (Reimer et al., 2009). All Th/U and calibrated ^{14}C dates are hereafter labelled 'yr BP' representing years before present.

3. Results and interpretations

3.1. Morphometric analysis of the modern reference material

Interpretation of the ANOVA results indicates that significant differences exist between pine species in each apophysis traits (Table 5). All traits seem to be relevant to discriminate pine apophyses.

Based on DA, 82.2% of the cone scales from the modern dataset were accurately classified (Table 6). Among these, 94.0%, 89.6% and 65.2% of the *P. sylvestris*, *P. mugo*, and *P. uncinata* cones were correctly classified, respectively. These percentages reflect the quality of our discriminative model. Several apophyses of *P. uncinata* were classified as *P. mugo* (n = 38) or *P. sylvestris* (n = 49). Consequently, the model's ability to identify the right species from apophyses is of 81.7%, 82.1% and 82.7% for *P. mugo*, *P. sylvestris* and *P. uncinata* respectively (Table 6). These results indicate that identification of scales of *P. mugo*, *P. uncinata* and *P. sylvestris* is relatively reliable. The discriminant functions created are presented in Table 7.

Table 5
Descriptive statistics of traits apophysis traits and one-way ANOVA results. For the descriptive statistics, values correspond to: Mean ± S.D. and (range).

Traits	*Pinus mugo* (μm)	*Pinus sylvestris* (μm)	*Pinus uncinata* (μm)	F-Value	p > F
HGT	494.7 ± 93.7 (266–757)	637.8 ± 121.7 (330–1072)	524.6 ± 139.3 (239–936)	90.6	<0.0001
WDH	768.5 ± 121.0 (493–1130)	635.1 ± 106.6 (353–904)	657.9 ± 137.4 (391–1142)	73.1	<0.0001
SLS	436.9 ± 85.2 (207–700)	401.2 ± 81.2 (193–663)	379.5 ± 94.9 (192–650)	24.1	<0.0001
IRS	473.2 ± 74.5 (294–739)	497.4 ± 84.3 (290–802)	465.0 ± 98.0 (256–722)	9.3	<0.0001
TOP	197.1 ± 59.0 (71–355)	245.8 ± 45.1 (127–365)	234.1 ± 106.7 (55–666)	24.9	<0.0001
LOW	193.4 ± 49.6 (73–314)	310.5 ± 65.0 (102–580)	252.2 ± 77.4 (44–452)	175.8	<0.0001
ABR	303.8 ± 56.4 (171–467)	314.0 ± 48.3 (170–448)	324.2 ± 90.4 (104–656)	5.0	0.0069
SRS	445.9 ± 84.2 (207–657)	413.2 ± 83.9 (182–610)	386.6 ± 100.2 (188–893)	24.0	<0.0001
UHT	185.1 ± 30.8 (97–265)	159.5 ± 21.7 (110–226)	188.9 ± 26.9 (118–266)	89.8	<0.0001
UWH	327.7 ± 42.0 (220–424)	262.9 ± 40.1 (143–386)	307.6 ± 45.5 (187–424)	139.4	<0.0001

Table 6
Classification results of modern specimens according to the 10 morphological traits. The numbers in brackets relate to the model's ability to identify the correct species. It's correspond to: 100×(number of observations classified in the correct group/total number of observations classified in this group).

	% of good classification	*A posteriori* classification (n)		
		Pinus mugo	*Pinus sylvestris*	*Pinus uncinata*
Pinus mugo	94.0	188 (81.7%)	0	12
Pinus sylvestris	89.6	4	224 (82.1%)	22
Pinus uncinata	65.2	38	49	163 (82.7%)
Total	82.9	230	273	197

Table 7
Discriminant functions for specie determination of *Pinus* type *sylvestris* cones.

Discriminant functions
Pinus mugo = $-93.87375 - 0.01522 \times \text{HGT} + 0.06511 \times \text{WDH} - 0.06226 \times \text{SLS} + 0.01460 \times \text{IRS} - 0.00078 \times \text{TOP} + 0.08242 \times \text{BOT} + 0.10648 \times \text{ABR} - 0.04973 \times \text{SRS} + 0.13118 \times \text{UHT} + 0.12443 \times \text{UWH}$
Pinus sylvestris = $-90.45675 + 0.05503 \times \text{HGT} + 0.07703 \times \text{WDH} - 0.06681 \times \text{SLS} - 0.03148 \times \text{IRS} + 0.13942 \times \text{TOP} - 0.05222 \times \text{BOT} + 0.06810 \times \text{ABR} - 0.08065 \times \text{SRS} - 0.14803 \times \text{UHT} + 0.13739 \times \text{UWH}$
Pinus uncinata = $-78.29601 + 0.02319 \times \text{HGT} + 0.02068 \times \text{WDH} - 0.01550 \times \text{SLS} + 0.02231 \times \text{IRS} - 0.02411 \times \text{TOP} + 0.02315 \times \text{BOT} - 0.00129 \times \text{ABR} - 0.02804 \times \text{SRS} + 0.13925 \times \text{UHT} + 0.10520 \times \text{UWH}$

3.2. Allocation of fossil cones

In total, 181 fossil cones were extracted from the travertine sequences. Among them, 131 cones exhibited hook-shaped apophyses and were morphologically identified as *P. uncinata*. So, only 50 fossil specimens displayed a centred umbo with thin apophyses, and required morphometric analysis to be identified. All fossil cones recovered in Tioures (n = 23) and St-Genix (n = 7) had thick hook-shaped apophyses, and belonged to *P. uncinata*. Most specimens collected in the travertines from the Col du Mont-Cenis (n = 79) and Termignon (n = 10) were *P. uncinata*. At San Dominico and Grand Puy, 4 and 8 fossil cones had thick hook-shaped apophyses, respectively.

Identification of the 50 fossil, and their associated allocation probabilities (Table 8) indicate that most specimens were *P. sylvestris* (n = 23) and *P. uncinata* (n = 14) with $p \geq 0.80$. Two cones were assigned as *P.* cf. *sylvestris* ($0.70 < p < 0.80$), three as *P.* cf. *uncinata* and one as *P.* cf. *mugo*. The remaining 7 fossil cones (of the 181 cones) were not classified as their allocation probability was below the 0.70 threshold probability.

Table 8
Allocation of fossil cones without a hook-shape apophysis. The numbers in brackets correspond to the number of remains identified. The site ordination is based on the chronological setting.

Sites	Species identified	Probability of allocation
Termignon	*Pinus sylvestris* (1)	0.93
	Pinus cf. *uncinata* (1)	0.77
Mont-Cenis	*Pinus* cf. *mugo* (1)	0.75
Grand Puy	*Pinus sylvestris* (5)	$0.96 \leq p \leq 1.00$
	Pinus cf. *sylvestris* (1)	0.70
	Pinus uncinata (1)	1.00
	Pinus cf. *uncinata* (1)	0.75
	Not classified (1)	
Prafanas	*Pinus sylvestris* (5)	$0.82 \leq p \leq 0.98$
	Pinus uncinata (9)	$0.96 \leq p \leq 1.00$
	Pinus cf. *uncinata* (1)	0.72
	Not classified (2)	
Selle	*Pinus sylvestris* (2)	$0.96 \leq p \leq 1.00$
San Dominico	*Pinus sylvestris* (10)	$0.85 \leq p \leq 1.00$
	Pinus cf. *sylvestris* (1)	0.74
	Pinus uncinata (4)	$0.85 \leq p \leq 1.00$
	Not classified (4)	

3.3. Temporal and altitudinal distributions

Dating showed that the cone imprints were fossilised between 11,500 and 1400 yr BP (Table 4). *P. sylvestris* and *P. uncinata* developed at the Late-Glacial/Holocene transition at San Dominico ca. 1340 m a.s.l. (Fig. 4a; see Appendix A S1 in supporting information). At 9800 yr BP, *P. uncinata* reached altitudes around 2200 m a.s.l. (Fig. 4a) near the Tioures sequence (see supporting information). *P. sylvestris* and *P. uncinata* were present up to 2000 m a.s.l. around Prafarnas, where sequences dated back to 8900 yr BP (Table 4). Macroremains of these two pines were less abundant and frequent in the travertine sequences that were dated after 8000–7000 yr BP (Fig. 4a). Currently, *P. uncinata* is absent at Tioures (2200 m), Grand Puy (1815 m) and St-Genix (1695 m), whereas *P. sylvestris* is absent around the Prafranas and Grand Puy sites. Our data were insufficient to allow us to precisely identify when these local extinctions occurred.

4. Discussion

Our data show that both *P. sylvestris* and *P. uncinata* were already present within upper forest ecosystems at the beginning of the Holocene in the western Alps. However, there were no definite *P. mugo* trees recorded, even though a previous analysis based on the same material concluded that this pine did occur near the San Dominico travertine during the Late-Glacial/Holocene transition (Ali et al., 2006). In our study, these fossil specimens (4 samples in total) were classified as *P. sylvestris* or were unclassified. It is important to stress that the unclassified specimens collected at the different sites had morphological features that were intermediate between the tree pine species, which could be a result of hybridization. Indeed, most travertine deposits are located in areas where populations are sympatric or nearby, favouring hybridization and introgression; this has already been reported for *P. sylvestris* and *P. mugo* (Wachowiak and Prus-Glowacki, 2008) and for *P. sylvestris* and *P. uncinata* (Probst and Rouane, 1984; Dzialuk et al., 2009).

4.1. Early Holocene upper tree-line composition

Between 11,500 and 8500 yr BP, we found a wide altitudinal spread of *P. sylvestris* and *P. uncinata*, the latter colonising the highest altitudes up to at least 2200 m. *P. sylvestris* and *P. uncinata* were the main tree species found within travertine layers, suggesting that these pines grew actively during the early Holocene afforestation period in mountain ecosystems in the western Alps. These conifers are well-adapted to colonise young soils, which are poorly differentiated from the bedrock; such soils characterised the beginning of the Holocene (Mourier et al., 2010). Our results match with pollen-based reconstructions indicating that *Pinus* section *sylvestris* began to spread across the Alps between 14,000 and 12,500 yr BP (Gobet et al., 2005; Cheddadi et al., 2006), from peripheral glacial refugia and/or nunatak glacial refugia (Birks and Willis, 2008; Holderegger and Thiel-Egenter, 2009). Our results also indicate that during the Late-Glacial–Holocene transition environmental conditions were suitable for trees to adopt sexual reproduction with production of female cones. Palaeo-climatic reconstructions (Fig. 4de) display that up to 8500 yr BP, the climate was drier (Ortu et al., 2008) and warmer than today (Heiri et al., 2004; Renssen et al., 2009). These conditions were likely to be suitable for sexual reproduction and assisted in the altitudinal range extension of *P. sylvestris* and *P. uncinata*. In the Swedish mountains, Kullman and Kjällgren (2000) also reported an exceptional altitudinal spread of *P. sylvestris* during the earliest part of the Holocene, probably favoured by a warmer and more continental climate.

Our data show that in the early Holocene the local vegetation in the study region was also composed of scattered individuals of *P. cembra*, *Abies alba*, *Larix decidua*, *Betula pendula*, *Populus tremula*, *Acer opalus* and *Salix* sp (see supporting information). These finding illustrate that the subalpine tree diversity and structuring were rapidly established after the deglaciation processes.

4.2. The development of competitively superior trees

P. uncinata has totally disappeared from sites like Tioures (2200 m a.s.l.), Grand Puy (1815 m) and St-Genix (1695 m), and *P. sylvestris* from Prafranas (2000 m) and Grand Puy. This highlights the fact that a local extinction of these two pine species occurred during the middle and late Holocene. In the same valley where Tioures and Prafarnas sequences were sampled (Queyras Massif), other subalpine travertines containing charcoal fragments and needle imprints revealed abundant *P. cembra* (Fig. 4b; Ali et al., 2005b) and cf. *L. decidua* remains. However, the identification of *L. decidua* from charcoal records is uncertain, it being hard to distinguish from *Picea abies* (Talon, 1997). Furthermore, dating of these sequences has shown that *P.*
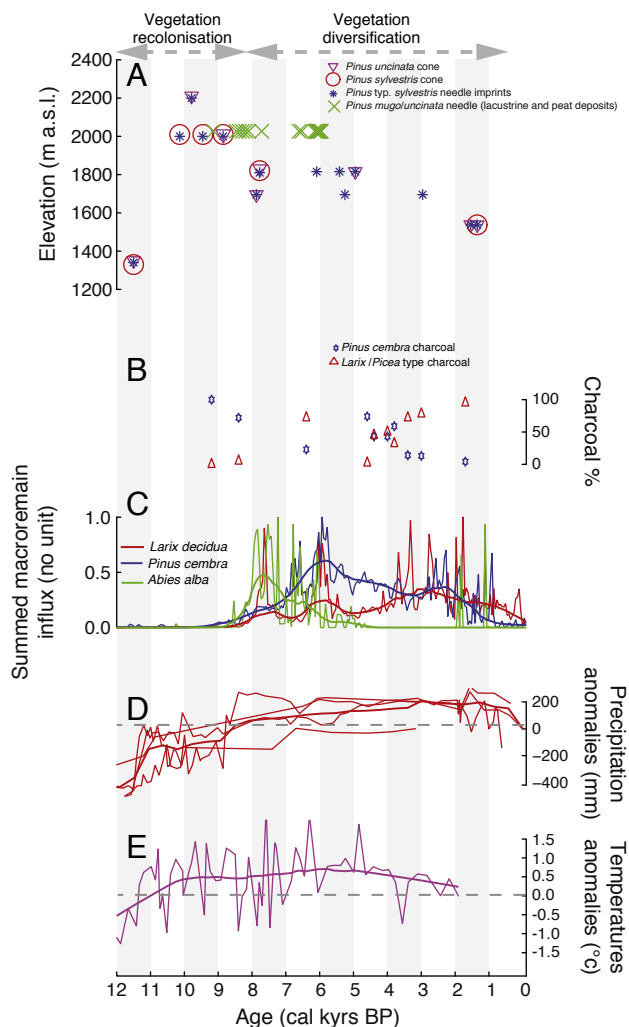

Fig. 4. Altitudinal distribution of *Pinus* section *sylvestris* compared to climate and vegetation reconstruction. a) Altitudinal distributions of *P.* section *sylvestris* macroremains from travertine (scale and needles imprints) and lacustrine deposits (*Pinus mugo/uncinata* needles; modified from Blarquez et al., 2010b). b) Relative abundance of charcoal fragments of *Pinus cembra* versus cf. *Larix decidua* in travertine sequences from the Queyras Massif (modified from Ali et al., 2005a). c) Dynamics of *P. cembra*, *L. decidua* and *Abies alba* inferred from sedimentary macroremains from 5 lakes (data from Blarquez et al., 2010a, 2010b; Genries et al., 2009a, 2009b). d) Precipitation anomalies for the South-western Alps (Ortu et al., 2008). e) Summer temperature anomalies of the Central Alps (Heiri et al., 2004).

cembra became locally abundant in the Queyras Massif between 8000–5000 yr BP as data from pollen analyses (Fauquette and Talon, 1995; Nakagawa, 1998; Nakagawa et al., 2000; Muller et al., 2006). This development of *P. cembra* at the middle of the Holocene is likely related to podzolization processes and the development of more mature soils compared to the early Holocene (Mourier et al., 2010). From 5000 to 3000 yr BP, the vegetation was characterised by mixed woodlands of *P. cembra/L. decidua* stands. Since ~4000 yr BP, *L. decidua* became the dominant taxa in these continental valleys of the inner Alps (Ali et al., 2005a), possibly in response to recurrent human-induced disturbance for agro-pastoral purposes. The same ecological transformation also occurred in the northern inner Alps according to sedimentary plant macroremains (Fig. 4c) analysed near the sites of St Genix and Grand Puy, where *A. alba*, was succeeded by *P. cembra* and *L. decidua.* Hence, these ecological changes in the vegetation have clearly contributed to the local extinction, or to *P. uncinata* and *P. sylvestris* becoming rarer in subalpine ecosystems.

5. Conclusion

Here the development of morphometric approach, based on the traits size apophyses of cone pines, proved to be an excellent approach to identify more accurately macroremains of fossil cones, compared to the qualitative approach, which was used in previous studies.

This study has improved our understanding of the historical biogeography of *P. sylvestris* and *P. uncinata* in the western central Alps. *P. sylvestris* and *P. uncinata* were dominant in terms of cones and needles within travertine deposits during the early Holocene. This suggests that these species composed the initial woodlands after the retreat of the alpine glaciers, with *P. uncinata* colonising the highest elevations up to at least 2200 m a.s.l. After 8000 yr BP, the expansion of other competitively superior conifers such as *P. cembra* likely prevented the development of *P. sylvestris* and *P. uncinata* in subalpine ecosystems and resulted in their local extinction at several sites. The altitudinal distribution and abundance of *P.* section *sylvestris* apparently results firstly from climate control, and secondly from competitive relationships with other tree species.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.revpalbo.2011.10.003.

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