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ORIGINAL ARTICLE

Rapid advance of climatic tree limits in the Eastern Alps explained by on-site temperatures

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Abstract
In the European Alps, mean temperature has risen by 2.5 K since the end of the nineteenth century. A 2 K warming of the growing season has taken place in the last 4 decades only. The 2.5 K warming should rise the position of the climatic treeline by about 400 m. Actual shifts in uppermost tree positions reported here for the Austrian Defereggen Valley and the Swiss Lower Engadine region of the Eastern Alps reach only around 140 m of elevation above the limit of old trees that date back to the nineteenth century. Uppermost *Pinus cembra* trees of > 2 m height currently occur at c. 2500 m, representing elevation records for the Eastern Alps. In situ temperature records for 2022–2023 revealed seasonal mean temperatures for uppermost trees that are 1–3 K higher than the equilibrium treeline isotherm of c. 6 °C in both regions (corrected for temperature anomalies from long-term records). The 2 K span reflects microhabitat differences and two ways to define the season. Thus, tree advances lag behind the upslope shift of the treeline isotherm, on average, by more than 200 m. The uppermost trees currently grow under quite warm conditions with annual shoot length increments frequently reaching 20 cm. Even without additional future warming, the new steady-state climatic treeline will exceed the Holocene maximum elevation in the Eastern Alps substantially.

Keywords Climate · Growth · Mountains · *Pinus cembra* · Treeline · Warming

Introduction

The global climatic treeline phenomenon is best explained by a thermal limitation of upright tree growth (Körner 2012a). The decline in air temperature with altitude is directly imposed on trees, while alpine plants with their smaller, more compact life forms, profit from aerodynamic decoupling and thus, warmer conditions near the ground (Körner and Hiltbrunner 2018, 2021; Körner and Hoch 2023). The reduction of atmospheric temperature with altitude has been hypothesized to constrain tree growth at the same critical temperature as in any cold adapted plant. But upright growth prevents significant departures from air temperature. Hence, the treeline mirrors atmospheric layering and often looks like a shoreline. A c. 6 °C isotherm of the growing season mean air temperature has been found to best correlate with the global treeline phenomenon, once a current lag of upslope shift in treeline position in response to the recent rapid climatic warming has been accounted for (called treeline isotherm hereafter; Körner and Paulsen 2004; Paulsen and Körner 2014, Körner and Hoch 2023). Importantly, this is a correlation, and this seasonal mean does not reflect the actual action of low temperature on a suite of life processes under strongly varying diurnal and seasonal in situ temperatures. The treeline isotherm is considered to represent the low temperature edge of the fundamental niche of the life form tree (Körner 2021).

Trees are often absent from treeline. A multitude of influences can prevent tree occurrence at treeline. Since these factors are not mountain specific, and include both physiological constraints (e.g., shortage of water) and various disturbances (e.g., logging, fire, avalanches, eroded soil), they are best attributed to the realized niche concept and addressed as local tree limit. It is obvious that trees are absent from the climatic treeline when people have cut or burnt them. Under annual precipitation < 250 mm a^{-1}, trees are absent from treeline (Paulsen and Körner 2014), just as

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they are under such conditions at low elevation. It is important to distinguish between drought-related slow growth of existing trees and the actual position of treeline. By including moisture shortage in a treeline definition, all arid range limits of trees would become treelines. Trees may also be absent from treeline, because the climate warms faster than trees can advance and thus, track the c. 6 °C treeline isotherm.

Although it is very hard to test hypotheses related to the realized patterns (niche) of tree distribution, the edge of the fundamental niche, the treeline, can be predicted with high confidence (Körner and Paulsen 2004; Paulsen and Körner 2014; Wang et al. 2022). On the other hand, the edge of the realized niche can be seen in the landscape, while that of the fundamental niche is often invisible (Körner and Hoch 2023). The distinction of these two types of forest edges assists in separating testable from hardly testable hypotheses, an idea that was already coined by Kerner (1865) and Däniker (1923). In the ideal case, both the realized and the fundamental niche edge are known, so that the distance between the two can become a research objective (e.g., Wang et al. 2022), requiring good knowledge of local temperatures.

It has been known for at least 120 years that the interior of large mountain systems is drier and warmer than front ranges. In other words, all isotherms move upslope as one moves from the periphery to the center of mountain systems, the so-called mass-elevation effect, first and exhaustively described by the Swiss climatologist De Quervain (1904). Generally, front ranges keep frontal weather out, causing sunshine hours to rise in the interior of mountain systems, and thereby temperatures and evaporative demand are rising, while precipitation declines (higher "continentality"). The climatic consequences of the mass-elevation effect cause a rise in treeline position as exemplified by our study regions in the Eastern Alps (Gams 1931–1932, Klebelsberg 1961).

Treelines reach their highest positions globally in dry and thus, warm climates as long as precipitation does not drop below 250 mm (extreme elevations at > 4800 m a.s.l. in Tibet and Bolivia; Miehe et al. 2007; Körner 2012a). In the Alps, treelines have always been highest in the interior of the western part, having reached almost 2550 m near Zermatt already in the early 1980s (Körner 2012a; Fig. 12.1 therein). In a recent assessment of highest elevations of *Pinus cembra* (André et al. 2023; LFI 2023), a number of tree individuals reached > 2 m height above 2800 m in the Western Alps in France. For the Valais, the highest located individual of *Pinus cembra* (2.9-m height) was spotted at 2740 m (LFI 2023). The historical elevation record in the Eastern Alps are the "trees" on a rock tower reaching 2465 m a.s.l., the Tristennöckl (near Taufers, S-Tyrol), close to our Defereggen study sites (Klebelsberg 1961). The problem of many lists of uppermost tree occurrences is that what is considered a tree is not always specified. With the term "tree," we refer to individuals > 2 m, a height at which trees are aerodynamically coupled to ambient air temperatures. Seedlings or saplings < 30 cm, nested in the warm boundary layer near the ground, do occur at much higher elevations, also at our study sites.

Climatic warming has been reported to be more pronounced at higher elevation compared to lowlands (Pepin et al. 2015); however, a global analysis revealed that this does not hold for all mountain regions (Pepin et al. 2022). There is no greater warming at high elevation within the Alps (Auer et al. 2007; DWD et al. 2022), but the European Alps belong to those mountainous regions with pronounced warming (Rebetez and Reinhard 2008): a 0.57 K warming per decade for 1974 to 2004 had been observed, leading to earlier snowmelt (2.5–2.8 days per decade for 1957–2022, Vorkauf et al. 2021; Marty et al. 2023) and to a greening trend observed from space (Rumpf et al. 2022). While warming over land has now reached a global mean of 1.4 K, the greater region of the Austrian and Swiss Alps has already seen a warming by around 2.5 K since the end of the nineteenth century (MeteoSwiss 2023). The temperature trend around 1980 is often considered a regime shift (Marty 2008), superimposed on a long-term trend of rising temperatures (Sippel et al. 2020). For the 1981–2023 period, the mean warming rate for the summer months only (JJA) in the most eastern part of Switzerland (six stations), including our Engadine study region, was 0.57 K per decade (2.3 K in total; MeteoSwiss 2023).

The warming in our study regions during the recent 48 years (Fig. 1) corresponds to an upward shift in isotherm elevation by c. 330 m (applying a 0.6 K/100 m lapse rate for summer for that region; Kollas et al. 2014). We expected that trees migrate upslope, and to the extent they lag behind the treeline isotherm shift, experience very favorable montane growth conditions. The current warming trends are likely to continue and are expected to reach more than 4 K in the part of the Alps studied here by the end of the twenty-first century (Kotlarski et al. 2023).

This paper explores recent trends in upslope shifts of climatic tree limits and the temperatures at the current position of uppermost trees in the Eastern Alps. With such data, we aim at identifying the potential lag of current tree limits behind the isotherm shift. We expect luxuriant conditions for tree growth when tree positions lag behind the upslope isotherm shift.

Materials and methods

Sites

The study sites in Austria (Defereggen valley, East Tyrol) and Switzerland (Val S-charl, Lower Engadine), known

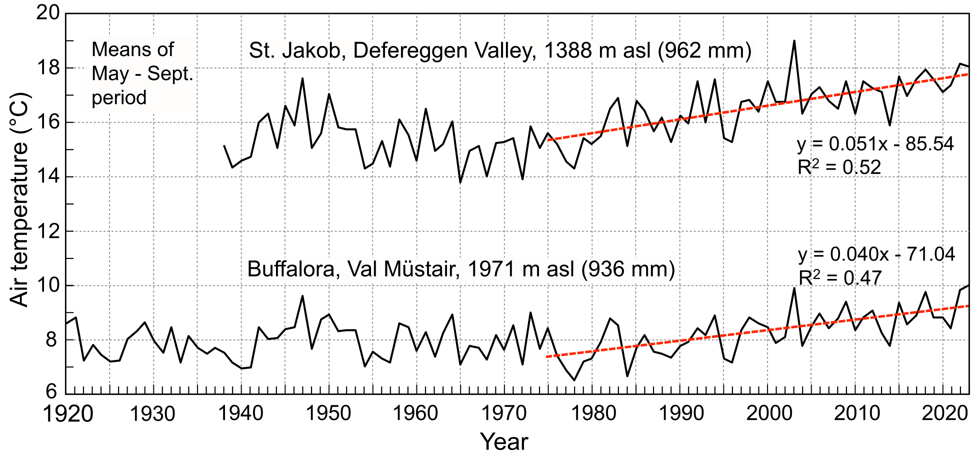

Fig. 1 Air temperature means for the May–September period, measured near the two study regions at the Austrian village St. Jakob in Defereggental, and the Swiss Buffalora station near the Val S-charl, Lower Engadine (Austrian and Swiss weather service data). Note the steady rise in temperature since the late 1970s in both regions, arriving at a regressed increase in mean growing season temperature by 2.4 and 1.9 K in 2023 compared to 48 years ago

for their continental, sunny climate, are c. 150 km apart and south of the main divide of the European Alps. These regions are screened from the dominant north-westerly weather as well as from southern fronts from the Mediterranean. Both regions are famous for their outstanding stands of *Pinus cembra* (Arolla pine, stone pine), a species that prefers continental climates. Known as the "Oberhauser Zirbenwald" (abbreviated as OZ; Kammerlander 1985) and the "God da Tamangur" (GT; Rikli 1909; Lopez-Saez et. al. 2023). These stands (Fig. 2) have attracted visitors since decades. Both have a history of threat during the seventeenth to nineteenth century mining boom. This led to the devastation, and a following recovery of the OZ forest beginning at the end of the eighteenth century, now under full protection by its inclusion in the Hohe Tauern National Park. Mining for silver and lead in the S-charl valley dates back to the fourteenth, sixteenth, and nineteenth centuries. In 1825, 3000 $m^3\ a^{-1}$ wood and > 25,000 bundles of twigs were needed for the smelters (Schreiber 2004), besides the needs for a year-round living in this valley. Although the last phase of mining was short in the S-charl valley (fully abandoned in 1850), trees older than 150–170 years are rare. Rikli (1909) documented a tree parkland with high grazing pressure and cone sampling that limited the rejuvenation in the post-mining decades. In 2007, the GT forest has become a protected forest area without any forestry management. Browsing pressure by red deer seems to represent a small fraction of the former grazing pressure, allowing massive tree recruitment (Brücker et al. 2015).

Today, both of these forests are believed to belong to the largest continuous *Pinus cembra* forests in the Eastern Alps. At closer inspection, both do not end at a natural climatic treeline. The prominent high elevation forest edge at 2250 m (OZ) and 2300 m (GT) elevation is the result of

Fig. 2 The famous *Pinus cembra* stands at Defereggen valley (Oberhauser forest, OZ, left, ending at 2250 m) and the Lower Engadine (God Tamangur, GT, right, ending at 2300 m), both with treeless plateaus above due to a long pastoralism history (not a climatic treeline), overtopped by old trees at c. 100 m higher elevation (not shown), and c. 4 m tall trees with upright stems < 40 years old at 2400–2450 m elevation (forefront)

geology (topography) and land use. The valleys show the classical U-shaped glacial profile, with the geological shoulders offering ideal grazing land. For the Defereggen Valley (OZ), documents of land use date back to the year 1212 (http://www.jagdhausalm.com) with year-round human presence at 2009 m elevation during the medieval warm period. Similarly, for the Alp S-charl (at GT), pastoralism was first mentioned in the year 1096 (Schreiber 2004). In addition, these topographic shoulders receive and stop avalanches, causing the below forests to remain largely unfragmented, while restricting the forests above the shoulder to ridges (Figs. 2 and 5). On these ridges, way above of what looks like a "treeline," tall, very old trees (by size and trunk diameter, we assume > 100 years) can be found around 2360 m at OZ and at 2420 m at GT. These tree locations, often on rocks, are unsuitable for grazing and most likely represent the equilibrium high elevation records for treelines in the Eastern Alps before climate warming came into action.

Long-term climate data for both regions are available from the weather stations at St. Jakob (Defereggen valley, 1388 m, c. 10 km E of our OZ study sites, starting in the year 1938) and Buffalora (Lower Engadine, 1971 m, 8.6 km SW to the study site, starting in 1920). Precipitation accumulates to a 1991–2020 mean of 962 mm a^{-1} at St. Jakob and 936 mm a^{-1} at Buffalora with a summer peak at both stations. For growing season air temperatures at the two stations, see Fig. 1. A much shorter-term reference is a weather station that had been installed only 7 years ago, right at the OZ forest by the Tyrolian hydrological service (Oberhauser Alm, 1740 m a.s.l, 46° 56′ 10″ N, 12° 13′ 36″ E). The June–August (2018–2023) air temperature means from that station were 12.1, 12.9, 11.4, 11.7, 12.8, and 12.5 °C (mean 12.2 °C), indicating that 2022 was 0.6 K and 2023 0.3 K warmer during that period than the mean for all 6 years (Tab. S2). From the St. Jakob and Buffalora chronologies (Fig. 1), the May–September means for 2022 and 2023 were also above that regressed for 1975–2023 by 0.3 K (OZ) and 0.8 K (GT). These data permit to place our in situ temperature data for the study years in a longer-term context. Hence, all seasonal means obtained by data loggers were adjusted to the regressed linear temperature trend (Fig. 1) by subtracting the regional above average temperatures during the two study seasons.

In situ temperature measurements

Defereggen site (OZ): For the temperature (T) monitoring, we selected in total four sites, two sites near the current local upper limit of trees, clearly above the OZ forest, at 2431 m (46° 57′ 23″ N; 12° 13′ 25″ E) and at 2494 m (46° 57′ 40″ N, 12° 12′ 48″), and two additional sites, one at the uppermost > 100-year-old trees (at 2357 m) and one at the prominent edge of the closed forest at the valley's shoulder that merges with pasture land at 2242 m.

God Tamangur (GT): T was recorded at 2535 m on Mot Falain (46° 41′ 11″ N, 10° 22′ 26″ E), with some 2–2.5 m trees found at 2560 m at this site in 2023 (but not equipped with a T logger).

In order to link up with existing data on temperatures at treeline, the same data loggers and installation procedures were employed as in the global assessment by Körner and Paulsen (2004) that included 12 sites in the Alps (serving as a regional reference). We used waterproof temperature loggers (TidbiT, v2 Temp UTBI-001, Onset HOBO, USA, accuracy ± 0.2 K) buried at 10 cm soil depth under 100% tree shade. Such temperatures were found to match 2 m air T, provided one integrates readings for one or few days (Körner and Paulsen 2004). In the absence of any solar radiation-driven soil heat flux, soils and air are in a convective equilibrium. The detailed analysis showed that a daily mean soil temperature of 3.2 °C corresponds to a mean air temperature of 0 °C (Körner and Paulsen 2004), a meteorological threshold to define the onset and end of the growing season (Körner et al. 2023). The T loggers were cross-checked in an ice-water slurry, and no deviations from zero > 0.1 K were detected. Additional loggers were exposed in shaded parts of the tree canopy to obtain air T, but a few high T extremes indicated that 100% shade was not warranted during the long summer days. The open canopy at the uppermost 2–2.5 m size trees made it difficult to assure permanent shading of the logger (Fig. S1). We thus refer to deep shade soil T in our analysis (in the shade of old trees at OZ 2242 m, we have only air T). However, the periods with a "radiation error" in the canopies of smaller, young trees must have been short enough, so that the air T means differed by only c. 1 K from soil T means for identical periods. Since soil T is thermally buffered compared to air T, such temperatures do not show the full range of temperatures that may occur in a tree canopy, both on bright days, as well as in clear nights.

Defining the onset and end of a season is key for site comparisons. Following the Körner and Paulsen (2004) protocol, the last and first passing above/below a 3.2 °C daily mean soil temperature was identified. The start of the season is commonly well defined by the time of snowmelt (abrupt rise in soil T and diurnal variation), while the end is much more difficult to define. In late 2022, there was a 2-week cold break (17–30 September) with daily air T minima between -3 and -6 °C (daily means down to -1.5 °C) with 10 cm soil T clearly cooler than the 3.2 °C threshold (daily mean 3.0 °C at OZ 2494 m, 2.1 °C at OZ 2431 m, and 2.4 °C at GT 2535 m, influenced by local snow differences), followed by a long period of mild weather until early November. Should this late period now be included or excluded into the growing season? Except for some ongoing photosynthesis, there is not much biological activity in treeline trees in October (Gruber et al. 2009), particularly after such a cold period,

and from all that we know about such trees, they are not carbon limited (Tranquillini 1979; Körner 2012a; Wieser et al. 2019; Cabon et al. 2020, 2022). We are thus presenting an analysis for both types of seasons, the short one calculated until late September only, versus the long one recorded until early November. In a third analysis for the year 2023 only, the season length was set to one common window from 25 May to 23 September, permitting a direct site comparison.

Temperature data collation

Temperature measurements started in late 2021 and cover 2 years (until late 2023) for three of the OZ sites, and 1 year for the OZ 2494 m site and the GT site, both starting in late 2022 (until late 2023). For 2023, all sites were logged concurrently. The data are presented as seasonal means (and medians), absolute minima and maxima, degree hours above 0 °C and above 5 °C, the duration of the growing season in days, and the frequency distribution of hourly records. Degree hours (°h) for an entire season produce large numbers, so, as in the reference works (Körner and Paulsen 2004), these sums were divided by 24 h (°h*), not resembling degree days which are based on daily means.

Tree measurements

In addition to searching for the regional uppermost 2–2.5 m tree individuals (current tree limit), the length increment of the leading shoots was measured in 31 trees at OZ 2320–2494 m (late season 2022) and 10 trees at GT 2488–2560 m (late season 2023), for the last 9–10 years per tree (a total of nearly 400 increment data). We selected straight and undamaged trees > 2 m. Annual shoot growth was regressed against elevation at OZ. Stem diameter at the base of the straight growing part and height above that point were used to calculate taper (cm of diameter per meter of height growth, same trees as for shoot growth at OZ).

Results

Highest tree limits

In both regions of the Eastern Alps, the current tree limits have advanced to 2494 m (OZ) and 2560 m elevation (GT), which is 134–140 m above the local limit of tall, old trees at 2360 m at OZ and 2420 m at GT, respectively, representing the highest growing trees > 2 m of Austria and, most likely, also the eastern part of Switzerland. Applying a 0.6 K per 100 m temperature lapse rate for the growing season, the uppermost young tree positions (compared to that of the uppermost old trees) correspond to a c. 1 K climatic warming—less than half of the warming that has actually occurred during the last four decades, based on the regional weather stations.

The climatic conditions at the Defereggen (OZ) sites

The climatic conditions measured at four elevations at OZ (Fig. 4) revealed much higher temperatures than ever measured at climatic treelines. Irrespective of whether the "long" season definition (including late 2022) or the short season was employed (Fig. 3). The temperatures (Fig. 4, Tab. S1) underline that (1) the prominent forest edge at 2242 m is clearly anthropogenic (the 10 °C mean at 2242 m is 4 K higher than the c. 6 °C equilibrium treeline isotherm), (2) the "old treeline" at 2357 m with a 9.2 °C mean grows under c. 3 K warmer conditions than the treeline isotherm, and also (3) the uppermost trees at 2494 m currently operate at local temperatures 2.3 K warmer than the treeline isotherm (8.3 °C; difference corrected for the 0.3 K 2022–2023 T-anomaly at OZ; 380 m below the potential climatic tree limit). These T differences are for the long season data. For the warmer short season variant (Figs. 3 and 4, Tab. S1; 9.3 °C minus 0.3 K), the difference to the treeline isotherm is 3 K (500 m below the potential climatic tree limit).

Across the studied c. 200 m elevation gradient at OZ, the thermal sums above 0 °C and 5 °C for the longer and thus, slightly cooler season variant, declined from 1773 to 1399 °h* > 0 °C, or 951 to 603 °h* > 5 °C, with 15–18% lower heat sums for the shorter season due to the reduced number of days (Tab. S1). Where both, soil T and air T were available, the sums for air T were a little higher than those for soil T by 0 to 140 °h* (> 0 °C) and 30–110 °h* (> 5 °C), when the same periods (25 May–23 September 2023) were compared, underpinning the close matching of shaded soil T and air T (air T not shown). The two uppermost tree sites exhibited a growing season of 162–179 days (long season) and 126–138 days (short season), respectively (Fig. 3).

Temperatures at the Tamangur (GT) forest

When comparing the same period in 2023, trees at GT 2535 m experienced very similar temperatures to those at OZ 2494 m, namely 8.7 °C compared to 8.9 °C (Fig. 4; Tab. S1). When the 2022 long season is included for a full season account, an all-season mean of 7.9 °C is resulting for GT compared to 8.6 °C at the OZ 2494 m site (Fig. 4). Once reduced by 0.8 K for the exceptional warmth in 2023 at the Buffalora station (Fig. 1), one arrives at 7.1 °C for a "normal" year, as estimated by the regression, that is c. 1.1 K warmer than the equilibrium isotherm. Using the shorter season, the seasonal mean was 8.0 °C (again after T-anomaly

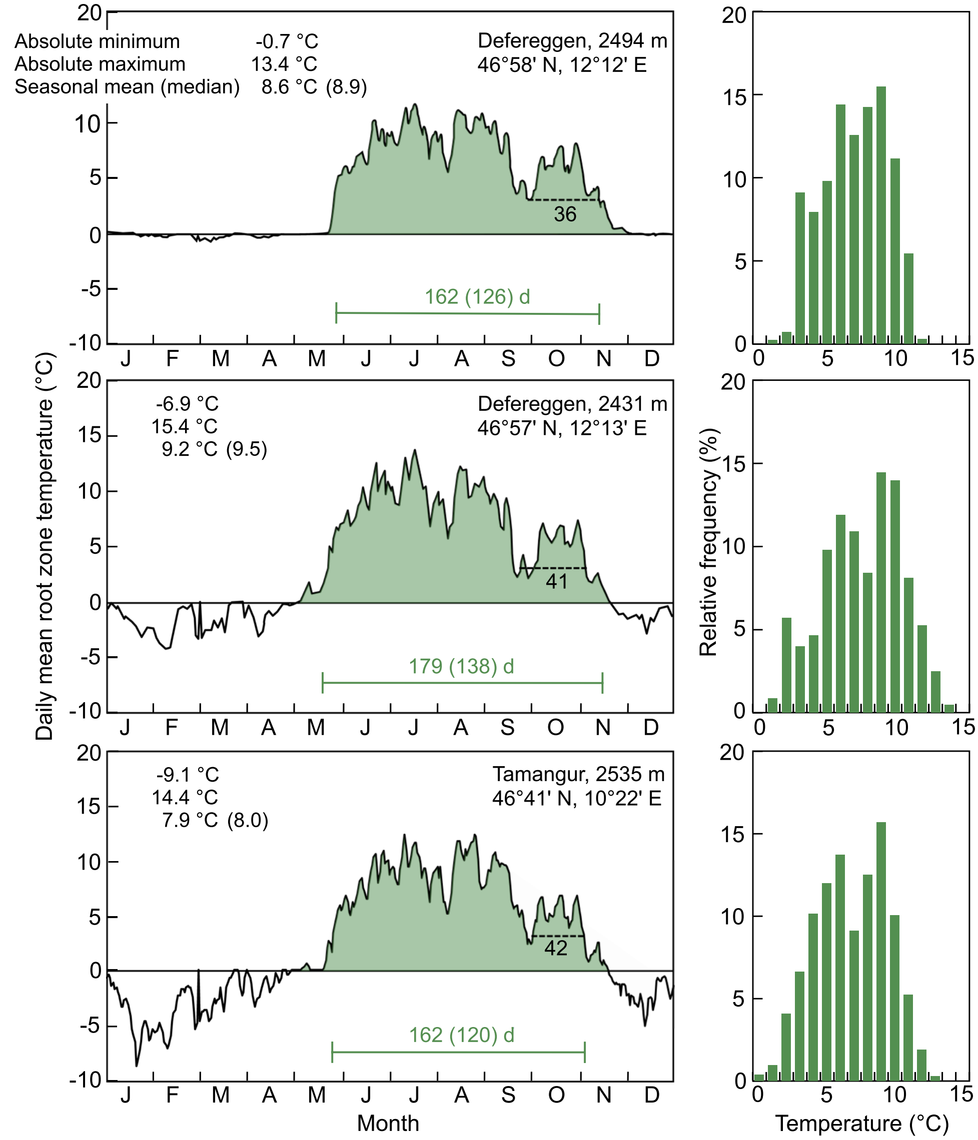

Fig. 3 Seasonal courses of shaded soil temperatures (T) in 10 cm depth (as proxies for mean air T) and frequency distributions (in %) of hourly T readings for the growing season under *Pinus cembra* trees at the current (2022–2023) upper limit of tree occurrence in the Defereggen valley (OZ sites) and Lower Engadine (GT site; Tamangur) in the Eastern Alps. The dashed line marks the period after the late September cold break, referring to the two alternative season definitions applied in Fig. 4. Mean T and median T are calculated for the "long" season variant

correction in 2023), that is 2 K warmer than the treeline isotherm. All-season heat sums at GT were slightly lower than at OZ (1273 °h* at GT vs 1399 °h* > 0 °C at OZ, long season). Seasonal mean canopy air T (not shown) was 1.1 K warmer than shaded soil T, a difference identical to that at OZ 2494 m for the same observation period (2023 only). Season length at GT was 162 days and 120 days for the long and short seasons, respectively, very similar to that at OZ 2494 m.

Tree growth responses above the Defereggen (OZ) forest

Pinus cembra individuals pass through three phases of tree growth: first, a potentially long-lasting seedling/sapling stage with very little gain in height. Second, a shooting phase with slender, acrotone advance (see Fig. S1). Third, a reduction in annual height increment and investment in crown volume. Trees develop a more elliptical silhouette as they approach coning age at around 30–50 years (Fig. 5). Several individuals measured between 2360 and 2420 m, that is closer to the "old" treeline (2360 m), have gone through a long krummholz period as seen in Fig. S2, with the crooked shoots confined to "dwarf-shrub" thickets not permitting age determinations. The data for shoot length increment are for straight trees of 2–2.5 m size that were all in the shooting phase (Fig. S1).

The young trees, growing above the "old" treeline at c. 2360 m elevation, gained in height between 10 and 20 cm per year, with mean rates of 15 cm a^{-1} per tree for the last 10 years not uncommon (Fig. 6). Fifteen years ago, these trees were saplings of < 1 m height and not considered "tree." Mean shoot increments varied little across the years (Fig. 7), with an overall mean of 16.5 cm a^{-1} < 2400 m and

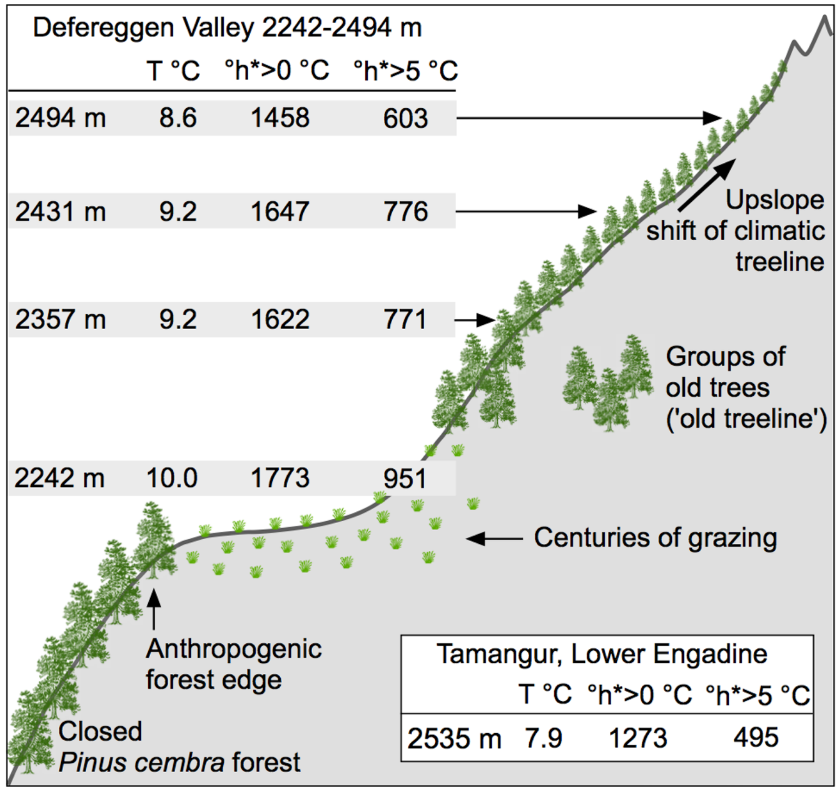

Fig. 4 Seasonal mean temperatures and thermal sums measured in 10 cm depth in shaded soils under individual trees at four different elevations at the OZ sites (Defereggen valley) and GT site (Lower Engadine). For the three lower OZ sites, seasonal data between late season 2021 and late season 2023 were averaged as in Fig. 3. For OZ 2494 m and GT 2535 m, the single season is composed of data from late 2022 until late 2023. In brackets data for 25 May–23 September 2023 only, for all sites. For the 2242 m site, full shade temperature in the canopy is available only, assumed to match soil temperature. Degree hours °h* = °h/24

of 12.4 cm a^{-1} > 2400 m. Minimum shoot length increments in 2013 and 2021 coincided with cold weather in May, while maximum growth (2015–2017, 2019) occurred despite cold May (2019) when the June–July temperatures were above average at the Oberhauser Alm weather station (Tab. S2). The coolest May–September period within 2013–2022 was in 2014, the warmest in 2022 (2 K difference). The data do not reveal obvious linkages between shoot length and concurrent seasonal mean temperatures (n. s.), with the variance declining with elevation.

As one approaches the current tree limit, stem diameter growth is less affected by the cooler conditions than height growth, causing the so-called taper to increase with elevation (Fig. 8). All in all, trees at upfront positions of the shifting tree boundary exhibited surprising vigor, currently gaining in height by more than 1 m per decade. Closer to the “old” treeline, at c. 2360 m elevation, c. 4 m tall, young trees occurred up to 2400 m, some of which started coning (inset in Fig. 5) with the upgrowing stem presumably less than 40 years old.

Tree growth at the God Tamangur site

Annual shoot increments in *Pinus cembra* at GT 2488–2560 m (Fig. 7) averaged at 13.9 cm a^{-1} for the last 9 years, including the year 2023, and they exhibited a record mean of 20 cm a^{-1} in 2023 (five out of 10 trees grew shoots > 20 cm a^{-1}, with a maximum of 26 cm a^{-1}). Trees at the GT site grew very similarly than the ones at the upper end of the OZ site, especially during the last 5 years and will most likely reach 4 m height with the current average growth rates in the next 10 years.

Discussion

To make a case for climate driven shifts in treeline position, the distinction between the climatic limit of the life form tree (fundamental niche) and the actually realized tree occurrences is essential (Körner 2021). On-site temperatures help to make that distinction. The data presented here show that the current uppermost tree positions are substantially above the historical treeline, but they are below the current treeline isotherm. These trees operate at much warmer than treeline temperatures, explaining why they grow so vigorously. Nevertheless, they represent the current regional high elevation record of tree occurrence.

The data indicate that uppermost *Pinus cembra* positions keep lagging behind climatic warming as they did 20–25 years ago, when the reference data had been assembled by Körner and Paulsen (2004) and despite the nutcracker-assisted dispersal of this species. The spotted nutcracker (*Nucifera caryocatactes*) is responsible for spreading *P. cembra* seeds, with lots of seedlings found above the

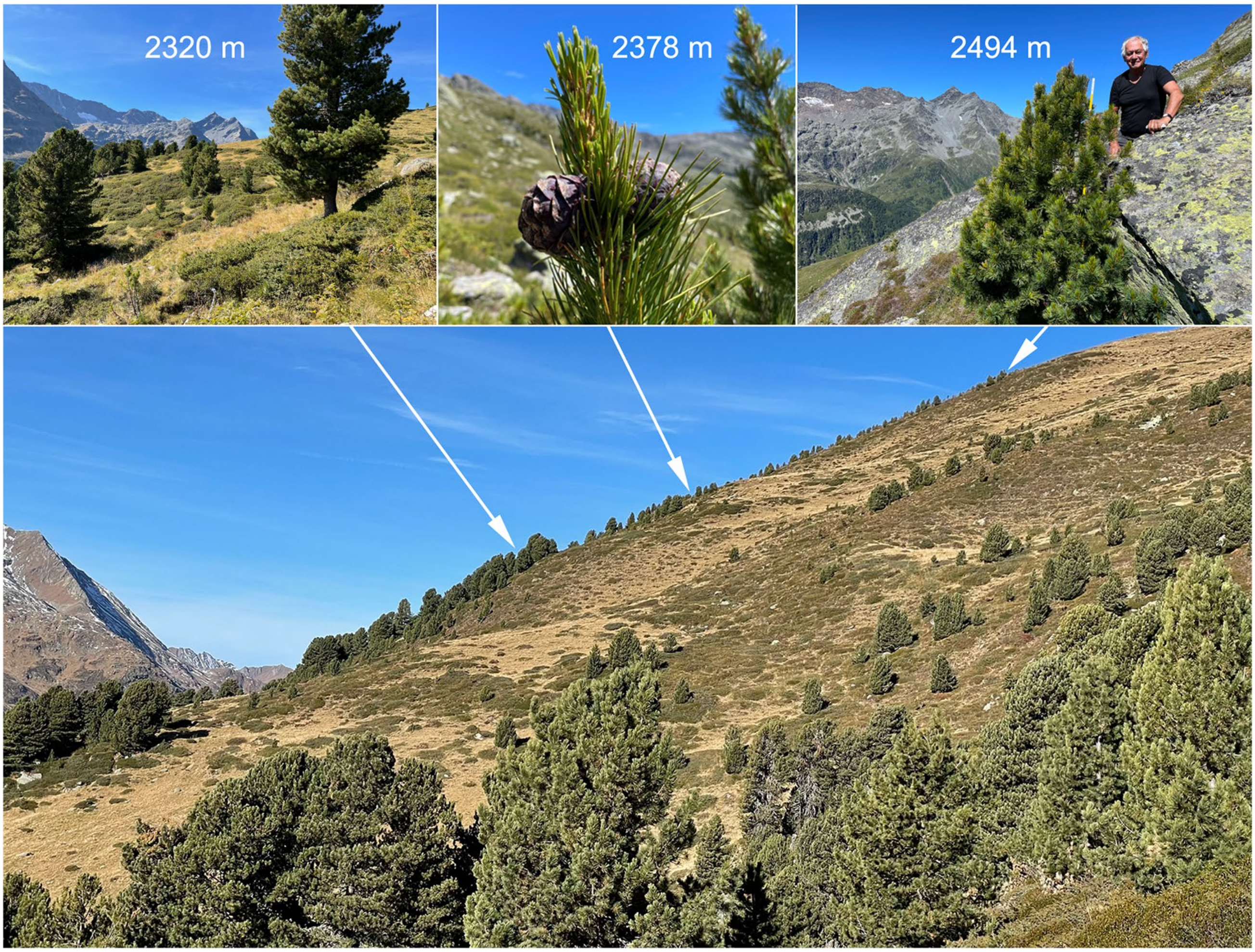

Fig. 5 The open, currently reforesting land above the Oberhauser forest in the Defereggen valley (OZ sites) reflects century long pastoralism. Old, tall individuals occur up to 2360 m, surpassing the closed forest edge at 2250 m elevation. The arrows point at the lower (2320 m) and upper range (2494 m) where annual shoot increments were measured, including new trees that start coning already at around 2380 m. The top right image indicates what is presumably the currently uppermost tree of Austria at 2494 m

current tree limit at both OZ and GT. Up to 100,000 seeds are spread by each bird per year, and on average, six seeds are buried together, one reason, why *P. cembra* recruits in clusters (e.g., Tomback et al. 1993; Müterthies 2002; Neuschulz et al. 2018; Gugerli et al. 2022). However, GPS bird tracking revealed that a great fraction of these seeds is also buried in places unsuitable for *P. cembra* (e.g., in dense spruce forests; Sorensen et al. 2022).

Had there been enough time for the uppermost tree positions to equilibrate with the concurrent climatic situation, they would be occurring at a c. 6 °C isotherm of seasonal mean T, rather than at 8.3 °C for OZ or 7.1 °C for GT (long season variant), after correcting for the 2022–2023 T-anomaly and assuming that the weather stations in St. Jakob and Buffalora captured the warmer 2022/2023 conditions representatively for these elevations. So, these trees currently operate at temperatures 2.3 or 1.1 K above the long-term equilibrium isotherm temperature, that is, at the same (GT), or even 1 K warmer temperature (OZ) than has been measured at 12 treeline sites across the Alps 20–25 years ago (7.0 ± 0.4 °C s.d.; Körner and Paulsen 2004) when climate warming had reached 1.0–1.2 K in the Alps (Fig. 1). With the temperature lapse rate for the growing season for the inner Alps of 0.6 K/100 m (Kollas et al. 2014), these T differences convert to 170 to 330 m of elevation below the position of the c. 6 °C treeline isotherm. Since the uppermost trees at OZ and GT are experiencing almost identical temperatures when comparing an identical time period in 2023, the T differences between the sites, when 2021–2022 data are included, reflect some unexplained in situ T variabilities and the difficulty to define the end of the season.

What we see in these landscapes is a massive encroachment of young trees onto higher slopes (Fig. S3), which currently grow 134–140 m above the > 100-year-old individuals

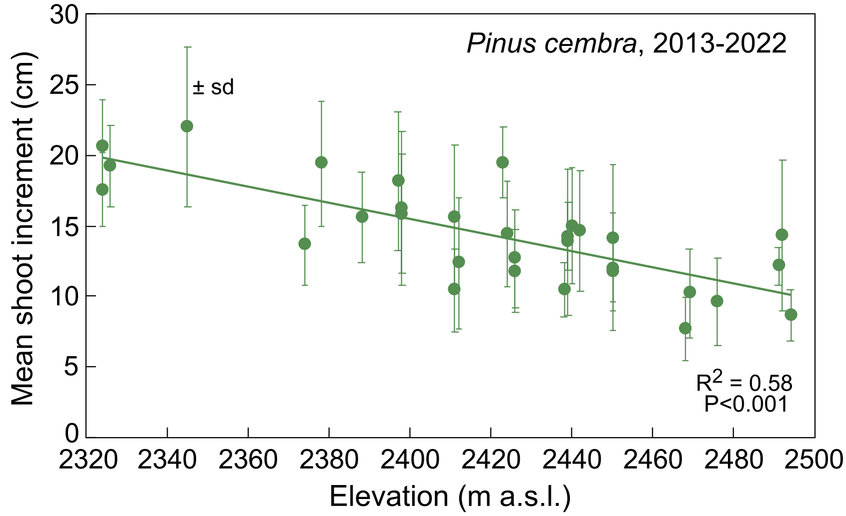

Fig. 6 Mean annual shoot increment per tree for the last 10 years (± s.d.; total of 31 trees) of *Pinus cembra* trees along the uppermost c. 200 m range (Fig. 5) above the highest old trees at OZ

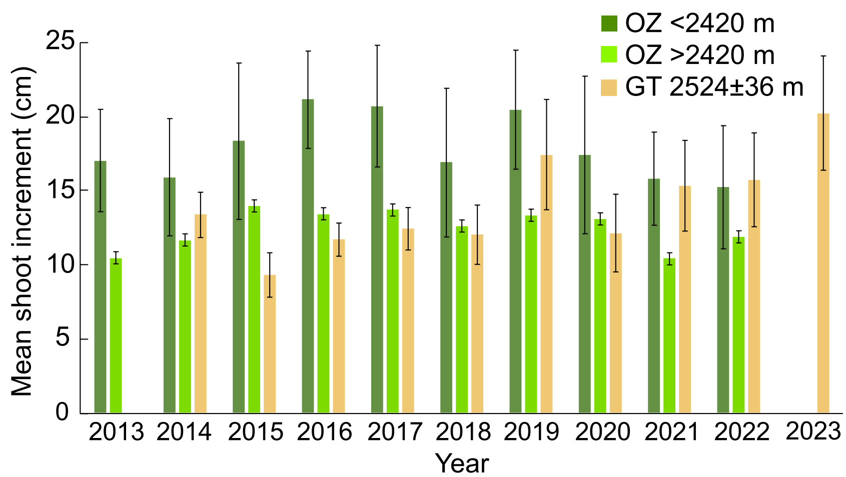

Fig. 7 The same OZ data as for Fig. 6, but grouped per year and separated in a lower (< 2420 m, green) and higher half (> 2420 m, dark-green). Yellow bars show the mean annual shoot increment at GT 2488–2560 m ($n = 10$ trees; 9 years). Means ± s.d. OZ are 16.5 ± 1.5 cm for < 2420 m, 12.4 ± 1.3 cm for > 2420 m for all 10 years, and at GT 13.9 ± 3.2 cm for the last 9 years

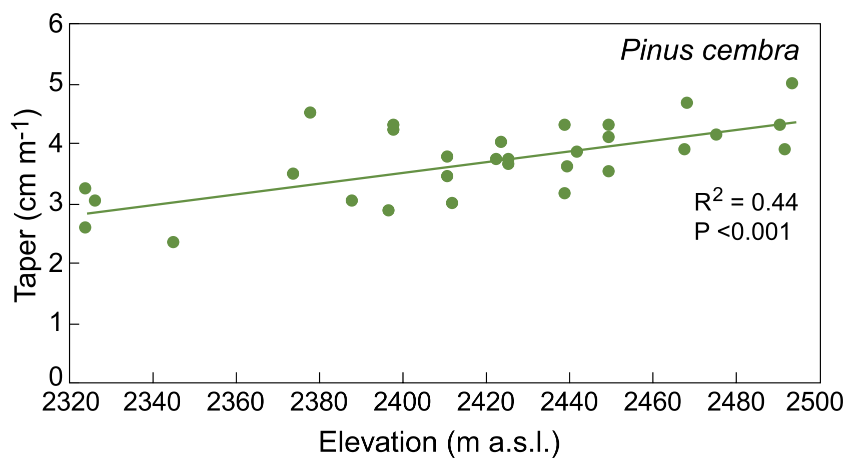

Fig. 8 Stem taper of *Pinus cembra* across the uppermost c. 200 m of elevation as in Fig. 6, Defereggen forest. For every cm in diameter, the uppermost trees grow 25 cm in height compared to 33 cm at the lower end of the elevational range

that mark the "old" treelines (2360 m OZ, 2420 m GT) at which trees may have been hardly growing during the late little ice age (Paulsen et al. 2000), but now find themselves under luxuriously warm life conditions. The fact that we find in two different regions (1) similar temperatures at these uppermost trees, (2) analogous patterns of "old" versus "new" tree distribution, and (3) close to identical, very high annual shoot increment rates over the last decade, suggests

that these dynamics in the treeline ecotone in response to climatic warming represent a general phenomenon in the inner part of the Eastern Alps.

While uppermost tree positions are largely hold by newly established individuals, trees at elevations between the "old tree limit" and c. 60 m above, often emerge from former krummholz-individuals (Fig. S2). Distorted krummholz forms under atmospheric conditions too cold for tree growth, with repeatedly unsuccessful shooting attempts, ending up in crooked growth, forming thickets that remain trapped in the warmer microenvironment they produce by aerodynamic decoupling (Körner 2012a, b; Millar et al. 2020). Once the climate warms above a threshold, upright tree stems emerge from such thickets (Pereg and Payette 1998; Gamache and Payette 2004). In line with our observations, Schickhoff et al. (2023) report a lagging of upper tree limits behind climatic change and high growing season mean soil temperature (7.5 ± 0.6 °C) at 10 cm depth in Rolwaling (Nepal).

The non-significant effect of growing season temperature on shoot growth near treeline (Fig. 7) matches the results by Paulsen et al. (2000) and Camarero et al. (2021) that annual radial stem growth increments saturate, once a threshold temperature has been surpassed. Unlike radial stem increment, the length (or height) growth is partly predefined in the bud formed in the previous autumn (the number of nodes, that is, the number of the 5-needle short shoots), while the concurrent growth conditions can influence the spacing of the short shoots on the stem (the length of the internodes). This way, the late season climate of the previous year can co-influences current season shoot length, as was found for tree ring width (Oberhuber and Kofler 2003), which is likely under demand-control by shoot vigor. Such carry-over effects may also explain the poor correlation between shoot increment and concurrent season climate (Fig. 7), but they do not preclude instantaneous, high-resolution temperature responses of tissue growth (Izworska et al. 2023). The elevational increase of taper near treeline observed here has been widely witnessed (Bernoulli and Körner 1999; Körner 2012a).

A rapid decline of shoot extension close to the 1900 m upper limit of a *Pinus cembra* plantation was observed in North-Tyrol in 1970–1995 (Kronfuss and Havranek 1999). Similarly, the annual height increment in young trees at the OZ site was found to decline with elevation, with only 4–5 cm a^{-1} at 2200 and 3 cm a^{-1} at 2290 m elevation in the early 1980s (Kammerlander 1985). Hence, the rate of shoot length growth quadrupled since then, but at 200 m higher elevation, where Kammerlander spotted no young trees at that time. We focused on > 2 m *Pinus cembra* because of the dominance of this species at the highest tree locations, but > 2 m *Larix decidua* is not far behind. In a side-valley, adjacent to our OZ sites (Trojer valley), 2–2.5 m tall *L. decidua* individuals were found at 2420 m with annual terminal shoot increments of c. 21 cm (6–35 cm), but there were lots of damaged shoots. In this climate, *Larix* seems to advance less successfully than *P. cembra*.

The rather warm conditions at current uppermost tree positions are also mirrored in thermal sums. For 12 sites, these were 940 ± 90 °h* > 0 °C for the growing seasons 20–25 years ago (Körner and Paulsen 2004), and arrived at 1399 °h* (OZ 2494 m) and 1273 °h* > 0 °C (GT 2535 m) in 2022/2023, employing the long season data (including October 2022) and 1176 vs. 1051 °h* > 0 °C for the shorter season (Fig. 4, Tab. S1). The heat sums > 5 °C were 300 ± 56 °h* in the old reference data (Körner and Paulsen 2004), and now arrived at 459–603 °h* across both season lengths. Since such data cannot be corrected for the above average seasonal warmth in 2022 and 2023, heat sums would be somewhat smaller at what currently could be considered "normal years." The mean season length for all 12 reference sites was 135 ± 10 days, compared to the current 162 days (long season, both regions) or 120–126 days (short season) observed at the uppermost OZ and GT sites. Körner and Paulsen (2004) had the same difficulty in defining the season end and adopted criteria closer to the short season type. From our numbers, we cannot deduce a lengthening of the climatic growing season at treeline, but as climate warming continues, the regime will more likely shift toward the long late-season type as the "normal" situation. The current 9.2 °C at OZ 2357 m (8.9 °C after correcting for the 2022–2023 T-anomaly) places these > 100-year-old trees c. 3 K below the presumed equilibrium isotherm at the end of the little ice age, that is, deep into the montane forest belt climate (c. 500 m below).

There are rather unique, historical climate data available for a location only 18 km south from our GT site, at 2473 m elevation, near Umbrail Pass (Kerner 1865; Tab. S3): a mean air temperature of 6.6 °C was recorded for June–September in the years 1854–1856. Including May would reduce the seasonal mean down to 5 °C. There are no daily data available that would have permitted delineating the season by our criteria (see the "Materials and methods" section), but the treeline season commonly starts in the second half of May, so a "true" seasonal mean of 6 °C for that period seems very plausible. There are scattered highest old *P. cembra* occurrences in that region at 2420 m including our GT site. With peak glacial advances during this terminal phase of the little ice age, this period most likely represents the equilibrium treeline temperature (plus 0.3 K for the 2473–2420 m elevation difference) for the oldest, still existing, uppermost trees. The data by Paulsen et al. (2000) indicate hardly any tree growth during that period (a "sit-out" state).

Although presumably more rapid, the elevation shifts of tree limits presented here, line up with results of many other surveys (Remy 2012; Hansson et al. 2021; Scherrer et al. 2020; André et al. 2023 for *P. cembra*; Schickhoff et al. 2023; Mienna et al. 2024). Several of these studies referred to the lag of such shifts behind the rise of temperature (Davis

et al. 2020; Rees et al. 2020; Lu et al. 2021). Except for Schickhoff et al. (2023), these observations suffer from two limitations: (1) often vague or inexistent definitions of what is a treeline and (2) lack of ground truth temperature data. So, it was difficult to separate temperature from land use-related tree abundance (Didier 2001; Gehrig-Fasel et al. 2007; Ameztegui et al. 2015; Shi et al. 2022; He et al. 2023). Although currently protected, both the OZ and GT sites are under browsing and grazing pressure (young cattle, red deer, chamois, ibex; Gugerli et al. 2022). Along our high slopes at OZ, it was hard to find trees that had not lost their terminal bud at least once during the past 10 years (2021 was a particularly "bad" winter with a lot of browsing damage).

The data presented here, not only evidence actual growth conditions at the current range limit of trees, but also permit projections as to where the tree limits will end up once in equilibrium with the current, warmer climate, with a several hundred meters leeway for effects of additional future warming. Our data support the suggestion that climatic warming can induce rapid advances of treeline over several hundred meters (Tinner and Kaltenrieder 2005), although our recorded tree limits still lag behind the position of the climatic treeline.

Pinus cembra suffers from long-laying snow in depressions (the species is sensitive to snow mold), and the nutcracker avoids places with long snow duration too (Holtmeier 1973; Müterthies 2002). Long before climatic warming facilitated upright tree growth at close to 2500 m elevation, the nutcracker had buried seeds at exposed sites above the treeline, and thus, is responsible for the positions of the current recruits on convex terrain. Plentiful seedlings at these uppermost elevations with trees and above, at both OZ and GT, indicate that successful novel seed dispersal is under way. However, the fraction of seeds dispersed that actually become vital seedlings can be very small. Explored in the Upper Engadine, the probability for seedling success was found to rise dramatically from 3 to 17% from 1850 to 2250 m (100 m above the local tree limit; Neuschulz et al. 2018). The presumed biotic limitation of tree spreading (reduced nutcracker visits) is compensated or even overcompensated by the more favorable abiotic conditions for seedlings in micro-shelters of open, and thus warm alpine terrain, compared to closed montane forests with dense undergrowth (Merges et al. 2020). Because trees are advancing upslope, the frontiers are diffuse (sensu Bader et al. 2020) and shaped by the nutcracker's site preferences (Holtmeier and Broll 2005). So, it is not the failure of trees to grow at higher elevation that limits the nutcracker's upslope activities (Engelhardt et al. 2020), but it is the other way round.

It has to be explored, if and how the "engineer" of the current tree distribution, the nutcracker, will adjust its seed allocation strategies in response to climatic warming and associated snow regimes. Birds have been known to track climatic warming at high elevations (Roth et al. 2014; Brambilla et al. 2022). A second biotic component is seed predation by rodents that removed almost half of the seeds buried in a field experiment, diminishing the contribution of abiotic conditions on seedling success (Neuschulz et al. 2018), similar to what had been observed for white bark pine seedlings (Pansing et al. 2017). Since seedbeds in open alpine terrain are thermally strongly decoupled from ambient air conditions (Körner and Hiltbrunner 2018), and are warmer than air temperatures scaled from meteorological stations, it does not come as a surprise that temperature plays a minor role for the early stages of tree recruitment.

Once in equilibrium, the expected future positions of the upper edges of tree distribution exceed the Holocene maximum of treeline elevation. Macrofossils and alpine lake sediments indicate that treeline in the central Alps was at most 150–200 m above the nineteenth century pre-climatic-warming positions (Tinner and Theurillat 2003; Tinner 2007; Körner 2012a, Fig. 12.6). The upslope-shift of the treeline isotherm currently exceeds the little ice age elevation (2360 m at OZ, 2420 m at GT) by more than 300 m in 2023. The uppermost trees currently grow 170–330 m below the treeline isotherm. We conclude that climate warming has advanced the frontiers of high elevation trees in the Eastern Alps by almost 140 m in less than 40 years. The current vigor of these trees and the on-site temperatures indicate that these trees currently operate at much warmer than the thermal equilibrium conditions at treeline.

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Author contribution CK designed the study, conducted the field work, and drafted the paper. EH suggested the work at Tamangur and was involved in literature work and in writing the paper.

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Data availability All relevant temperature data used in this study are available from the Figshare repository https://doi.org/10.6084/m9.figshare.25242796.v3.

Declarations

Competing interests The authors declare no competing interests.

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