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Tales from the past: remapping dynamic tree- and forest lines in response to changing climate and current land use

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Abstract. Average temperatures are rising more rapidly in high-latitude and alpine regions than elsewhere, leading to a gradual compression of the alpine bioclimatic zone due to the upward shift of the tree- and forest lines (TFLs). While most studies on TFL dynamics indicate advance, the rate at which regional and local treelines respond to climate warming remains uncertain. Furthermore, not every empirical TFL is determined by climate alone; edaphic conditions, species traits, and, in particular, land use, affect tree growth and distribution. In many regions, domestic grazing and other forms of traditional mountain summer farming have historically depressed forest lines. Previous research has been limited by the comparison of data sampled with mixed methods and poor temporal data coverage. Additionally, there is still a lack of studies accounting for time lags, thus including data spanning a long time.

In this study, we used consistently remapped in situ measurements of mountain birch (*Betula pubescens* ssp. *czerepanovii*) in Norway, dating from 50 to 130 years back, to: (1) document the rate of TFL change; (2) understand the impact of land use and climate change on regional TFL dynamics; and (3) discuss regional aspects and quality components of the data.

We find that Norwegian TFLs are advancing at rates exceeding 0.5 m yr^{-1}, primarily driven by climate change for TLs and land use for FLs. Still, the rates of TFL change vary considerably between regions, likely due to stochastic disturbances (e.g. snow avalanches, insect outbreaks, pests, landslides, rockfalls).

We highlight the need for better quantification of time lags in treeline responses and for consistent definitions and methodologies when assessing long-term TFL dynamics in boreal–alpine ecotones.

1 Introduction

Average temperatures are rising more rapidly in high-latitude and alpine regions than elsewhere on the planet (Pepin et al. 2022), a phenomenon known as the Arctic amplification (Pithan et al. 2014). Anticipated ecological consequences of a warmer climate are range shifts of species and ecosystems, habitat loss, changed species interactions, and increased invasion pressure from non-native species (Pykälä, 2017). While the full range of consequences of global climate change is still not understood, it is well documented that mountain ecosystems are undergoing significant changes (Dainese et al., 2024; Körner 2014). One such change is the gradual compression of the alpine bioclimatic zone due to upward shift of the forest line (Harsch et al., 2009).

Tree- and forest lines (TFLs) represent the highest elevations at which trees can establish, grow, and reproduce. TFLs are not sharp borders but ecotones where the growing season gradually becomes too short for trees to survive (Körner 2021). However, not every empirical TFL is climatic; other factors than climate may influence tree growth and distribution (e.g. nutrient availability, soil conditions, landscape fragmentation, and species-specific traits) (Körner and Hoch, 2023). Yet, the strongest elevational limitation for upright tree growth is low temperature (Körner 2021). With increasing average surface temperatures, TFLs along the boreal-alpine ecotone serve as potential model systems for investigating the effects of climate change on alpine ecosystems (Smith et al., 2009).

Since year 1900, and particularly since the 1980s, a notable increase in temperature as well as precipitation has been recorded in Norway (Hanssen-Bauer et al., 2015). Globally, mountain ecosystems are undergoing pronounced changes (Körner, 2014; Dainese et al., 2024); however, the comprehensive impacts of climate change on TFLs in Norway have not yet been systematically studied (Bryn & Potthoff, 2018). Assessing Norwegian TFLs provides the opportunity to account for the complex variation of factors impacting empirical TFL elevation, including the effects of climate change.

Despite its moderate extent, mainland Norway (323 810 km^2) encompasses substantial variation across regional or climatic (Bakkestuen et al., 2008) as well as local or edaphic gradients (Halvorsen et al., 2020), and in landscape types (Simensen et al., 2021). This heterogeneity is mainly the result of a complex topography shaped by glacial erosion over millions of years (Sulebak, 2007). The locally highest-situated TFL locations occur at lower elevations in the northern and western parts of the country rather than the south-central mountain massif, due to either lower mean summer temperatures, 'summit syndrome' (Körner, 2012: i.e. that TFLs close to a summit tend to be regulated by non-thermal abiotic disturbance (for empirical support, see Wistrand, 1962)), proximity to the coast, or a combination of multiple factors (Odland, 2015). Megafossil and pollen records indicate that mountain forests covered a more extensive area in the past than at present, with birch forests established at higher elevations in the early Holocene (Paus and Haugland, 2017). Since then, the TFLs have fluctuated in response to long-term climatic fluctuations (e.g. Bjune et al., 2005; Nesje, 2009). While most studies on TFL dynamics indicate advance, the rate at which regional and local treelines respond to climate warming remains uncertain (Hofgaard et al., 2013; Rannow, 2013; Rees et al., 2020), with potentially significant impacts on TFLs in Norway, where mountain birch (Betula pubescens ssp. czerepanovii) predominates.

The time it takes for a new generation of trees to establish (or a tree stand to die back) results in a time-delayed impact of climate change on TFLs (Woods, 2014). Consequently, it is essential to study TFL dynamics over timescales that span potential demographic time-lags. As far as we know, the length of these time-lags has not been specifically studied. Woods (2014) suggests 50 years as a minimum, which is broadly consistent with the 40–50 years proposed by Rees et al. (2020). Time-lags of ca. 50 years make most high-resolution satellite remote sensing products and methods, commonly applied in long-term retrospective studies, unsuitable for studies of TFL dynamics, as most images do not date back further than 50–60 years (e.g. the Landsat mission launched in 1972). Older aerial photos or perspective photos, which could cover larger time spans, tend to have very scattered coverage. Macrofossil and pollen records, widely used for reconstructing historical TFLs (Birks & Birks 2000, Kullman 2013), confirm the presence of specific tree species at specific points in time and space but do not resolve the precise position and elevation of TFLs. Therefore, it has been emphasized that retrospective TFL studies should rather use site-specific in situ observations and compare historical records with current TFLs positions (Bryn & Potthoff, 2018).

A factor contributing to the complexity of TFL responses to climate change is land use, which commonly results in anthropogenically depressed TFLs (Körner and Hoch, 2023). For Norway, the millennial history of land use involves rangeland grazing, fodder collection, and forest logging (Bryn et al., 2012). In particular, empirical TFLs have been lowered by mountain summer farming comprising practices such as livestock grazing, dairy farming, and firewood cutting (Olsson et al., 2000). From the mid-19th century, mountain summer farming has gradually declined, most strongly over the last decades, due to the availability of mineral fertilizer and rationalization of agricultural production (Potthoff et al., 2020). Consequently, extensive regrowth is now occurring in formerly deforested areas (Bryn et al., 2013). Although climate is considered the main limiting factor of TFLs, the changing land use regimes also influence the dynamics of empirical TFLs. In areas with previous mountain summer farm activity, the impacts of land use change are particularly difficult to separate from the impacts of climate change, as both processes result in regrowth and shift of TFLs to higher elevations (Bryn & Potthoff, 2018; Bryn & Potthoff, 2022).

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2 Material and Methods

2.1 Definitions of treeline and forest line (TFL)

We define treelines and forest lines as the elevation of the topmost tree and the topmost forest, respectively. To qualify as a tree, a plant must have a distinct main wooden stem that is rigid at breast height. The stem must be at least 2.5 m tall from the base to the top of the crown. By that definition, trees typically protrude above the snow in winter, with crowns exposed to ambient temperatures throughout the year. Furthermore, they respond to ambient climate at heights similar to those addressed by standard meteorological weather stations, which are positioned 2 meters above ground. By definition, a forest consists of at least 15 trees with a maximum distance of 15 m between neighbouring trees. Several main stems splitting off above ground, that have a common vegetative below-ground origin, are counted as individual trees. The elevation of the forest line is represented by the tree at the highest elevation within the forest patch, see Tjessem et al. (2025) for the complete and consistent definitions.

2.2 Study area and data on TFLs

To assess spatiotemporal TFL dynamics, we analyzed the dataset compiled by Tjessem et al. (2025), which includes 274 TFLs of mountain birch (*Betula pubescens* ssp. *czerepanovii*), all remapped in situ using a standardized, common methodological approach (Fig. 1). The study area spans mainland Norway from 60°30'49" and 68°58'10" Latitude to 4°53'25" and 19°15'57" Longitude (Fig. 1). The TFLs range from 200 to 1300 meters above sea level (m a.s.l.).

The TFLs were originally recorded by Finn Frost (FF), Johannes Musæus Norman (JMN), Hanna Resvoll-Holmsen (HRH), Søren Ve (SV), and Børre Aas (BAA), who are hereafter referred to as originators of the historical records (OHR). Because the OHRs mapped TFLs during different periods (1887−1967) and in different parts of Norway (Fig. 1), the full TFL dataset consists of four data subsets (i.e. JMN, 130 years, n=32; HRH, 100 years, n=104; SV, 80 years, n=93; FF, 70 years, n=1; BAA, 50 years, n=44). The historical sites were relocated as precisely as possible for in situ *r*emapping of TFLs between 2015 and 2024. Only records that could be positioned with certainty on a specific hillside, with a given aspect, were included. The elevational position of each TFL was recorded by a barometer and a Global Positioning System (GPS) for historical and repeated records, respectively. The elevational uncertainty, measured as the elevational difference in meters (mean ± SD) from the Norwegian Mapping Authority’s digital elevation model (DEM), was low for both barometer (2.06±21.0 m) and GPS (0.11±6.5 m) (Tjessem et al., 2025).

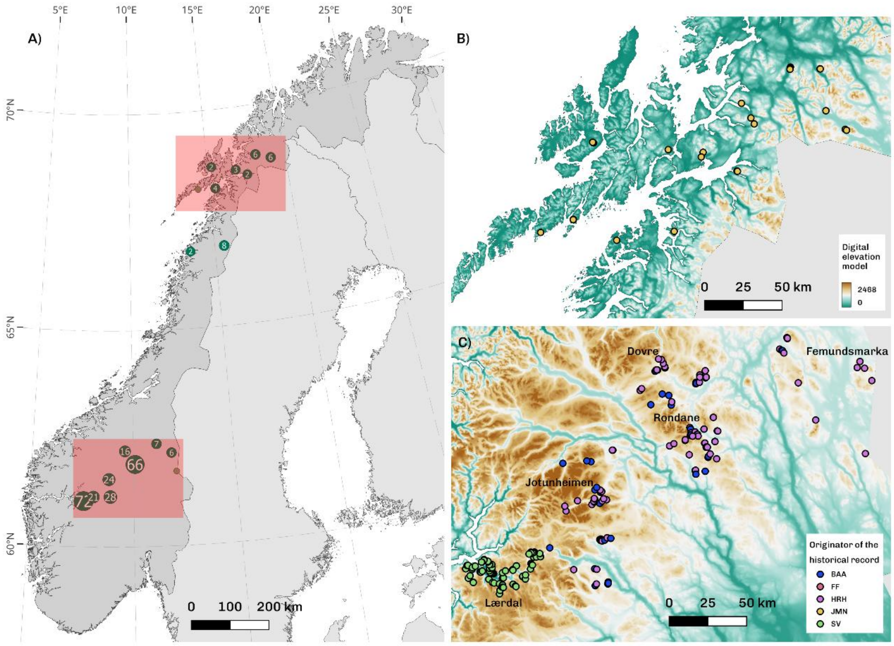

Figure 1: The study area (A), with mainland Norway indicated by a darker grey colour. The 274 localities are displayed as circles representing clusters of localities, with numbers indicating the number of individual localities in each cluster. The red rectangles represent the bounding boxes of the detailed maps (B and C), in which points represent individual localities in northern Norway and central southern Norway, coloured according to the originators of the historical records (OHR) (see also Tjessem et al., 2025). The TFL records are superimposed on a digital elevation model with a green-to-brown elevation gradient (low to high elevation) (downloaded from the Norwegian Mapping Authority). CRS: ETRS89 / UTM zone 32N (EPSG 25832).

2.3 Climate variables

To describe the long-term effect of climate on TFLs, two model-based datasets were used. The first dataset was obtained from observation-based long-term 1x1 km gridded data for monthly temperature and precipitation covering the period 1901–2019 (Tveito, 2021; 2023). For the second dataset, covering the period 1868–1900, we also used long-term observation data records of temperature and precipitation, but only from meteorological stations that correlated strongly with gridded data in the 1901–2019 period. Regression analysis was used to make the 1868–1900 data directly comparable with the 1901–2019 grid data for each of the TFL localities. Finally, we extracted the mean monthly temperature and monthly precipitation for each TFL locality for the entire study period 1868–2019. From these monthly data, we derived a set of 19 variables, 15 representing temperature and four representing precipitation (Table 1).

Table 1. Predictor variables representing potential drivers of tree and forest line (TFL) dynamics, grouped by effect type (land use, site, temperature, precipitation). For each variable, and unit of measurement are also given. Two predictors are based on static values (i.e. aspect favourability and proximity to mountain summer farms), and the rest (i.e. mean grazing pressure, and all temperature and precipitation variables) include temporal change (i.e. change in predictor values between the first and last TFL record). The warmest and coldest quarters refer to the warmest three consecutive months of the year (July, August, and either June or September) and the coldest three consecutive months of the year (January, February, and either December or March), respectively. The term tetratherm refers to the four warmest months of the year (June, July, August, and September). For further description, see Table A1.

Effect	Predictor variable	Unit
Land use	Mean grazing pressure	Grazing pressure per km^2
	Proximity to mountain summer farms	m
Site	Aspect favourability	° N
Temperature	Mean annual temperature	°C
	Monthly highest temperature	°C
	Monthly lowest temperature	°C
	Annual temperature deviation	°C
	Warmest quarter	°C
	Coldest quarter	°C
	Tetratherm mean temperature	°C
	Tetratherm temperature deviation	°C
	Monthly temperature > 0 °C	Number of months
	Monthly temperature > 5 °C	Number of months
	Monthly temperature > 5.5 °C	Number of months
	Monthly temperature > 6 °C	Number of months
	Monthly temperature > 6.5 °C	Number of months
	Monthly temperature > 7 °C	Number of months
	Monthly temperature > 7.5 °C	Number of months
Precipitation	Annual precipitation sum	mm
	Annual precipitation deviation	mm
	Tetratherm precipitation sum	mm
	Tetratherm precipitation deviation	mm

The climate data were processed to account for time-lags in the response of TFLs to climate (Alexander et al., 2018) by first calculating the mean value for each climate variable over a 20-year period prior to the first, second, and third TFL record. Second, the mean annual difference between the first and the second or the first and the third 20-year averages were calculated (Fig. 2). Similarly, averages were calculated for the climate reference period 1981–2010.

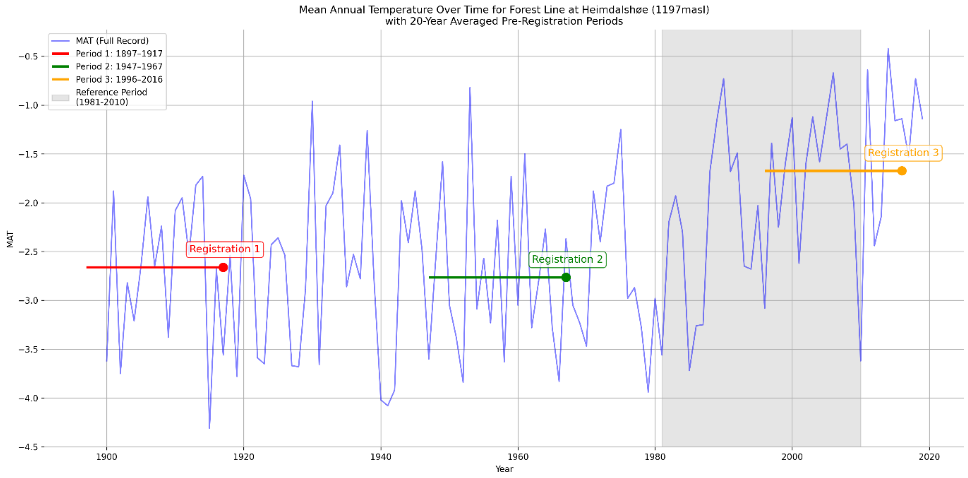

Figure 2: Visualization of the climate variable "Mean Annual Temperature" (MAT, °C) for the period 1900–2019, also showing the 20-year averages prior to one specific TFL record (the red, green, and orange horizontal lines), for the north-west-facing forest line locality at Heimdalshøe. The reference period for the calculation of MAT, 1981–2010, is shown by grey shading.

In addition to the long-term climate variables, aspect favourability was included to represent local site conditions related to incoming radiation and thermal conditions for growth. Aspect was derived from the compass direction of the maximum slope. To derive aspect favourability, the aspect values were converted to a linear scale from 0 (least favourable, NNE; 22.5°) to 1 (most favourable aspect, SSW; 202.5°) with all intermediate directions scaled proportionally (Dargie, 1984).

2.4 Land use variables

To describe land use history (i.e., land use change from first to last TFL record), two different datasets were assembled. The first dataset contains the number of livestock grazers on rangelands in each municipality in 2003, 2004, and 2019, according to applications for agricultural subsidies (data downloaded from the Norwegian Agriculture Agency (https://www.landbruksdirektoratet.no, accessed May 2020). The second dataset contains the number of livestock grazers registered in each municipality in 1891, 1907, 1917, 1929, 1939, 1949, 1959, and 1969. Although this dataset includes livestock grazers in both rangelands and infield pastures, the livestock grazers were primarily restricted to rangeland areas during that time period. The 1891 data were obtained from the precursor of Statistics Norway (*Norges officielle statistik*, 1895). Data for the remaining years were obtained from the Census of Agriculture, downloaded from "Historisk statistikk" (accessed March 2020). Because census dates varied across years, all records were adjusted to reflect typical summer/early autumn livestock numbers to ensure comparability (see Appendix B). Furthermore, because the administrative division of Norway changed throughout the study period, reaching a maximum of 747 municipalities in 1930 and a minimum of 357 in 2024, both datasets were adapted to the division of Norway into 422 municipalities as of 2019 (see Appendix B).

Livestock numbers in both datasets were converted to livestock units, which were used as a measure of grazing pressure. The following conversion key was used: adult cattle × 5, young cattle × 3, sheep × 1, goats × 1, and horses × 3 (Tveitnes, 1949; Rekdal & Angeloff, 2021). The total number of livestock units per municipality was divided by municipality area to obtain a measure of grazing pressure per km^2. We used the mean value of the grazing pressure variable over 20 years prior to each TFL record to represent the potential impact of grazing on the observed TFL changes (i.e. mean grazing pressure). As the grazing data only extends back to 1890, no data on grazing pressure is available prior to the earliest historical records of TFLs from 1887. For TFL records prior to 1890, the 1890 grazing pressure data were used. Because the effect of mean grazing pressure on tree establishment and growth was considered first to be present when the grazing pressure was above 4 livestock units per km^2, we clamped lower recorded values to 4. To account for the expected nonlinear effect of mean grazing pressure on TFLs, we applied a base-2 logarithmic transform to the (clamped) mean grazing pressure variable.

The effect of mountain summer farming (i.e., land use) was estimated by the 'proximity to mountain summer farms' variable (Table 1), which was obtained by surveying aerial photos in 'Norge i Bilder' (www.norgeibilder.no) and measuring the distance from each TFL record to the nearest mountain summer farm. The measured distance was log-transformed to meet the assumption of normality and homoscedasticity.

Hereafter, we use the term "predictor" to refer to all explanatory variables, including those with static values (i.e. aspect favourability and proximity to mountain summer farms) and those representing temporal change (i.e. the change in predictor values between the first and last TFL record, such as all climate variables and mean grazing pressure).

2.5 Statistical analyses

Empirical frequency distributions of both response and explanatory variables were evaluated before further analyses to detect potential inhomogeneity of variances, as indicated by the skewness of variables. Additionally, quantile-quantile plots (QQ plots) and Shapiro–Wilk tests were used to examine if the two response variables (TL change and FL change) were homogeneously distributed. An initial descriptive analysis of spatial structure (semi-variance analysis, e.g. Rossi et al., 1992) was carried out using the *geoR* package (Ribeiro et al., 2025), to ascertain that no spatial structure was present in either of the two response variables, TL change and FL change. Spatial structure was considered to be absent in distance intervals where the semi-variance was enclosed within a confidence interval, which was constructed from semi-variances of 99 randomizations of between-observation distances. If absent, the spatial structure was not further evaluated or commented.

One-sample Wilcoxon-Mann-Whitney signed-rank tests were used to test the null hypotheses that the rates of TL change and FL change (m yr^{-1}) did not differ significantly from zero. Furthermore, a two-sided Wilcoxon-Mann-Whitney rank-sum test was used to test the null hypotheses that the two response variables, TL and FL change, did not differ significantly from each other.

To explore the impact of land use and climate change on TFL dynamics, we analyzed the full rate of change (i.e. the change in m from first to last record) using linear regression. In order to address the summit syndrome, we removed the 10 TL and 6 FL records that, at the timepoint of the first record, were situated closer to a summit than their overall mean change (in m). To account for the possibility that drivers of TL advance may differ from drivers of overall TL change, we analyzed four response variables (TL change, TL advance, FL change, and FL advance). Whereas TL change (n = 124) and FL change (n = 122) included all records, TL advance (n = 94) and FL advance (n = 84) were subsets of TL and FL change, respectively, both restricted to records with an upward shift of 20 meters or more.

To prevent multicollinearity, we carried out a preselection of variables by, for each subset of variables with pairwise Kendall's rank correlation coefficients $|\tau| > 0.7$, selecting the variable with the strongest correlation with the response variable in question and discarding the rest. The four response variables were subjected to modelling by Analysis of Variance (ANOVA), using forward selection of preselected predictor variables. Nested models were compared using the *F*-test with Bonferroni correction (Dunn, 1961) in each step. Only predictor variables, including single-effect interactions, that were significant at the $\alpha = 0.05$ level in marginal tests, were included in final models. Four-fold cross-validation was used to compare and evaluate the final model with the null model.

Statistical analyses were carried out in R version 4.3.0 (R Core Team 2023).

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3 Results

3.1 Rate of change

The overall rates of change for TLs and FLs (median ± standard deviation, in m yr^{-1}) were both positive and significantly different from zero: 0.69 ± 0.62 (p < 0.001) and 0.55 ± 0.54 (p < 0.001), respectively (Fig. 3). The upward shift was significantly larger for TLs than for FLs (p = 0.033, Fig. 3).

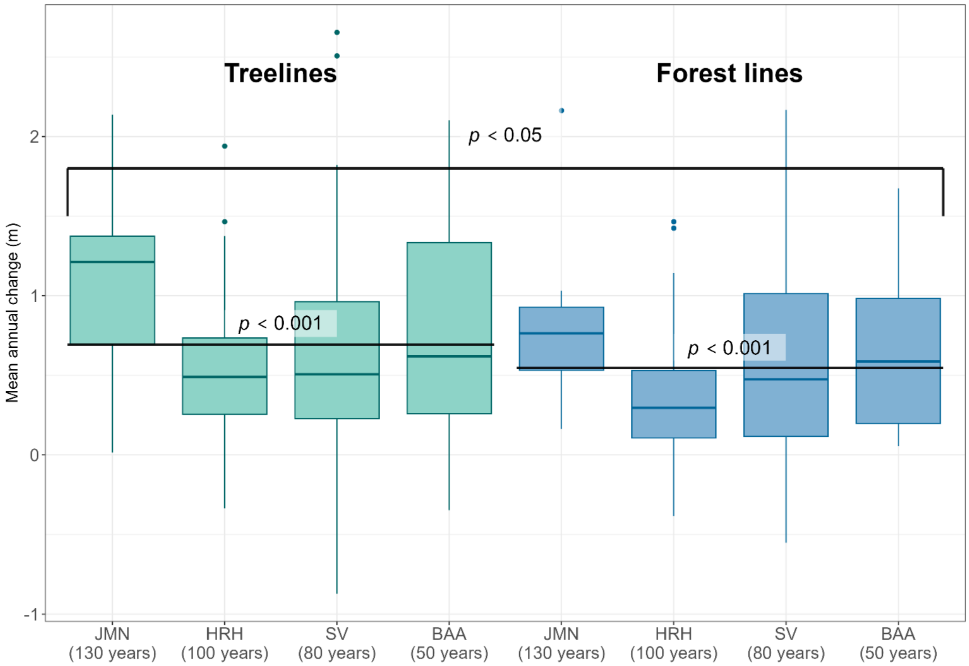

Figure 3: Box plot of mean annual change (m yr-1) from first to last record for treelines (TLs) and forest lines (FLs), respectively, categorized by originators of the historical records (OHR). The box represents the interquartile range (IQR) and the line inside the box shows the median. Whiskers extend to the smallest and largest values within 1.5 times the IQR from the lower and upper quartiles, respectively. Observations outside this range are shown as points beyond the whiskers. The p-values below refer to two unpaired one-sample Wilcoxon-Mann-Whitney signed-rank tests, one for TLs and one for FLs, of the null hypotheses that the overall medians (one thick line for each of TLs and FLs) are significantly different from zero. The p-value above refers to a two-sided Wilcoxon-Mann-Whitney rank-sum test of the null hypothesis that the medians for TLs and FLs do not differ statistically.

The largest annual mean changes (TLs: 1.10 ± 0.53 m yr^{-1} ; FLs: 0.84 ± 0.61 m yr^{-1}) were observed for the northernmost data subset, originally mapped by J. M. Norman (Fig. 3), which includes the longest time interval of 130 years (Fig. 3). The smallest mean annual changes (TLs: 0.53 ± 0.45 m yr^{-1}; FLs: 0.36 ± 0.42 m yr^{-1}; Fig. 3) were found in the subset from southeastern Norway (Fig. 1), originally mapped by H. Resvoll-Holmsen.

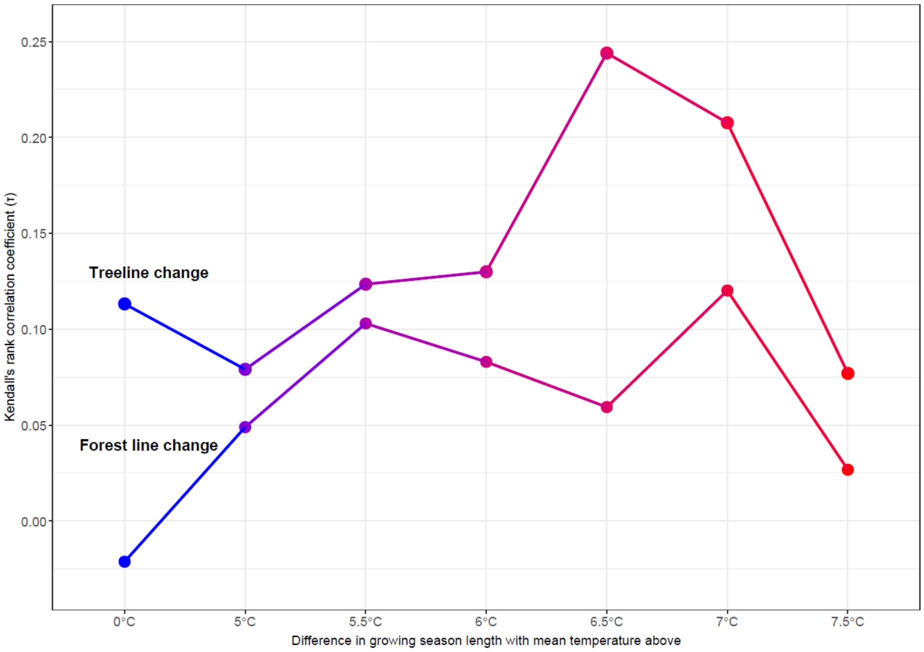

Figure 4: Line plot of Kendall's rank correlation coefficient (τ) between treeline change and the seven predictors representing difference in growing season length between first and last TFL record, using mean temperature above 0°C, 5°C, 5.5°C, 6°C, 6.5°C, 7°C, and 7.5°C.

3.2 Impact of land use vs climate

Both TL change and TL advance were positively correlated with the difference in growing-season length, when defined as the number of months with mean monthly temperatures above $5.5 < T < 7.0$ °C. The strength of these relationships peaked for $T = 6.5$ °C (Table 2, Fig. 4). TL advance was positively correlated with the same predictors as TL change, except monthly temperature above 6 °C, which only showed a significant positive correlation with TL change (Table 2). Due to the strong correlation between annual temperature deviation and mean annual temperature, only one of these two variables was preselected and subjected to model fitting: TL change had a stronger relationship with annual temperature deviation, whereas TL advance had a stronger relationship with mean annual temperature (Table 2). Warmest quarter was positively correlated with both TL change and TL advance (Table 2).

No FL variable was significantly correlated with any climate variable (Table 2). All response variables except FL advance (TL change, TL advance, and FL change) were positively correlated with proximity to mountain summer farms (Table 2). As the only response variable, FL advance was correlated with aspect favourability (Table 2).

Table 2. Kendall's rank correlation coefficients (τ) and corresponding p-values for all combinations of predictor and response variables (see Table 1 for explanation of variables). Variables in bold were preselected for fitting linear models (see explanation in text).

Predictor variables	**Treeline change**		**Treeline advance**		**Forest line change**		**Forest line advance**	
	τ	*p*	τ	*p*	τ	*p*	τ	*p*
Annual precipitation deviation	0.0551	0.3654	0.0373	0.5700	0.0997	0.1047	0.1054	0.1768
Annual precipitation sum	0.0611	0.3152	0.0485	0.4607	0.1054	0.0863	0.1109	0.1553
Annual temperature deviation	**0.1494**	**0.0141**	0.1502	0.0223	0.0891	0.1471	0.071	0.3487
Aspect favourability	0.0578	0.3921	0.1162	0.1098	0.1234	0.0689	**0.1701**	**0.0449**
Coldest quarter	0.0884	0.1466	0.1183	0.0717	0.0777	0.2063	0.0899	0.2491
Mean annual temperature	0.1445	0.0176	**0.1518**	**0.0209**	0.0872	0.1560	0.0707	0.3648
Mean grazing pressure	-0.0877	0.1694	-0.0585	0.3932	0.0509	0.4393	0.0095	0.9083
Monthly highest temperature	0.0055	0.9277	-0.0142	0.8295	0.0196	0.7499	-0.0635	0.4157
Monthly lowest temperature	-0.0275	0.6517	-0.0405	0.5375	0.0162	0.7923	-0.0326	0.6760
Monthly temperature > 0 °C	0.1132	0.0641	0.1068	0.1056	-0.0212	0.7314	0.0121	0.8776
Monthly temperature > 5 °C	0.0791	0.1965	0.0674	0.3074	0.0489	0.4297	0.0623	0.4281
Monthly temperature > 5.5 °C	**0.1234**	**0.0434**	**0.1428**	**0.0306**	0.1030	0.0966	0.0913	0.2468
Monthly temperature > 6 °C	**0.1299**	**0.0337**	0.1053	0.1114	0.0830	0.1810	0.1032	0.1908
Monthly temperature > 6.5 °C	**0.2440**	**0.0001**	**0.2475**	**0.0002**	0.0594	0.3383	0.0385	0.6249
Monthly temperature > 7 °C	**0.2076**	**0.0007**	**0.2331**	**0.0004**	0.1201	0.0535	0.1244	0.1165
Monthly temperature > 7.5 °C	0.0770	0.2082	0.0751	0.2567	0.0267	0.6667	0.0056	0.9438
Tetratherm mean temperature	0.1311	0.0313	0.1279	0.0516	0.0411	0.5039	0.0007	0.9930
Tetratherm precipitation deviation	0.0902	0.1384	0.0384	0.5591	0.0366	0.5516	0.0051	0.9474
Tetratherm precipitation sum	0.0882	0.1472	0.0364	0.5791	0.0401	0.5138	0.0148	0.8500
Tetratherm temperature deviation	0.1320	0.0301	0.1286	0.0503	0.0415	0.4996	-0.0003	0.9965
Proximity to mountain summer farms	**0.1508**	**0.0132**	**0.1537**	**0.0193**	**0.1360**	**0.0250**	0.0718	0.3476
Warmest quarter	**0.1356**	**0.0259**	**0.1378**	**0.0360**	0.0501	0.4154	-0.0127	0.8707

Linear models for TLs (TL change and TL advance) both contained one significant predictor only: difference in growing season length with mean temperature above 6.5 °C (Fig. 5A and 5B). The relationship was slightly stronger for TL advance ($b = 112.4$, $SE = 23.5$, $R^2 = 0.20$) than for overall TL change ($b = 110.9$, $SE = 22.6$, $R^2 = 0.16$) (Fig. 5A and B).

The linear model for FL change contained one significant predictor: proximity to mountain summer farms (Fig. 5C). FL change was predicted to increase with increasing distance from mountain summer farms ($b = 16.9$, $SE = 5.5$) (Fig. 5C). The model for FL advance (Fig. 5D) also contained one predictor only: aspect favourability. FL advance was predicted to be higher in the more favourable, S- to SW-facing mountainsides than in less favourable aspects ($b = 30.2$, $SE = 13.1$). Both FL models only accounted for 7 % of the variation ($R^2 = 0.07$; Fig. 5C and 5D). Yet, all models (TL change, TL advance, FL change, and FL advance) had lower prediction error than the respective null models (TL change = 5932.108; TL advance = 4278.539; FL change = 4307.954; FL advance = 2363.531) using 4-fold cross-validation (Table C1).

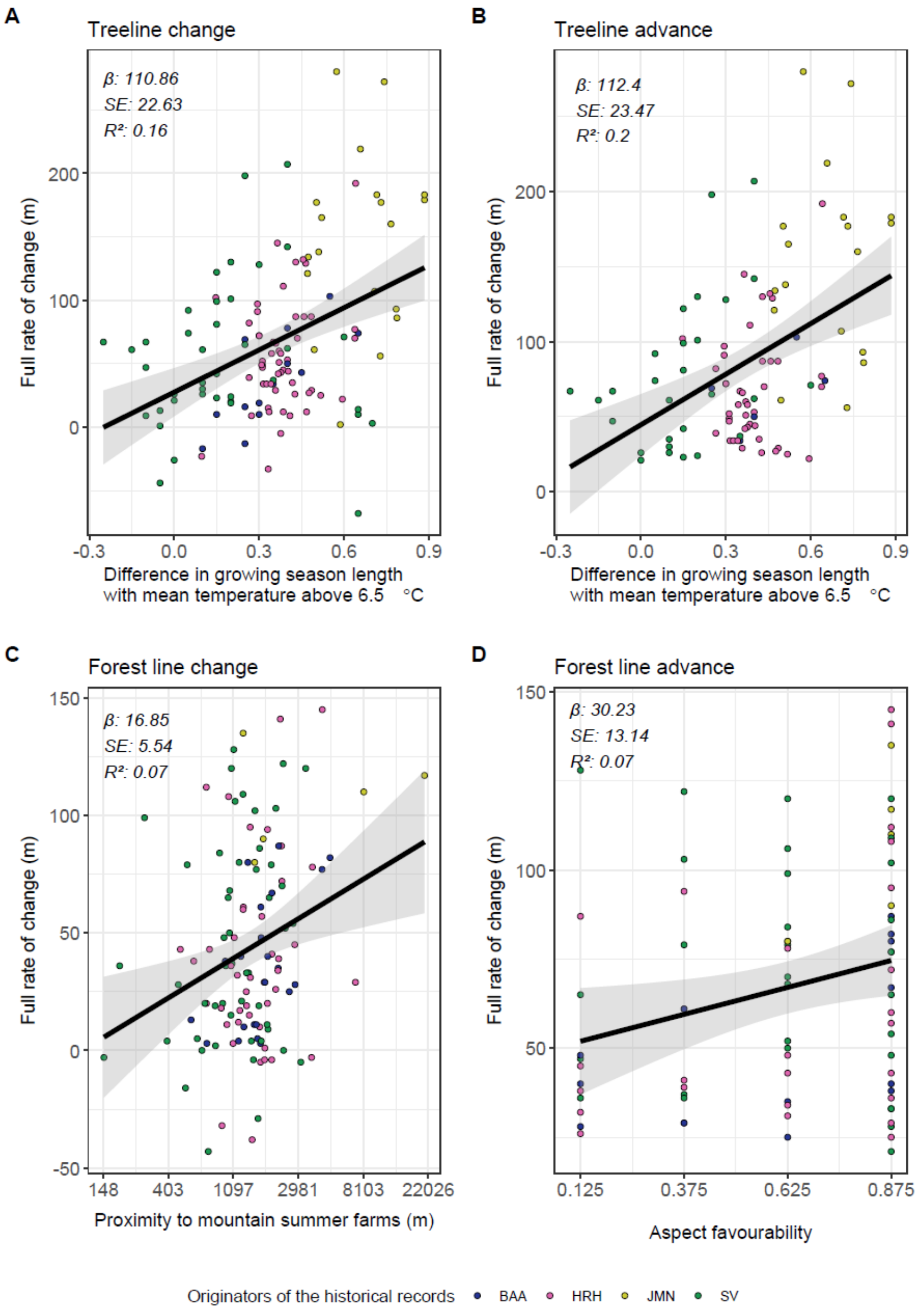

Figure 5: Linear models (LM) with 95 % confidence interval for the response of (A) treeline change (m) and (B) treeline advance (m) to difference in growing season length (months) with mean temperature above 6.5 °C; (C) forest line change (m) and proximity to mountain summer farms (m); and (D) forest line advance (m) to aspect favourability. Originators of the historical records (OHR) (e.g. BAA – Børre Aas, HRH – Hanna Resvoll-Holmsen, JMN – Johannes M Normann, SV – Søren Ve) are shown in different colours. Slope (β), standard error (SE), and the coefficient of determination (R^2) for the four linear models are shown in the upper left corner of each figure.

4 Discussion

This study documents the rate of TFL change over a timespan of nearly 130 years, thereby accounting for potential time-lags between drivers and TFL responses. TLs and FLs both show a significant advance of more than 0.5 m yr^{-1} (Fig. 3), which is, according to our models, related to climate change and land use (Table 2). Our findings corroborate previous research on TL shifts, showing advancement in Norway averaging 0.6–0.8 m yr^{-1} from the early to mid-1900s to the early 2000s, with some variation between regions (Cudlín et al., 2017). However, previous reviews on TFL dynamics often synthesize studies using different methods and various TFL definitions. Furthermore, the number of relevant studies is limited, and most rely on sparse and spatially scattered data (Bryn and Potthoff, 2018; Cudlín et al., 2017; Tattoni et al., 2010). In this study, all records are based on consistent TL and FL definitions, and both the historical and recently repeated observations are obtained by in situ barometer measurements of elevation (Tjessem et al., 2025), which have been argued to provide higher spatial precision than methods relying on historical photographs and map interpretation (Bryn and Potthoff, 2018). Our study thus confirms a general upward shift of TFLs along the boreal-alpine ecotone, while also accounting for potential demographic time-lags.

4.1 Rate of change

The rate of TFL change found in our study (Fig. 3) falls well within the range of upward shifts reported from elsewhere in Europe, ranging from 0.43 m yr^{-1} in the Giant Mountains, Czech Republic, to 1.92 m yr^{-1} in the Central Pyrenees (Cudlín et al., 2017). This substantial variability, reviewed by Cudlín et al. (2017), underscores the highly dynamic nature of TFLs and is primarily attributed to differences in bedrock, soil, microclimatic conditions, and the interplay between historical land use and present socio-economic factors. Nonetheless, variation in TFL dynamics has also been attributed to climatic conditions (Hofgaard et al., 2013; Rees et al., 2020) or a combination of climate and land use (Bryn, 2008; Hofgaard et al., 2009; Aune et al., 2011). A potential natural forest model for Norway has predicted that 15.9 % of mainland Norway has been deforested due to the long-lasting historical land use (Bryn et al., 2013). Much of this land use is abandoned, and forests are regenerating and expanding. The same pattern is seen for central Europe: forests have been predicted to regenerate >10 % of previously open areas depending on future climate and land use scenarios (Tasser et al., 2017). Globally, both upslope and downslope shifts of TFLs have been observed and explained by various effects; nevertheless, the general worldwide pattern is consistent with our results, showing a clear TFL advance (Harsch et al., 2009; Liang et al., 2025).

4.2 Regional variation

The overall largest mean TL advance is found in the subset from N Norway, originally recorded by J. M. Norman between 1887 and 1894 (Fig. 3). This subset encompasses the longest period between two records (i.e. 130 years). However, TFL dynamics cannot be explained by time alone if the drivers do not change during the study period. This is more clearly expressed within the boreal-alpine ecotone in Norway, where the availability of birch seeds is rarely a limiting factor as mountain birch has high capacity for long distance-dispersal and is commonly found with high seed density in upper soil layers (Tiebel et al., 2018). This contrasts with TFLs defined by coniferous species, such as mountain pine in the Pyrenees (Anadon-Rosell et al., 2020) and black spruce in northern Quebec (Sirois, 2000), where seed limitation constrains forest expansion. With a persistent soil seed bank near TFLs defined by mountain birch, TFL advance is expected primarily to be dependent on favourable conditions for germination. Once the minimum time needed for a new generation to establish is accounted for, including potential time-lags, additional time alone does not drive TFL advance. When the records by Norman were excluded from the correlation analysis, no correlation was found between time and TFL dynamics (Table D1). However, the originators of historical records (OHR) collected data in different time periods (circa 130, 100, 80, and 50 years before the repeated records were made) and in different geographic areas. Consequently, variations among the OHR may reflect local or regional differences rather than the timespan alone.

The smallest mean TFL change is found in the westernmost and the eastern regions of S Norway, originally mapped by Ve and Resvoll-Holmsen, respectively. The largest negative values (TL: –0.87 m yr^{-1}; FL: –0.55 m yr^{-1}; Fig. 3A and C) are found in sites around Sognefjorden (Fig. 1) mapped by Ve, where mass movement (i.e. snow avalanches, landslides, and rockfalls) frequently causes instant lowering of TFLs (Fig. 6). Although some areas are more prone to disturbance than others, the stochastic nature of disruptive events such as insect outbreaks, pests, landslides, and rockfalls makes them difficult to predict (Cudlín et al., 2017). The overall effect of disturbance events is assumed to be small, and they are difficult to trace back in time. Consequently, we did not include direct measures of stochastic disturbances in our predictor variable dataset. Nonetheless, some of these events may have been captured indirectly through the temperature variables given that, for example, insect infestations are known to increase in severity and frequency with rising temperatures (Jepsen et al., 2008). The range of insect infestations is likely to expand, particularly northwards, under continued warming (Vindstad et al., 2022). Outliers and other idiosyncratic patterns of single observations are expected and inevitable in dynamic systems such as TFLs (Fig. 6).

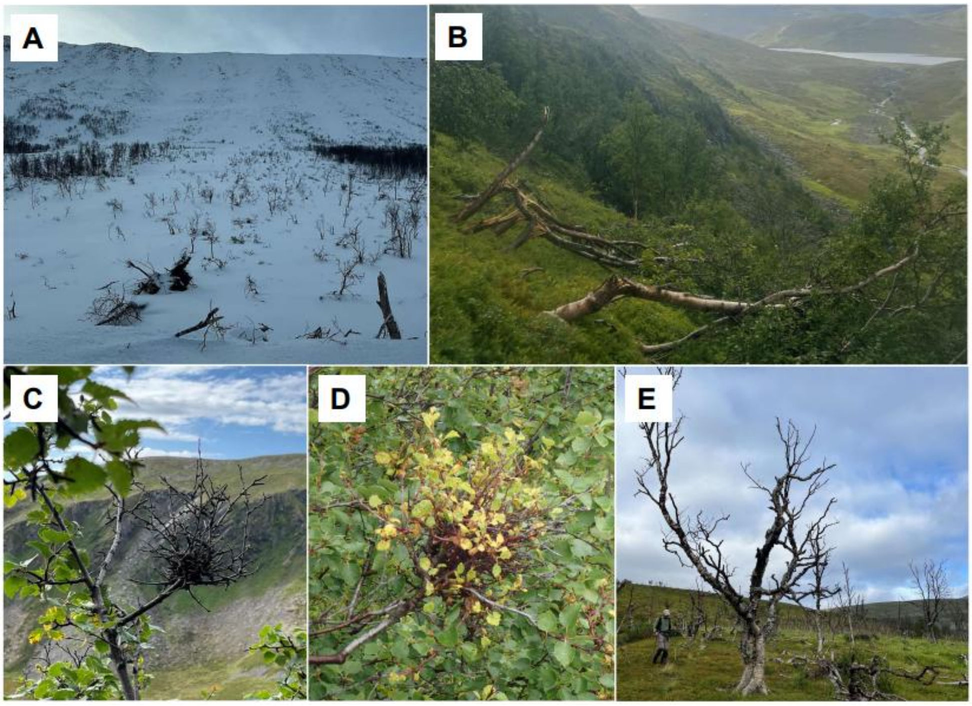

Figure 6: Examples from five different localities in Norway where tree- and forest lines (TFLs) may be instantly lowered due to various stochastic effects: (A) and (B) snow avalanche; (C) and (D) fungal infections by Taphrinales and Melampsoridium betulinum, respectively; (E) insect infestations by Epirrita autumnata, Operophtera brumata or Agriopis aurantiaria.

4.3 Impact of land use vs climate

Both TL models (i.e. for TL change and TL advance) identify longer growing seasons as a major predictor. More specifically, the strongest predictor is the difference in growing season length, calculated with mean temperature above 6.5 °C. Furthermore, the model for TL advance accounted for slightly more of the variation in (R^2 = 0.20) than the model for overall TL change (R^2 = 0.16). This indicates that a longer growing season, with an optimal thermal limit at 6.5 °C (Fig. 4), is a major contributor to TL advance. Previous studies support our findings that the lower temperature limit for tree growth is approximately 6.5 °C. For example, Paulsen and Körner (2014) find that the global positions of 376 TLs were best predicted

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by a seasonal (periods with daily minimum temperatures at 0.9 °C) air temperature of 6.4 °C ± 0.4 °C. Our results for Norwegian TL dynamics support previous global assessments indicating that TLs are limited by low temperatures (Körner & Paulsen, 2004; Paulsen & Körner, 2014).

We find a positive relationship between the magnitude of climate warming and TL change (Figure 4) while land use (i.e. proximity to mountain summer farms) is the only variable included in the model for FL change. The latter result may at first sight appear paradoxical, as a majority of FLs included in our study were first mapped by Hanna Resvoll-Holmsen, who had a strong focus on climatically determined TFLs (Resvoll-Holmsen, 1918). Accordingly, Resvoll-Holmsen intentionally selected sites that were minimally impacted by land use (i.e. deforestation and rangeland grazing). However, it is well documented that almost all available mountainous land resources were in use around 100 years ago, as a result of expanding populations since the 16th century (Reinton, 1965; Bryn & Daugstad, 2001). Therefore, Resvoll-Holmsen likely found few climatic FLs completely unaffected by land use (Bryn et al., 2013; Bryn & Potthoff, 2022), whereas individual trees forming TLs could more easily escape rangeland grazing, for example, on steep slopes or within boulder fields. Although the summer farm system in Norway was complex (see e.g. Bryn & Daugstad, 2001), a key point is that the summer farms were established close to the FLs, where forests provided fuel for cheese production, and mountains served as rangeland for summer grazing. Scattered trees at high elevations, forming the TLs, however, were likely not influenced by summer farm settlements (Fig. E1). This is consistent with our results showing a strong impact of land use (i.e. proximity to mountain summer farms) on FL change and a non-significant effect on TL change.

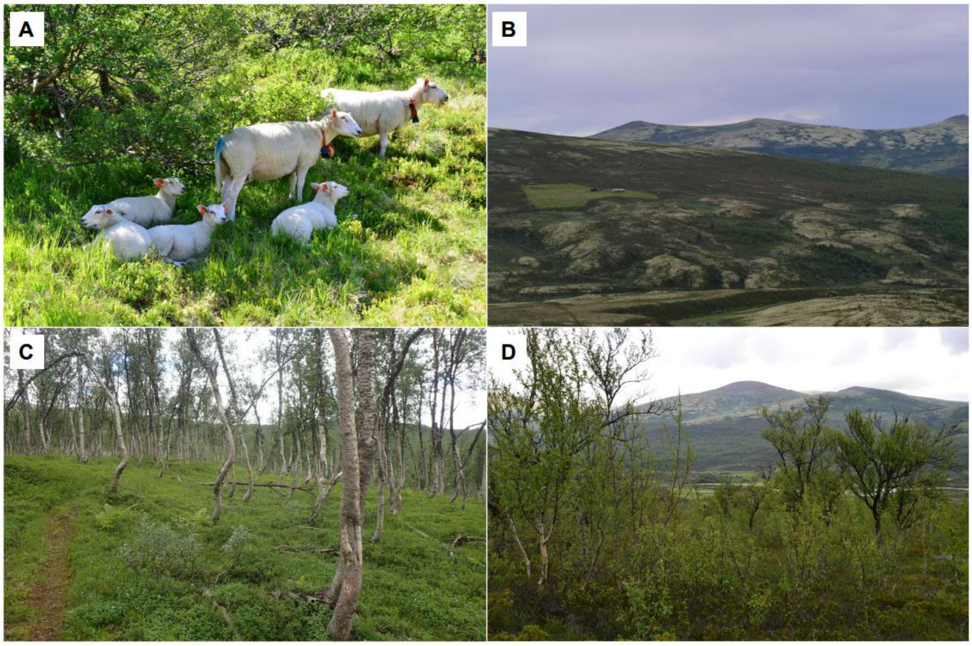

Figure 7: Examples of four different forest lines in Norway at which land use is a driver of forest line dynamics: (A) grazing livestock minimize recruitment of new trees; (B) the extent and local impact from forest logging and grazing around mountain summer farms to promote graminoids at the expense of boreal vegetation; (C) mountain birch forest that lacks recruitment of new trees due to livestock grazing; (D) site without grazing livestock, with substantial recruitment of birch.

Land use is pinpointed as a major driver of TFL dynamics in many studies (e.g. Palombo et al., 2013). In a study by Vitali et al. (2018), land use measured as population density per municipality emerged as the primary driver of recent forest-cover shifts, both upward and downward. In our study, land use was measured as mean grazing pressure (land use change) and proximity to mountain summer farms (land use). We did not record or estimate other anthropogenic activities such as development of cabin settlements, outdoor recreation, and broader effects of increasing demographic pressure. This is

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because (1) we do not have historical data on cabins or recreational activities; (2) there were, and are, no permanent settlements close to TFL locations included in this study; (3) since 1965 the uppermost forest belt has been protected by law against forestry (§ 12. Vernskog, Skogbruksloven 1965); and (4) because the only human physical land use activities that could influence the remote TFLs locations are related to domestic rangeland grazing and previous summer farming. On the other hand, the impact of both summer farming and domestic rangeland grazing on the TFLs is documented in previous studies from different mountain regions in Norway. In an experiment with sheep grazing, Speed et al. (2010) documented a clear reduction of seedlings and saplings at the FL compared with fenced enclosures. Similar results are also found in several landscape ecological studies, in which a clear elevational drop of FLs is attributed to domestic rangeland grazing (Sickel et al., 2004; Potthoff, 2009; Wehn et al., 2012; Mienna et al., 2022), and around summer farms, where combinations of logging for fuel wood and herded grazing have lowered the TFLs (Hofgaard, 1997; Bryn, 2008; Rössler et al., 2008; Potthoff, 2017).

In our study, proximity to mountain summer farms emerges as an important driver of FL change (Table 2), whereas the mean grazing pressure shows no significant impact. Similar findings are reported by Kucsicsa and Bălteanu (2023) from the Carpathian mountains, where the distance to farms captures the effect of grazing animals better than actual animal counts. Our interpretation of the lacking relationship between mean grazing pressure and TFLs in our analysis (Table 2), is the low spatial resolution of our grazing data. Although the grazing data cover the same period as the initial and subsequent TFL records, estimates of grazing pressure per km^2 from municipality-level counts (Table 1) are likely to be too coarse to capture the substantial variability in grazing impact among TFL sites, i.e. on more local spatial scales. The impact of rangeland livestock grazing on vegetation may vary with factors such as elevation, resource availability, and grazer food preferences. Consequently, the actual grazing pressure may vary considerably between TFL localities, even where numbers of domestic animals are similar.

4.4 Quality components

The importance of accounting for time-lags for trees and forests to establish is stressed in many previous studies (e.g. Bryn and Potthoff, 2018), as well as the importance of avoiding the assumption that vegetation is in equilibrium with climate (Loehle, 2018). Woods (2014) maintains that even a temporal lag of 50 years may be too short for slow-growing trees. However, according to Hofgaard et al. (2009), the time needed for mountain birch to establish and grow tall enough to satisfy the definition of a tree is highly variable. In our study, we accounted for a disequilibrium between our predictor and response variables by including a time-lag of 20 years. The choice of time-lag may have influenced the strength of the relationships identified in our models. Establishing more precise estimates of time lag duration is beyond the scope of this study, but we acknowledge the uncertainty associated with the selected 20-year lag.

Whereas the time-lag for establishment of TFLs, in our opinion, is likely around 20 years, the time-lag related to TFL dieback is likely to be much more varied. The time it takes for a forest to recover from an insect outbreak has been estimated at 30 years (Tenow, 2000), whereas post-fire regeneration in conifer-dominated FLs in Yellowstone has been estimated at around ten years (Donato et al., 2016). Moreover, snow avalanches can instantly erase the TFLs locally, whereas dieback related to climate deterioration or extensive rangeland grazing likely exceeds the mean demographic life expectancy of mountain birch at the TFL (approximately 100 years; Holtmeier, 2009). For example, sheep grazing cannot kill fully grown birch trees but can remove seedlings and saplings (e.g. Speed et al., 2010), thereby preventing forest recruitment. Over time, when the established trees die of age, the result may be TFL dieback to lower elevations. To ensure that potential diebacks of TFLs were included in our study, we focused on repeating TFL data older than 50 years, spanning up to 130 years (Tjessem et al., 2025).

The summit syndrome is a widespread phenomenon that results in TFLs around mountain tops that are lower than the regional climatic FLs (Körner, 2012). This syndrome implies that, even when conditions favour TFL advance, upward expansion may be constrained by summit conditions and lack of suitable sites at higher elevations. In such cases, the

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empirical TFL represents a disturbance-driven edge rather than a climatic limit (Körner, 2021). Accordingly, studies not accounting for the summit syndrome could potentially register a false TFL stability. In our study, we accounted for the summit syndrome by removing records from sites for which the first recording was situated closer to the summit than the total average increase for TLs and FLs, respectively. Previous research indicates that wind, microclimate, erosion, and limited substrate availability are factors that influence the summit syndrome (Körner, 2012; Holtmeier et al., 2003; Kašpar and Treml 2018). A study by Beloiu et al. (2022) found no shift in the treeline over the past 70 years, despite increasing temperature in the study area. They reported that the TL was strongly correlated with topographic exposure to wind ($R^2 = 0.74$, $p < 0.001$) and suggested that the lack of TL advance could be explained by a combination of topographic and microclimatic factors, such as the absence of shelter and reduced moisture availability. In our data, we observe the summit syndrome to fade out for FL sites that, when first recorded by the OHR, were situated more than 150 m below the summit (Fig. F1). However, for TL records, the effect does not diminish (Fig. F2). In other words, we could not fully remove the summit syndrome effect without discarding the entire TL dataset.

5 Conclusion

While previous research has been limited by temporal data coverage, this study quantifies TFL change up to 130 years and relates it to changes in climate and land use spanning more than 150 years.

We show that Norwegian TFLs are advancing at rates exceeding 0.5 m yr^{-1}, primarily driven by climate change for TLs and land use for FLs. Still, the rates of TFL change vary considerably between regions, likely due to stochastic disturbances (e.g. snow avalanches, insect outbreaks, pests, landslides, rockfalls). As with other datasets, the TFLs in our study may be in disequilibrium with climate and limited by the summit syndrome. Although these effects are addressed in our analysis, we suggest further research on these topics to improve our understanding of how TFLs are influenced by climate change.

Overall, our findings underscore the need for more precise estimates of the duration of time-lags in a dynamic system such as the boreal-alpine ecotone. We emphasize the necessity of applying consistent definitions and methodologies when quantifying TFL shifts over long temporal scales.

Appendix A: Description of all predictor variables

Table A1. Predictor variables representing potential drivers of tree and forest line (TFL) dynamics, grouped by effect type (land use, site, temperature, precipitation). For each variable, a thorough description is given. Two predictors are based on static values (i.e. aspect favourability and proximity to mountain summer farms), and the rest (i.e. mean grazing pressure, and all temperature and precipitation variables) include temporal change (i.e. change in predictor values between the first and last TFL record).

Effect	Predictor variable	Description
Land use	Mean grazing pressure	Grazing pressure per km^2. For full description, see section 2.4.
	Proximity to mountain summer farms	The log-transformed distance from each TFL record to the nearest mountain summer dairy farm.
Site	Aspect favourability	A converted linear variable of the compass direction faced by the maximum slope, where the least favourable aspect is NNE = 22.5° and set to 0, and the most favourable aspect is SSW = 202.5° and set to 180.
Temperature	Annual average temperature	The mean of monthly temperature values during a year.
	Monthly highest temperature	The mean monthly temperature of the warmest month of the year.
	Monthly lowest temperature	The mean monthly temperature of the coldest month of the year.
	Annual temperature deviation	The difference from the mean annual temperature based on the climatological standard normal for 1981–2010.
	Warmest quarter	The mean temperature during the warmest three consecutive months of the year (July, August, and either June or September).
	Coldest quarter	The mean temperature during the coldest three consecutive months of the year (January, February, and either December or March).
	Tetraterm mean temperature	The mean temperature of the four warmest months of the year (June, July, August, and September).
	Tetraterm temperature deviation	The difference from the tetraterm temperature based on the climatological standard normal for 1981–2010.
	Monthly temperature > 0 °C	Number of months with monthly temperature above 0 °C.
	Monthly temperature > 5 °C	Number of months with monthly temperature above 5 °C, April-October.
	Monthly temperature > 5.5 °C	Number of months with monthly temperature above 5.5 °C, April-October.
	Monthly temperature > 6 °C	Number of months with monthly temperature above 6 °C, April-October.
	Monthly temperature > 6.5 °C	Number of months with monthly temperature above 6.5 °C, April-October.
	Monthly temperature > 7 °C	Number of months with monthly temperature above 7 °C, April-October.
	Monthly temperature > 7.5 °C	Number of months with monthly temperature above 7.5 °C, April-October.
Precipitation	Annual precipitation sum	The sum of monthly precipitation values during the year.
	Annual precipitation deviation	The difference from the annual precipitation sum based on the climatological standard normal for 1981–2010
	Tetraterm precipitation sum	The precipitation sum of the four warmest months of the year (June, July, August, and September).
	Tetraterm precipitation deviation	The difference from the tetraterm precipitation sum based on the climatological standard normal for 1981–2010.

Appendix B: Additional information on the land use variables

Census dates

The census dates were as follows: January 1st, 1891, the end of September 1907 and 1917, and mid-June from 1929 to 1969. Due to the autumn slaughter, livestock numbers are generally smaller in winter than in summer/early autumn. Accordingly, the 1891 data were adjusted to reflect the summer/early autumn livestock conditions to be comparable with later years. The percentage differences between census data from September 1917 and an additional census from January 1918 were used to estimate the difference between a winter and a summer/early autumn situation, and thus, provide estimated livestock numbers for the summer/early autumn of 1890.

Municipality borders

Municipality borders have changed throughout history comprising division of one municipality into two or several and merging of (parts of) two or several municipalities (Juvkam 1999). Moreover, borders between municipalities have been adjusted. While we have considered the former changes, border adjustments have not been taken into account. Consideration of border adjustments would have required data on farm level in terms of municipality affiliation and number of livestock. These data were not available. All livestock data were adjusted to reflect municipality borders in 2019.

Municipalities have been grouped in accordance with the border changes that have occurred:

- Municipalities without any border changes: Bardu, Dovre, Hamarøy, Lom, Øystre Slidre, Oppdal, Ringebu, Sortland, Tysfjord, Vang, Vestre Slidre
- Municipalities that were merged; livestock data were summed for the years before the merger of the municipalities: Lærdal, Stor-Elvdal, Harstad
- Municipalities that were divided; livestock data for the years before the division were estimated based on the percentagewise distribution of heads of livestock after the division: Alvdal, Evenes, Folldal, Vågå
- Municipalities that were divided and merged; if the same municipalities were divided and merged data were summed for the years the municipalities were divided; if a municipality was merged with a different municipality it was divided from, percentagewise distribution of heads of livestock after division was used to estimate numbers before the division and data for the years before the merger of the municipalities were summed: Målselv, Narvik, Sel, Vågan
- Municipalities were divided, merged and divided; if the same municipalities were divided, merged and divided, data for the years when the municipalities were merged were estimated based on an average of the percentagewise distribution of heads of livestock before and after the merger;
- if municipalities were merged with a different municipality they were divided from, percentagewise distribution of heads of livestock after the first division were used to estimate data before the first division, and percentagewise distribution of heads of livestock after the second division were used to estimate livestock numbers for the time municipalities were merged: Lavangen, Nord-Fron, Sør-Fron
- Municipalities with complex border changes: a) parts of municipalities were merged to become a new municipality; in such a case the land area of the municipality before and after merger was used to estimate the distribution of heads of livestock before the merger; b) a municipality was divided and merged again but one municipality was excluded from the merger; in such a case the heads of livestock in this municipality were subtracted from the data before municipalities were merged; c) borders changes mentioned for previous groups have happened in addition; data were adjusted in accordance with the already presented rules: Engerdal, Harstad, Os, Rendalen, Tolga,

Appendix C: 4-fold cross-validation

Table C1. Total prediction error from 4-fold cross-validation for both response variables on TLs (TL change and TL advance) and FLs (FL change and FL advance) under three model formulations (null, alternative, and final models). Lower values indicate better predictive performance.

	Total prediction error			
	Treeline change	**Treeline advance**	**Forest line change**	**Forest line advance**
Null model	5932.108	4278.539	4307.954	2363.531
Final model	5701.148	4044.945	4158.87	2264.917

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Appendix D: Correlation between time and TFLs

Table D1. Kendall's rank correlation coefficients (τ) and corresponding p-values in parentheses for the number of years between two records and the total change in m for TLs and FLs, when both including and excluding records by J. M. Norman.

Correlation between n years (between first and last record)	***Including* J. M. Norman**	***Excluding* J. M. Norman**
TLs	0.28 ($p = 0$)	0.08 ($p = 0.29$)
FLs	0.07 ($p = 0.30$)	- 0.02 ($p = 0.81$)

510

Appendix E: Frequency plot of TLs and proximity to mountain summer farms

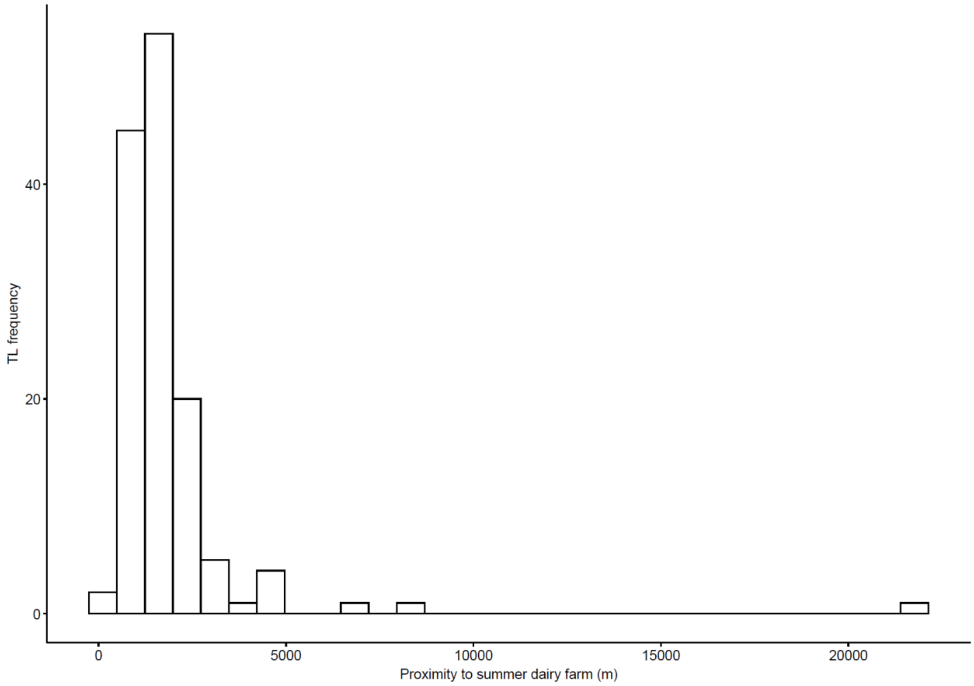

Figure E1. Frequency plot of proximity to summer dairy farm in m (x-axis) and number of TL records (y-axis).

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Appendix F: Summit syndrome

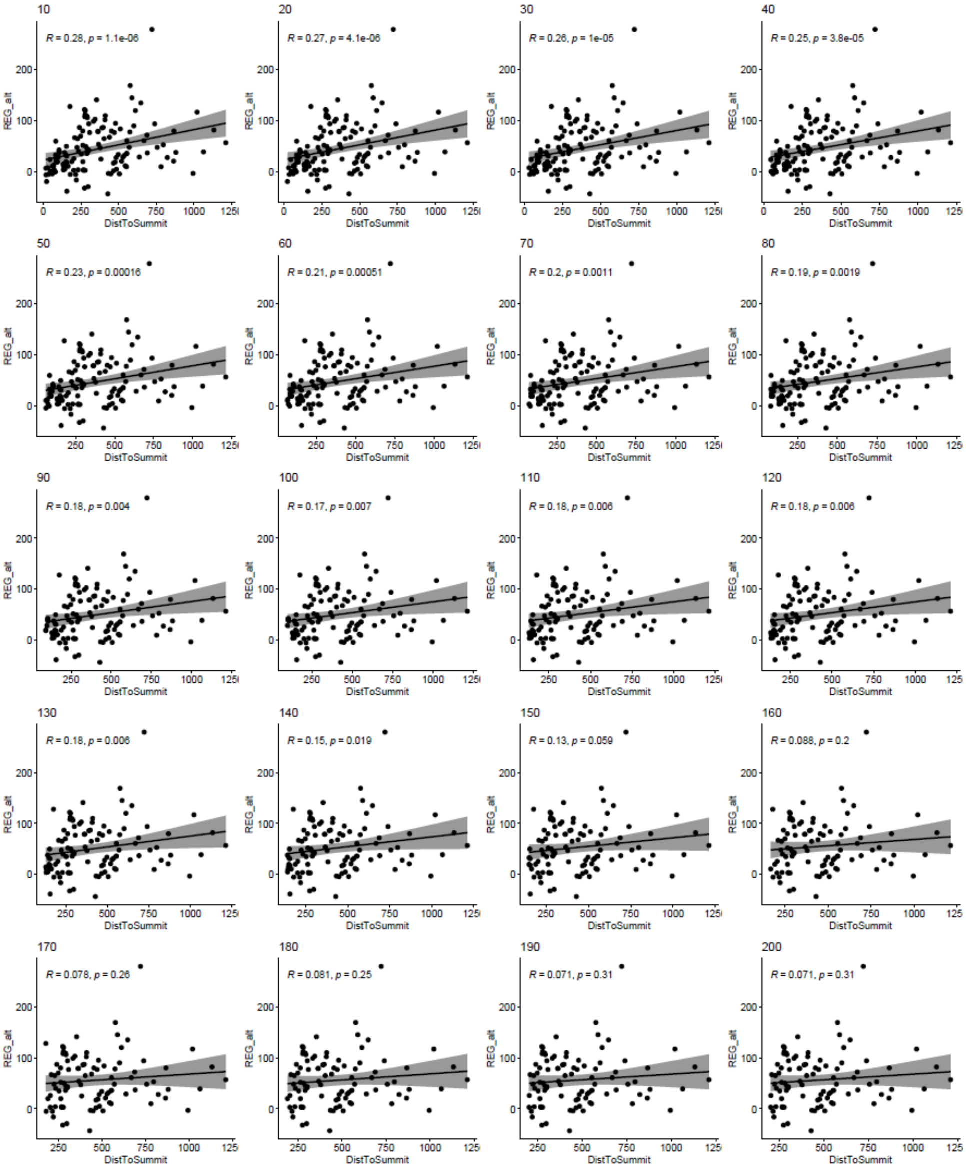

Figure F1. Kendall's rank correlation coefficients (τ) marked as *R* and corresponding p-values for the distance to the summit and the total change in m for FLs.

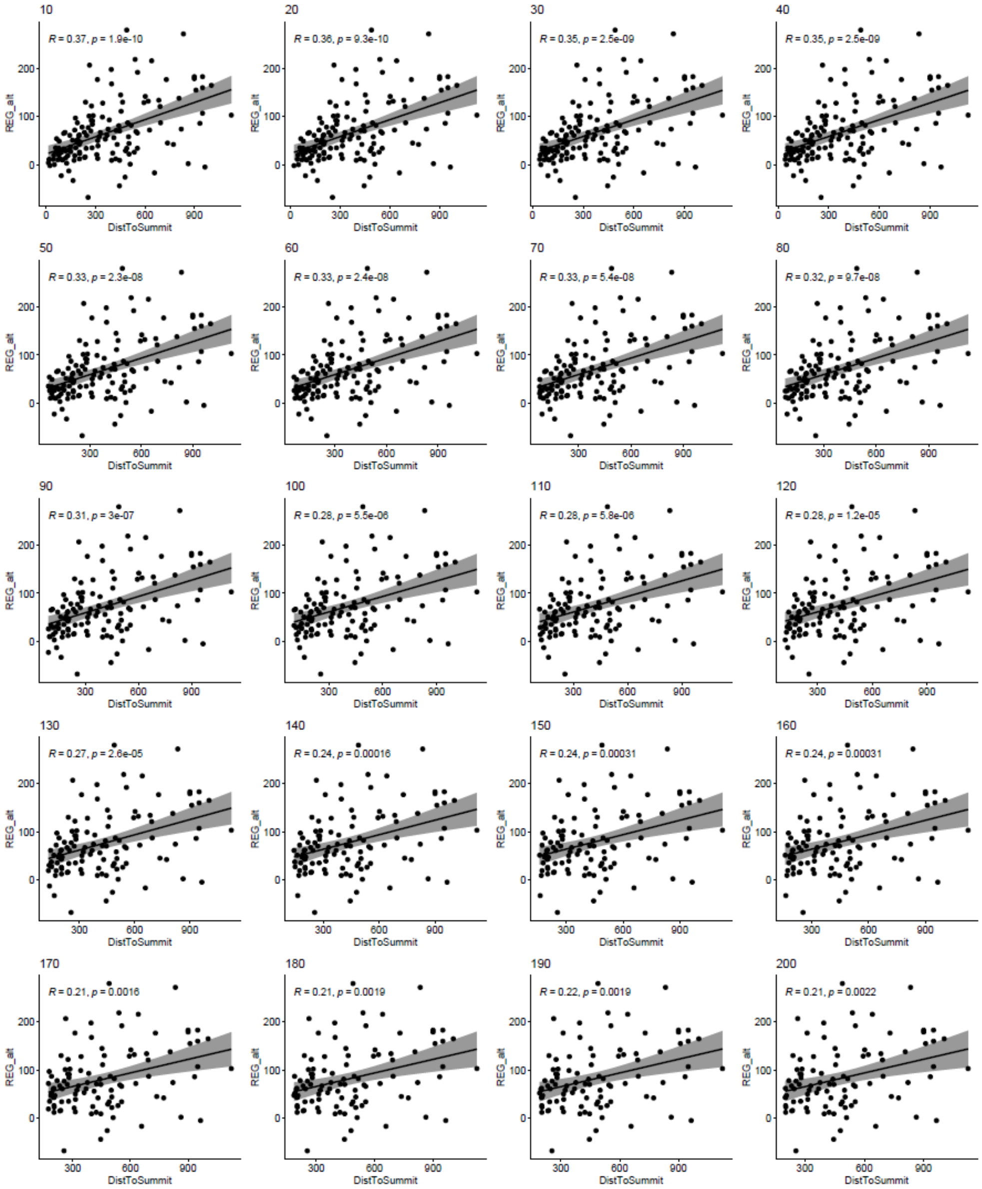

Figure F2. Kendall's rank correlation coefficients (τ) marked as *R* and corresponding p-values for the distance to the summit and the total change in m for TLs.

Code and data availability

All data, code, and scripts will be made publicly available upon acceptance and publication of the manuscript, and can be downloaded from: [will be included in a revision upload once the dataset link is accessible].
Until then, access will be restricted to reviewers.

Author contributions

AB, PH, and IVT designed the study, and AB, PH, IVT, and AEN carried it out. IVT, AB, and RH decided on the formal analyses. IVT, AB, PH, AEN, KP, KI, and OET prepared the data. IVT, PH, AEN, KP, KI, and OET developed the code and performed the modelling. IVT prepared the manuscript with contributions from all co-authors. AB was responsible for funding acquisition.

Competing interests

The authors declare that they have no conflict of interest.

Disclaimer

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Artificial intelligence was used as an aide in the writing of this manuscript: for English improvement and rephrasing, and never for writing original text.

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Review statement

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