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1 Climate, not land-use, drives a recent acceleration of Larch expansion at the 2 forest-grassland ecotone in the Southern French Alps.

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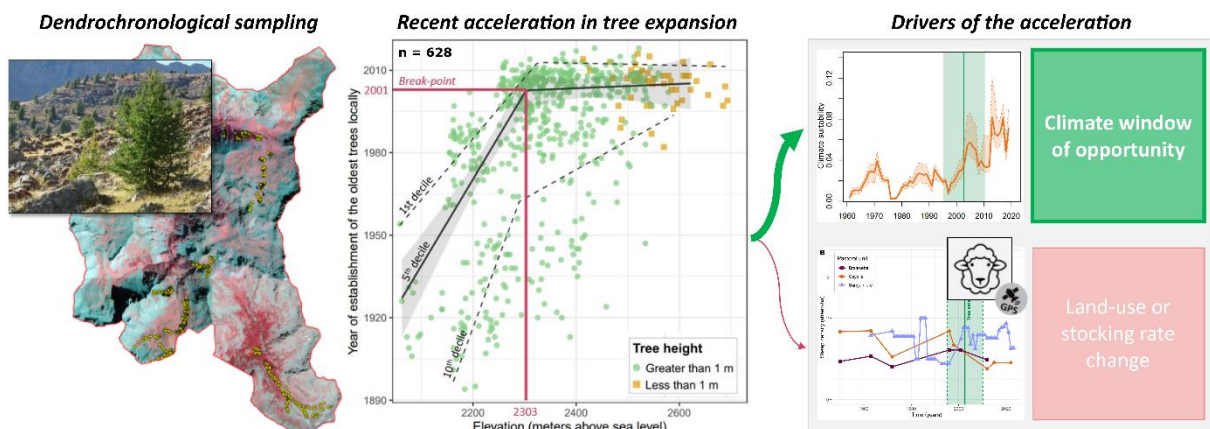
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12

13 Graphical abstract.



14 Abstract

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

29

30

31 **Highlights**

- 32 ● A massive wave of larch establishment, dating to the early 2000s, has been detected in the
33 southern French Alps using dendrochronology and high-resolution imagery.
- 34
- 35 ● Tree expansion is progressing in mountain pastoral systems across various elevations, despite
36 the absence of significant land-use changes in recent decades.
- 37
- 38 ● Since the late 1990s, favourable thermal and water conditions have created a climatic window
39 of opportunity for tree establishment, with warming continuing to support rapid expansion
40 independent of grazing pressure.
- 41
- 42 ● Although past land-use changes have been a predisposing factor for larch dynamics, its
43 spectacular acceleration over the recent decades is primarily caused by climate change.

44

45 **Keywords:** treeline, tree establishment wave, climate change, land-use change, French Alps, *Larix*
46 *decidua*

47

48 **1. Introduction**

49 In recent decades, forest expansion into previously treeless alpine areas have been documented in
50 mountain ranges across Asia (Cazzolla Gatti et al., 2019; Du et al., 2018), North America (Beckage et
51 al., 2008; Trant et al., 2020) and Europe (Bayle et al., 2024; Carlson et al., 2014; Gehrig-Fasel et al.,
52 2007). The upward shift of the treeline ecotone significantly influences land-atmosphere interactions,
53 altering albedo, heat storage, evapotranspiration, and carbon sequestration (Mienna et al., 2024). These
54 shifts impact ecosystem biodiversity and community functioning by causing habitat loss for endangered
55 species (Dirnböck et al., 2011; Pornaro et al., 2013; Ripa et al., 2011), modifying biogeochemical
56 cycles and soil properties (Guidi et al., 2014), reducing pastoral resources (Espunyes et al., 2019) and
57 driving landscape changes (Ameztegui et al., 2021; Dirnböck et al., 2011). Given the wide array of
58 impacts of treeline elevation changes on alpine ecosystems, understanding the mechanisms driving
59 upward treelines shift is crucial.

60 As the treeline marks the physiological tolerance limit of ‘tree’ life form (Dandan et al., 2022;
61 Körner, 2012; Körner and Paulsen, 2004), its position is partly controlled by temperature. The upward
62 shift of treelines has thus been linked to global climate warming (Harsch et al., 2009), particularly
63 pronounced at high-elevations (Pepin et al., 2015). However, climate variables account for only about
64 30% of global alpine treeline migration (Hansson et al., 2021; Harsch et al., 2009; Lu et al., 2021; Rees
65 et al., 2020) indicating that the substantial role of non-climatic factors in mediating treeline advance
66 (Mienna et al., 2024). These include topography (Ramírez et al., 2024), pedogenesis and geomorphic
67 processes (Cudlín et al., 2017; Körner and Hoch, 2023), and human land-use, such as logging, fires,
68 summer farming, and livestock grazing which historically constrained tree establishment and growth. In
69 many regions, current treelines reflect historical land-use legacies and expand towards higher elevations
70 as anthropogenic activity decreases (Mienna et al., 2022).

71 In Europe, the upward shift of treelines since the mid-19th century coincides with both rising
72 temperatures (Choler, 2023; Gobiet et al., 2014) and reduced land-use intensity following mass exodus
73 and declining livestock densities (Chhetri et al., 2017; Collantes, 2006; Vitali et al., 2018). Attributing
74 advancing treelines to global warming or land-use changes remains challenging, and few studies have
75 quantified their respective contributions (Ameztegui et al., 2016; Gehrig-Fasel et al., 2007; Hofgaard et

76 al., 2009; Mienna et al., 2020; Vittoz et al., 2008). In the Alps and the Pyrenees, these studies have
77 produced contradictory results. Ameztegui et al. (2016) and Gehrig-Fasel et al. (2007) suggest that land-
78 use changes play a predominant role, whereas Vittoz et al. (2008) suggest a stronger role for climate
79 change. The attribution is further complicated by pulses, lags and threshold effects in the response of
80 the treeline to environmental changes (Cullen et al., 2001; Danby and Hik, 2007; Liang and Camarero,
81 2018; Rupp et al., 2001). Waves in tree establishment more likely result from a combination of
82 concurrent factors, such as specific meteorological events and abrupt land-use changes (Frei et al.,
83 2018), than from long-term climate warming trends. Similarly, peaks in tree establishment, often
84 observed following grazing cessation, suggest windows of opportunity for trees, during which biotic
85 competition remains low before herbivory-sensitive plant species recover (Speed et al., 2010). Rupp et
86 al. (2001) and Camarero et al. (2021) respectively explain the delayed response of treeline trees to
87 changes by their inability to keep pace with rising temperatures, as their physiological processes are too
88 slow.

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

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

114

115 **2. Materials and Methods**

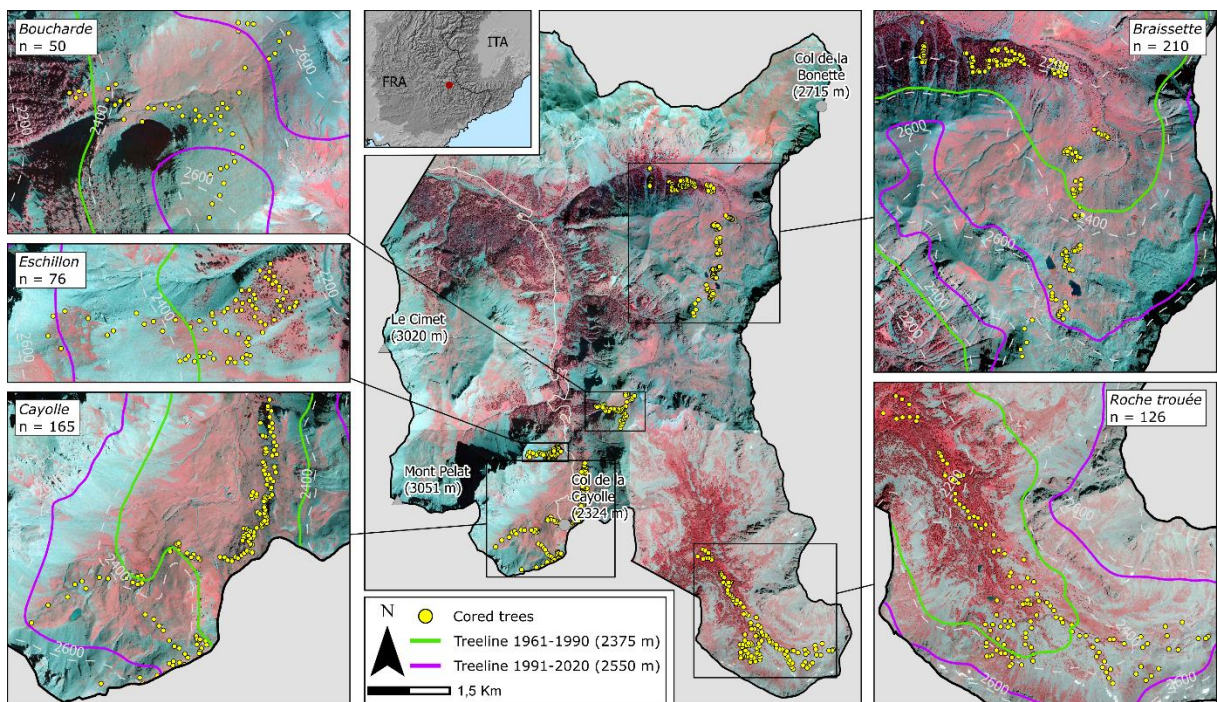
116 **2.1. Study area**

117 We conducted this study in the upper watersheds of the Ubaye valley, near to the Cayolle pass in
118 the northern Mercantour National Park (Fig. 1). The study site spans approximately 6,500 hectares of
119 high elevation landscapes characterised by relatively gentle slopes. The primary bedrock is the “Grès
120 d’Annot” sandstone. Below 2300 m asl, the vegetation is dominated by forests of European larches
121 (*Larix decidua* Mill.), a pioneering deciduous conifer that forms monospecific stands at this elevation
122 in this region. Above the forested areas, the landscape transitions to high elevation grasslands, sparsely
123 vegetated areas, screes, and rocky outcrops. Individual larch trees are scattered in these higher areas,

124 particularly in sparsely vegetated zones. The study area experiences a continental climate characteristic
125 of inner alpine valleys with Mediterranean influences and seasonal snow cover. This region has features
126 of a greening hotspot, i.e. with a significant increase of vegetation cover over the last decades (Choler
127 & al., 2021). Recent studies indicate that larch expansion is a major contributor to this pronounced
128 greening (Bayle et al., 2024).

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

134



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

142 *2.2. Tree dynamics*

143 During 2022 and 2023, we conducted dendrochronological sampling campaigns across five
144 elevation gradients ranging from 2,000 to 2,700 m asl, in areas named Braissette, Cayolle, Roche trouée,
145 Boucharde and Eschillon (Fig. 1). These gradients, selected for their varying aspects, steepness, and
146 grazing pressures span from dense forests to isolated high-elevation larch tree individuals. Notably, the
147 Roche trouée gradient has been excluded from sheep grazing since 1988. To document the colonisation
148 patterns along these gradients, sampling targeted the oldest trees along the elevation range. To select
149 these trees, we considered their height, crown size and trunk diameter, comparing these traits to those
150 of surrounding trees. This approach allows us to determine the age structure of the larch population and
151 trace the timeline of colonisation.

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

157 **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
158 Roche trouée	2062-2510	NW	Not since 1988	126

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

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

178 **2.3. Land-use history**

179 We sourced livestock data from pastoral surveys conducted by local authorities for three pastoral
 180 units: Braissette, Cayolle and Sanguinière. Records for Braissette and Cayolle are partial and cover the
 181 years 1950, 1963, 1972, 1995 and 2012. For the Sanguinière mountain pasture, a more extensive dataset
 182 allowed for a more detailed reconstruction of sheep numbers. For each year, we retrieved data on the
 183 number of sheep, the surface area of the pastoral unit, and the duration of grazing. Given changes in
 184 surface area over time, we calculated sheep density per hectare to assess variations in grazing pressure.

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

192 span from the late 18th century to 2021, although records before 1850 are sparse and irregular. After
193 1850, the data became consistently available.

194 **2.4. Grazing pressure**

195 To relate grazing pressure to larch dynamics, we used individual tree locations from Bayle et al.
196 (2024), derived from photo-interpretation of very high-resolution aerial infrared images. We also used
197 estimates of stocking rates obtained from position tracking of sheep (Perron Chambard et al., 2024).
198 Between 4 and 8 sheep per pastoral unit were tracked at 10-minute frequency throughout the grazing
199 season. Hidden Markov Models were applied to classify sheep behaviour into three categories: (i)
200 moving; (ii) grazing; and (iii) resting. The sub-trajectories for each behaviour were then converted into
201 stocking rates using a Brownian Bridge Movement Model (Horne et al., 2007). This yielded stocking
202 rates per pixel at a spatial resolution of 30 metres, expressed as the number of sheep-days per hectare.
203 Monitoring was conducted in the summers of 2022 and 2023 within the Cayolle and Sanguinière pastoral
204 units. Data from the two pastures were merged and averaged across the two years.

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

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

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

217 **2.5. Climatic trends**

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

226 Meteorological data are interpolated based on elevation, slope steepness (up to a maximum slope of
227 40°), slope aspect, and an orographic mask with a 20 km radius. The slope and mask data are extracted
228 from a 30 m digital elevation model to account for shadow effects due to terrain relief. At our
229 dendrochronological sampling points, corresponding to 81 pixels of 250 m each, we extracted annual
230 climatic indices including snow melt-out day (SMOD), snow fall day (SF), heat wave index (HWI), cold
231 wave index (CWI), and cumulative rainfall (RR). The SMOD is defined as the first day of the year when
232 snowpack depth falls below 10 cm, while SF is the first day when snowpack exceeds 10 cm late in the
233 season. This threshold was chosen as it aligns with the average error of the model. These metrics allowed
234 us to calculate the length of the snow-free period for each year, which is critical for the germination and
235 survival of seedlings. All climate indicators were calculated during the snow-free period.

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

$$240 \quad T_{mean} = 0.5 * (T_{min} + T_{max})$$

241 where T_{min} and T_{max} represent the minimum and maximum daily temperature, respectively.

242 We then computed the quantiles of T_{mean} for each day of the year, centred on a moving window of
243 15 days over the reference climate period 1991-2020. Afterward, we compared the T_{mean} value of each
244 day of each year to the corresponding quantiles for the same day within the reference period. We defined
245 a heatwave as a sequence of at least three consecutive days where T_{mean} exceeded the 8th decile. For
246 cold waves, the definition was similar, but in this case, T_{mean} had to be below the 20th percentile of
247 daily maxima. Finally, we computed the cumulative length of HWI and CWI per year (Fig. 5A).

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

$$255 \quad \text{Standardised anomaly} = \frac{\text{Gross value} - \text{mean}(REF)}{\text{sd}(REF)}$$

256 where the Gross value is the annual value of the variable, REF represents the reference period (1991-
257 2020), mean (REF) is the average value over the reference period and sd(REF) is the standard error over
258 the reference period. We then normalised each index using the following formula:

$$259 \quad \text{Normalised anomaly} = \frac{\text{Standardised anomaly} - \text{Min value}}{\text{Min value} + \text{Max value}}$$

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

263 In this process, we applied prior knowledge about each variable. For HWI, we assumed that high
264 temperatures favour tree establishment at this elevation, (Liu and El-Kassaby, 2015; Loranger et al.,
265 2016). Therefore, the Max value was assigned to the longest cumulative HWI. For CWI, since cold
266 events are frequently associated with frost episodes in high-elevation ecosystems, the Max value was
267 assigned to the shortest cumulative CWI. Early snowmelt has been shown to positively affect tree
268 survival at treelines (Barbeito et al., 2012; Moir et al., 1999), so the max value for SMOD was assigned
269 to the earliest snowmelt. For RR, moisture availability is a critical factor for early tree establishment, as
270 drought can cause seedling damage and mortality (Loranger et al., 2016; Plesa et al., 2018). Therefore,
271 the Max value was assigned to the highest RR.

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

$$274 \quad \text{Climate suitability function} = SMOD * HWI * CWI * RR$$

275 The closer the function's value is to 1, the more suitable the climate is for tree establishment.
276 Conversely, lower values indicate less suitable conditions. This methodology was applied independently
277 to the 81 pixels. For each year, we calculated the median and the first and third quartiles. This indicator

278 can be used to assess the suitability of the climate for different stages of establishment, such as
279 germination, survival and growth taking into account water availability, growing season length and
280 thermal regime.

281 The location of the climatic treeline was calculated according to the method proposed by Körner
282 and Paulsen (2004) based on three criteria: (i) tree growth requires a minimum growing season length
283 of 94 days; (ii) all days of the season must have a daily mean temperature >0.9 °C; and (iii) the mean
284 temperature over the growing season must exceed 6.4°C. Using the air temperature data from the S2M
285 re-analysis, we estimated the average temperature every 25 m of elevation by applying a constant
286 environmental lapse rate (ERL), which reflects the temperature decrease with elevation. We used an
287 ERL of 0.56°C per 100m, consistent with the mean value observed in the Alps during late spring and
288 summer (Rolland, 2003). Finally, we plotted the season's average temperature as a function of elevation
289 to identify the elevation at which the 6.4°C threshold was crossed (Supp. Mat. 3). We applied an
290 uncertainty of ± 0.05 °C to this thermal threshold to determine the position of the treeline. We estimated
291 the elevation of the climatic treeline for two distinct periods: 1961-1990 and 1991-2020.
292

293 **3. Results**

294 ***3.1. Wave of tree establishment***

295 In total, 628 trees were sampled across the five gradients: Braissette (n = 210), Cayolle (n = 165),
296 Roche Trouée (n = 126), Boucharde (n = 50), and Eschillon (n = 76). The lowest sampled tree was at
297 2,058 m asl, and the highest at 2,693 m asl. Figure 2 shows the age structure of tree stands along
298 elevation gradients across the five study sites. Over time, trees have progressively established at higher
299 elevations, with younger trees appearing at greater elevations. This upward shift is corroborated by
300 photo-interpretation, which shows an increase in the number of recorded trees from 312,027 in 1983 to
301 603,449 in 2018 (Supp. Mat. 1).

302 The analysis using segmented linear regressions by quantile and elevation bin reveals a non-linear
303 pattern in the upward movement of trees (Fig. 2). For the 5th decile curve, a simple linear regression
304 (AIC = 534.7576, Adjusted R-squared: 0.41) was less effective in representing the data compared to a
305 segmented regression (AIC = 499.6862, Adjusted R-squared = 0.67). Moreover, the analysis suggests
306 at least one significant breakpoint in the relationship (P-value < 0.001), located at an elevation of
307 approximately 2300 m asl, occurring around 2003 (Fig. 2A). The 95% uncertainty for the breakpoint
308 year is [1995.2 - 2010.2]. This elevation is below both the climate treeline of the 1961-1990 period
309 (2375 m asl) and the recent one of 1991-2020 (2550 m asl) indicating a 200 m rise in the climate treeline
310 over the past 30 years (Fig. 2B and Supp. Mat. 3A). Additionally, growing season length has slightly
311 increased during this period (Supp. Mat. 3B), remaining well above the 94-day threshold necessary for
312 the transition to tree life form (Körner and Paulsen, 2004). Notably, above 2550 m asl, all larch
313 individuals were under 1 m in height and displayed multiple twisted stems.

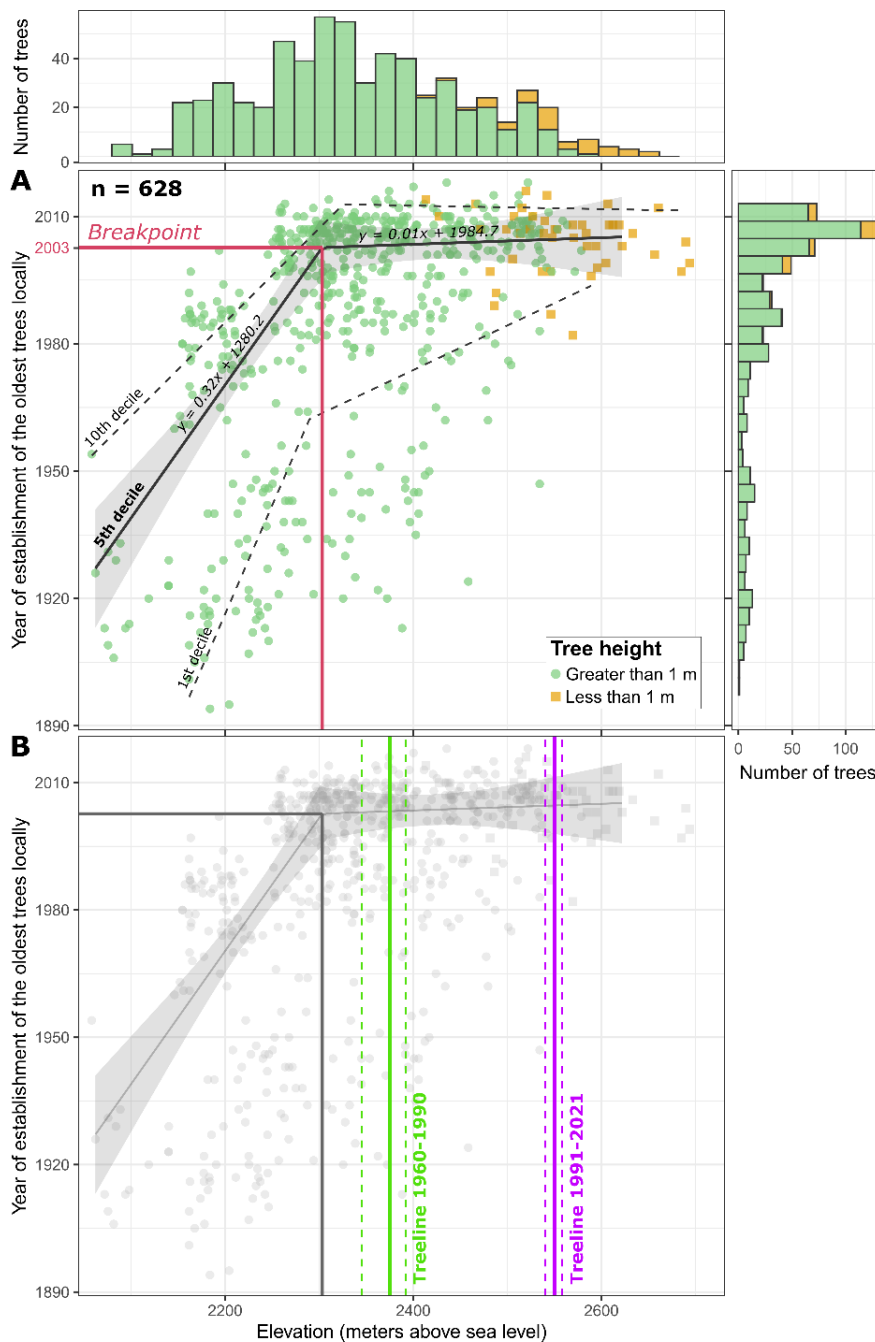
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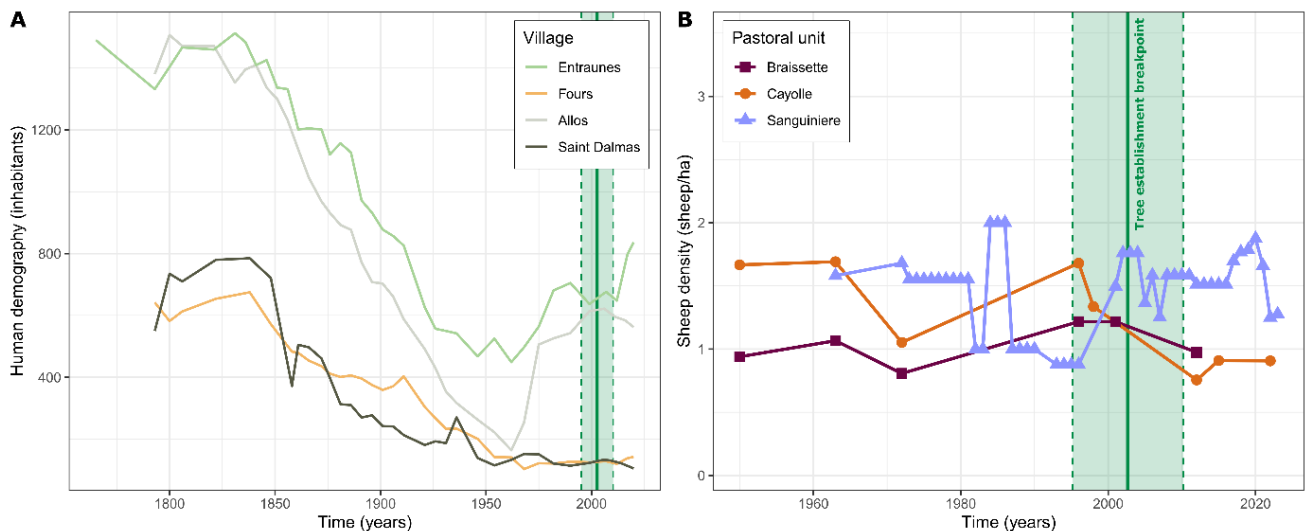


320 **Figure 2. Age structure of the oldest trees along an elevation gradient of expansion.** On panel A,
 321 each point represents a cored tree, with data combined across all five gradients. Black lines represent
 322 segmented linear regressions for different quantiles (1st, 5th, 10th). The shaded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

328 **3.2. No drastic land-use and stocking rate changes**

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

339



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

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

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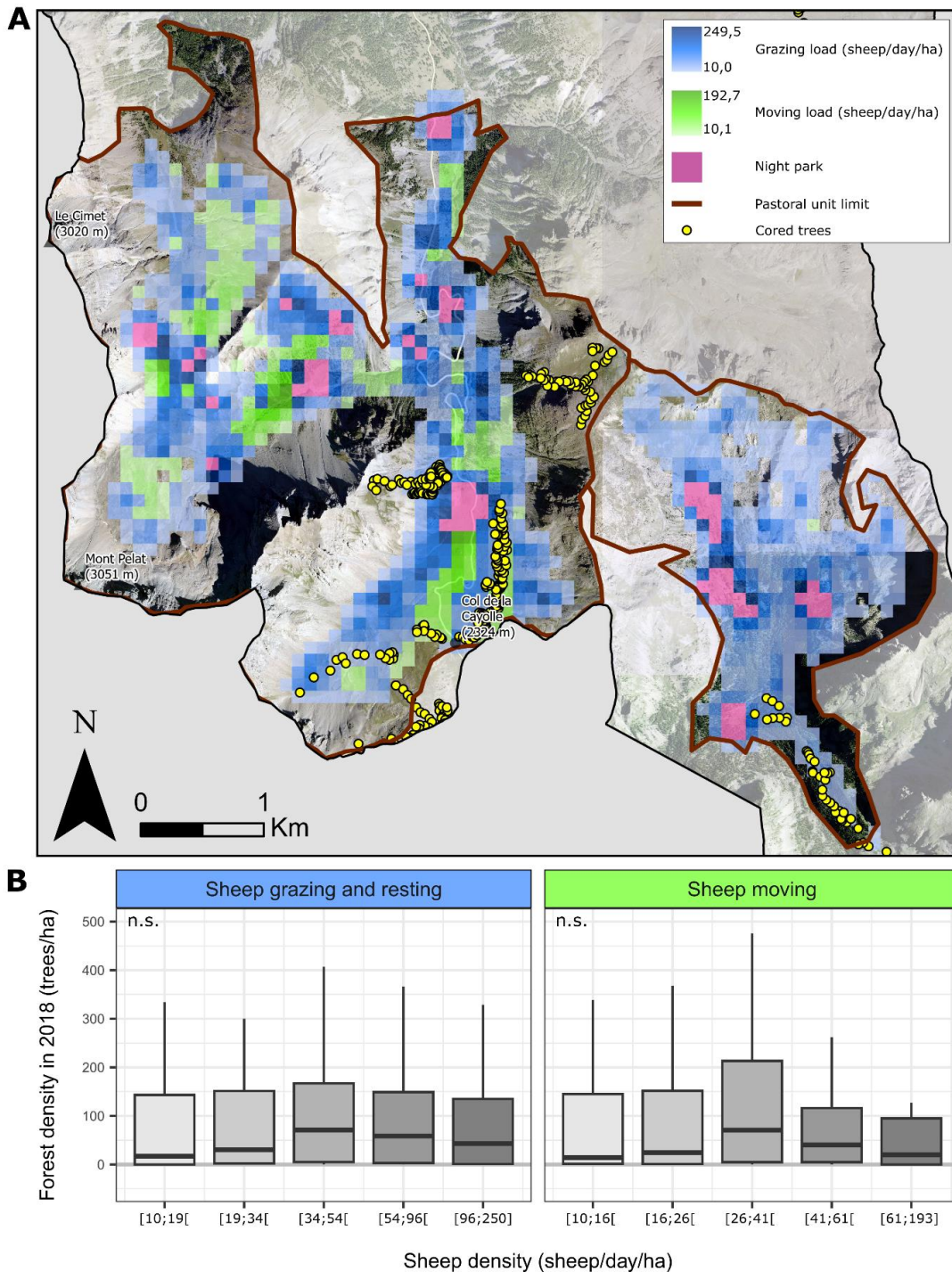
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358 **Figure 4. Relationship between current livestock distribution and current larch density.** Panel A
 359 illustrates the spatial distribution of sheep stocking, categorised by two behaviours: grazing/resting (blue
 360 gradient) and moving (green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

363 **3.3. Climate window of opportunity for tree establishment**

364 The analysis of climate trends shows a marked reduction in the snow melt-out date (SMOD) since
 365 the 1990s, alongside a decrease in the cumulative length of cold waves and an increase in very warm

366 episodes since 1960 (Fig. 5A and B). The trends for these thermal extremes became more pronounced
367 during the 1990s, with the number of summer heat waves stabilising from the early 21st century onwards
368 (Fig. 5A). Cumulative precipitation during the snow-free season shows considerable inter-annual
369 variability with a slight decrease in the 5-year moving average trend since the early 1990s (Fig. 5C).
370 The probability of climate conditions suitable for tree establishment remained low until 1995, showing
371 only slight decadal fluctuations (Fig. 5E). However, after 1995, the probability increased sharply, around
372 2005, then slightly declining until 2012 before rising sharply again. The acceleration in tree
373 establishment aligns closely with the rise in the climate suitability function (Fig. 5E). The peak observed
374 between 1995 and 2005 (Fig. D) is synchronous with a sharp reduction in cold waves, an increase in
375 heatwaves and an earlier snowmelt. After 2005, while thermal indicators continued trending towards
376 warmer seasons, the snowpack began to melt slightly later (Fig. 5D).

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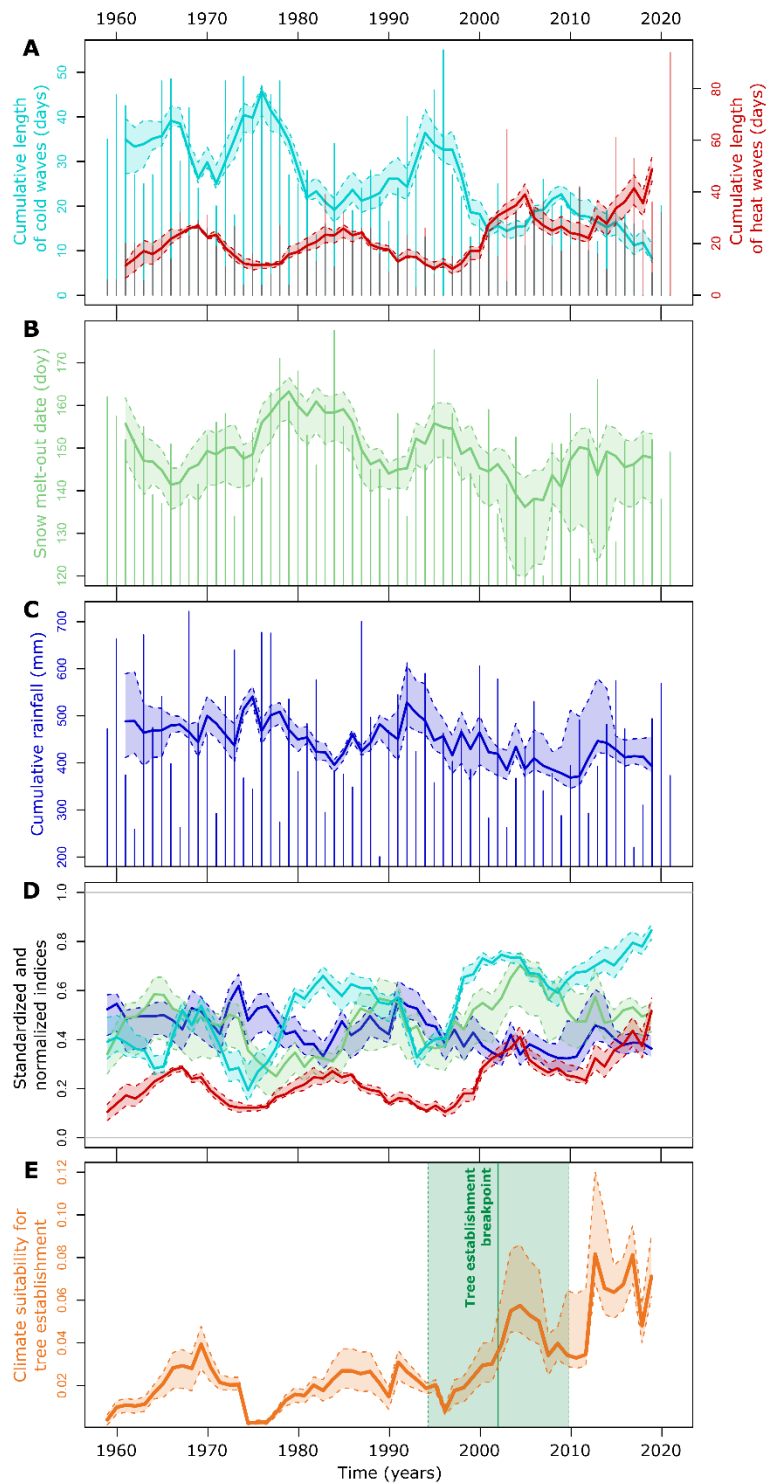
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386 **Figure 5. Time series of climatic indicators relevant to tree establishment in the study area.** Panel
 387 A shows the cumulative length of heat and cold waves during the snow-free period each year. Panel B
 388 depicts the snow melt-out date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

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

438 (Frei et al., 2023), our research included an in-depth historical reconstruction of stocking rates
439 (Anselmetto et al., 2024; Garbarino et al., 2013). Several studies have linked forest expansion to a
440 decline in domestic grazing over recent centuries (Gehrig-Fasel et al., 2007; Malfasi and Cannone,
441 2020). However, our extensive livestock dataset spanning the past 80 years shows that sheep stocking
442 rates have remained relatively stable since the 1950s at our study site. This constancy during the period
443 of accelerated tree establishment challenges the hypothesis that variations in sheep density directly drove
444 the observed tree expansion.

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

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

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

473 In 1993, the wolf returned to France, spreading throughout the Alps and forcing mountainous agro-
474 pastoral systems to adapt. The main change involves gathering sheep in protected night enclosures,
475 rather than allowing them to sleep freely in high-elevation, treeless areas. This shift led to more
476 movement towards these enclosures and tighter herding, which may increase trampling. However, the
477 lack of relationship between sheep behaviour and current tree distribution suggests that changes in
478 herding practices are unlikely to explain the observed accelerated tree expansion. Further studies are
479 needed to clarify the impacts of livestock behaviour on woody plants.

480 Another possible explanation for the recent wave of tree establishment involves the biotic factors
481 specific to larch trees. Larch cones are heavily predated by several species of fly, which decreases the
482 number of viable seeds (Poncet et al., 2009). To counteract this, larch trees employ a masting strategy

483 to maximise reproductive success (Poncet et al., 2009), resulting in highly variable seed production,
484 with occasional years of very high output (Bisi et al., 2016). A rain of seeds could potentially explain
485 the recent wave of tree establishment. However, larch seeds can remain dormant in the soil for several
486 years, awaiting favourable germination conditions (Alain Roques, personal communication).

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

489 ***4.3. Climatic factors driving recent acceleration in treeline expansion***

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

507 To better understand tree establishment, we estimated a climate suitability function recognising that
508 tree establishment depends on a combination of multiple factors (Frei et al., 2018). Our findings suggest
509 that the recent acceleration in tree establishment at the treeline ecotone is largely driven by climatic
510 factors, particularly thermal indicators and the length of the growing season, which have improved the
511 climate suitability for tree growth since the 2000s. These findings align with several studies showing
512 that tree establishment is sensitive to climate (League and Veblen, 2006) and responds positively to
513 rising temperatures (Malfasi and Cannone, 2020). However, there is some uncertainty regarding the
514 exact timing of this acceleration. We cannot exclude that the climatic window may have occurred in the
515 1990s, a period characterised by cold, wet conditions and late snow clearance. These conditions could
516 have led to a high germination rate in the 1990s, with favourable conditions in the subsequent decade
517 supporting tree survival and growth. Regardless, it is clear that climate change has accelerated the
518 upward shift of treelines.

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

525 The current climatic context still appears favourable for a high rate of tree establishment in the
526 study area (Fig. 5). Trees over 1m tall now reach elevations of 2550 m asl (i.e. the 1991-2020 treeline),
527 and beyond that, only disturbed individuals close to the ground are found, indicating that trees are

528 catching up with the theoretical climatic life-form limit. Furthermore, the observed rise of the climatic
529 treeline in recent decades (an average of 200 metres) suggests that trees will continue to ascend. The
530 acceleration in the upward shift, combined with the increasing elevation of the climatic limit, points to
531 a potential for massive forest expansion in the southern French Alps.

532 However, projections show that the climate in ecosystems with seasonal snow cover will continue
533 to warm in the coming decades (Lee et al., 2023). Camarero & Gutiérrez (2007) noted that high summer
534 temperatures began to negatively affect *Pinus uncinata* establishment in the Iberian system since the
535 1990s. In relatively dry environments like the Southern Alps, this could become the limiting factor for
536 mountain tree expansion. The negative impact of heat episodes during dry summers on tree survival has
537 been demonstrated in the Alps (Gazol and Camarero, 2022). Our study, therefore, raises important
538 questions about the future trajectory of mountain forest ecosystems.

539 ***4.4. Long-term trajectory of mountain socio-ecosystems***

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

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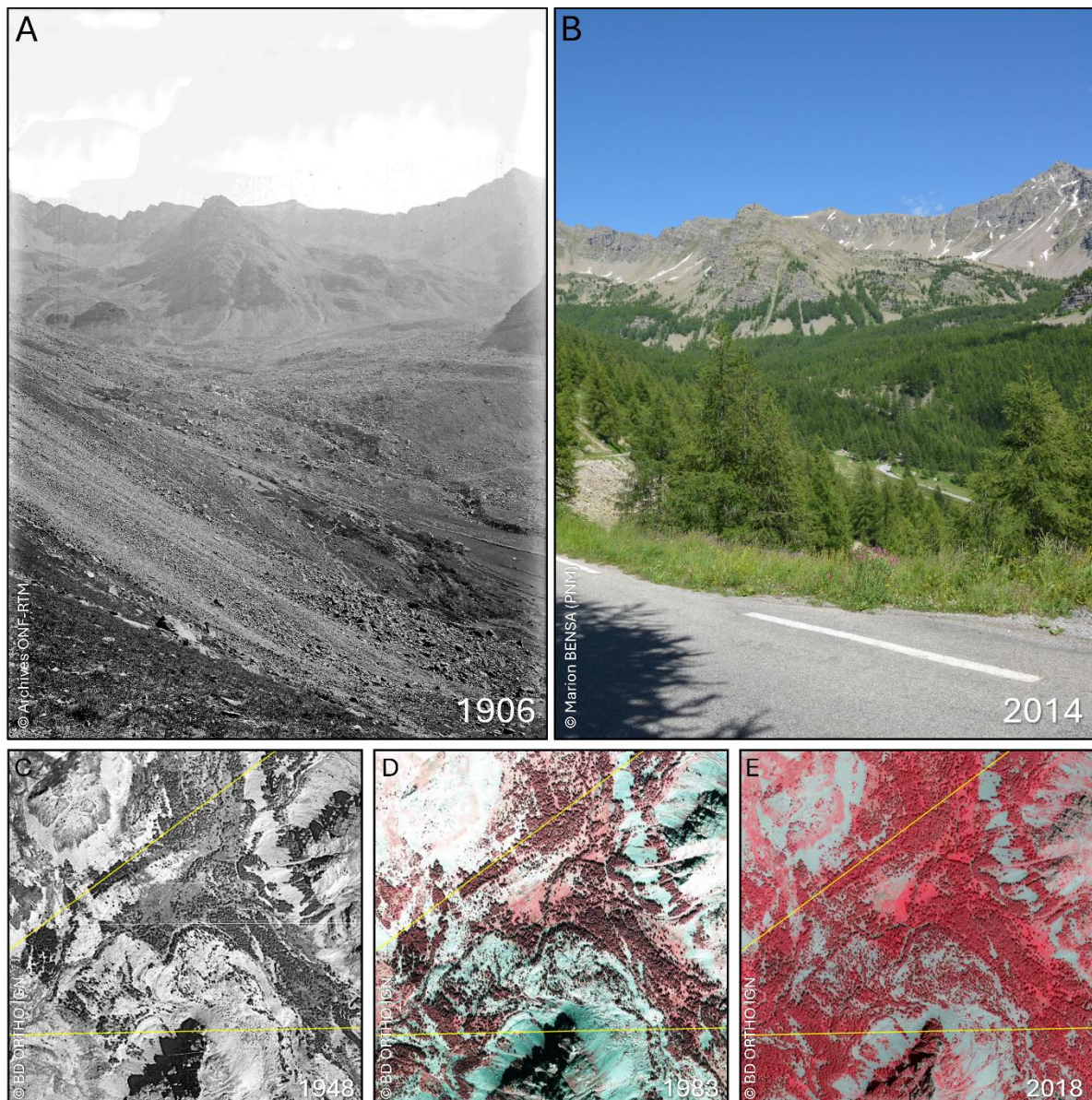
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571 **Figure 6. Landscape evolution at the study site from the early 20th century to the present.** Panel
 572 A shows a 1906 photograph from the French National Forestry Office. Photograph B taken by Marion
 573 BENSA (Mercantour National Park) in 2014, captures the same location over a century later. Panels C,
 574 D and E present aerial images from the French National Geographic Institute dated 1948, 1983 and
 575 2018, respectively. The yellow lines in Panels C, D, and E indicate the angle of view corresponding to
 576 the photographs in Panels A and B.

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

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

592 The combined effect of changing land-use practices and climate change, has led to a complete
593 transformation of the landscape in the study area - from open, rocky ecosystems to dense larch forest -
594 within just a century (Fig. 6). This trajectory has significant implications for alpine ecosystems
595 (Ameztegui et al., 2021) including habitat loss for endangered species (Dirnböck et al., 2011; Pornaro
596 et al., 2013; Rippa et al., 2011), alterations in biogeochemical cycles and soil properties (Guidi et al.,
597 2014) and a decline in pastoral resources (Espunyes et al., 2019).

598

599 **5. Conclusion**

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

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

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

615

616 ***CRedit authorship contribution statement***

617 **Baptiste Nicoud:** Conceptualisation, Data curation, Formal analysis, Investigation, Writing – original
618 draft, reviewing and editing. **Arthur Bayle:** Conceptualisation, supervision, Data curation, Writing –
619 review and editing. **Christophe Corona:** Conceptualisation, supervision, Data curation, Writing –
620 review and editing. **Rémy Perron-Chambard:** Data curation, Writing – review and editing. **Loïc**
621 **Francon:** Data curation, Writing – review and editing. **Mathieu Fructus:** Data curation. **Marion**
622 **Bensa:** Data curation. **Philippe Choler:** Conceptualisation, Supervision, Data curation, Writing –
623 review and editing.

624

625 ***Declaration of competing interest***

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

628

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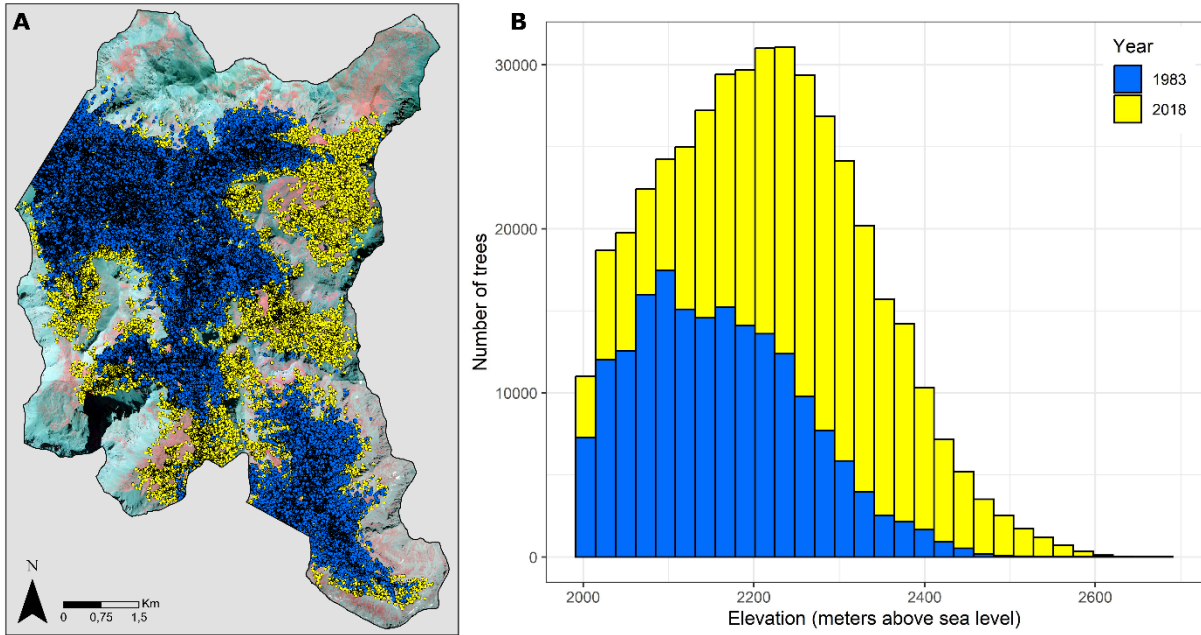
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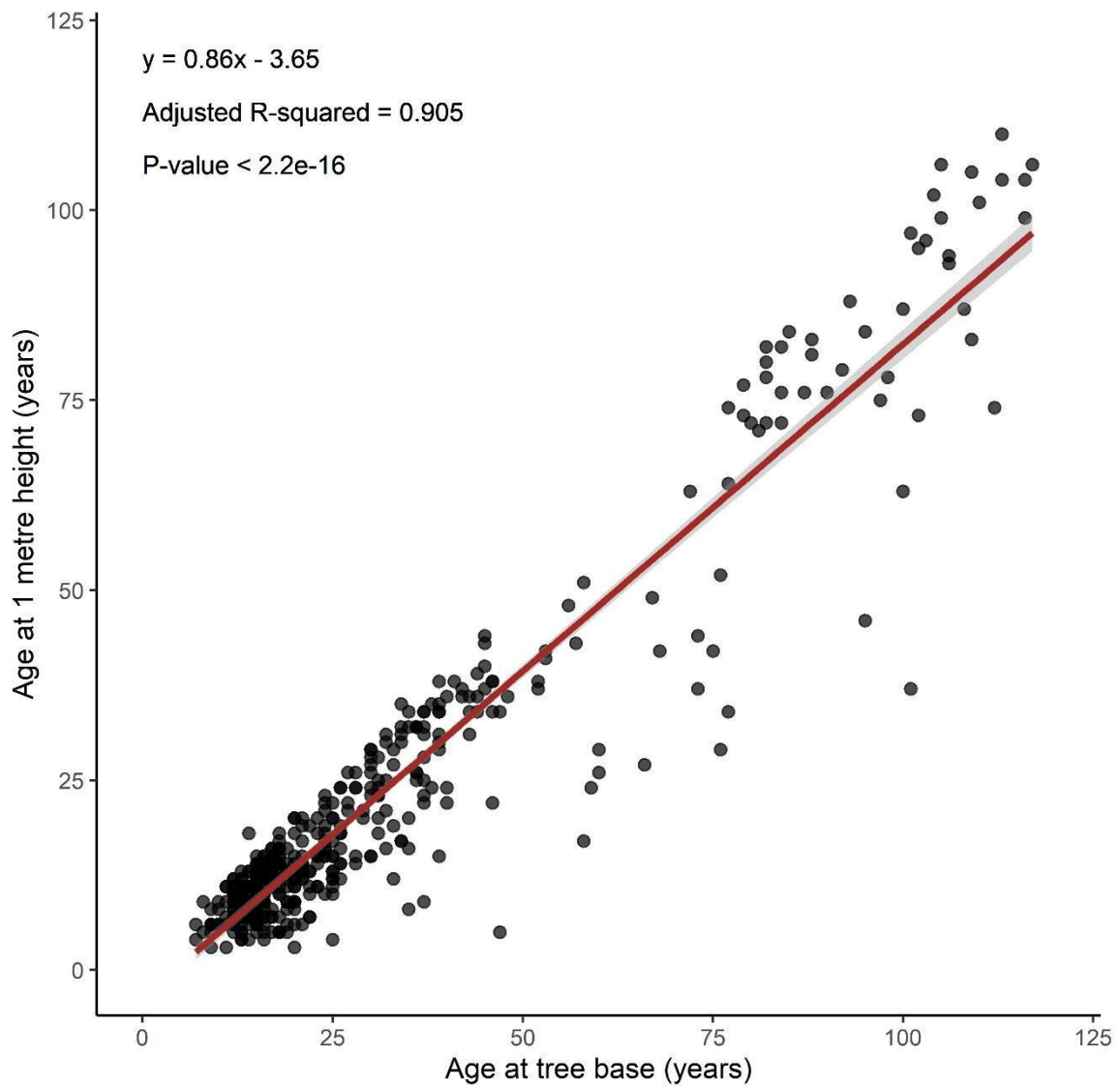
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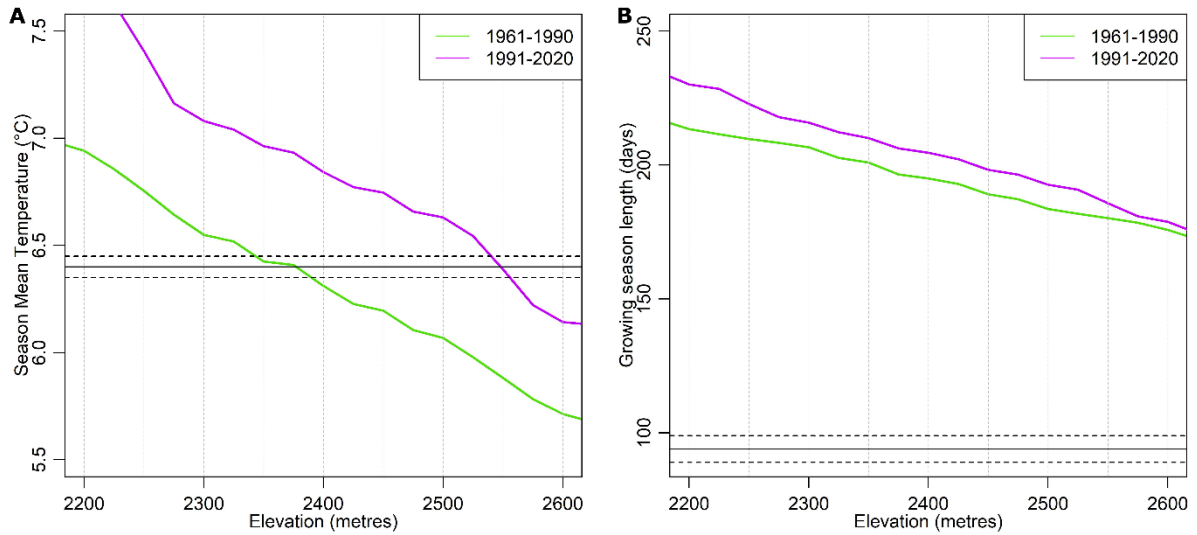
930 **Supplementary Material 1. Expansion of larch trees in the study area over the last four decades.**

931 Panel A shows a photo-interpretation map depicting the distribution of larch trees in 1983 (blue) and
 932 2018 (yellow). Panel B presents a histogram showing the number of trees in 1983 and 2018 categorised
 933 by elevation. To highlight the increase in the upper limit of the forest, only trees above 2000m asl are
 934 included.



935
 936 **Supplementary Material 2. Linear regression analysis for estimating tree age.** This figure presents
 937 a linear regression analysis between the age at the base of the stem and the age at 1 metre height, used
 938 to estimate the age of trees lacking basal core samples. Black dots represent trees with increment cores
 939 taken at both 0- and 1-metre height. The red line represents the linear regression fitted to these data
 940 points. The shaded area surrounding the linear regression indicates the 95% confidence interval.

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944 **Supplementary Material 3. Parameters used for determining the climatic treeline elevation over**
 945 **time.** This figure summarizes the key climatic parameters used to evaluate the elevational position of
 946 the climatic treeline in the study area. Panel A shows the mean temperature during the growing season
 947 plotted against elevation, with the solid black bar indicating the 6.4°C threshold and dotted lines
 948 representing $\pm 0.05^\circ\text{C}$ uncertainty. Panel B illustrates the length of the growing season as a function of
 949 elevation. The solid black bar corresponds to the 94-day threshold, with the dotted lines indicating the
 950 ± 5 days uncertainty. For a detailed explanation of the methods and calculations, please refer to the
 951 Methods section.