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Climate, not land-use, drives a recent acceleration of larch expansion at the forest-grassland ecotone in the southern French alps

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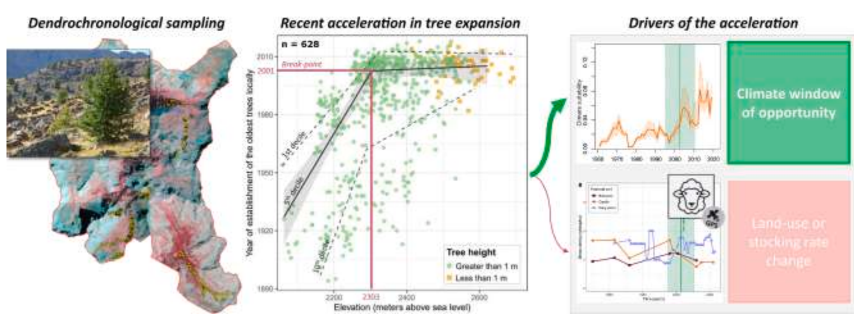
HIGHLIGHTS

- A wave of larch establishment in the early 2000s was detected in the southern French Alps via dendrochronology and imagery.
- Tree expansion occurs in mountain pastoral systems at various elevations, despite minimal land-use changes in recent decades.
- Since the late 1990s, favourable climate has enabled tree establishment, with warming driving expansion regardless of grazing.
- Past land-use changes enabled larch dynamics, but its recent acceleration is mainly driven by climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

In recent decades significant forest expansion into treeless alpine zones has been observed across global mountain ranges, including the Alps, driven by a complex interplay of global warming and land-use changes. The upward shift of treelines has far-reaching implications for ecosystem functioning, biodiversity, and biogeochemical cycles. However, climate variables alone account for only a fraction of treeline dynamics, highlighting substantial research gaps concerning the influence of non-climatic factors. This study addresses these gaps by combining dendrochronological methods, high-resolution bioclimatic data, and historical land-use records to investigate treeline dynamics in the southern French Alps. Our results reveal a marked acceleration in tree establishment, starting in the early 2000s, attributable primarily to climate change rather than the pastoral abandonment of the 19th century. We demonstrate that historical land-use changes created predisposing conditions for tree establishment, while recent climate change has increasingly acted as an accelerator for this dynamic. While key climatic factors, such as thermal indicators and growing season length, are identified as significant contributors to treeline shifts, our study highlights the need for further research to disentangle the specific drivers of tree recruitment and survival in the context of ongoing climate change.

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1. Introduction

In recent decades, forest expansion into previously treeless alpine areas have been documented in mountain ranges across Asia (Cazzolla Gatti et al., 2019; Du et al., 2018), North America (Beckage et al., 2008; Trant et al., 2020) and Europe (Bayle et al., 2024; Carlson et al., 2014; Gehrig-Fasel et al., 2007). The upward shift of the treeline ecotone significantly influences land-atmosphere interactions, altering albedo, heat storage, evapotranspiration, and carbon sequestration (Mienna et al., 2024). These shifts impact ecosystem biodiversity and community functioning by causing habitat loss for endangered species (Dirnböck et al., 2011; Pornaro et al., 2013; Rippa et al., 2011), modifying biogeochemical cycles and soil properties (Guidi et al., 2014), reducing pastoral resources (Espunyes et al., 2019) and driving landscape changes (Ameztegui et al., 2021; Dirnböck et al., 2011). Given the wide array of impacts of treeline elevation changes on alpine ecosystems, understanding the mechanisms driving upward treelines shift is crucial.

As the treeline marks the physiological tolerance limit of 'tree' life form (Dandan et al., 2022; Körner, 2012, 2021; Körner and Paulsen, 2004), its position is partly controlled by temperature. The upward shift of treelines has thus been linked to global climate warming (Harsch et al., 2009), particularly pronounced at high-elevations (Pepin et al., 2015). However, climate variables account for only about 30 % of global alpine treeline migration (Hansson et al., 2021; Harsch et al., 2009; Lu et al., 2021; Rees et al., 2020) indicating that the substantial role of non-climatic factors in mediating treeline advance (Mienna et al., 2024). These include topography (Ramírez et al., 2024), pedogenesis and geomorphic processes (Cudlín et al., 2017; Körner and Hoch, 2023), and human land-use, such as logging, fires, summer farming, and livestock grazing which historically constrained tree establishment and growth. In many regions, current treelines reflect historical land-use legacies and expand towards higher elevations as anthropogenic activity decreases (Mienna et al., 2022).

In Europe, the upward shift of treelines since the mid-19th century coincides with both rising temperatures (Choler, 2023; Gobiet et al., 2014) and reduced land-use intensity following mass exodus and declining livestock densities (Chhetri et al., 2017; Collantes, 2006; Vitali et al., 2018). Attributing advancing treelines to global warming or land-use changes remains challenging, and few studies have quantified their respective contributions (Ameztegui et al., 2016; Gehrig-Fasel et al., 2007; Hofgaard et al., 2009; Mienna et al., 2020; Vittoz et al., 2008). In the Alps and the Pyrenees, these studies have produced contradictory results. Ameztegui et al. (2016) and Gehrig-Fasel et al. (2007) suggest that land-use changes play a predominant role, whereas Vittoz et al. (2008) suggest a stronger role for climate change. The attribution is further complicated by pulses, lags and threshold effects in the response of the treeline to environmental changes (Cullen et al., 2001; Danby and Hik, 2007; Liang and Camarero, 2018; Rupp et al., 2001). Waves in tree establishment more likely result from a combination of concurrent factors, such as specific meteorological events and abrupt land-use changes (Frei et al., 2018), than from long-term climate warming trends. Similarly, peaks in tree establishment, often observed following grazing cessation, suggest windows of opportunity for trees, during which biotic competition remains low before herbivory-sensitive plant species recover (Speed et al., 2010). Rupp et al. (2001) and Camarero et al. (2021) respectively explain the delayed response of treeline trees to changes by their inability to keep pace with rising temperatures, as their physiological processes are too slow.

In this context, understanding the timing of woody encroachment at an annual resolution over extended periods, ranging from several decades to centuries, is crucial for characterising non-linearities and disentangling the interplay of land-use legacies and climate change (Ameztegui et al., 2016; Anselmetto et al., 2024; Gehrig-Fasel et al., 2007). Schematically, two primary methods have been used to study tree line dynamics over long time periods (Feuillet et al., 2020). The first considers elevational variation or forest densification using aerial photographs, which results in discrete time series of tree line positions (see, e.g., Ameztegui et al., 2016; Camarero and Gutiérrez, 2007, Camarero and Gutiérrez, 2004; Gehrig-Fasel et al., 2007; Leonelli et al., 2011). The second, based on dendrological analyses (see, e.g., Cannone and Malfasi, 2024, for a recent review), theoretically offers continuous, annually resolved series of tree encroachment. However, the majority of the 46 studies reviewed by Cannone and Malfasi (2024) aggregate tree establishment data into multi-year windows rather than leveraging the annual resolution provided by dendrochronological analysis. These datasets are often compared with temperature series but are rarely contrasted with local, highly resolved climatic variables and detailed trajectories of land-use.

To address this gap, we documented larch expansion across five watersheds in the French south-western Alps using dendrochronology. We applied quantile-segmented linear regressions to visualise age structures along elevation gradients and conducted breakpoint analyses to detect potential non-linearities in tree establishment patterns. To assess anthropogenic influences, we utilised detailed datasets, including population censuses, pastoral surveys, and sheep stocking rates. Additionally, we considered several rarely studied climatic drivers, including snow melt-out date (SMOD), date of the first snowfalls (SF), heat wave (HWI) and cold wave index (CWI), and cumulative rainfall (RR), using highly resolved climate reanalysis data from Météo-France (1959–present). Specifically, we aimed to (i) determine whether the upward expansion of larch is a continuous trend or driven by episodic establishment waves, (ii) disentangle the respective roles of climatic and anthropogenic factors in treeline dynamics and (iii) identify key climatic drivers of the treeline shift.

2. Materials and methods

2.1. Study area

We conducted this study in the upper watersheds of the Ubaye valley, near to the Cayolle pass in the northern Mercantour National Park (Fig. 1). The study site spans approximately 6500 ha of high elevation landscapes characterised by relatively gentle slopes. The primary bedrock is the "Grès d'Annot" sandstone. Below 2300 m asl, the vegetation is dominated by forests of European larches (*Larix decidua Mill.*), a pioneering deciduous conifer that forms monospecific stands at this elevation in this region. Above the forested areas, the landscape transitions to high elevation grasslands, sparsely vegetated areas, screes, and rocky outcrops. Individual larch trees are scattered in these higher areas, particularly in sparsely vegetated zones. The study area experiences a continental climate characteristic of inner alpine valleys with Mediterranean influences and seasonal snow cover. This region has features of a greening hotspot, i.e. with a significant increase of vegetation cover over the last decades (Choler et al., 2021). Recent studies indicate that larch expansion is a major contributor to this pronounced greening (Bayle et al., 2024). (See Table 1.)

This landscape has been shaped by centuries of agro-sylvo-pastoralism. Summer pastures are extensively grazed by sheep herds for approximately three months, from mid-June to mid-September. The high-elevation grazed lands are organised into three distincts pastoral units, each representing mountain pastures grazed by different herds and subject to specific grazing rules. These pastoral units are named Cayolle, Sanguinière and Braissette.

2.2. Tree dynamics

During 2022 and 2023, we conducted dendrochronological sampling campaigns across five elevation gradients ranging from 2000 to 2700 m asl, in areas named Braissette, Cayolle, Roche trouée, Boucharde and Eschillon (Fig. 1). These gradients, selected for their varying aspects, steepness, and grazing pressures span from dense forests to isolated high-elevation larch tree individuals. Notably, the Roche trouée gradient has been excluded from sheep grazing since 1988. To document the colonisation patterns along these gradients, sampling targeted the oldest trees along the elevation range. To select these trees, we considered their height, crown size and trunk diameter, comparing these traits to those of surrounding trees. This approach allows us to determine the age structure of the larch population and trace the timeline of colonisation.

We used a Pressler increment borer to extract two cores per tree and sapling: one close to the ground to precisely determine the age, the second at approximately 1 m in height. This second sample allows us to establish a relationship between the age at ground level and at 1 m in cases where the first core is missing. Our sampling protocol, designed to target the oldest trees at each location, enabled us to determine the onset of tree establishment (i.e. the year of initial colonisation) (Figs. 1 and 2).

The cores were sanded and scanned using a high-resolution scanner. Tree-ring counting and cross-dating were performed using CooRecorder and Cdendro softwares (Maxwell and Larsson, 2021). Cross-dating was not possible for saplings due to the limited number of rings. In cases where the lowest core was missing, we estimated tree age using a linear regression between the number of rings at 0 and 1 m height (Supp. Mat. 2). For increment cores that did not reach the pith, we estimated the number of missing rings using the "DistanceToPith" tool in CooRecorder (Maxwell and Larsson, 2021). This tool estimates the number of missing rings based on the radius to the estimated pith position and the spacing of preceding rings. It is noteworthy that our sampling protocol may slightly underestimate tree ages, as coring at the root collar level was not always possible and some cores did not reach the pith.

To visualise the age structure along the colonisation gradient, we first merged data from the five gradients for a comprehensive analysis. We applied the quantile-segmented linear regression method, which examines the relationships between different quantiles of a distribution and an explanatory variable, with particular focus on the lower and upper quantiles. This approach is particularly useful for identifying the envelope of tree age distribution along the elevation gradient. Since the age structure appeared to vary with elevation, we refined our analysis by using segmented regressions, dividing elevation range into 20 classes of approximately 30 m each. For each elevation class, the dataset was further divided into deciles based on tree age. We then performed quantile-segmented linear regressions to visualise the age structure along the elevation gradient. This analysis was conducted using the 'segmented' package in R (Muggeo, 2008).

Table 1
Features of the surveyed *Larix decidua* treeline ecotone sites in the southern French Alps.

Name	Elevation range (m asl)	Aspect	Domestic grazing	Number of trees cored
Boucharde	2354–2633	W	Yes	50
Braissette	2058–2693	N-NW	Yes	210
Cayolle	2228–2660	NE	Yes	166
Eschillion	2244–2550	E	Yes	76
Roche trouée	2062–2510	NW	Not since 1988	126

2.3. Land-use history

We sourced livestock data from pastoral surveys conducted by local authorities for three pastoral units: Braissette, Cayolle and Sanguinière. Records for Braissette and Cayolle are partial and cover the years 1950, 1963, 1972, 1995 and 2012. For the Sanguinière mountain pasture, a

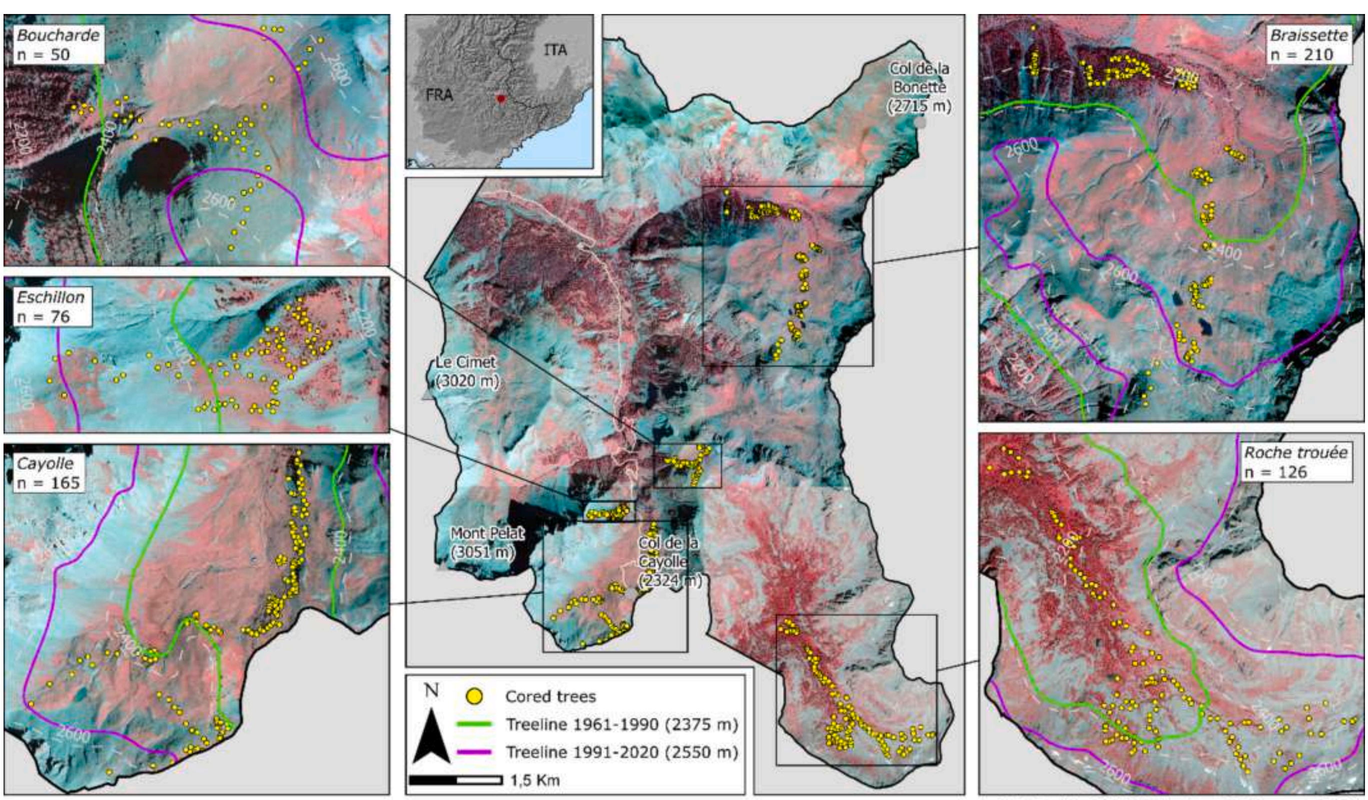

Fig. 1. Map showing the locations of the five elevation gradients where tree coring was conducted. Yellow dots represent the positions of the cored trees. The green and pink lines indicate the climatic treelines for the periods 1961–1990 (2375 m) and 1991–2020 (2550 m), respectively. The inset map highlights the location of the study area within the Alps, shaded in dark grey. Each of the five panels provides a zoomed-in view of the sampled gradients with colour infrared images as the background. The name of each gradient and the corresponding number of cored trees are noted in each panel. Additional methodological details can be found in the methods section.

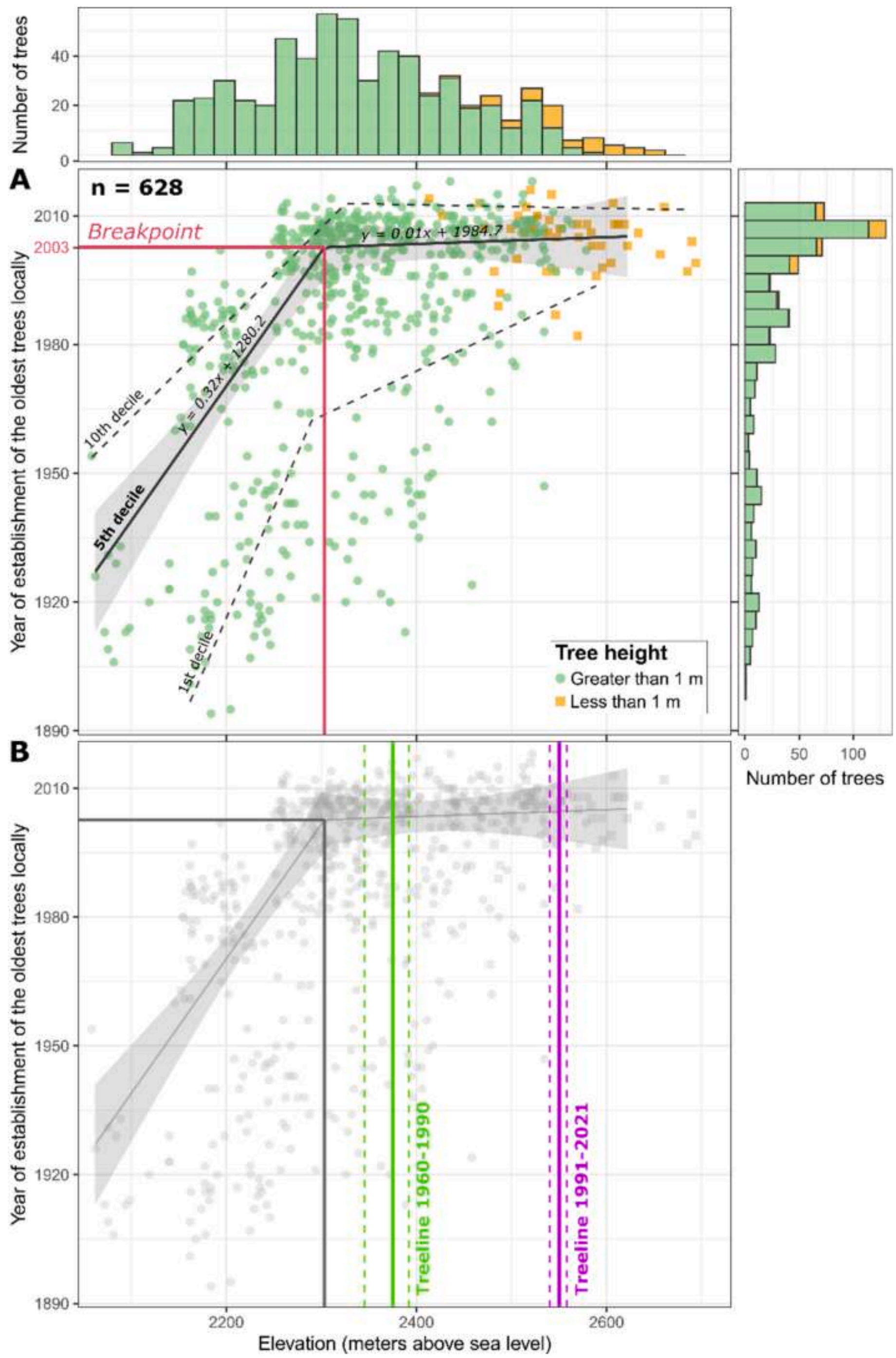

Fig. 2. Age structure of the oldest trees along an elevation gradient of expansion. On panel A, each point represents a cored tree, with data combined across all five gradients. Black lines represent segmented linear regressions for different quantiles (1st, 5th, 10th). The shaded area indicates the 95 % confidence interval for the segmented linear regression of the median. The pink line represents the breakpoint in the relationship, showing the elevation and year when this breakpoint occurred. Green circles represent trees taller than 1 m, while orange squares represent trees shorter than 1 m. Panel B displays the elevation of the climatic treelines for two periods: 1961–1990 (green) and 1991–2020 (purple). See Supplementary Material 2 for additional details.

more extensive dataset allowed for a more detailed reconstruction of sheep numbers. For each year, we retrieved data on the number of sheep, the surface area of the pastoral unit, and the duration of grazing. Given changes in surface area over time, we calculated sheep density per hectare to assess variations in grazing pressure.

To reconstruct the history of agro-sylvo-pastoral farming, we used the number of inhabitants over the past two centuries as a proxy. This approach is relevant since the workforce in traditional pastoralism was closely tied to the environmental pressure exerted by human activities (Mather et al., 1999; Rosenberg, 1988). Previous studies have similarly used human population changes to explain shifts in practices and land cover, such as in the Italian Alps (Falcucci et al., 2007). We obtained population records from the four towns surrounding the study area - Uvernet-Fours, Entraunes, Saint Dalmas-le-Selvage and Allos - from the French National Institute for Statistics and Economic Studies. These data span from the late 18th century to 2021, although records before 1850 are sparse and irregular. After 1850, the data became consistently available.

2.4. Grazing pressure

To relate grazing pressure to larch dynamics, we used individual tree locations from Bayle et al. (2024), derived from photo-interpretation of very high-resolution aerial infrared images. We also used estimates of stocking rates obtained from position tracking of sheep (Perron Chambard et al., 2024). Between 4 and 8 sheep per pastoral unit were tracked at 10-min frequency throughout the grazing season. Hidden Markov Models were applied to classify sheep behaviour into three categories: (i) moving; (ii) grazing; and (iii) resting. The sub-trajectories for each behaviour were then converted into stocking rates using a Brownian Bridge Movement Model (Horne et al., 2007). This yielded stocking rates per pixel at a spatial resolution of 30 m, expressed as the number of sheep-days per hectare. Monitoring was conducted in the summers of 2022 and 2023 within the Cayolle and Sanguinière pastoral units. Data from the two pastures were merged and averaged across the two years.

We set thresholds to focus on areas with significant sheep presence: a minimum density threshold of 10 sheep/day/ha to exclude ungrazed or minimally grazed areas and a maximum of 250 sheep/day/ha to exclude areas of high density due to nightly penning.

We divided the space explored by the flock into two categories: (i) areas used for moving, likely associated with high trampling rates, and (ii) areas used for grazing and resting, where herbivory was the dominant factor. Moving behaviours accounted for at least 50 % of the total stocking rate in the first category, while all other areas were included in the second.

We used tree density data from 2018 to assess the impact of sheep on tree expansion. Data were aggregated at the hectare scale to better represent landscape-level dynamics and minimize localised station effects. We compared tree density across five quantiles of sheep stocking density, independently for both behaviours. Statistical differences between distributions were evaluated using pairwise Wilcoxon tests, allowing for comparisons between group levels.

2.5. Climatic trends

We conducted a detailed climate analysis based on the following considerations: (i) the snow-free period is critical for tree establishment, (ii) indicators relevant to larch ecophysiology were prioritised, (iii) a fine temporal resolution is necessary to capture short-term events affecting seedling germination and survival. We used the S2M reanalysis developed by Météo France for the French Alps, available since 1959 (Durand et al., 2009a, 2009b). This model integrates observed data from a network of weather stations with estimates from numerical weather forecasting models, providing hourly atmospheric data (e.g. precipitation, solar radiation) and snow metrics for 23 massifs of the French Alps across 300 m elevation bands.

Meteorological data are interpolated based on elevation, slope steepness (up to a maximum slope of 40°), slope aspect, and an orographic mask with a 20 km radius. The slope and mask data are extracted from a 30 m digital elevation model to account for shadow effects due to terrain relief. At our dendrochronological sampling points, corresponding to 81 pixels of 250 m each, we extracted annual climatic indices including snow melt-out day (SMOD), snow fall day (SF), heat wave index (HWI), cold wave index (CWI), and cumulative rainfall (RR). The SMOD is defined as the first day of the year when snowpack depth falls below 10 cm, while SF is the first day when snowpack exceeds 10 cm late in the season. This threshold was chosen as it aligns with the average error of the model. These metrics allowed us to calculate the length of the snow-free period for each year, which is critical for the germination and survival of seedlings. All climate indicators were calculated during the snow-free period.

HWI and CWI were calculated using the method of Russo et al. (2014). These indices are more informative than an average trend analysis, as they account for extreme events at a yearly resolution, which we considered the most relevant for influencing germination and seedling survival. To compute the HWI, we first calculated the mean daily air temperature as follows:

$$Tmean = 0.5^*(Tmin + Tmax)$$

where Tmin and Tmax represent the minimum and maximum daily temperature, respectively.

We then computed the quantiles of Tmean for each day of the year, centred on a moving window of 15 days over the reference climate period 1991–2020. Afterward, we compared the Tmean value of each day of each year to the corresponding quantiles for the same day within the reference period. We defined a heatwave as a sequence of at least three consecutive days where Tmean exceeded the 8th decile. For cold waves, the definition was similar, but in this case, Tmean had to be below the 20th percentile of daily maxima. Finally, we computed the cumulative length of HWI and CWI per year (Fig. 5A).

Next, we calculated the cumulative rainfall (RR) during the snow-free period for each year (Fig. 5C). Our objective was to integrate temperature and water-related drivers (i.e. SMOD, HWI, CWI, RR) into a function that quantifies the climatic suitability for tree establishment (Fig. 5E). To achieve this, we first calculated a standardised anomaly for each annual indicator relative to the 1991–2020 reference period. Standardisation is crucial as it allows for the comparison of indicators by assigning them equal weight in the analysis. Additionally, the anomaly transformation helps reduce the impact of extreme values. The standardised anomaly for each indicator was computed as follows:

$$Standardised\ anomaly = \frac{Gross\ value - mean(REF)}{sd(REF)}$$

where the Gross value is the annual value of the variable, REF represents the reference period (1991–2020), mean (REF) is the average value over the reference period and sd(REF) is the standard error over the reference period. We then normalised each index using the following formula:

$$Normalised\ anomaly = \frac{Standardised\ anomaly - Min\ value}{Min\ value + Max\ value}$$

where the Standardised anomaly is the annual value to be normalised and Min and Max values are the minimum and maximum annual values of the index time series, respectively. This normalisation step ensures that each variable contributes equally to the anomaly (Fig. 5D).

In this process, we applied prior knowledge about each variable. For HWI, we assumed that high temperatures favour tree establishment at this elevation, (Liu and El-Kassaby, 2015; Loranger et al., 2016). Therefore, the Max value was assigned to the longest cumulative HWI. For CWI, since cold events are frequently associated with frost episodes in high-elevation ecosystems, the Max value was assigned to the shortest cumulative CWI. Early snowmelt has been shown to positively affect tree survival at treelines (Barbeito et al., 2012; Moir et al., 1999), so the max value for SMOD was assigned to the earliest snowmelt. For RR, moisture availability is a critical factor for early tree establishment, as drought can cause seedling damage and mortality (Loranger et al., 2016; Plesa et al., 2018). Therefore, the Max value was assigned to the highest RR.

Next, we multiplied the standardised annual anomaly value of all the indices (i.e. SMOD, HWI, CWI AND RR) to construct a climate suitability function.

$$Climate\ suitability\ function = SMOD^*HWI^*CWI^*RR$$

The closer the function's value is to 1, the more suitable the climate is for tree establishment. Conversely, lower values indicate less suitable conditions. This methodology was applied independently to the 81 pixels. For each year, we calculated the median and the first and third quartiles. This indicator can be used to assess the suitability of the climate for different stages of establishment, such as germination, survival and growth taking into account water availability, growing season length and thermal regime.

The location of the climatic treeline was calculated according to the method proposed by Körner and Paulsen (2004) based on three criteria: (i) tree growth requires a minimum growing season length of 94 days; (ii) all days of the season must have a daily mean temperature > 0.9 °C; and (iii) the mean temperature over the growing season must exceed 6.4 °C. Using the air temperature data from the S2M re-analysis, we estimated the average temperature every 25 m of elevation by applying a constant environmental lapse rate (ERL), which reflects the temperature decrease with elevation. We used an ERL of 0.56 °C per 100 m, consistent with the mean value observed in the Alps during late spring and summer (Rolland, 2003). Finally, we plotted the season's average temperature as a function of elevation to identify the elevation at which the 6.4 °C threshold was crossed (Supp. Mat. 3). We applied an uncertainty of ±0.05 °C to this thermal threshold to determine the position of the treeline. We estimated the elevation of the climatic treeline for two distinct periods: 1961–1990 and 1991–2020.

3. Results

3.1. Wave of tree establishment

In total, 628 trees were sampled across the five gradients: Braissette ($n = 210$), Cayolle ($n = 165$), Roche Trouée ($n = 126$), Boucharde ($n = 50$), and Eschillon ($n = 76$). The lowest sampled tree was at 2058 m asl, and the highest at 2693 m asl. Fig. 2 shows the age structure of tree stands along elevation gradients across the five study sites. Over time, trees have progressively established at higher elevations, with younger trees appearing at greater elevations. This upward shift is corroborated by photo-interpretation, which shows an increase in the number of recorded trees from 312,027 in 1983 to 603,449 in 2018 (Supp. Mat. 1).

The analysis using segmented linear regressions by quantile and elevation bin reveals a non-linear pattern in the upward movement of trees (Fig. 2). For the 5th decile curve, a simple linear regression (AIC = 534.7576, Adjusted R-squared: 0.41) was less effective in representing the data compared to a segmented regression (AIC = 499.6862, Adjusted R-squared = 0.67). Moreover, the analysis suggests at least one significant breakpoint in the relationship (P-value <0.001), located at an elevation of approximately 2300 m asl, occurring around 2003 (Fig. 2A). The 95 % uncertainty for the breakpoint year is [1995.2–2010.2]. This elevation is below both the climate treeline of the 1961–1990 period (2375 m asl) and the recent one of 1991–2020 (2550 m asl) indicating a 200 m rise in the climate treeline over the past 30 years (Fig. 2B and Supp. Mat. 3 A). Additionally, growing season length has slightly increased during this period (Supp. Mat. 3B), remaining well above the 94-day threshold necessary for the transition to tree life form (Körner and Paulsen, 2004). Notably, above 2550 m asl, all larch individuals were under 1 m in height and displayed multiple twisted stems.

3.2. No drastic land-use and stocking rate changes

An analysis of demographic trends reveals a sharp decline in population between 1840 and 1950 (Fig. 3A). The population then stabilised in the municipalities of Uvernet-Fours and Saint-Dalmas-le-Selvage, while an increase in the 1960s was followed by stagnation in Entraunes and Allos. The wave of tree establishment occurred during a period of demographic stability. Sheep stocking in the study area remained consistently low, with minimal variation since 1950 (Fig. 3B). Although there was a slight increase in sheep density in the 1980s, it decreased somewhat after 1995. The stocking rate and inter-annual variations have been relatively uniform for the three pastoral units within the study area. Notably, the upper section of the Roche Trouée gradient has not been grazed since 1988. In this area, the wave of tree establishment coincided with a period when the stocking rate experienced a slight decline.

The stocking rate inferred from GPS tracking of sheep shows important spatial variation (Fig. 4A). The rangeland comprises a few flat areas with night parks (in pink). Most of the pixels in the zone correspond to resting or grazing areas, with a few paths associated with sheep movements (Fig. 4A). We found no significant relationship between sheep stocking rates and tree density in 2018, and this held true for the two distinguished sheep behaviours (Fig. 4B and Supp. Mat. 1).

3.3. Climate window of opportunity for tree establishment

The analysis of climate trends shows a marked reduction in the snow melt-out date (SMOD) since the 1990s, alongside a decrease in the cumulative length of cold waves and an increase in very warm episodes since 1960 (Fig. 5A and B). The trends for these thermal extremes became more pronounced during the 1990s, with the number of summer heat waves stabilising from the early 21st century onwards (Fig. 5A). Cumulative precipitation during the snow-free season shows considerable inter-annual variability with a slight decrease in the 5-year moving

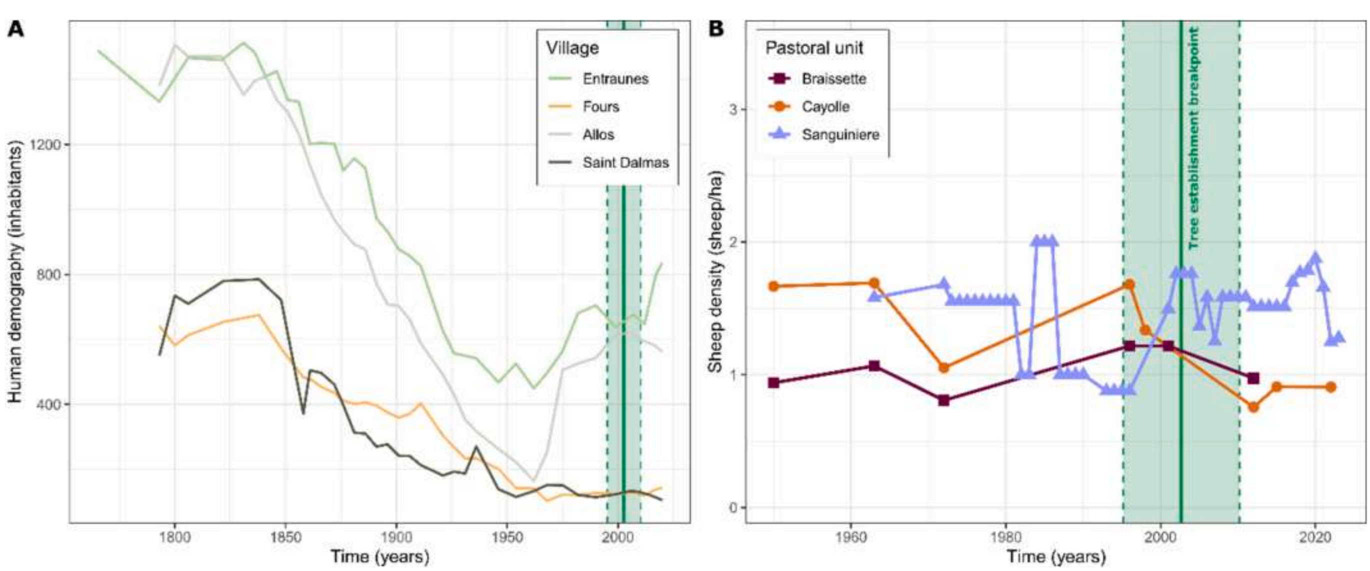

Fig. 3. Demographic history and livestock trends in the study area. Panel A shows human demographic trends for the four villages surrounding the study area. Panel B presents trends in livestock density (sheep per hectare) across the three pastoral units covering the study area. The green vertical line represents the year when tree establishment accelerated, as identified in Fig. 2, with green dashed lines representing the uncertainty in the breakpoint year.

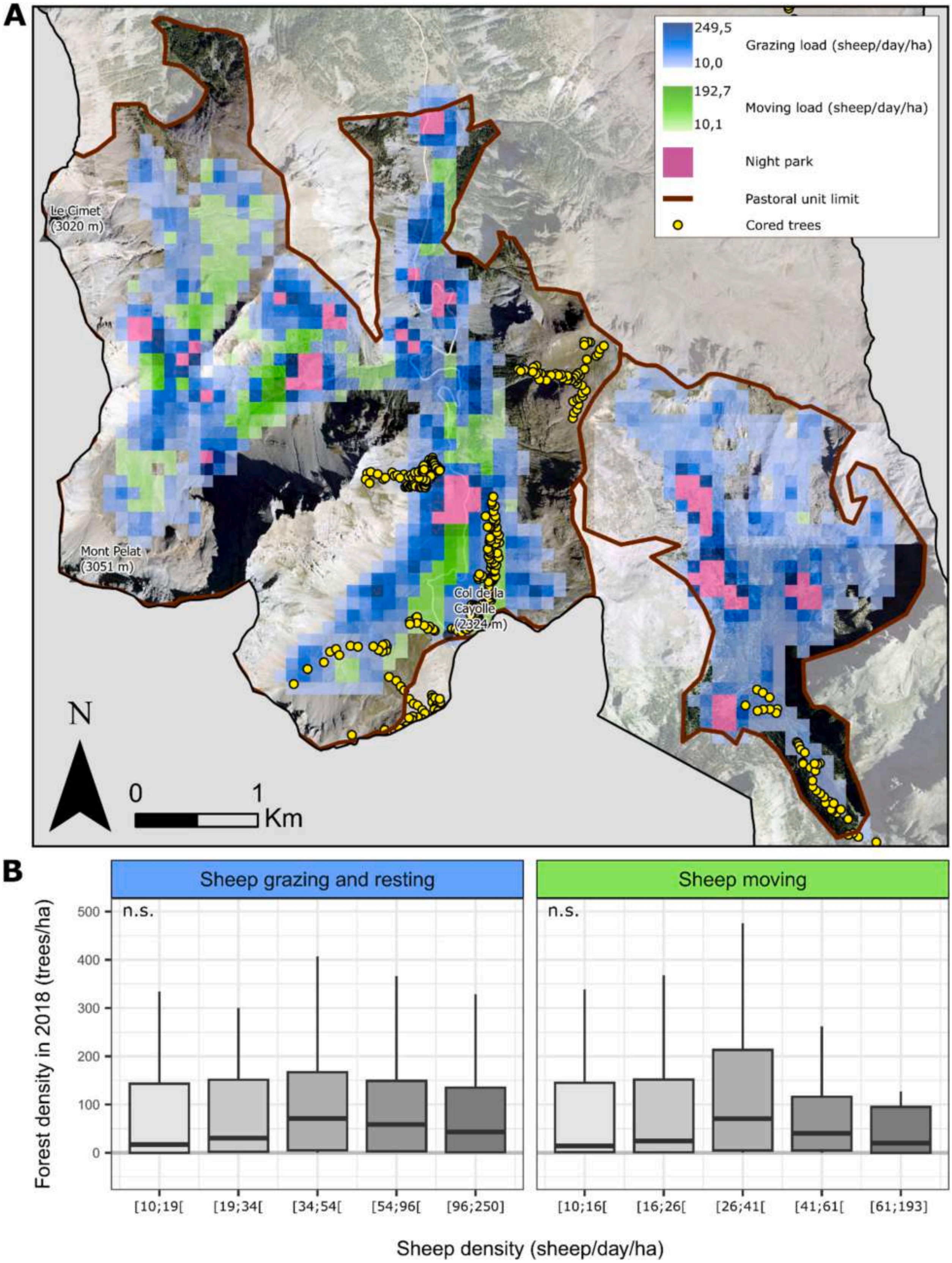

Fig. 4. Relationship between current livestock distribution and current larch density. Panel A illustrates the spatial distribution of sheep stocking, categorised by two behaviours: grazing/resting (blue gradient) and moving (green gradient). Panel B shows the impacts of these two sheep behaviours on tree distribution in 2018. Sheep loadings are divided into five quantiles, and differences between distributions were tested using a Wilcoxon test.

average trend since the early 1990s (Fig. 5C). The probability of climate conditions suitable for tree establishment remained low until 1995, showing only slight decadal fluctuations (Fig. 5E). However, after 1995, the probability increased sharply, around 2005, then slightly declining until 2012 before rising sharply again. The acceleration in tree establishment aligns closely with the rise in the climate suitability function (Fig. 5E). The peak observed between 1995 and 2005 (Fig. D) is synchronous with a sharp reduction in cold waves, an increase in heatwaves and an earlier snowmelt. After 2005, while thermal indicators continued trending towards warmer seasons, the snowpack began to melt slightly later (Fig. 5D).

4. Discussion

In this study, we coupled tree-ring analysis with diachronic analyses of aerial photographs to document treeline upward shifts with high temporal precision since the early 20th century. By integrating bioclimatic indices relevant to tree establishment and historical livestock data, we contextualised forest expansion and treeline shifts within the long-term framework of climate and land-use changes. Our findings confirmed that forest dynamic is not a linear phenomenon over time, with constant rates of tree establishment. Instead, tree establishment occurs episodically in response to interacting factors. The analysis of changes in sheep stocking rates ruled out the possibility of a recent drastic change in grazing pressure as the primary driver of forest expansion. Instead, our analysis supports the hypothesis that a climatic window of opportunity for tree germination and survival has driven the observed acceleration of tree expansion, rather than recent changes in grazing practices.

4.1. Non-linear recolonisation by larch

The observed patterns of stand densification and treeline shifts at our study site (Fig. 2, Fig. 6 and Supp. Mat. 1), align with findings from arctic and temperate mountain ecosystems across the Northern Hemisphere (Cannone and Malfasi, 2024), the European Alps (Carlson et al., 2014; Gehrig-Fasel et al., 2007), and the Pyrenees (Feuillet et al., 2020). Notably, Choler et al. (2021) identified a greening hotspot in the southern French Alps within the broader European Alps. Bayle et al. (2024) demonstrated that the expansion of larch trees largely contributed to the rapid greening in this region.

Our data reveal that forest expansion during the 20th century has not occurred at a steady rate (Fig. 2A), with a marked acceleration around the year 2000. This trend is consistent across a wide range of elevations and exposures and corroborates studies reporting similar accelerations in tree establishment for *Larix decidua*, *Pinus cembra* and *Rhododendron ferrugineum* in the Alps (Malfasi and Cannone, 2020; Vittoz et al., 2008) for *Pinus uncinata* in the Pyrenees (Batllori and Gutiérrez, 2008) and for *Pinus nigra* in the Apennines (Piermattei et al., 2016). Similarly, pulses in tree establishment patterns have been documented for *Pinus ponderosa* in Colorado (League and Veblen, 2006). Alpine studies conducted at similar elevations (above 2000 m asl) identified overlapping periods of strong acceleration, such as 1995–2003 (Piermattei et al., 2016) and 2000–2004 (Malfasi and Cannone, 2020). In the Pyrenees, Batllori and Gutiérrez (2008) documented an earlier acceleration in the 1980s.

Danby and Hik (2007) describe such episodic patterns as threshold-dependent responses, rather than gradual adjustments of forests and treelines to climate warming. In the same vein, Camarero et al. (2021) observed that regeneration at treelines coincides with periods of higher tree growth rates but noted a non-linear response which appears to be dependent on the crossing of climatic thresholds (Liang and Camarero, 2018). While long-term climate warming trends are often cited as drivers of these patterns, our results suggest a combination of interacting factors, including specific meteorological events (Frei et al., 2018) which appear to trigger waves of tree establishment.

4.2. Land-use changes fail to explain recent acceleration of forest expansion

The recent wave of forest expansion raises questions about the relative contributions of climate and land-use changes (Ameztegui et al., 2016; Gehrig-Fasel et al., 2007). To disentangle these two processes, we closely examined the timing of changes in land-use and climate, while also exploring the factors contributing to the observed wave of tree establishment.

For this purpose, we conducted a detailed analysis of land-use practices since World War II (WW2). While many studies on the impact of land-use changes in forest expansion provide only partial insights (Frei et al., 2023), our research included an in-depth historical reconstruction of stocking rates (Anselmetto et al., 2024; Garbarino et al., 2013). Several studies have linked forest expansion to a decline in domestic grazing over recent centuries (Gehrig-Fasel et al., 2007; Malfasi and Cannone, 2020). However, our extensive livestock dataset spanning the past 80 years shows that sheep stocking rates have remained relatively stable since the 1950s at our study site. This constancy during the period of accelerated tree establishment challenges the hypothesis that variations in sheep density directly drove the observed tree expansion.

Moreover, the observed sheep densities are low compared to those used in experiments testing the effects of herbivory on treeline ecotone dynamics (Speed et al., 2010). Chauchard et al. (2018) demonstrated that low livestock densities in Mediterranean mountain pastures did not hinder fir colonisation. Similarly, on the Roche trouée gradient - grazed only by a small number of wild ungulates since 1988 - the trend of tree expansion further challenges the hypothesis that changes in sheep stocking drive this process.

To complement this, we employed a novel approach to explore potential spatial interactions between livestock presence and forest expansion (Fig. 4). By distinguishing the impacts of sheep based on specific behaviours - such as herbivory and trampling which can exert contradictory effects on woody plants (Buttler et al., 2009) - our results indicate no significant link between grazing and movement patterns and tree density (Fig. 4B). In other words, this means that the grazing and movement patterns of sheep are not influenced by the presence or absence of larch trees. This suggests that sheep presence or absence is unlikely to be the main driver of forest expansion.

In addition to analysing sheep numbers, considerable effort was devoted to gathering information on other human practices through archival research, interviews with local residents, and consultations with land managers. Although this information is more fragmented, it provides valuable insights into long-term changes in practices. Notably, the study area has not been mown since at least the 1970s, as evidenced by pastoral surveys conducted in 1972 and 2012. Testimonies from a local shepherd indicate that mowing likely ceased around WW2. Furthermore, this region, located within the Mercantour National Park, has not experienced forestry activities such as felling or planting for several decades (M. Bensa, personal communication). Similarly, the uprooting or cutting of shrubs and trees has been absent since WW2 as corroborated by communications with National Park rangers and local shepherds. From the 1950s onwards, mountain communities "stopped cutting the larches, leaving them in place without any maintenance". This abandonment of mowing and uprooting practices - linked to post-WW2 rural exodus - is a widely observed phenomenon across European mountain regions (MacDonald et al., 2000). Finally, no evidence or testimonies suggest the use of fire as a landscape management tool in this area. These findings collectively indicate that there have been no significant recent changes in human practices that could reduce the role of land-use in accelerating tree dynamics.

In 1993, the wolf returned to France, spreading throughout the Alps and forcing mountainous agro-pastoral systems to adapt. The main change involves gathering sheep in protected night enclosures, rather than allowing them to sleep freely in high-elevation, treeless areas. This

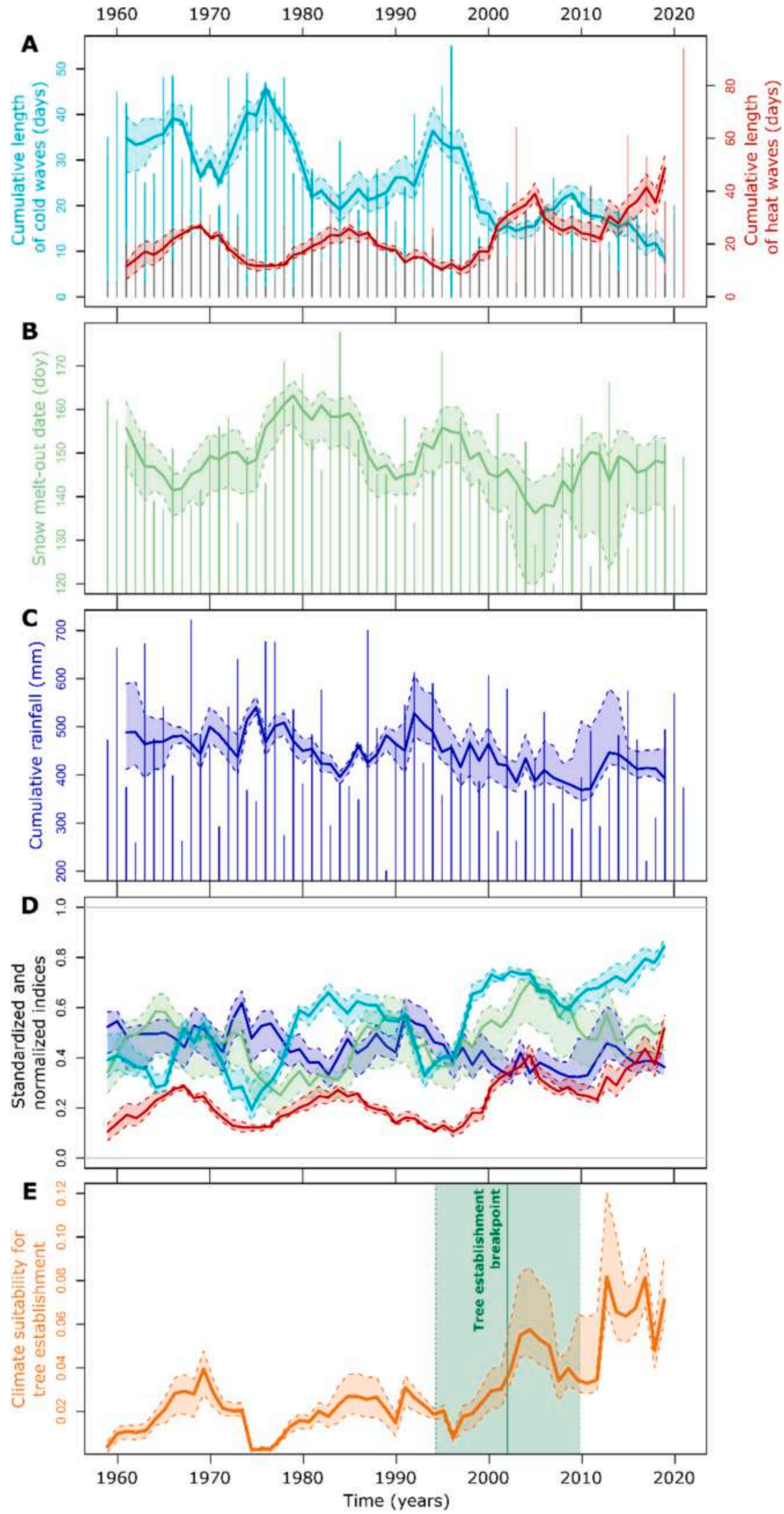

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Fig. 5. Time series of climatic indicators relevant to tree establishment in the study area. Panel A shows the cumulative length of heat and cold waves during the snow-free period each year. Panel B depicts the snow melt-out date per year. Panel C presents cumulative rainfall during the snow-free period. Panel D displays the standardised and normalised values of the climatic indices from panels A, B and C. Panel E illustrates the overall climatic function derived from these four indicators, representing the suitability of the climate for tree establishment. The green vertical line marks the year when tree establishment accelerated as identified in Fig. 2, while green dashed lines indicate the breakpoint year uncertainty. Annual values are shown as bars, with the curve representing a 5-year moving average and the dotted lines indicating the first and third quartiles. See methods, for more details.

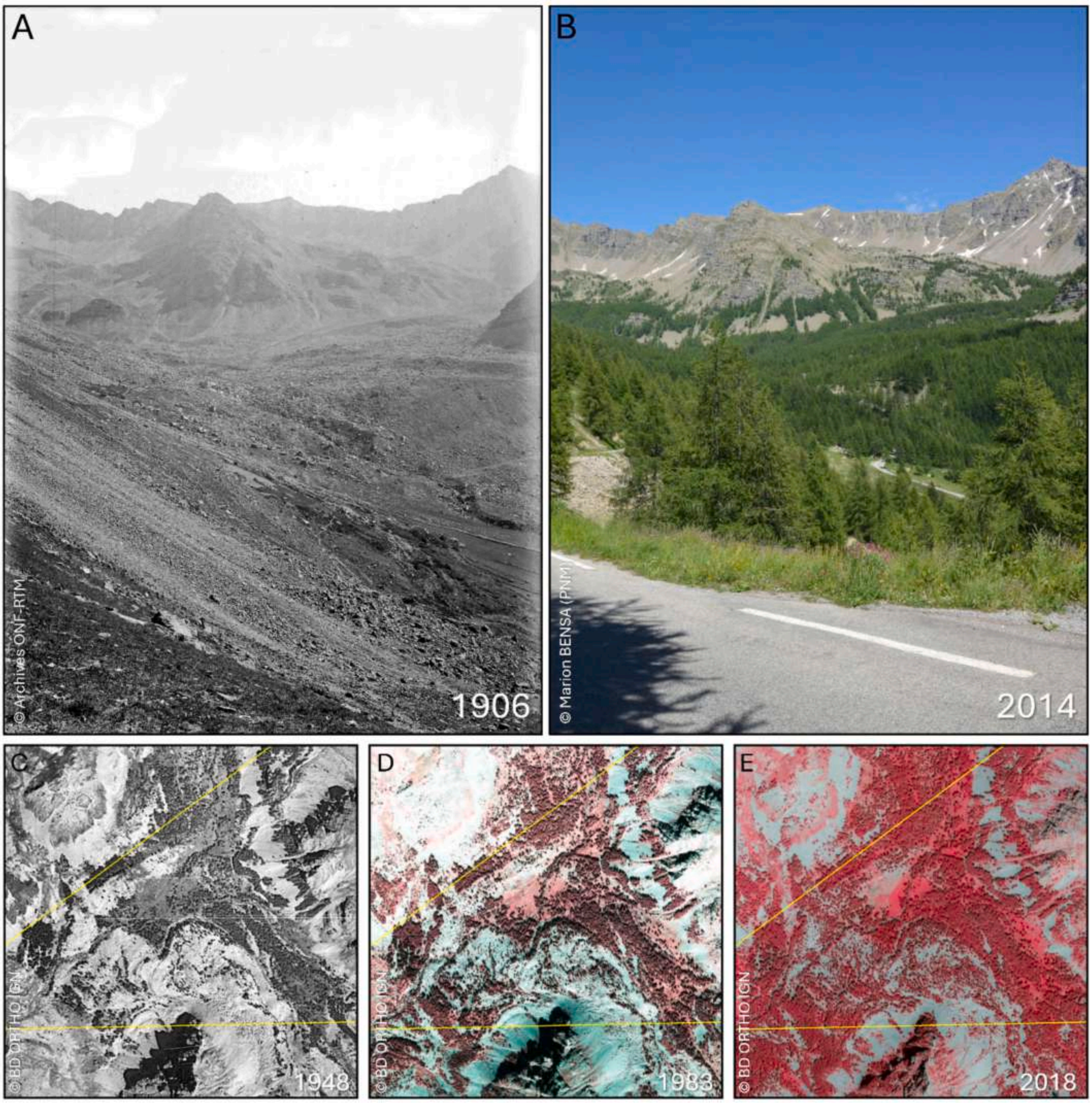

Fig. 6. Landscape evolution at the study site from the early 20th century to the present. Panel A shows a 1906 photograph from the French National Forestry Office. Photograph B taken by Marion BENSA (Mercantour National Park) in 2014, captures the same location over a century later. Panels C, D and E present aerial images from the French National Geographic Institute dated 1948, 1983 and 2018, respectively. The yellow lines in Panels C, D, and E indicate the angle of view corresponding to the photographs in Panels A and B.

shift led to more movement towards these enclosures and tighter herding, which may increase trampling. However, the lack of relationship between sheep behaviour and current tree distribution suggests that changes in herding practices are unlikely to explain the observed accelerated tree expansion. Further studies are needed to clarify the impacts of livestock behaviour on woody plants.

Another possible explanation for the recent wave of tree establishment involves the biotic factors specific to larch trees. Larch cones are heavily predated by several species of fly, which decreases the number of viable seeds (Poncet et al., 2009). To counteract this, larch trees employ a masting strategy to maximise reproductive success (Poncet et al., 2009), resulting in highly variable seed production, with occasional years of very high output (Bisi et al., 2016). A rain of seeds could potentially explain the recent wave of tree establishment. However, larch seeds can remain dormant in the soil for several years, awaiting favourable germination conditions (Alain Roques, personal communication).

Despite this, no significant forest expansion was observed until the late 1990s, suggesting that masting alone does not fully explain the dynamics we observed.

4.3. Climatic factors driving recent acceleration in treeline expansion

The abrupt increase in the probability of a climate suitable for larch establishment observed in the mid-1990s coincides closely with the wave of tree establishment at our study sites (Fig. 5). During this period earlier snowmelt, more frequent hot episodes, fewer cold periods, and significant cumulative rainfall were observed. These climatic changes align with broader warming trends in the Alps (Gobiet et al., 2014), where temperature has been recognised as a critical factor for the establishment of cold ecosystem trees (Hantemirov et al., 2008; Malfasi and Cannone, 2020). Our results indicate that a combination of higher temperatures and fewer frost events, along with a reduction in snow cover duration, has created favourable conditions for tree establishment in mountainous regions. These findings are consistent with studies that have shown positive effects of early snowmelt on tree establishment (Barbeito et al., 2012; Moir et al., 1999; Vittoz et al., 2008). While early snowmelt can sometimes lead to frost damage (Havranek and Tranquillini, 1995; Neuner, 2014), the simultaneous decrease in cold episodes likely mitigates this risk in our study area. Similarly, although severe drought is driving mortality of young larch (Plesa et al., 2019; Plesa et al., 2018), the slight downward trend in precipitation at our sites does not appear to have significantly impacted tree establishment. Since our analysis focused on the snow-free period, which is crucial for seed germination and the early survival of seedlings (Germino et al., 2002; Körner, 2012), we cannot exclude the possibility that, in years or locations without snow, drought and frost can still cause winter mortality of young trees (Frey, 1983).

To better understand tree establishment, we estimated a climate suitability function recognising that tree establishment depends on a combination of multiple factors (Frei et al., 2018). Our findings suggest that the recent acceleration in tree establishment at the treeline ecotone is largely driven by climatic factors, particularly thermal indicators and the length of the growing season, which have improved the climate suitability for tree growth since the 2000s. These findings align with several studies showing that tree establishment is sensitive to climate (League and Veblen, 2006) and responds positively to rising temperatures (Malfasi and Cannone, 2020). However, there is some uncertainty regarding the exact timing of this acceleration. We cannot exclude that the climatic window may have occurred in the 1990s, a period characterised by cold, wet conditions and late snow clearance. These conditions could have led to a high germination rate in the 1990s, with favourable conditions in the subsequent decade supporting tree survival and growth. Regardless, it is clear that climate change has accelerated the upward shift of treelines.

While our study aimed to identify relevant indicators, it did not fully assess the respective importance of various climate variables on tree establishment. Future research should focus on pinpointing the specific drivers of germination and survival of treeline trees, as well as their relative significance. This could involve growing trees in communal gardens under controlled conditions or closely monitoring treeline bioclimatic conditions in the field to gain a more detailed understanding of the factors influencing tree establishment (Lechler et al., 2024).

The current climatic context still appears favourable for a high rate of tree establishment in the study area (Fig. 5). Trees over 1 m tall now reach elevations of 2550 m asl (i.e. the 1991–2020 treeline), and beyond that, only disturbed individuals close to the ground are found, indicating that trees are catching up with the theoretical climatic life-form limit. Furthermore, the observed rise of the climatic treeline in recent decades (an average of 200 m) suggests that trees will continue to ascend. The acceleration in the upward shift, combined with the increasing elevation of the climatic limit, points to a potential for massive forest expansion in the southern French Alps.

However, projections show that the climate in ecosystems with seasonal snow cover will continue to warm in the coming decades (Lee et al., 2023). Camarero and Gutiérrez (2007) noted that high summer temperatures began to negatively affect *Pinus uncinata* establishment in the Iberian system since the 1990s. In relatively dry environments like the Southern Alps, this could become the limiting factor for mountain tree expansion. The negative impact of heat episodes during dry summers on tree survival has been demonstrated in the Alps (Gazol and Camarero, 2022). Our study, therefore, raises important questions about the future trajectory of mountain forest ecosystems.

4.4. Long-term trajectory of mountain socio-ecosystems

The elevation of the breakpoint in upward tree expansion (averaging 2300 m asl) reflects the position of the colonisation front during the early 2000s, when tree establishment accelerated. This limit was below the climatic treeline of the 1961–1990 and 1991–2020 periods, suggesting that the absence of trees was linked to factors other than climate (Körner, 2012). Sampling sites have been carefully selected to avoid local abiotic disturbances, such as geomorphic processes or soil deficiencies, that could affect the presence of trees. Many studies have shown that most treelines in Europe are lower than expected due to agro-sylvo-pastoral practices (Leonelli et al., 2009; Piermattei et al., 2016). Thus, we can reasonably hypothesise that the absence of trees could be attributed to the legacy of human activities.

A comparison of historical images of the study area from 1906, which show a treeless and barren landscape, with those from 2014, depicting tall larch forests with trees several dozen metres high, highlights both a lowered treeline and a significant expansion of trees over the past century (Fig. 6). This transformation coincides with a massive rural exodus in the region, occurring from the late 18th century to shortly after WW2 (Fig. 3A). This trend, observed across the French Alps, was largely driven by the Industrial Revolution (Collantes, 2006). The resulting labour shortages led to profound changes in land management practices, including the cessation of woody plant uprooting and mowing, as well as the gradual abandonment of hay meadows and mountain pastures (Marini et al., 2011). As a result, maintaining mountain pastures became increasingly incompatible with modern agricultural methods.

The cessation of the practices related to the abandonment of the traditional agro-sylvo-pastoral system acts as a predisposing factor for woody plant expansion (Motta et al., 2006; Tasser et al., 2007). Trees have successfully established in areas previously opened by sheep movement, where erosion patterns created regeneration niches for species such as larch (Soraruf and Carrer, 2007). Climate change has recently acted as an accelerator of this ongoing forest expansion, enabling a higher rate of tree establishment at higher elevations.

The combined effect of changing land-use practices and climate change, has led to a complete transformation of the landscape in the study area - from open, rocky ecosystems to dense larch forest - within just a century (Fig. 6). This trajectory has significant implications for alpine ecosystems (Ameztegui et al., 2021) including habitat loss for endangered species (Dirnböck et al., 2011; Pornaro et al., 2013; Rippa et al., 2011), alterations in biogeochemical cycles and soil properties (Guidi et al., 2014) and a decline in pastoral resources (Espunyes et al., 2019).

5. Conclusion

By integrating dendrochronological methods, detailed bioclimatic analysis, and a study of the impacts of pastoralism, we have conducted a comprehensive investigation into the temporal dynamics of treeline upward shifts in the southern French Alps. Our results demonstrate that tree expansion has been gradual but has recently accelerated. Despite some temporal uncertainty regarding the precise timing, the massive wave of tree establishment detected around the 2000s, was not driven by changes in pastoral practices or sheep stocking but rather by the opening of a climatic window of opportunity.

Our study reaffirms that 19th-century land-use changes, particularly the abandonment of pastoral activities, played a crucial role in creating the conditions for forest expansion. Furthermore, our findings underscore the role of climate change as a catalyst, accelerating these dynamics by fostering conditions favourable to tree establishment at higher elevations.

Despite these insights, the study does not fully quantify the relative importance of various climatic variables influencing tree establishment. This limitation highlights the need for future research to explore the specific drivers of tree germination and survival more deeply. Ultimately, our study provides new perspectives on the vulnerability of treeline trees during their early life stages and offers a methodological framework to better understand the effects of livestock on forest expansion.

CRediT authorship contribution statement

Baptiste Nicoud: Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Arthur Bayle:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Christophe Corona:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Rémy Perron Chambard:** Writing – review & editing, Data curation. **Loïc Francon:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Mathieu Fructus:** Data curation. **Marion Bensa:** Data curation. **Philippe Choler:** Writing – review & editing, Supervision, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.178326.

Data availability

Data will be made available on request.

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