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Unsuspected prevalence of *Pinus cembra* in the high-elevation sky islands of the western Alps

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Abstract

A survey of *Pinus cembra* (Arolla pine) growing above 2800-m elevation was conducted in an ecoregion of the western Alps, where the highest treeline is at ~2650 m. The concepts of treeline and species line are discussed based on these field observations. The species line is the biological limit of a species, with inherited nested historical and current processes of high-mountain socio-ecosystems, while the treeline strictly concerns the limit of erect trees. Arolla pines were located and described (height, physiognomy) and their habitats recorded (elevation, slope, aspect). Individuals occurred up to 3200 m on east-facing steep and rocky slopes, with density decreasing exponentially with increasing elevation (halving every 40 m). East-facing habitats benefit from the main atmospheric moisture coming from the east (Italy). Individuals were mostly dwarf-shaped/prostrate (58%) or trees (39%; max height 3.8 m). They usually do not bear female cones, and needles are smaller by half compared to those of pines growing in lower elevation forests. Their morphology indicates harsh growing conditions due to elevation (aridity, frost) and disturbances (wind, snow, rockfall). Habitat preference primarily on grass-free steep rocky slopes and cliffs at high elevation is likely explained by the exclusion of livestock impacts (grazing, trampling). These pines constitute noteworthy “sky island” populations. *Larix decidua* and *Pinus uncinata* were also recorded above the treeline, but with lower maximum elevation and density than *Pinus cembra*. These observations highlight a complex pattern of species treeline in the western Alps, and probably beyond, with relevance to issues in conservation science.

Keywords Biogeography · Mountain · Species line · Topography · Treeline

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Introduction

The altitudinal treeline has long been a topic of studies (Tranquillini 1979; Wieser and Tausz 2007), notably because it is primarily climate driven (Körner 2021) and can be used as a climate proxy (Kullman 1995). Treeline is often defined based on the physiognomy of plant rather than of species occurrence, with physiognomy being a functional life trait (Körner 2012). The *treeline* concept considers that plants must be erect and taller than a few meters (Payette 1983; Eronen and Huttunen 1993; Kašpar and Treml 2018), growing in woodland or tree islands (Holtmeier and Broll 1992), or even visible by remote sensing (Paulsen and Körner 2001; Gehrig-Fasel et al. 2007). Therefore, the concepts of *treeline* and *species line* must be distinguished. The species line, which is less conservative, is the ecological limit of a species regardless of its physiognomy and stand structure, while the *treeline* concerns only the erect trees.

Tree physiognomy depends on the micro-scale environment that regulates plant physiology (Körner 2012). During

their lifetime, trees can alternate between erect and prostrate (*krumholz*) stature, due to variations in climate (e.g., snow depth) altering the winter survival of meristems (Lavoie and Payette 1994; Brodersen et al. 2019) or to changes in herbivory or parasitism (Körner 1998). Therefore, the species line represents either a relic of stressed treeline with formerly erect trees potentially > 100 years old (Laberge et al. 2001; Wurth et al. 2018), or the forefront of tree expansion due to the release of stressors (Kullman 2001; Brodie et al. 2019), or a *status quo* of occasional and stochastic recruitment above treeline. Indeed, tree height and shape are largely independent of age and result from mechanisms that have affected plants during their lifetime; thus, small individuals are not necessarily “seedlings.” Further, scattered trees can inherit features from non-climatic historical factors, e.g., domestic grazing (Carrer 2015) and anthropogenic burning (Carcaillet et al. 2022), that may have excluded or hindered tree recruitment for centuries and therefore lowered the treeline. If individual physiognomy is, for a time, shaped by these historical factors, then the mere presence of tree species—largely overlooked and underestimated (Oberg and Kullman 2011)—could be considered part of the treeline, especially if the individuals are not growing in their best nutritional habitat (gentler slopes, deeper soils) but in places that exclude domestic grazers (e.g., rocky outcrops, cliffs). Therefore, the treeline and its surroundings form a socio-ecosystem (Liu et al. 2007) resulting from coupled natural and anthropogenic processes, including legacies of past conditions, producing non-linear trends and patterns that are sometimes delayed.

In the European Alps, woody species show a current slight upward trend (Vitasse et al. 2021), largely controlled by land use abandonment since at least the 1950s (Chauchard et al. 2010; Frei et al. 2023). Above treeline, which typically occurs in the range 2100–2400 m above sea level (asl), the alpine belt has been greening since the 1990s due to the expansion of denser herb cover and shrubs on north-facing slopes and outcrops or in screes (Carlson et al. 2017; Choler et al. 2021). The present paper reports a systematic census of high-elevation *Pinus cembra* L. (Arolla pine) growing above 2800 m asl in a small area of the western Alps. The aim is to demonstrate that the conventional treeline of erect individuals does not always capture the reality, which can differ significantly from species lines that are generally ignored or understated. The survey area is large enough to allow a significant number of observations and was conducted in an ecoregion where *P. cembra* has been recorded up to 2800 m asl (Bono and Barbero 1971; Motta and Nola 2001; Carcaillet and Blarquez 2019). Because higher occurrences of *P. cembra* were also reported (André 2016), the lower threshold of 2800 m appeared meaningful for the study. Elevation, slope and aspect, and rock cover are the main drivers of pine occurrence and height (Motta and Nola 2001; Housset et al.

2021). We hypothesized that the species line for *P. cembra* should be higher on south-facing slopes (longer growing season) and on gentler slopes with more developed soils (better water storage, nutrient availability).

These data, supplemented by more extensive data collected in the western Alps, contribute to a discussion of the regional species line for *P. cembra* in light of past and current environmental processes. With ongoing global warming and land use abandonment, pine outposts far above the line of erect individuals provide suitable habitat nuclei for further successful establishment of individuals dispersed from lower elevations (facilitation) or could be possible sources of pine expansion if climatic conditions change sufficiently to allow in situ seed production. They could potentially contribute to the greening of the alpine belt. This study seeks to contribute to the definition and framing of future research on the ecology and biology of pines living considerably above the conventional treeline.

Material and methods

Study area

The present study area comprises inner valleys and massifs in the western Alps, between 6.75°E–7.15°E and 44.60°N–44.78°N (Fig. 1). From west to east, the area covers the Queyras Massif and the Guil Valley, France and the Vaira Valley with the Mount Viso Massif, Italy (Supplementary Figure S1). The survey area is assessed to encompass around 31 km² (Table S1).

In the western Alps, the treeline is considered to occur at nearly 2100–2200 m asl in the northern massifs, and approximately 2300–2400 m in the southern ones. The treeline follows a clear gradient, being lower in colder and wetter massifs (e.g., Ecrins) than in warmer and drier massifs (e.g., Queyras, Mount Viso) at the same latitude. On the south-facing slopes of Mount Viso, the highest treeline was reported up to 2650 m (Motta and Nola 2001) and scattered pines up to 2810 m (Bono and Barbero 1971; Motta and Dotta 1994).

Study species

Pinus cembra (Arolla pine) co-dominates the upper forests of inner valleys with *Larix decidua* Mill. and sometimes *Pinus uncinata* Ram. ex. DC or *Picea abies* (L.) H. Karst. It is a long-lived species (> 500 years) with long generation intervals and maintains stable population sizes over a long time without inbreeding depression with high genetic variation (Gugerli et al. 2009; Toth et al. 2019). *Pinus cembra* produces heavy seeds, dispersed only by a mutualistic bird (*Nucifraga caryocatactes* L., nutcracker), which specializes

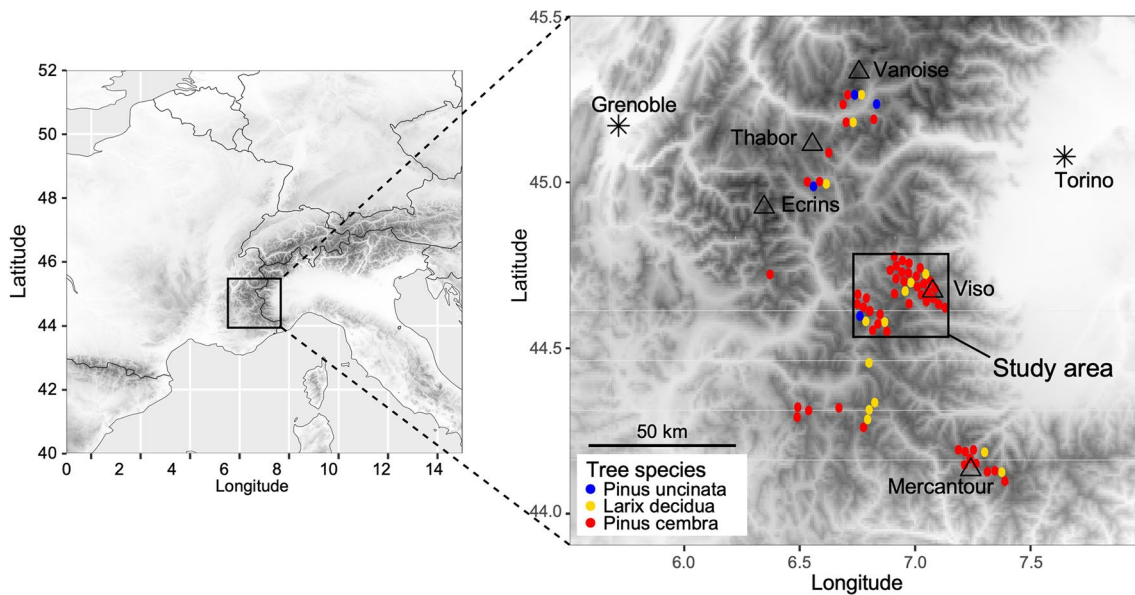


Fig. 1 Study area in the southwestern Alps straddling France and Italy; the small box that delineates the study area is detailed in Supplementary Information using a topographical map 1/25 000 (Fig. S1). The map illustrates the maximal elevations of isolated *Larix*

in caching nut-like seeds in the soil, up to hundreds of meters from the source pine, as a winter food resource. This ornithochory strictly controls seed dispersion and shapes colonization to specific landscape elements selected by nutcrackers. *Pinus cembra* interacts both with fungi, symbiotic for nutrients and water acquisition, and pathogens (Merges et al. 2018). These interactions with bird and fungi drive pine recruitment (Neuschulz et al. 2018).

Data collection

All observed occurrences of *Pinus cembra* above 2800-m elevation in the survey area were mapped using GPS. Elevation, slope, and aspect were recorded and subsequently verified using online public maps and satellite/aerial images on the Geoportail website (geoportail.gouv.fr/) or the Google Earth Pro program.

Plant height was measured or visually estimated (± 10 cm) for individuals that were inaccessible. Other data collected included the individual physiognomy, isolated *versus* clustered structure, and environment (substratum, aspect, and slope). At least one photograph was taken to support and expand upon the description of stand contexts, habitats (rock cover, aspect, slope, etc.), and growth form. Based on photographs, some clustered individuals could not be distinguished from each other for growth form description, i.e., 79 out of 544. Pine density was calculated as the number of individuals per elevation or aspect class.

decidua, *Pinus cembra*, and *Pinus uncinata* we observed in the southwestern Alps; only individuals above the classic treeline were recorded; names of main massifs evoked in the text are indicated

The aspect of high-elevation individuals/clusters recorded here was compared to the 1747 field observations with aspect data among the 3100 containing *P. cembra* community relevés and habitat descriptions, including geographical coordinates (all below 2800 m asl), from the botanical database of the French National Alpine Botanical Conservatory (CBNA; www.cbn-alpin.fr/). Because the individual density differed between the CBNA database and our data, and in order to graphically represent aspect, the pine density per aspect class was min–max rescaled between 0 and 1 by subtracting the minimum number per elevation class and dividing by the range of values of this class:

$$x'_i = (x_i - x_{min}) / (x_{max} - x_{min}),$$

where x'_i is the rescaled pine number of x_i and x_{max} and x_{min} are the maximum and minimum numbers of pines per class, respectively.

Results

Elevation, habitat, slope, and aspect

In total, 544 *Pinus cembra* were recorded above 2800 m asl in 24 stands (Supplementary Fig. S1). The individual frequency decreased with site elevation, reaching a maximum elevation of 3200 m asl (Fig. 2). The median pine elevation was 2835 m (mean \pm sd: 2853 ± 58 m); 75% of all

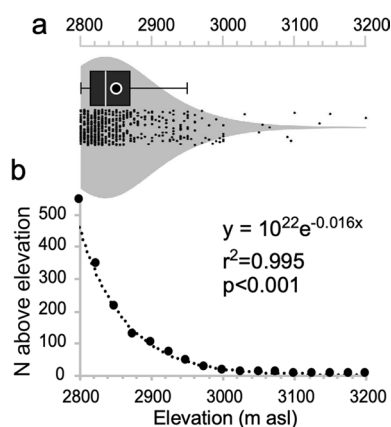


Fig. 2 **a** Elevation distribution of *Pinus cembra* from 2800 to 3200 m asl illustrated by box plot and violin plot; box plot: the white circle represents the mean value, the black rectangle is the interquartile range with the median value (white line), and the whiskers correspond to $1.5 \times$ the upper or lower interquartile values and violin plot: the envelope is a kernel density estimation of the pine distribution illustrated by small black dots. **b** Exponential distribution of number of individuals (N) above the 25-m elevation class

recorded individuals occurred below 2870 m. The frequency distribution of pines across elevation classes was negative exponential ($r^2 = 0.99$; Fig. 2), with a halving of individuals for every 40 m of elevation. While *Pinus uncinata*, *Larix decidua*, and *Picea abies* are also found in the inner valley treeline forests of this region, *Larix* was encountered only infrequently above 2800 m (3 occurrences) and *P. uncinata* and *P. abies* not at all.

Individuals of *P. cembra* were generally situated on steep (cliff) and rocky habitats and on ridges. The modal

slope class was $50\text{--}60^\circ$. About 94% of all individuals were found on slopes between 40° and 70° ($n = 511$; Fig. 3a). Rarely, some pines grew with grasses, but always embedded between rocks or within rocky outcrops in a grass-free habitat. In cliff habitat, individuals were rooted in cracks or between bedrock layers, which offered a weathered mineral substrate (Fig. 4). Pines grew on extremely heterogeneous bedrock, including dolomitic limestone (Fig. 4kl), calcareous sandstone (Fig. 4d), calcschist, flysch, and ophiolites (Fig. 4gh), basalt, quartzite (Fig. 4ij), acidic schist, and sandstone, demonstrating that the chemical quality of bedrock did not control their occurrence.

The modal aspect for pines above 2800 m was east and ranged from northeast to southeast (Fig. 3b). When sorted by elevation and latitude and clustered by percentile, all pines located below 2870 m (75th percentile) were on slopes facing east to northeast. In contrast, the upper quartile of individuals, situated between 2870 and 3200 m, mostly faced southeast, and when considering only the 95th percentile ($n = 27$, 2960–3200 m), they were all facing southeast. These aspect patterns are strikingly different to the *Pinus cembra* aspect data from the CBNA database for forest stands below 2800 m with the main aspect in the Queyras and French Alps mostly north-facing (Fig. 3b).

Spatial pattern and physiognomy

Pines generally grew in stands consisting of a few up to tens of individuals. They often grew in disconnected stands sometimes hundreds of meters from the nearest woodlands in both distance and elevation (Fig. S1). Some stands were

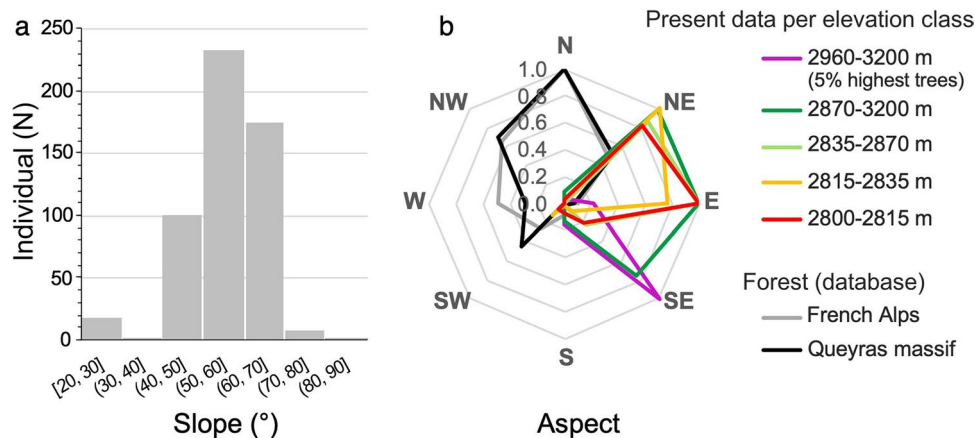


Fig. 3 Slope **a** and aspect **b** patterns of *P. cembra* distribution in the Queyras-Viso ecoregion, western Alps. The data for isolated *P. cembra* ($n = 544$) above 2800 m are sorted per elevation class (red, yellow, green, and purple perimeters) and are compared to values for *P. cembra* stands mostly in lower elevation forests of the Queyras massif (black perimeter) and from the French Alps (gray) ($n = 1747$). To

compensate for differences in observation numbers, densities were minimax-rescaled from 0 to 1 by subtracting the minimum numbers per elevation class and dividing by the range of values of this class. The 95th centile represents the highest 5% of all the elevations where pines were found

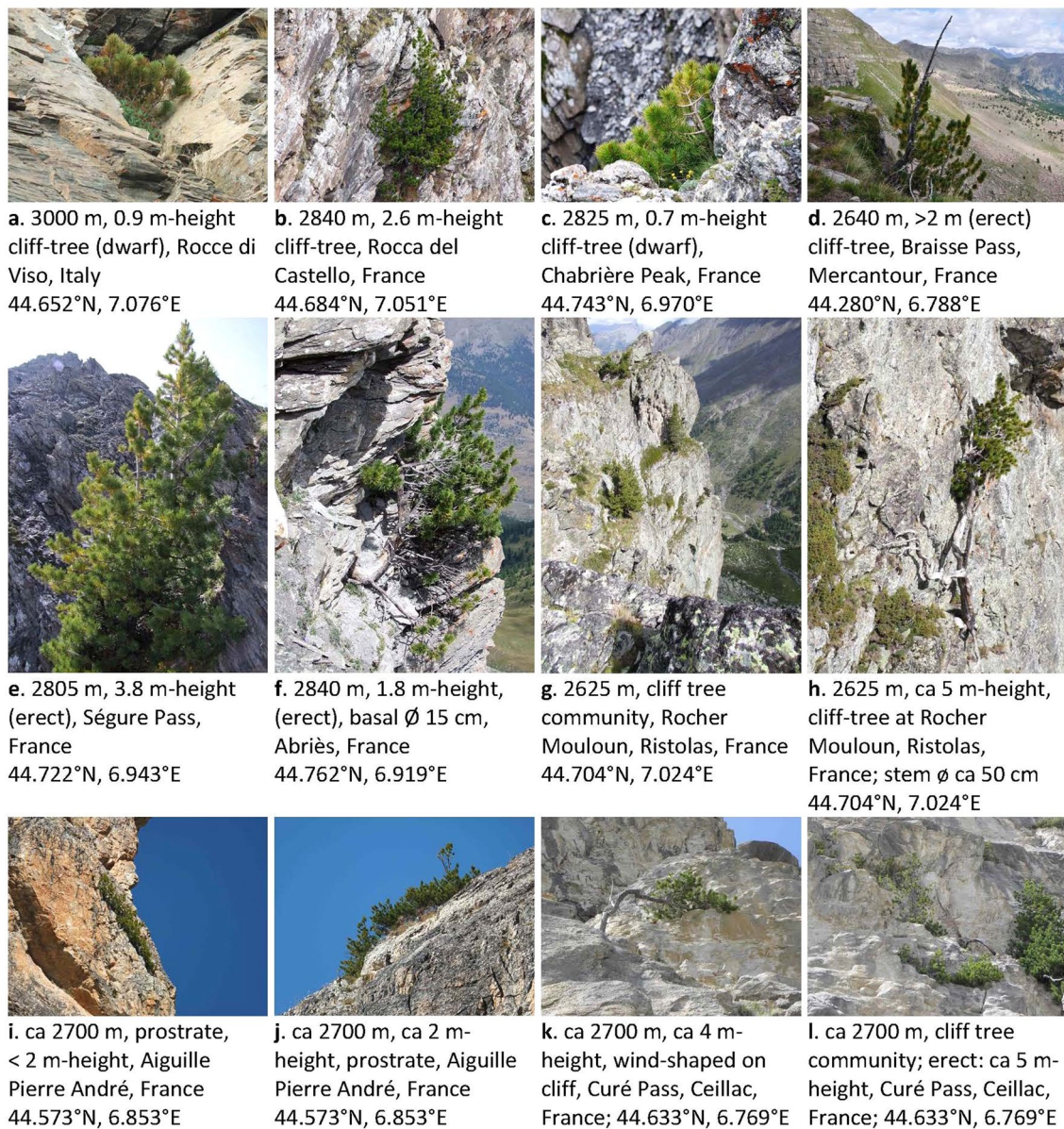


Fig. 4 Examples of *Pinus cembra* growth forms between 2600 and 3200 m asl in the western Alps, in France and Italy. These examples illustrate different contexts of growth (cliff, outcrop) on different

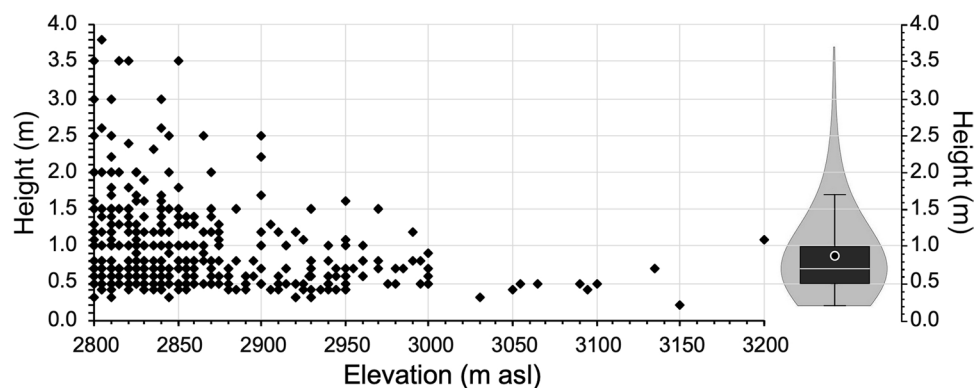
rock types (ophiolite [g,h], quartzite [i,j], limestone [k,l], calcareous sandstone [d]), and of pine physiognomy (dwarf, erect, prostrate, flag shaped). All pictures are from GA, except [d] from CC

connected to lower elevation forests by a narrow corridor of individuals growing among rocks from the forest limit to the isolated stands.

The physiognomy of 465 pines out of 544 were characterized based on photographs. A few were prostrate (18%; Fig. 4ij), but most were dwarf shaped (40%; Fig. 4a–c) or erect (39%; Fig. 4d–g). A few (3%) were flag shaped (Fig. 4hk). The median height was 0.7 m, with a range of

0.2 to 3.8 m (Fig. 5). Malformed female cones of *P. cembra* were observed on a few individuals up to 2855 m asl and male cones up to 2870 m asl (Fig. S2).

Fig. 5 Height of *Pinus cembra* plotted against elevation; the median height is 0.7 m and the 75th percentile is 1.0 m (right: box plot and violin plot distribution of heights)



Discussion

We show that *Pinus cembra* can grow at elevations as high as 3200 m asl in the western Alps, which is about 800 m above the regional observed treeline. Although studies have reported pines growing at high elevation in the western Alps (Bono and Barbero 1971; Motta and Nola 2001; André 2016; Carcaillet and Blarquez 2019) and central Alps (Paulsen et al. 2000; Körner 2012), they have never reported such pine prevalence at exceptional elevations. The peculiar topographic situation of these pine stands, often disconnected from the main range of pines by 400–800-m elevation, recalls that of trees growing on isolated mountains in Arizona, popularized under the metaphor of “sky islands” (Heald 1967). We hereafter discuss the ecological context of these sky island pines and put into perspective their habitats with a history of land use.

Trees in cliffs or steep and rocky slopes

The observed pines exclusively occur on rocky outcrops, steep slopes, cliffs, and ridges (Fig. 4). Such inhospitable habitats raise questions about pine nutrition, because of the limited water storage capacity and nutrient supply. Soil moisture depends on precipitation, but gravity rapidly drains water. Significant cloudiness on summits during the growing season provides moisture in the form of vapor, in the study area notably from humid and warm easterlies coming from the Po River plain. However, pines need mycorrhiza to capture this moisture, as well as to recycle nutrients (Smith and Read 2008). Fortunately, ectomycorrhization seems not to be affected by elevation and may help in securing pine nutrition (Merges et al. 2018), although access to nitrogen may be limiting.

Elevation is a strong driver of pine distribution. The negative exponential model of pine density indicates that survival depends on elevation (Fig. 2), probably regulated by constant mortality or regeneration (Hett and Loucks 1976). The dispersal of *P. cembra* seeds depends on nutcrackers, which

preferentially cache seeds in dry soil, but there is a low probability of seedling establishment in dry habitats (Neuschulz et al. 2015). Above 2800 m on steep slopes and cliffs, the habitat is dry and far from seed sources, thus unfavorable for seedlings, especially on south-facing slopes, which undergo severe evapotranspiration due to too strong solar irradiance and low-temperature photoinhibition (Germino and Smith 1999). However, east-facing slopes, where 95% of pines are located (Fig. 3b), are more humid thanks to higher cloud-based moisture and lower irradiance. Above 2960 m, most pines grow on south-facing slopes that are warmer (Fig. 3b), perhaps to compensate for the shorter growing season due to higher elevation.

Growth forms: stress and disturbances

The growth form of sky island pines mostly corresponds to a dwarf or prostrate stature (58%), which is an advantage in a cold environment by decoupling the atmospheric temperature from their own under the canopy close to or connected to the ground (Körner 2012). Similar observations of decreasing pine height with elevation indicated a reduced length of annual shoots in similar environments prone to strong wind and low temperature (Takahashi and Yoshida 2009). We also found that needles of pines above 2800 m were smaller than those from forest trees (about 4 cm vs 10–12 cm; Fig. S2). The observed reduced leaf length, shoot length, radial growth (Fig. S5), and individual height (Fig. 5) appear to be morphological plasticity in response to abiotic stresses (Schoettle 1990; Kajimoto 1993), notably due to difficulties with building cells and tissues (Rossi et al. 2007).

While 39% of pines were erect, almost all were damaged by wind, snow, rockfall, or lightning (Fig. 4). These local peculiarities lead to the question of why only erect trees above a certain height are considered to determine treeline, since size is partly controlled by severe disturbances at these elevations. Pine height decreasing with elevation (Fig. 5) is of course partly due to physiological difficulties to producing erect stems (Körner 2012) but is also due to disturbances that break stems. The small physiognomy of sky island trees

a. Hypothetical scenario

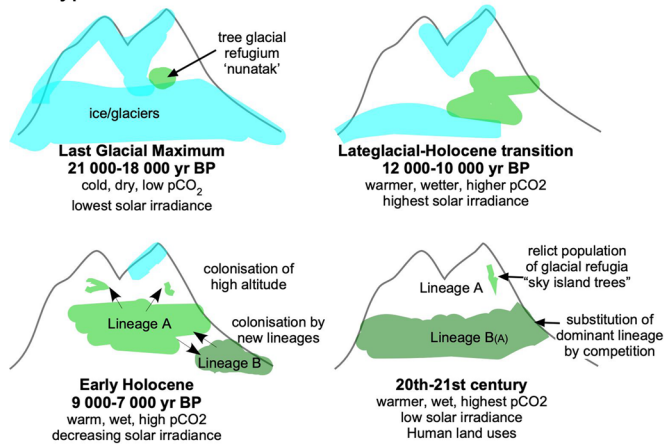


Fig. 6 a Hypothetical scenario of a glacial refugium that would contain a genetic lineage of trees adapted to peri-glacial environmental conditions (climate, soil), which first expanded with the early-Holocene warming and was confronted with a lineage that was outside the inner Alps during glacial times; here, we assume that the colonizing lineage was more competitive than glacial relict lineage; last, due to

must be considered as a result of the combination of stress and disturbances.

Past land uses: a species line driver

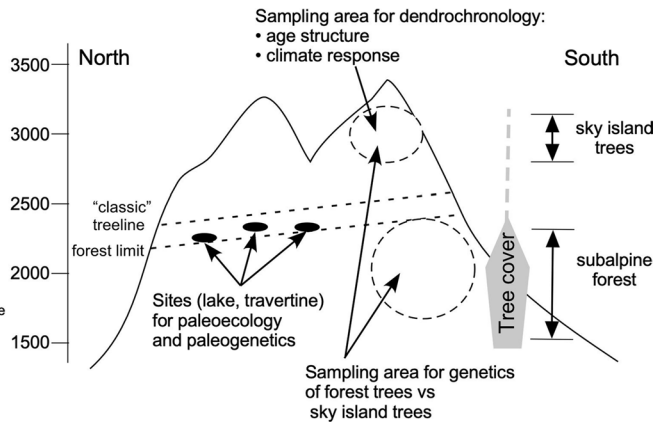
The localization of these elevated rocky and grass-free habitats of isolated pines strongly argues for introduced livestock grazing as the chief mechanism to exclude tree species from alpine grasslands (Fig. S6). Livestock, which do not feed in rocky habitats, control seedlings through grazing and trampling and saplings and small trees by browsing. Wild herbivores are marginally involved because they naturally have low-density populations.

Soil charcoal studies have revealed that pines and larches burned where grasslands occur today, suggesting tree suppression above 2400 m for the needs of animal husbandry (Saulnier et al. 2015; Carcaillet et al. 2022). Locally, burning above 2400 m occurred chiefly between 5000 and 500 years ago (Saulnier et al. 2015), with fire frequency peaking about 3500 years ago (Carcaillet and Blarquez 2017). Even though all evidence of past fires shows they were below 2800 m asl, we assume that past livestock grazing combined with anthropic fires explain the scattered distribution of pines above 2400 m or, more often, their total extinction in many alpine areas.

Species line of *Pinus cembra*

Pinus cembra are growing up to 800 m above the regional treeline (Fig. S7), an observation which appears largely new to the literature, and may be considered as the limit of the

b. Sampling design



competition and thanks to adaptation, the glacial relict lineage moves to higher elevation, experiencing harsh conditions similar to those found during glacial times, but in the absence of a more competitive lineage; **b** general study design for genetics and paleogenetics, and historical ecology for testing hypotheses of genetic differentiation, population dynamics in response to climate variations

fundamental niche of the species. These extreme elevations in the Alps up to 3200 m asl are perhaps facilitated by the southern location of the study area compared to northern and western massifs that are colder and wetter. One high-elevation occurrence of *P. cembra* has been reported in the central Swiss Alps, up to 700 m above the classic treeline, which would be at 3050 m asl (C. Körner, pers. com.). Such observations of isolated elevated pines have largely been overlooked due to a lack of botanical prospecting in harsh, poorly accessible areas with steep cliffs that often prevail in these high mountains (Boucher et al. 2021).

Conclusion

The occurrence of *Pinus cembra* up to 3200 m asl in the Alps is a significant finding that questions their biology and ecology facing ongoing global changes, but also those of the past. First, it is obvious that their ages and their establishment chronology must be studied. The age structure inferred from dendrochronology would provide a net demographic result helpful to explore (i) the balance between mortality and regeneration thanks to demographic hypotheses (Hett and Loucks 1976) and (ii) the function of past climate and land use drivers by comparison of the age structure with temporal and spatial high-resolution climate reconstructions (<https://climexp.knmi.nl/>) and local domestic husbandry reports (e.g., Fortuny et al. 2014). However, sampling problems of small and fragile individuals must be first resolved, as well as counting problems of incomplete tree rings (e.g., Mathaux et al. 2016). Second, this high-elevation population

questions its genetic origin knowing that glacial refugia of *P. cembra* were found in the same area (Carcaillet and Blarquez 2017) and that present-day population genetics have shown that Arolla pine living in local subalpine forests belong to the most common lineage of western Alps (Toth et al. 2019). We hypothesize (Fig. 6) that this sky island pines could be relicts of a glacial population, which would have moved in high elevation due their adaptation to peri-glacial conditions and because forest elevations were better used by more competitive trees, which would have survived to the glacial times near north Italian plain where refugia were evidenced (Vescovi et al. 2007). Such hypothesis would need genotyping of modern populations with best sequencing methods and microsatellite development (Lepais et al. 2020), completed by high-throughput sequencing of ancient DNA extracted from subfossil needles to get species genetic chronicles since glacial times (e.g., Wagner et al. 2023).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11258-023-01341-1>.

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Author contributions AG carried out the fieldwork and collected most of the data. CC produced a draft of the manuscript, and all co-authors contributed to further versions. All authors approved the final version.

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Data availability All data are available by contacting the authors.

Declarations

Conflict of interest The authors have no conflict of interest to declare. Part of the data used in this article has already been used in a previous article published in a French regional naturalist journal (André 2016). However, the scientific findings and the analysis presented here have not been published and are not under consideration for publication elsewhere. All the authors have approved this submission and all people entitled to authorship have been named.

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