Distribution modelling of a century with tree- and forest line changes in south Norway

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Abstract

Altitudinal tree- and forest lines (TFLs) are two boundaries (but often abbreviated with one word to save space) in the transition zone that separates closed forest from treeless tundra in alpine regions. Due to the last century's trend of advancing TFLs there is a growing need to understand and predict their distributions. In this study, we aimed to: (1) identify climatic predictors of TFLs in south Norway dominated by mountain birch (*Betula pubescens* ssp. *czerepanovii*); (2) analyse elevational changes and estimate distributional changes from 1917 to 2017; and (3) discuss the most likely explanations for the observed changes. The maximum entropy algorithm was used for distribution modelling of past and present TFLs with wall-to-wall coverage of 40 explanatory variables (EVs) with 100×100 m resolution and presence-only data collected *in situ* from the study area covering 69 000 km^2 from 60°26 to 62°43 N and 6°58 to 12°13 E. Stepwise forward selection with the likelihood ratio test for nested models was used to obtain present TFL models with and without topographical variables, evaluated by AUC-ROC and AUC-PR with independently collected evaluation data. Model coefficients were estimated for past TFL models with fixed EVs derived from modelling of present TFLs and evaluated by 4-fold cross-validation. Inverse distance weighting with the elevation of the highest local predictions from past and present TFL models without topographic variables as interpolation attributes was used to obtain interpolated raster layers. Through comparison with a digital elevation model, areas above and below TFLs were identified, and the resulting binary maps were used to estimate changes in distribution. In addition, elevational changes were analysed statistically. We found that: (1) the present treeline distribution was predicted by mean temperature of the warmest quarter, maximum temperature in November, slope inclination and snow water equivalent in March, while mean temperature of the warmest quarter, minimum temperature in November and slope inclination predicted the forest line distribution; (2) TFLs significantly moved upslope from 1917 to 2017 with treelines and forest lines moving on average 0.53 and 0.36 m/year, respectively. The estimated reduction of 6 688 km^2 in areas above the treeline (27.6% decline) from 1917 to 2017 was much higher than the estimated 1 137 km^2 reduction of areas above the forest line (5.3% decline) but might be affected by the data quality of past TFL observations; (3) the observed changes are most likely a result of climate and land use changes, but it is hard to separate their relative influences. Potential consequences of the observed changes for climate and biodiversity are discussed briefly.

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Introduction

Mountain areas worldwide have been largely impacted by changes in land use and climate the last century (Gehrig-Fasel *et al.* 2007, IPCC 2013, Cudlín *et al.* 2017, Li and Li 2017), which have contributed to changes in the distribution of forest and mountain ecosystems, conventionally approximated by monitoring boundary shifts (Harsch *et al.* 2009, Rees *et al.* 2020). Tree- and forest lines (TFLs) – the altitudinal or latitudinal positions above which trees and forests, respectively, are absent – are such boundaries, and they represent the transition zone that separates closed forest from treeless tundra (Elliott 2016).

Globally, TFL distributions are strongly correlated with summer temperature, and thus, they are assumed to be good climatic indicators (Jobbágy and Jackson 2000, Körner and Paulsen 2004). At smaller scales, factors controlling TFL distribution encompass a broad range of abiotic, biotic and historical factors, often working in combination (Holtmeier and Broll 2007). The distribution of TFLs in south Norway also correlate strongly with summer temperature but other climatically limiting factors in the region are less known (Bryn 2008). Identification of climatic and ecological predictors may generate new hypotheses of factors limiting distributions (Dormann *et al.* 2012) and thereby improve predictions of past and future TFL dynamics.

Historically, elevations of TFLs in Fennoscandia were higher than today throughout much of the Holocene, although fluctuating since trees colonized after the Last Ice Age (Bjune 2005, Kullman 2013). Macrofossils from Jotunheimen in south Norway indicate that treelines in the area most likely became climatically depressed from around 8900 BP, while human land use started to gain more importance in the area around 2000 BP (Bjune 2005). As a result of past land use many TFLs in Norway are still situated at positions below their climatic potential (Bryn and Daugstad 2001). Empirical studies from Norway indicate that TFLs have mainly been advancing, but in some locations, they have been stable or declining the last century (Bryn and Potthoff 2018), and regionally, they are moving slower than expected from changes in temperature (Dalen and Hofgaard 2005, Rannow 2013). Coinciding with elevational changes, intensity of summer farming in the mountains has declined in many areas (Bryn and Daugstad 2001), while annual temperature has increased (Hanssen-Bauer *et al.* 2006). Therefore, abandonment of agricultural land and climate change are considered the two main driving forces of the observed elevational changes (Bryn 2008). However, their relative importance is unknown and due to time lags in establishment, TFLs respond to environmental changes in a non-linear fashion, which makes it hard to disentangle and quantify the effects of these two driving forces (Malanson 2001).

TFL advance is thought to initiate substantial feedback mechanisms because closed forest and treeless tundra ecosystems have completely different effects on surface albedo, carbon storage and turnover, evapotranspiration and release of biogenic volatile organic compounds, (de Wit *et al.* 2014, Rydsaa *et al.* 2017). Changes in TFL distribution might also have negative consequences for alpine biodiversity because TFL rise entails shrinkage of alpine ecosystems, increasing the extinction probability of alpine species (Moen *et al.* 2004). Although several studies report elevational changes of TFLs in the 20th century (Kullman 2010a, Bryn and Potthoff 2018, Trant *et al.* 2020), we do not know how these observations translate into changes in areas above and below TFLs. Such estimates do not yet exist from south Norway but are needed because they allow calculations of the radiative forcing from TFL induced climate feedbacks, and assessments of the potential impacts on alpine biodiversity.

Areal estimates of changes in distribution and identification of ecological predictors can be investigated with distribution modelling, commonly used for predicting distributions in past, present and future conditions (Guisan and Zimmermann 2000). They are commonly used to model the distribution of targets like species, communities, species diversity or land-cover types (Halvorsen 2012), and not continuous lines in the landscape, which are modelled in this study and are what TFLs theoretically represent (see Bryn *et al.* (2013) for an exception). In correlative distribution modelling a target's distribution is predicted from a statistical relationship between target occurrence data and explanatory variables within a given area, followed by projecting the resulting distribution onto geographical space (Elith and Leathwick 2009). These methods have some properties that might be problematic for their use to model past and present TFL distributions. They assume that the target is in equilibrium with the environment and that the explanatory variables are capturing relevant mechanisms that affect the target's distribution, which refers to the types of explanatory variables, as well as their temporal and spatial scale (Dormann *et al.* 2012). Moreover, for extrapolation of models, explanatory variables that affect the target's distribution directly might be preferable because they can change differently than their proxies in time and space (Austin 2002).

Distribution models often rely on information about where a target is present and absent (Mateo *et al.* 2010), but methods that only require presence observations, like MaxEnt, have gained popularity in recent years due to the lack of absence observations in many data sets (Graham *et al.* 2004), such as Resvoll-Holmsen's (1918) field observations of TFL elevations in south-east

Norway. Data collected in the field, have higher spatial precision than the aerial photos and satellite data often used in studies on TFL dynamics (Harsch *et al.* 2009). In addition, old data sets enable detection of changes in slow processes that occur over long time periods (Tingley and Beissinger 2009), such as TFL dynamics.

Aims

The objective of this thesis is to improve the understanding of TFL dynamics through modelling of their past and present distributions in south Norway. The main questions are:

1. What are the climatic and ecological predictors of TFLs?
2. What changes have occurred in TFL elevation and what are the estimated changes in distributional area?
3. What can explain the changes in TFL distribution?

Material & Methods

Study area

The study area extends from 6°58 to 12°13 E and 60°26 to 62°43 N with a total area of approximately 69 000 km^2 and was chosen based on observations from Resvoll-Holmsen (1918) and more recently collected data from south Norway (mentioned in detail in section "Training data" below) (Figure 2). The mean elevation of the landscape is 922±389 m a.s.l. and mountain heights generally decrease in all directions from the highest point in the middle of the study area, at Galdhøpiggen, 2 469 m a.s.l. TFLs in south Norway are primarily formed by mountain birch (*Betula pubescens* ssp. *czerepanovii*), while Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and rowan (*Sorbus aucuparia*) sometimes form TFLs locally. The uppermost forests are mostly dominated by mountain birch and usually extend vertically more than 50 m (Odland 1992). According to Resvoll-Holmsen (1918), logging of mountain forests followed by maintenance of their positions by grazing had been extensive in the region in the 1910s. The mountain forest in the region is primarily situated on deposits of glacial till but soil conditions depend more on the bedrock, which mainly consists of gabbro in Jotunheimen and Tron, gneiss in Dovre and sparagmites in Rondane and Femunden (Ramberg *et al.* 2008). The study area spans four bioclimatic sections from markedly oceanic in the western most parts to slightly continental eastwards and five bioclimatic regions from the boreonemoral zone, especially in south and at the lowest elevations, to the alpine zone at the highest (Bakkestuen *et al.* 2008). The mean annual precipitation ranges from 318 mm in east to 2204 mm in western parts, while the mean annual temperature ranges from -6.4°C at high elevations to 7.2°C at lowland locations.

Data collection (ref. Figure 3, step 1)

For the statistical analysis of elevational changes 57 treelines and 47 forest lines were remapped in the field between July and October from 2013 to 2017 in the mountains/valleys and aspects previously mapped by Resvoll-Holmsen (1918). Aas (1969), who like Resvoll-Holmsen (1918) measured elevation with a barometer, had previously remapped 37 of the treelines and 28 of the forest lines and these were also used in the analysis. In the remapping, we measured aspect with a compass at each observation point, divided into eight sectors of equal range, representing north, north-east, east, etc. Only the uppermost tree or forest was mapped in each aspect and coordinates and elevation was registered with a GPS. All characteristics (species, elevation, aspect, coordinates) of a forest were defined based on its uppermost tree. The georeferenced positions of all observations (from our remapping) used in the statistical analysis of elevational changes are depicted in Figure 1.

Definitions (ref. Figure 3, step 1)

Resvoll-Holmsen (1918) and Aas (1969) adopted Normann's treeline definition: "the highest point where predominantly upright, single trunked birch (or other species), higher than a man is found", while they categorized forest lines as "the highest limit of continuous forest". During remapping, the most important criteria considered for classification of trees were that they had a height of at least 2.5 m measured vertically from the ground and a tree crown established above the snow cover in winter periods. Forests were defined as groups of at least 15 trees, where only trees within 15 m of the other trees in a group were considered part of it. All criteria are listed in the unpublished guidelines from Bryn (2020) for mapping of TFLs (see Appendix for the guidelines).

Training data (ref. Figure 3, step 1 and 3)

Presence-only data for distribution modelling of present TFLs consisted of remapped georeferenced observations (see the section "Data collection" above, and Figure 1) and additional TFLs mapped in the field between July and October from 2013 to 2020 (Figure 2 shows a subset of the data, due to filtering described later). Some of the data were collected as part of another remapping project and the other were mapped for the first time, but all observations used as presences were collected by registering the same variables with the same definitions of TFLs (see the section "Definitions" above). Although the data used for distribution modelling and analysis of elevational changes also included observations from other years than 2017, that year was regarded as the most recent year in the results for all analysis due to practical purposes. As presences for distribution modelling of past TFLs, data from Resvoll-Holmsen (1918) were georeferenced with assistance from a digital elevation model (DEM) with 10×10 m resolution following the same procedure as Bryn and Potthoff (2017). Past TFL presence points were assumed to be located in the nearest grid cell relative to their corresponding remapped TFL presence points, provided that they were in the same mountain/valley, aspect and elevation as reported in Resvoll-Holmsen (1918). Uncertainties were measured as the distance from the presence points to their most distant possible positions, given the same mountain/valley, aspect and elevation. Analyses of past treelines, past forest lines, present treelines and present forest lines were further handled separately with the same procedure, unless otherwise specified. Presence points were rasterized in a grid covering the entire study area with 100×100 m resolution with maximum one presence point inside each grid cell. To reduce potential influences of sampling bias, the data was filtered by lowering the density of presence points geographically (Vollering *et al.* 2019a). From presence points within a subjectively chosen distance of 2 km in both latitude and longitude of other presence points, the presence point situated at the lowest annual temperature was retained, as it more likely represent a climatic tree- or forest line, which by definition are limited by temperature (Odland 1992). Presence points for 40 past treelines, 36 past forest lines, 115 present treelines and 109 present forest lines remained after filtering (Figure 2). Each modelled target was divided into a separate training data set with a 1:3 ratio of presences to randomly generated pseudo-absences (Støa *et al.* 2018) and five replicates were made for each set obtaining 20 training data sets in total. MaxEnt models generated with a ratio of 1:1 presences to pseudo-absences perform slightly worse than models generated with a ratio of 1:9 or lower (Grimmett *et al.* 2020), but a higher number of replicates compensates by increasing model performance when the presence to pseudo-absence ratio is high (Barbet-Massin *et al.* 2012).

Evaluation data (ref. Figure 3, step 2 and 3)

To evaluate present TFL models, georeferenced observations of 389 treelines and 354 forest lines in the study area were gathered from the citizen science project *Natur i endring* (www.naturiendring.no, accessed 11.01.21). These data were registered with a mobile application between February and October from 2018 to 2020 (Bryn *et al.* 2019) and were independently collected from the training data. Registering occurs through a questioning procedure to ensure that TFLs are classified according to the unpublished guidelines of TFL mapping from Bryn (2020) which also was used in this study. A recent analysis of the data showed that treelines and forest lines were classified correctly 57.7% and 63.2% of the times, respectively, while the altitudinal errors in terms of distance from the true line were 14.64 m for treelines and 8.84 m for forest lines (Torma 2019). Presence points were rasterized in a 100×100 m resolution grid covering the entire study area with maximum one presence point inside each grid cell and from presence points within a distance of 5 km in both latitude and longitude of other presence points, the presence point situated at lowest annual temperature was retained. Lower distance threshold for removal of close samples was used due to the higher classification error in the evaluation data. Presence points within 2 km in longitude and latitude of presence points in the training data were also removed to make the evaluation data more independent of the training data. Filtering reduced the sample sizes to 107 observations of treelines and 53 forest lines (Figure 2). Five replicates of each separate data set for treelines and forest lines were generated with a 1:3 ratio presences to randomly generated pseudo-absences.

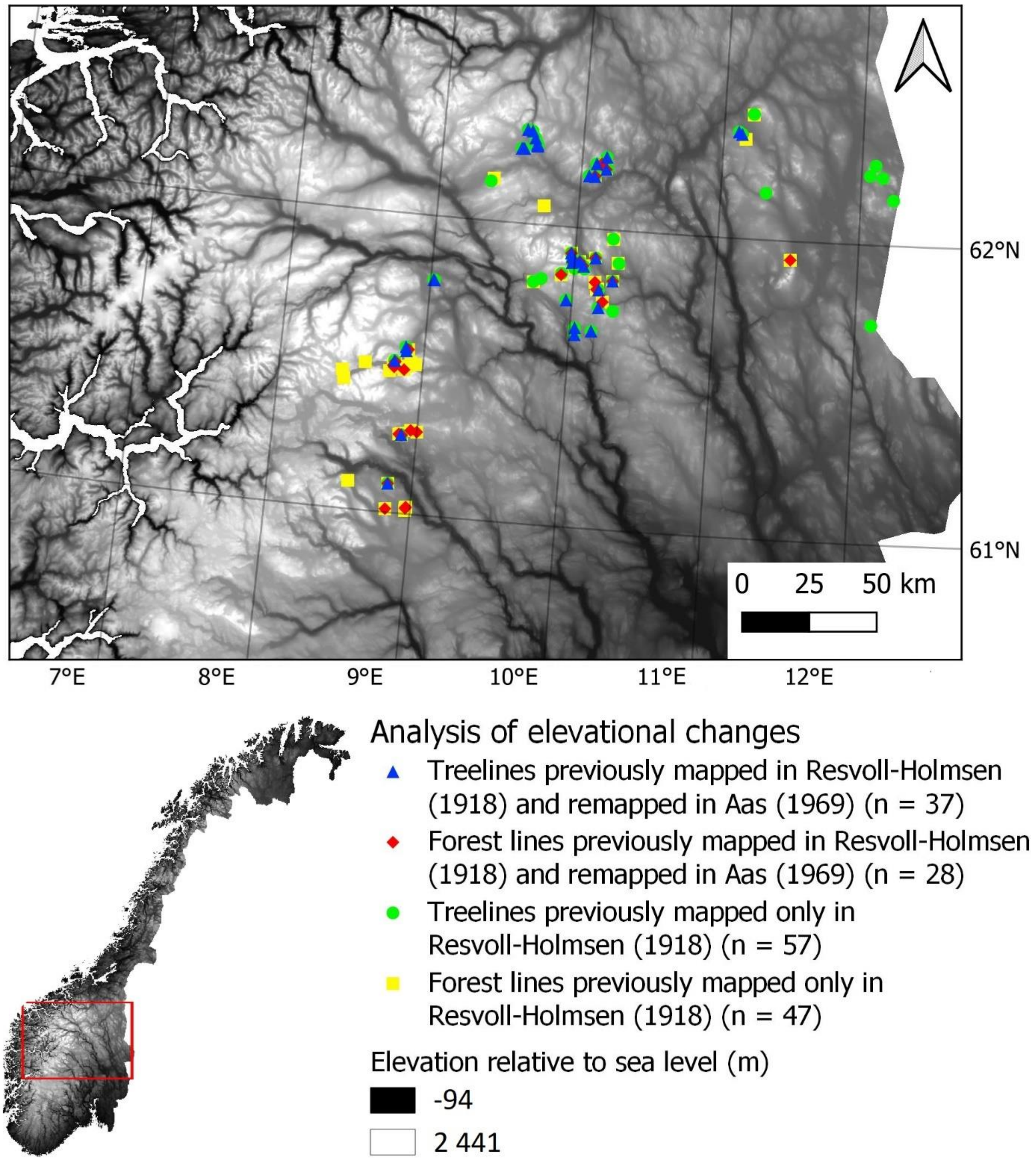

Figure 1. Location of the study area in south Norway based on a digital elevation model (DEM) derived from the Norwegian Mapping Authority with 100×100 m resolution. Observations of tree- and forest lines used in the analysis of elevational changes are marked with different symbols and elevation relative to sea level is indicated on a continuous scale, where whiter shades represent higher elevations. Note that many of these observations are the same as those depicted in Figure 2. Coordinate reference system: WGS 84/UTM zone 33N.

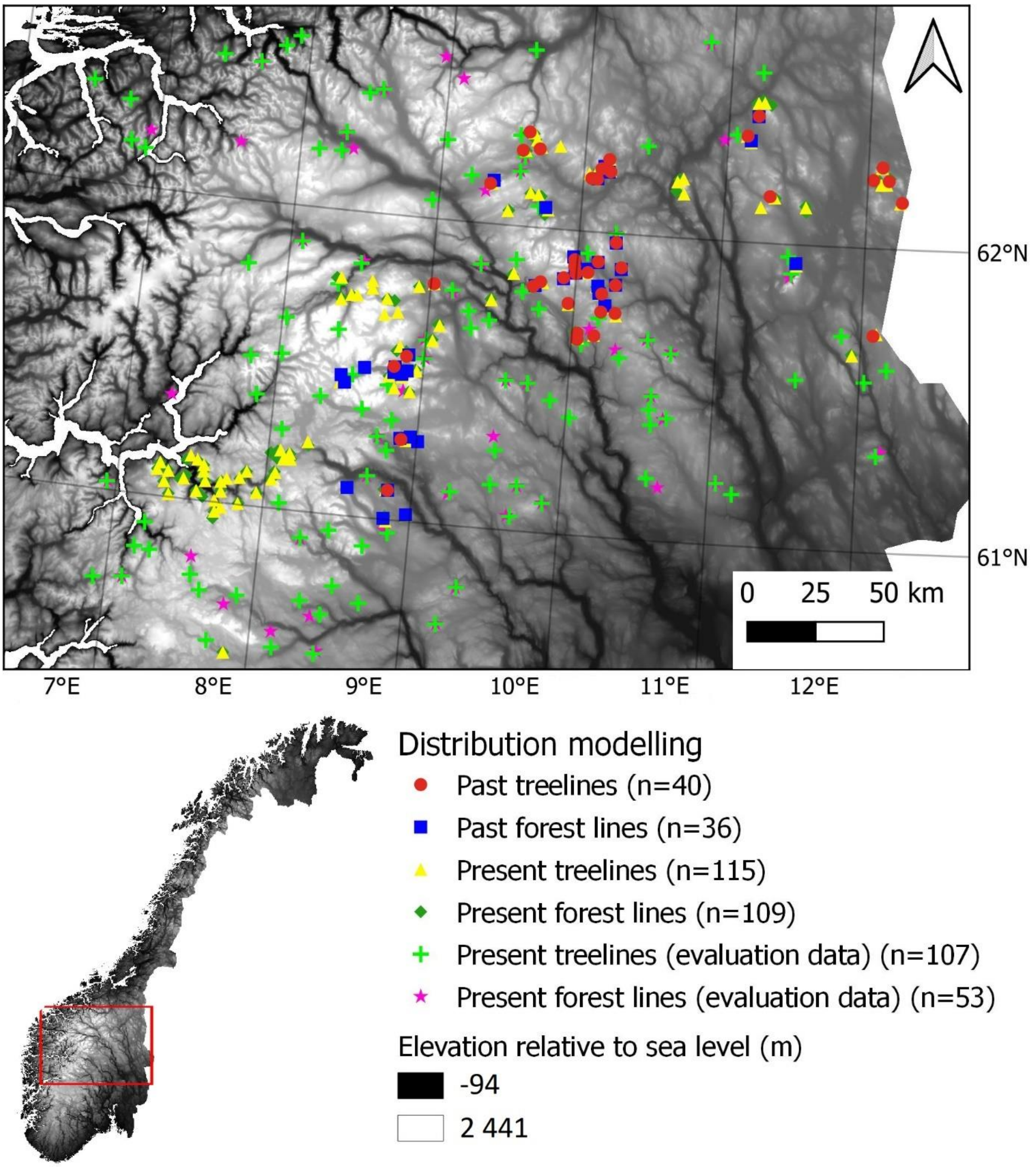

Figure 2. Location of the study area in south Norway based on a digital elevation model (DEM) derived from the Norwegian Mapping Authority with 100×100 m resolution. Observations of tree- and forest lines used for distribution modelling marked with different symbols and elevation relative to sea level is indicated on a continuous scale, where whiter shades represent higher elevations. Note that many of these observations are the same as those depicted in Figure 1. Coordinate reference system: WGS 84/UTM zone 33N.

Explanatory data (ref. Figure 3, step 4 and 5)

125 explanatory variables (EVs) covering the entire study area were derived from Horvath *et al.* (2019). These consist of climatic (monthly variables for mean temperature, extreme temperature and precipitation and 19 BIOLCLIM variables (Fick and Hijmans 2017) generated from these) and snow variables (monthly variables for snow covered area and snow water equivalent) obtained from interpolated weather station data (Lussana *et al.* 2016, Lussana *et al.* 2018) with 1×1 km resolution recorded daily between 2004 and 2014. They also include topographic variables derived from a DEM (upscaled to 100×100 m from 50×50 m) obtained from the Norwegian Mapping Authority, and geological and land cover variables. All the other EVs, except the topographical were further interpolated to 100×100 by Horvath *et al.* (2019). EVs considered uninformative were excluded along with all the categorical variables, which were mapped at low resolution. Uninformative EVs includes for example snow covered area in January that was 100% for almost all presence observations of TFLs. Kendall's rank correlation coefficients of 1000 random values from the entire study area were calculated for all pairs of remaining EVs and the less relevant EV from all pairs with $|\tau| > 0.7$ was excluded. Here, the degree to which the EV could be directly causing a response was considered. For instance, temperature was regarded as more direct than altitude because temperature is directly related to plant physiological processes (Tranquillini 1964), whereas altitude only serves as a proxy for the adiabatic change of atmospheric temperature (Körner 2007). Others, like the mean temperature of the warmest quarter were preferred based on literature (Helland 1912). The remaining set of 40 EVs consisted of snow, climatic and topographic types.

Model fitting and selection (ref. Figure 3, step 6-9)

Model fitting and selection was executed on all replicates of present and past TFL training data sets, 20 in total. Models were parameterized with the maximum entropy method using the "MIAmaxent" package (version 1.2.0) (Vollering *et al.* 2019b) in R version 4.0.3 (R Core Team 2021). The model selection consists of two steps, first selecting sets of derived variables (DVs) to represent each EV, then selecting from these sets of DVs to obtain a set of DVs that predict the distribution of the modelled target in the final model. DVs are single parameter transformation types of EVs, supposed to represent realistic response curves, or truncated ones (Halvorsen 2013). These are useful because species (but also TFLs= do not respond in a linear fashion to most variables, assuming that they are measured across the entire range of the species' tolerance. Instead, they are more likely to occur around an optimum value and decline towards higher and lower values (Halvorsen 2012). Frequency of observed presence (FOP) plots were made to guide the decision about which types of DVs to include (Vollering *et al.* 2019b). These plots show the FOP at selected intervals for a given EV in the data set, with a local regression line fitted to the points. They also include the estimated kernel density of values of the plotted EV in the data set, which at low density is an indication of high model uncertainty (Vollering *et al.* 2019b). Guided by the FOP plots, but also to avoid overfitted models only linear (L), monotonous (M) and three deviation types (D1, D2, D05: decreasing kurtosis from left to right) of DVs for each EV were fitted. The different deviation types represent unimodal responses with an optimum at the EV value with the highest frequency of presence, while the linear and monotonous type represent truncated response curves (Halvorsen *et al.* 2015). In both steps of the model selection, DVs were selected with a stepwise forward selection procedure using residual variation explained as selection criteria until reaching a significance threshold for the model, thereby obtaining parsimonious sets of DVs (Halvorsen 2013). Here, the likelihood ratio test for nested models was used to quantify residual variation explained by DVs and model significance. Low significance threshold ($\alpha = 0.001$) was used as the frequency of type I error (i.e., rejection of a true null hypothesis) increases with number of parallel tests in each step (Blanchet *et al.* 2008). The model output – probability ratio output (PRO) - indicates the probability of presence in each grid cell relative to the other grid cells in the study area (Halvorsen 2013) and are therefore not comparable among models.

In addition to using the entire set of EVs, model selection was also performed using a set of only snow and climatic variables to obtain a set of DVs for EVs for present and past TFL models used to estimate changes in area. Topographic variables, like slope inclination, curvature and topographic position index were left out because the uncertainty in the positions of past TFLs was substantially higher in longitudinal and latitudinal compared to altitudinal direction. In these directions, the topographic variables vary strongly on smaller scales, whereas the snow and climatic variables vary mostly with altitude. Because EVs for past conditions were lacking, we were unable to extrapolate the present models to past environmental conditions, which is usually done when predicting past or future distributions (for examples, see Svenning *et al.* (2008), Fløjgaard *et al.* (2009) or Jaeschke *et al.* (2013)). Instead, EVs with the same temporal range were used to predict present and past TFLs but with different presence points. Estimation of model coefficients for past TFL models with fixed EVs obtained from modelling of present TFLs without topographic variables was carried out with the same procedure as for present TFL modelling.

Model evaluation (ref. Figure 3, step 10)

The predictive power of each final model of present TFLs was determined by calculating the area under the receiver operator curve (AUC-ROC) and the area under the receiver precision-recall curve (AUC-PR) for all five replicates of the evaluation data sets. The resulting AUC-ROC and AUC-PR scores were separately averaged for each final model, and the model with highest average AUC-ROC score was assumed to represent the best model. When using presence-only data, AUC-ROC is a measure of the model's ability to discriminate presence from pseudo-absence observations (Halvorsen 2013). The discrimination ability increases from slightly higher than 0 to slightly lower than 1, calculated on presence-only data, where 0.5 is no better than random (Phillips *et al.* 2009). Although AUC-PR was ignored when selecting among models, it was calculated as an alternative model performance measure to AUC-ROC, because AUC-ROC scores tend to inflate when the modelled targets are rare, whereas AUC-PR are independent of the number of true absence observations (Sofaer *et al.* 2019). AUC-PR is a measure of precision (the ratio of correctly predicted presences to all predicted presences) as a function of recall (the ratio of correctly predicted presences to all observed presences), and theoretically, model performance increases from 0 to 1, where scores equal to the sample prevalence (the ratio of presence observations to total observations) is no better than random (Sofaer *et al.* 2019). However, the minimum score of AUC-PR also depends on sample prevalence and is 0.137 when it equals 0.25 as in all our data sets, calculated with equations from Boyd *et al.* (2012). Since the data sets have identical prevalence AUC-PR is comparable among models (Boyd *et al.* 2012).

Because independently collected occurrence data from 1917 was lacking, past TFL models were evaluated by 4-fold cross-validation (Fushiki 2011). This method consists of, without replacement, splitting the training data set randomly into four subsets of equal size with the same ratio of presence to pseudo-absence observations. Three of the subsets are then used to estimate model coefficients for models with fixed parameters, and the following model is used to predict values for the observation points in the remaining validation subset. This is repeated until all subsets have been used for validation and the sum of prediction errors for all validation test subsets is the total prediction error, used to measure model performance. The lowest total prediction errors were used to determine which of the final past TFL models were best.

Estimation of changes in area (ref. Figure 3, step 11 and 12)

To estimate changes in land cover of TFLs, grid cells with the highest prediction value within 20×20 km grids wall-to-wall covering the entire study region were extracted from the best models of present TFLs without topographic variables and past TFLs. Although the model output is not comparable among models, we assume that the highest local prediction values in each map represent the most likely elevation of TFLs locally. The elevation of TFLs in all grid cells (100×100 m) in the study area was interpolated using elevation from the extracted cells, obtained from a DEM, as interpolation attribute with inverse distance weighting (IDW) (Lu and Wong 2008) in QGIS version 3.16.3 (QGIS Development Team 2021). With IDW, values in unsampled grid cells are interpolated under the assumption that they are more similar to values of sampled nearby grid cells rather than distant ones, and the similarity decays with distance. The strength of this decay is determined by and inversely related to a distance coefficient weight, which is usually determined *a priori* (Lu and Wong 2008). Therefore, the same weight (P=3.5) was used in interpolation of all models, which was determined by experimenting. To obtain binary maps of TFL distributions the resulting interpolated raster layer was subtracted from the DEM raster layer, and all grid cells with values above and below zero were regarded as above and below the TFLs, respectively. Raster layers with changes in area were generated by subtracting the raster layers of binary transformations of past TFL models from the raster layers of binary transformations of present TFL models (modelled without topographic variables). Changes in area were estimated by subtracting the number of grid cells with advance from the number of grid cells with decline in the raster layer. Areas above and below the TFLs were calculated from the binary raster maps and percent reduction of areas above the TFLs was calculated by dividing the area above each line by net changes in land cover of the corresponding TFL.

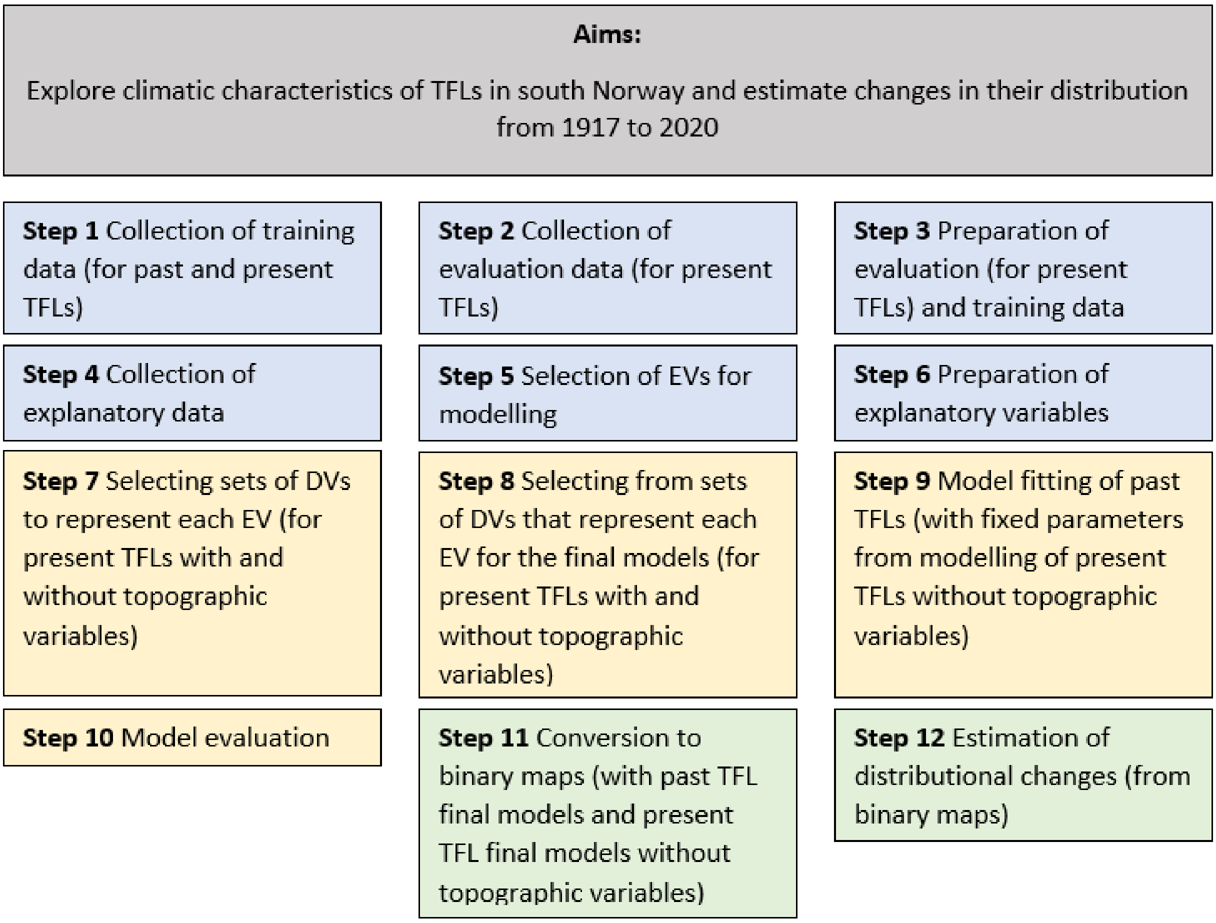

Figure 3. Aims and conceptual model of the methodology related to distribution modelling. Colours indicate groups with steps involved in data collection and preparation (blue), statistical modelling (yellow) and further use of the model (green), similar to Halvorsen (2012). The steps do not always follow a linear order. TFL = tree- and forest line, EV = explanatory variable, DV = derived variable

Statistical analysis of elevational changes

Mean and standard deviation of changes in elevation of remapped TFLs was calculated and mean elevational changes were tested for significance with a two-tailed Student's t-test (Al-Achi 2019). Elevational movement per year was calculated as the mean elevational change divided by the average number of years between first and second registry. Percentage advance and decline was also calculated, while stability, defined as 0 m elevational change, was ignored as it only comprised a small proportion.

Results

The main findings of this study were that TFLs in south Norway generally advanced upslope from 1917 to 2017. The climatic and topographic variables were able to predict the present TFL distribution in the study area reasonably well, which were shown to depend strongly on temperature. We also estimated large changes in the distribution of treelines between 1917 and 2017, and somewhat smaller changes in forest line distribution.

Modelled distributions

The present distribution of treelines modelled with topographic variables was predicted by mean temperature of the warmest quarter, maximum temperature in November, snow water equivalent in March and slope inclination in the respective order of decreasing fraction of total variation accounted for (FTVA) in the model (Table 1). All derived variables (DVs) were of the D2 type, and thus, treelines responded unimodally to all the predictors (Table 1; Figure 4). The frequency of observed presence (FOP) plots for almost all the explanatory variables (EVs) had high estimated kernel density in the range where probability ratio output (PRO) values were high (Figure 4a-c and 5a-c). An exception was slope inclination, where the density was low in the upper range (Figure 4d and 5d), which makes the model less reliable in this range (Vollering *et al.* 2019b). With decreasing order in terms of FTVA, the forest line distribution modelled with topographic variables in 2017 was predicted by mean temperature of the warmest quarter, slope inclination and minimum temperature in November, which also were represented by DVs of the D2 type (Table 1). As for treelines, all the EVs had high estimated kernel density in the range with high PRO values in the model (Figure 6a, 6c, 7a and 7c), except for slope inclination that had low data density in the upper range (Figure 6b and 7b).

The distributions of both present TFL models were explained almost exclusively by temperature predictors when they were modelled without topographic variables (Table 1). Notably, the minimum temperature in November from the distribution of forest lines, was replaced by the maximum temperature in November when topographic variables were excluded (Table 1). Past and present treelines modelled without topographic variables were situated at a position where the current mean temperature of the warmest quarter is 9.9°C and 8.8°C, respectively, whereas it is 9.4°C in the location of past forest lines and 9.2°C in that of present forest lines modelled without topographic variables (Table 1). The current maximum temperature in November and snow water equivalent in March is higher in the locations of past than present treelines modelled without topographical variables, while past forest lines were situated at a position where the current maximum temperature in November is lower compared to what it is in their positions today (Table 1).

Snow water equivalent in March lowered PRO values around the glacier Jostedalsbreen, west in the study area in all treeline models (Figure 8, Appendix: Figure S1 and S7). In all models, the magnitude of PRO values was unequally distributed with a similar pattern across the study area, with high PRO values in a transect from south-west to north-east of the study region, whereas outside this transect they were generally low (Figure 8 and 9; and Appendix: Figure S1, S4, S7 and S10). Due to the lack of slope inclination as a predictor, the modelling of present TFLs without topographic variables and past TFLs resulted in predictions of less spatial small-scale variation (Appendix: Figure S1, S4, S7 and S10).

Present treelines and present forest lines modelled with topographic variables obtained AUC-ROC scores of 0.800 and 0.791, respectively (Table 2). When topographic variables were excluded from modelling AUC-ROC scores decreased slightly and the resulting scores for treelines and forest lines were 0.788 and 0.768, respectively (Table 2). AUC-PR scores coincided well with AUC-ROC scores, and all the best models evaluated by AUC-ROC, except the present treeline model without topographic variables, also scored highest with AUC-PR (Appendix: Table S4, S8, S12 and S16).

Table 1. Explanatory variables, their estimated optima, transformations and fraction of total variation accounted for (FTVA) in the final models of past and present tree- and forest lines (with and without topographic variables) in south Norway. L = linear, M = monotonous, D = deviation (D1, D2 or D05)

Present treelines (with topographic variables)			
Explanatory variables	**Current conditions at georeferenced positions**	**Transformation**	**FTVA**
Mean temperature of warmest quarter	8.8°C	D2	0.648
Maximum temperature in November	6.1°C	D2	0.192
Snow water equivalent in March	2608.0 mm	D2	0.096
Slope inclination	0.5 (ratio)	D2	0.064
Present treelines (without topographic variables)			
Mean temperature of warmest quarter	8.8°C	D2	0.692
Maximum temperature in November	6.1°C	D2	0.205
Snow water equivalent in March	2608.0 mm	D2	0.103
Past treelines (without topographic variables)			
Mean temperature of warmest quarter	9.9°C	D2	-
Maximum temperature in November	6.9°C	D2	-
Snow water equivalent in March	2805.2 mm	D2	-
Present forest lines (with topographic variables)			
Mean temperature of warmest quarter	8.9°C	D2	0.810
Slope inclination	0.6 (ratio)	D2	0.100
Minimum temperature in November	-20.5°C	D2	0.090
Present forest lines (without topographic variables)			
Mean temperature of warmest quarter	9.2°C	D2	0.782
Maximum temperature in November	6.4°C	D2	0.218
Past forest lines (without topographic variables)			
Mean temperature of warmest quarter	9.4°C	D2	-
Maximum temperature in November	6.2°C	D2	-

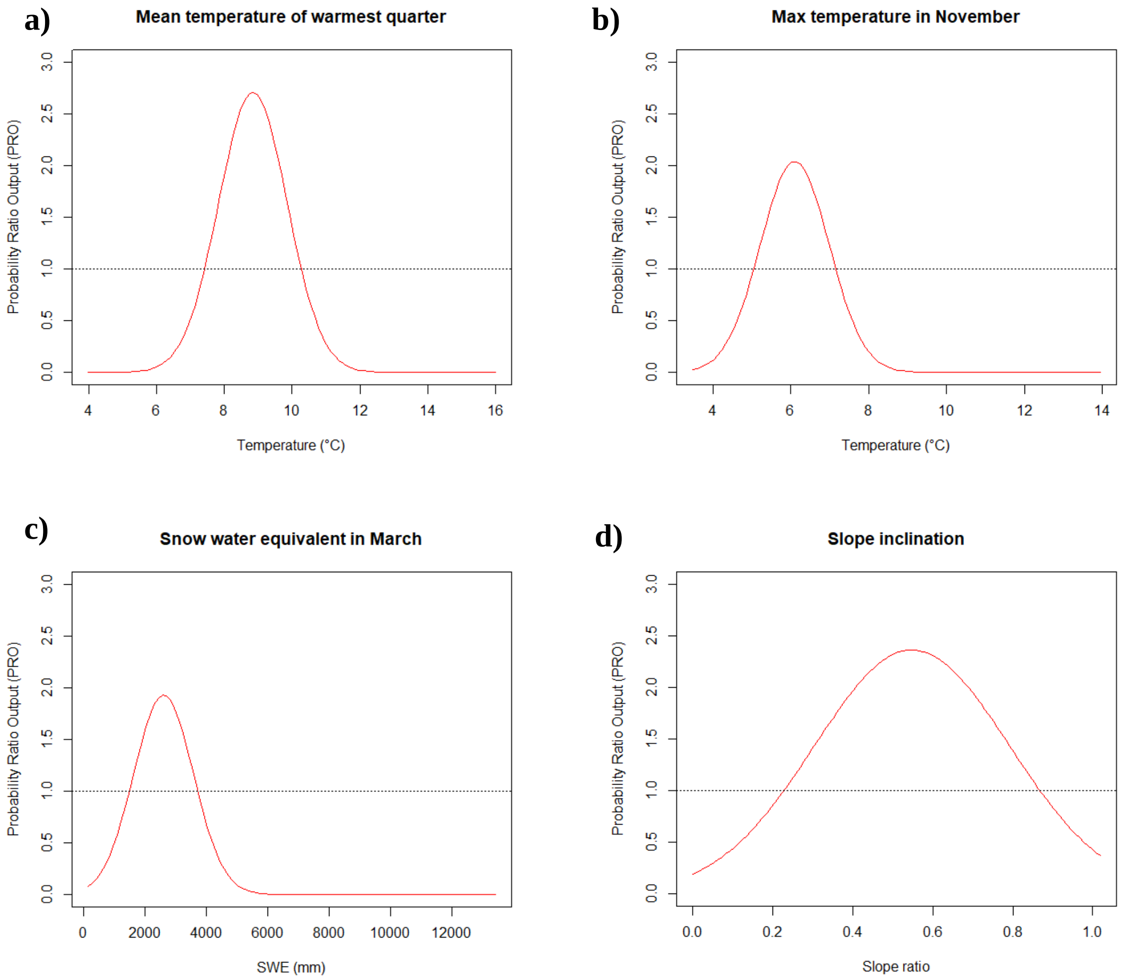

Figure 4. Response plots showing probability ratio output (PRO) values as a red line for the **(a)** mean temperature of the warmest quarter, **(b)** maximum temperature in November, **(c)** snow water equivalent in March and **(d)** slope inclination in the model of present treelines, modelled with topographic variables (see Table 1 for details, and Figure 5 for frequency of observed presence (FOP) plots).

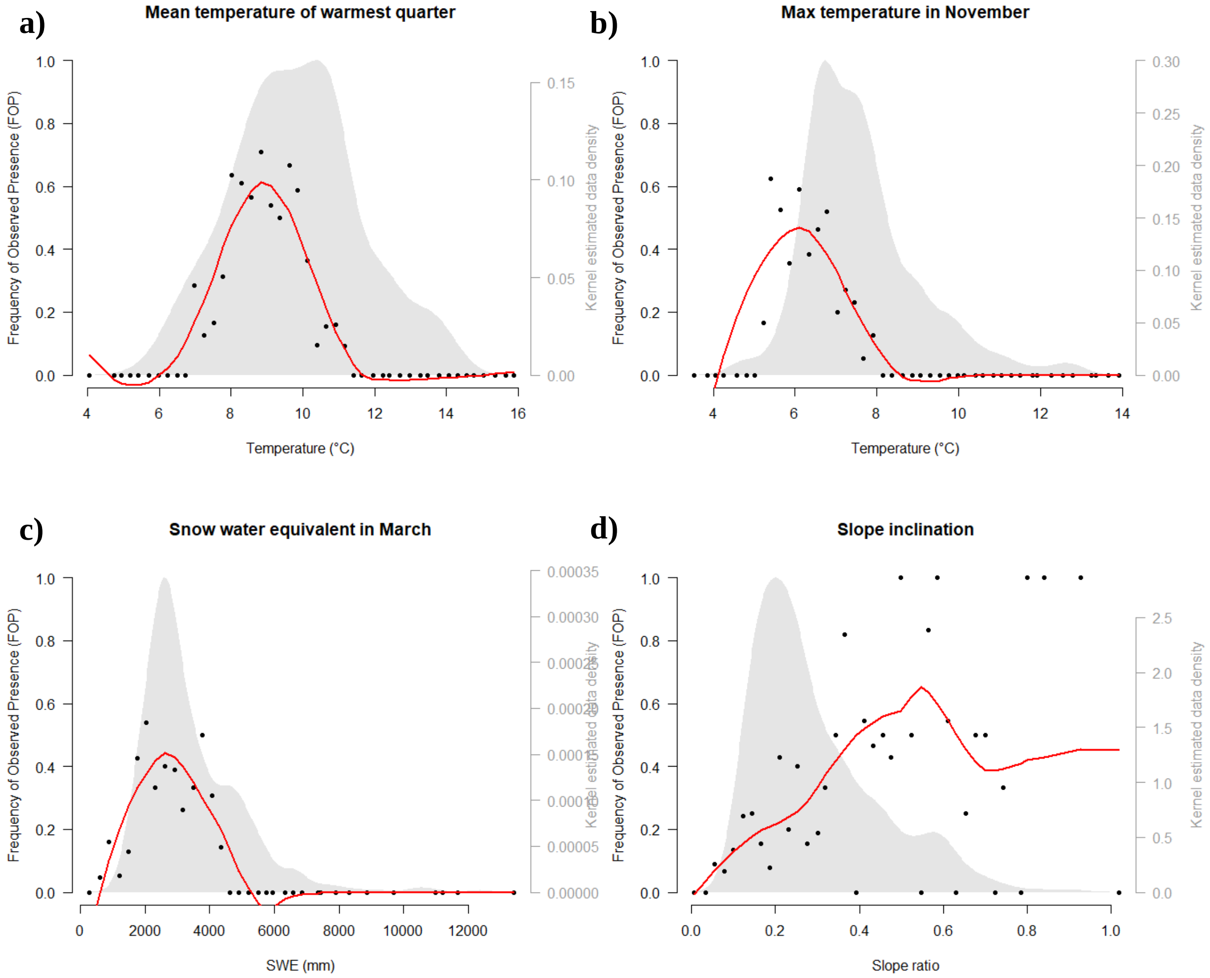

Figure 5. Frequency of observed presence (FOP) plots of present treelines modelled with topographic variables (see Table 1 for details, and Figure 4 for modelled response of the predictors) for the **(a)** mean temperature of the warmest quarter, **(b)** maximum temperature in November, **(c)** snow water equivalent in March and **(d)** slope inclination presented as black dots. The red line is fitted to the points by a local regression with the MIAmaxent package and the density of values for each explanatory variable in the data set is presented in grey.

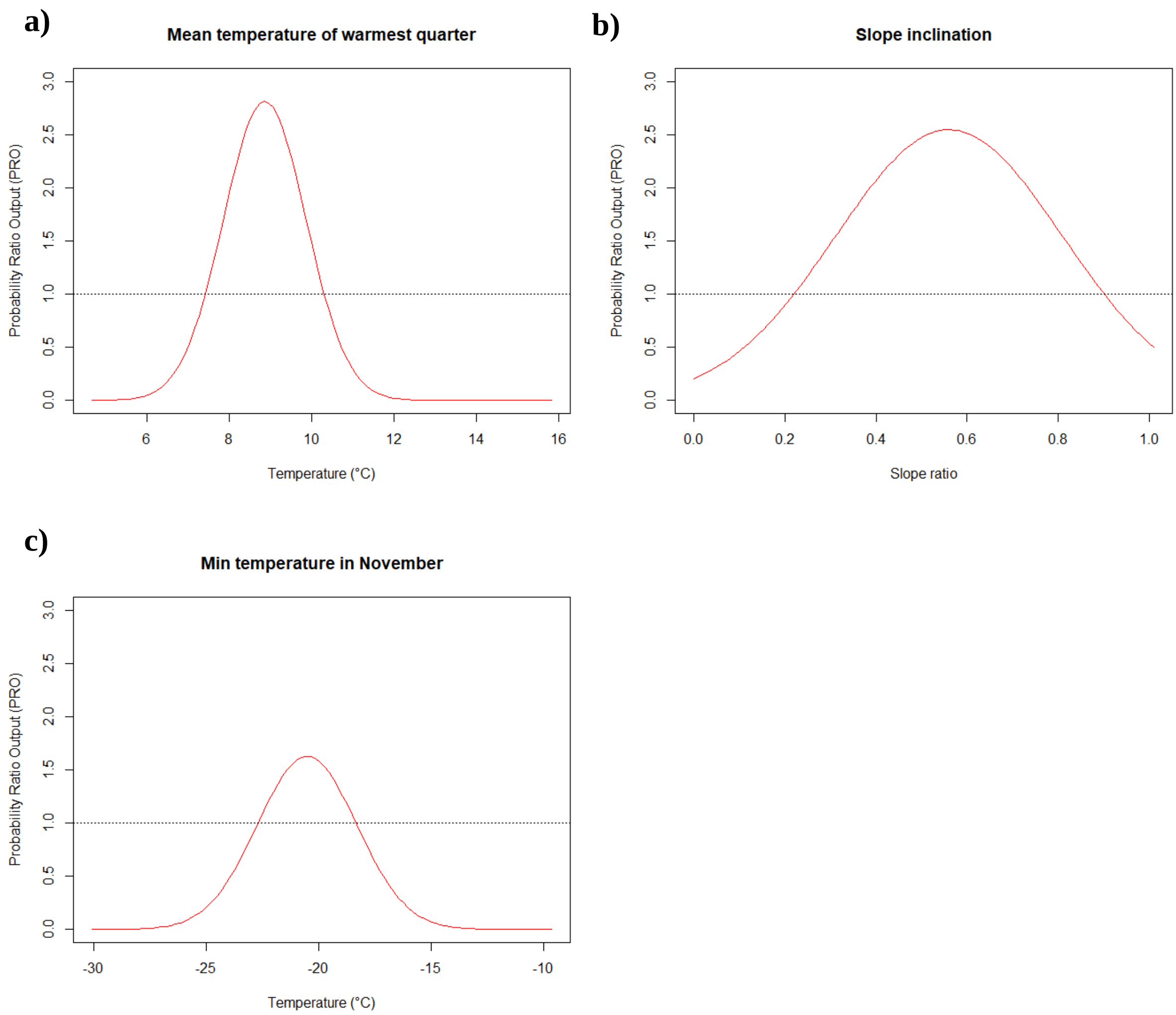

Figure 6. Response plots showing probability ratio output (PRO) values as a red line for the **(a)** mean temperature of the warmest quarter, **(b)** slope inclination and **(c)** minimum temperature in November in the model of present forest lines, modelled with topographic variables (see Table 1 for details, and Figure 7 for frequency of observed presence (FOP) plots).

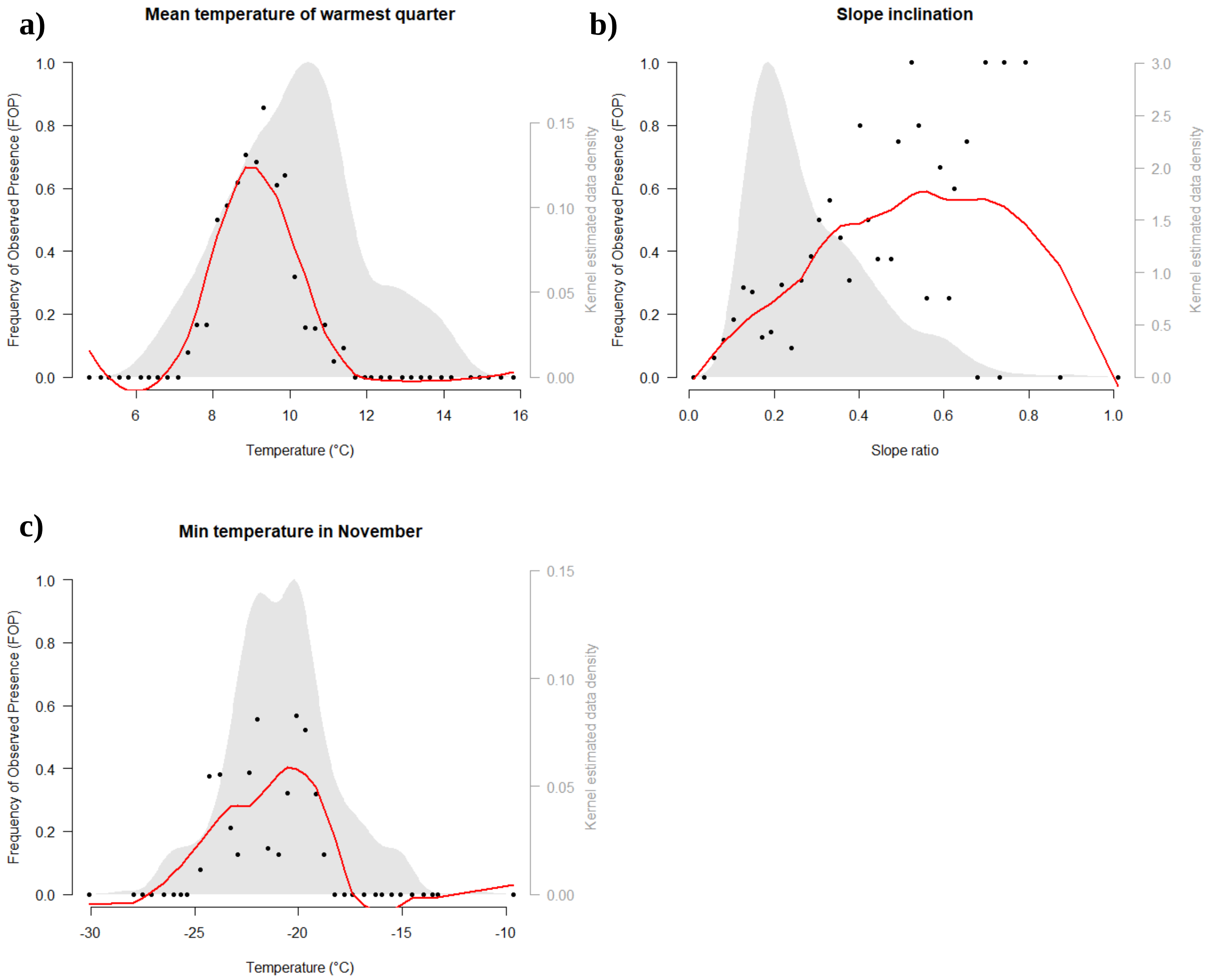

Figure 7. Frequency of observed presence (FOP) plots of present forest lines modelled with topographic variables (see Table 1 for details, and Figure 6 for modelled response of the predictors) for the **(a)** mean temperature of the warmest quarter, **(b)** slope inclination and **(c)** minimum temperature in November presented as black dots. The red line is fitted to the points by a local regression with the MIAmaxent package and the density of values for each explanatory variable in the data set is presented in grey.

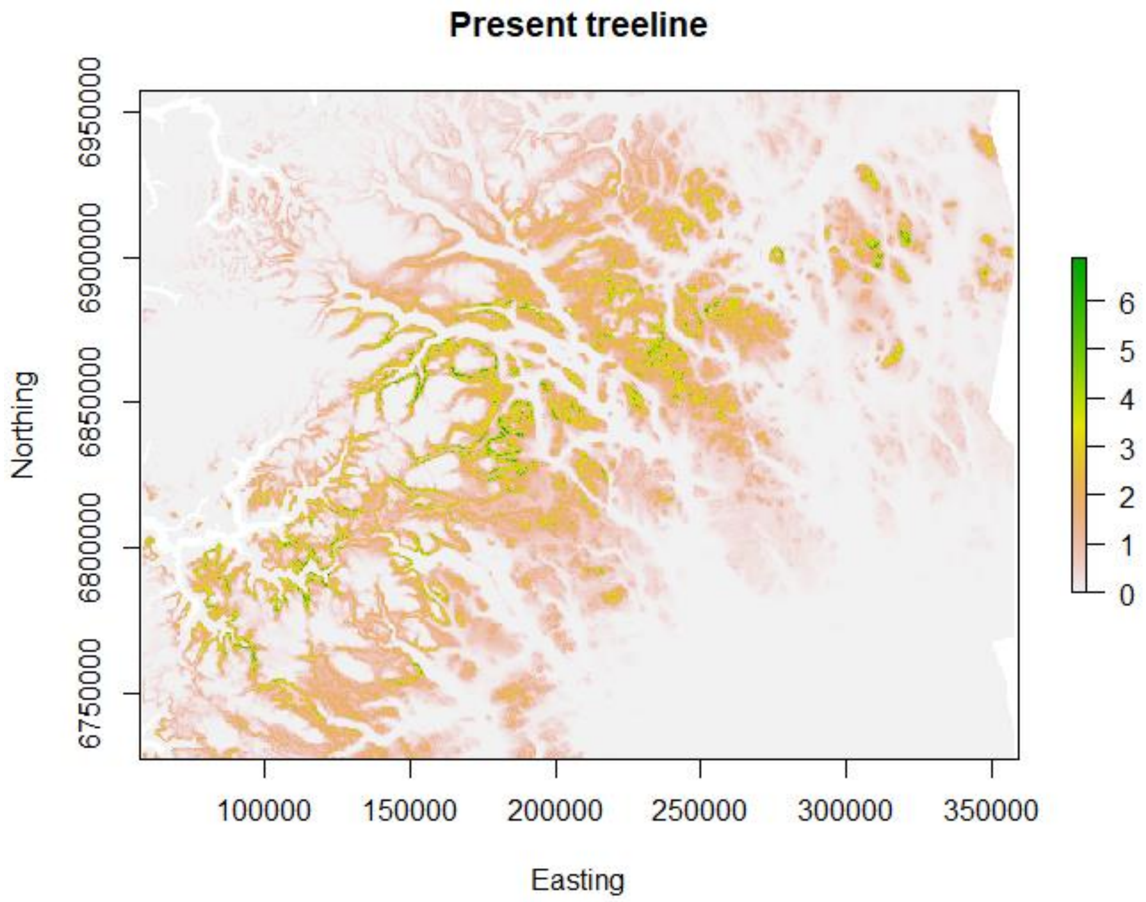

Figure 8. Modelled distribution of present treelines with topographic variables (see details in Table 1, Figure 4 for modelled response of the predictors) in south Norway with probability ratio output (PRO) values indicated on a continuous scale, where white indicates low relative probability of presence and green indicates high. Because the values are relative, a given value in this model may not correspond to the same value from another model. Coordinate reference system: WGS 84/UTM zone 33N.

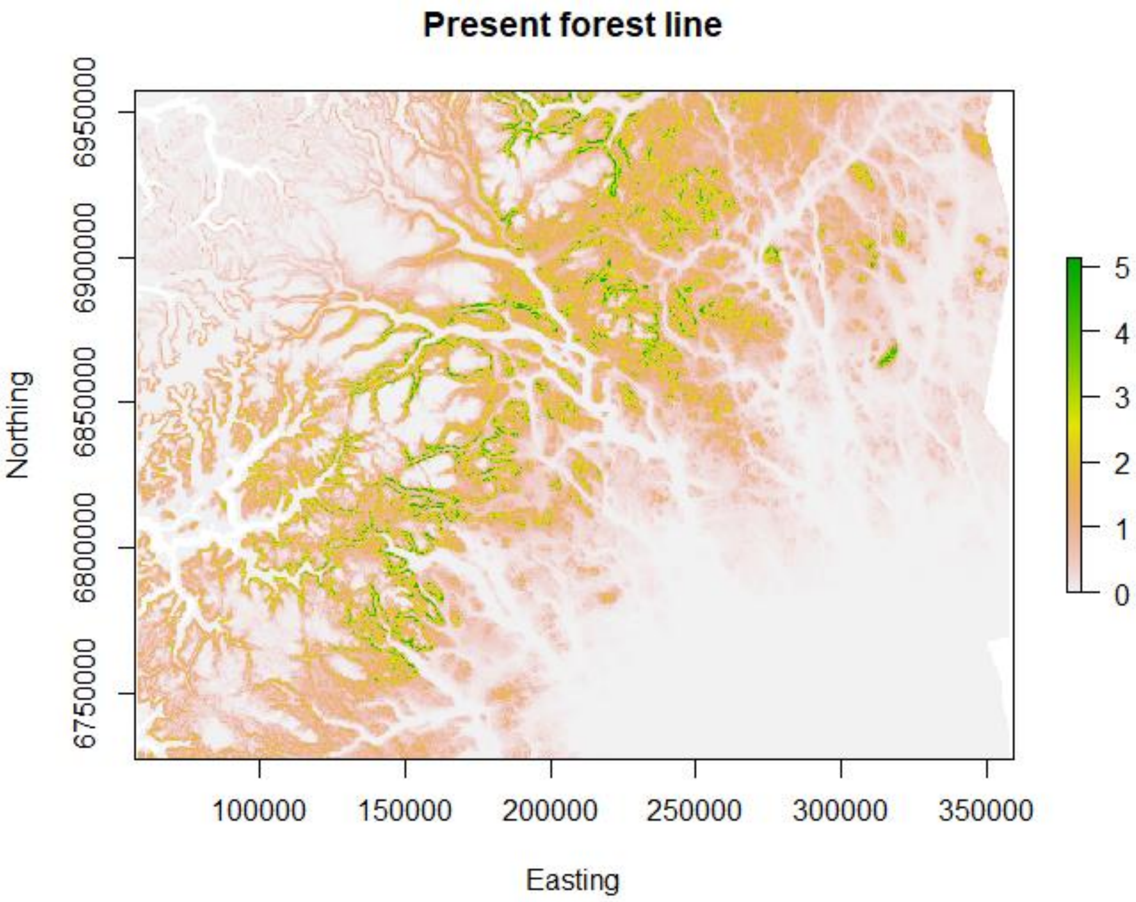

Figure 9. Modelled distribution of present forest lines with topographic variables (see details in Table 1, and Figure 6 for modelled response of the predictors) in south Norway with probability ratio output (PRO) values indicated on a continuous scale, where white indicates low relative probability of presence and green indicates high. Because the values are relative, a given value in this model may not correspond to the same value from another model. Coordinate reference system: WGS 84/UTM zone 33N.

Table 2. Model performance of final models of past and present tree- and forest lines, with and without topographic variables (see Table 1 for details). Present tree- and forest line models were evaluated by the area under the receiver operator characteristic (AUC-ROC) and the area under the precision-recall curve (AUC-PR), while past tree- and forest line models were evaluated by total prediction error.

	Present treelines	Present forest lines	Present treelines (without topographic variables)	Present forest lines (without topographic variables)	Past treelines	Past forest lines
Total prediction error	-	-	-	-	99.28	106.55
AUC-ROC	0.800	0.791	0.788	0.768	-	-
AUC-PR	0.562	0.493	0.530	0.462	-	-

Distributional changes

From 1917 to 2017 the treeline land cover was estimated to increase from 43 086 to 49 774 km^2, corresponding to a net increase in land cover of 6 688 km^2, and a reduction of 27.6% areas above the treeline (Table 3). The forest line land cover in 1917 was estimated to be 46 057 km^2 (larger than the treeline land cover in 1917) and increased to 47 194 km^2 in 2017 (Table 3). Both due to less advance and more decline the net land cover increase of forest lines was smaller in comparison to that of treelines, in total 1 137 km^2, which was a 5.3% decline in areas above the forest line (Table 3). Treeline land cover increased almost throughout the entire study region and most of the decline were in small areas at the margins (Figure 11). The largest declines in forest line land cover were mainly in south-east, whereas advances were distributed throughout the region (Figure 12). In mountain areas where there has been a change of land cover, TFL land covers have changed less in steeper than gentler slopes. (Figure 11 and 12).

Table 3. Estimates of areas above and below tree- and forest lines in 1917 and 2017, changes in land cover of tree- and forest lines and areas above them, between the two time points (see Appendix: Figure S13 for binary maps used for these estimates).

	Areas below (km^2)		Areas above (km^2)		Areal expansion (km^2)	Areal declin e (km^2)	Net land cover increase (km^2)	Percent decline of area above lines (%)
	1917	2017	1917	2017				
Treelines	43 086	49 774	24 266	17 578	6 841	153	6 688	27.6
Forest lines	46 057	47 194	21 296	20 158	1 989	859	1 137	5.3

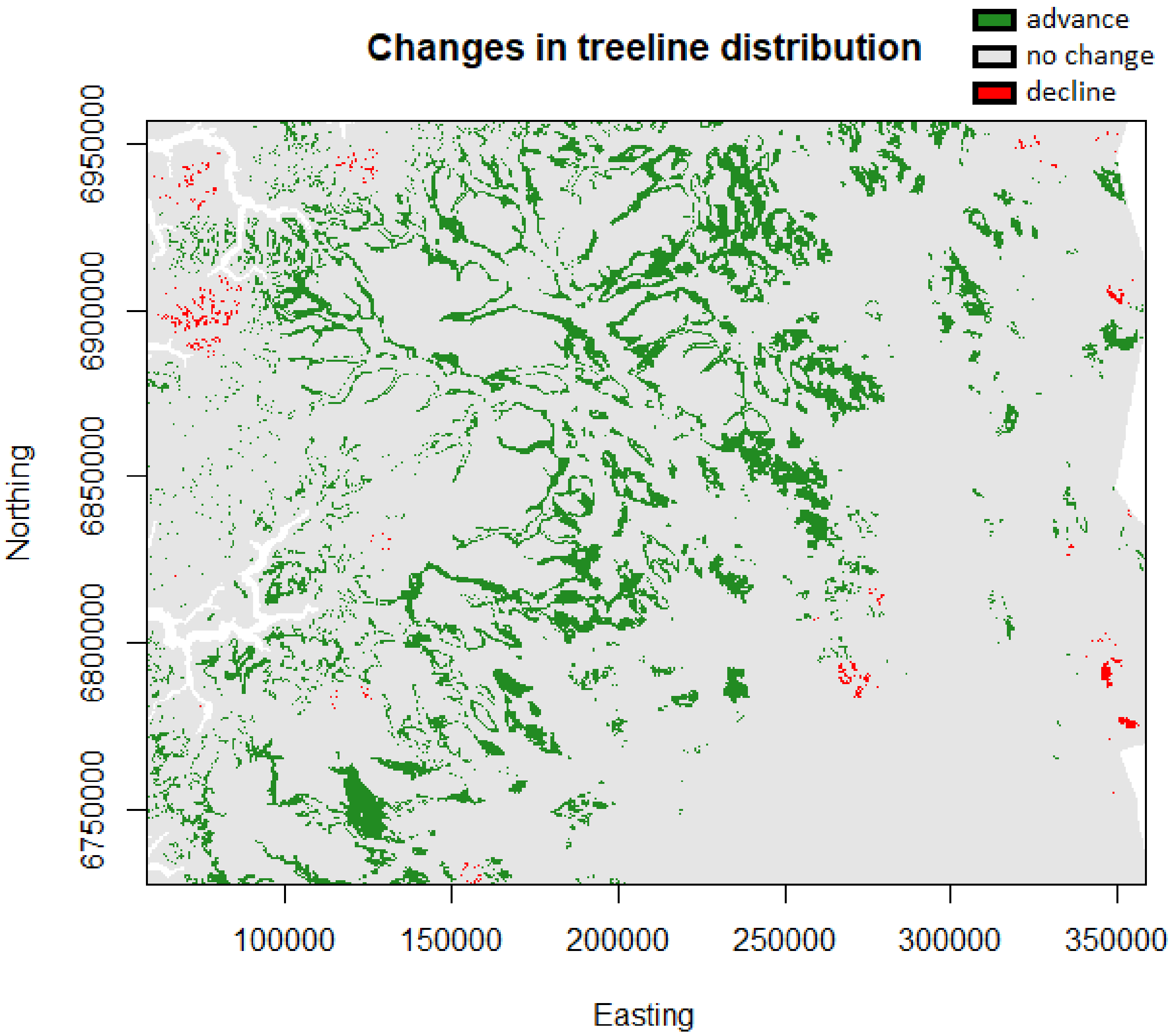

Figure 11. Changes in treeline distribution in south Norway from 1917 to 2017 with advance indicated in green, grey as no change and decline in red (see Table 3 for estimates). The map is based on differences between past and present treeline models, modelled without topographic variables (see Appendix: Figure S1 and S7), where values are relative. Thus, the models are not comparable, but the maps (Appendix: Figure S13) used to calculate changes are, under the assumption that the highest local prediction values in each model represent the most likely elevation of tree- and forest lines locally. Coordinate reference system: WGS 84/UTM zone 33N.

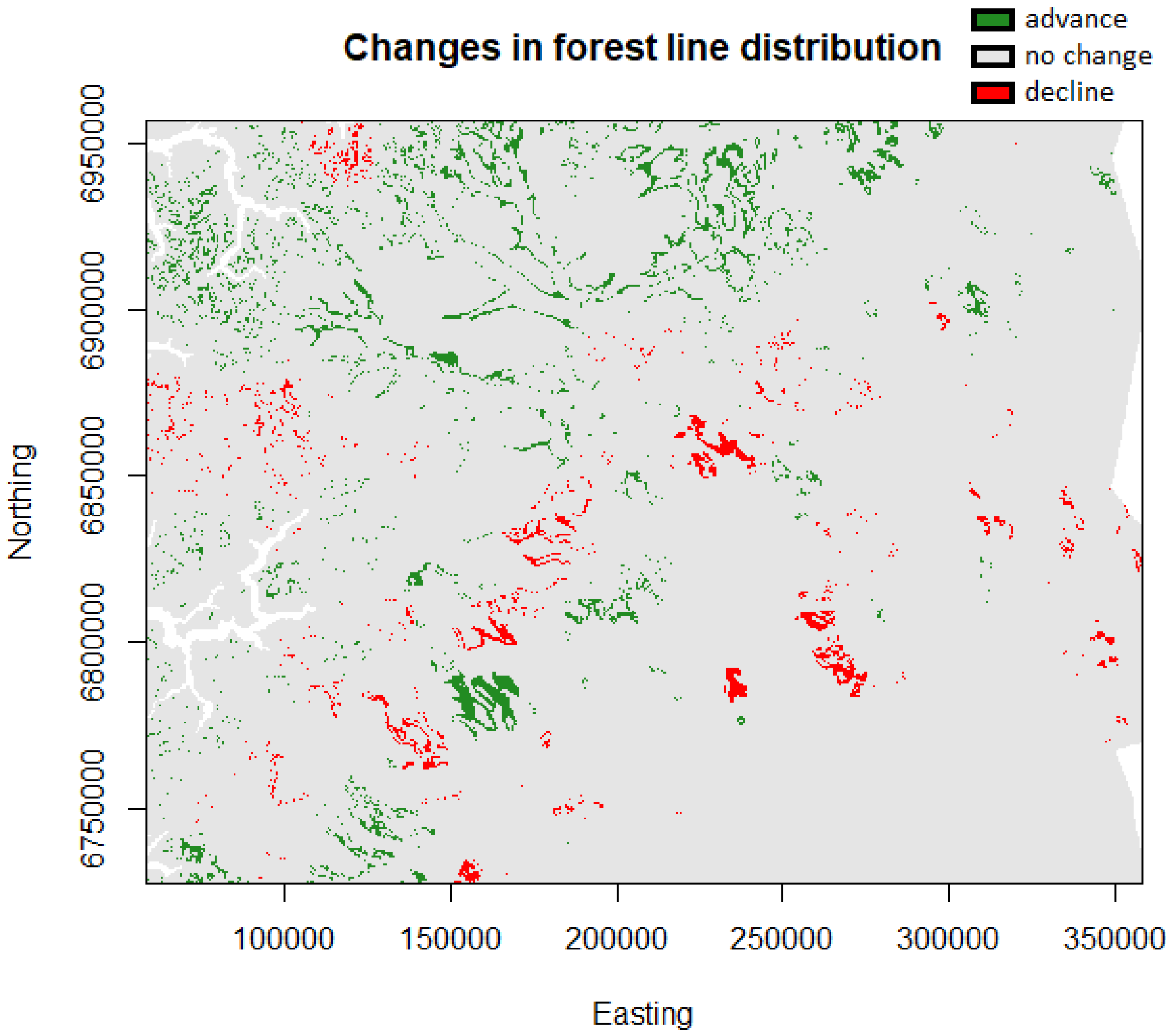

Figure 12. Changes in forest line distribution in south Norway from 1917 to 2017 with advance indicated in green, grey as no change and decline in red (see Table 3 for estimates). The map is based on differences between past and present forest line models, modelled without topographic variables (see Appendix: Figure S4 and S11), where values are relative. Thus, the models are not comparable, but the maps (Appendix: Figure S13) used to calculate changes are, under the assumption that the highest local prediction values in each model represent the most likely elevation of tree- and forest lines locally. Coordinate reference system: WGS 84/UTM zone 33N.

Elevational changes

On average, treelines (51±44 m, Student's t-test: $p < 0.001$, 0.53 m/year) and forest lines (36±41 m, Student's t-test: $p < 0.05$, 0.36 m/year) in the region have advanced upslope from 1917 to 2017. Although there was high variation in elevational changes for individual TFLs, few declined (Table 4). The largest elevational advances and declines for individual treelines were 192 m and 33 m, while they were 145 m and 38 m for individual forest lines. Large differences were observed between the first to second and the second to third mapping, with no significant trend in TFL movement between 1917 and 1967 and a nearly equal percentage of advance and decline in TFL elevation (Table 4). From 1967 to 2017 treelines (47±36 m, Student's t-test: $p < 0.05$, 0.99 m/year) and forest lines (30±27 m, Student's t-test: $p < 0.005$, 0.62 m/year) advanced strongly, and almost all individual TFLs advanced (Table 4). In all periods, treelines advanced upwards at a higher rate than forest lines, and there was high variation in TFL movement with at least some percent decline (Table 4).

Table 4. Statistical analyses of elevational changes in treelines and forest lines between 1917 and 2017 in south Norway. Note that percentage advance and decline of forest lines from 1917 to 1967 only adds up to 97% due to 3% stability, defined as 0 m elevational movement.

Treelines							
Period (year)	**n**	**Mean**	**SD**	**p-value**	**Movement/year**	**% advance**	**% decline**
1917-1967	37	3.89	37.10	.	0.08	54	46
1967-2017	37	47.27	36.07	*	0.99	97	3
1917-2017	57	51.49	43.64	***	0.53	91	9
Forest lines							
Period (year)	**n**	**Mean**	**SD**	**p-value**	**Movement/year**	**% advance**	**% decline**
1917-1967	28	-4.86	39.69		-0.10	43	54
1967-2017	28	29.86	26.93	**	0.62	96	4
1917-2017	47	35.72	41.13	*	0.36	81	19

p-values calculated for mean elevational changes (two-tailed Student's t-tests): 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Discussion

Several indicators of improved growth conditions have been reported in mountains worldwide the last century, which includes increased stand density, and enhanced growth and recruitment of trees (Camarero and Gutiérrez 2004, Gehrig-Fasel *et al.* 2007, Hofgaard *et al.* 2009, Gaire *et al.* 2014). Another trend is the advance of TFLs in the northern Hemisphere (Harsch *et al.* 2009, Rees *et al.* 2020), including Norway (Bryn and Potthoff 2018), which is supported by our analysis of TFL elevational changes and estimations of their distributional changes in south Norway since Resvoll-Holmsen mapped TFLs in 1917.

Ecology of TFLs

It is generally accepted that summer temperature is fundamental to TFL distribution from local to global scales (Körner 1998, Holtmeier and Broll 2005). The growth limitation hypothesis suggests that trees due to low temperature are limited by conversion of non-structural carbohydrates into supportive tissues (Körner and Paulsen 2004). In Norway, summer temperature has also been identified as the primary controlling factor of TFL distribution, which has shown strong correlation with several summer temperature indicators like the mean temperature of the three warmest months, mean temperature of the warmest quarter and the maximum temperature of the warmest month (Helland 1912, Aas 1969, Bryn 2008).

Outside the growing season, the effect of temperature for the survival of trees have been well documented, but is thought to be less important for determining TFL distribution (Körner 1998). In northern Alaska and the Alps, radial growth of tree rings in the treeline ecotone the last two centuries was positively correlated with the autumn temperature of the previous year (Garfinkel and Brubaker 1980, Oberhuber 2004). Oberhuber (2004) suggests that warm temperatures in the previous autumn might promote carbon storage and growth of mycorrhizal roots by impeding soil freezing. In addition, autumn temperature may serve as a proxy for freeze-thaw cycles (Charrier *et al.* 2014) or accumulation of photosynthates for the following growing season (Garfinkel and Brubaker 1980). However, many of these factors are primarily relevant for evergreen trees, which only formed 6% of the treelines and none of the forest lines used as presence observations in modelling. More investigation is needed to understand the relationship between autumn temperature and deciduous TFLs.

Inclusion of slope inclination allowed the models to predict more heterogenous TFL distributions at smaller scales and predicted the highest suitabilities at medium inclinations.

Trees and forests at low inclinations are more susceptible to human impact and grazers, as they are often more accessible (Kjällgren and Kullman 1998, Wehn *et al.* 2011). At high inclinations trees and forests might be prevented from establishing due to frequent disturbances from mass wasting or avalanches (Holtmeier and Broll 2005). Slope inclination might also serve as a proxy for solar radiation, wind exposure, soil conditions, soil moisture and snow distribution patterns (Holtmeier and Broll 2012). Possibly, the predictor captures suitable microclimates that the other variables are unable to because slope inclination is upscaled from 50×50 m, whereas the snow and climatic variables are interpolated from weather stations in Norway.

The treeline models differed most notably from the forest line models in that snow water equivalent in March was selected as a predictor, which caused low predictions in the area around Jostedalsbreen, west in the study region. The amount of snow might affect treeline distribution positively or negatively by modifying soil moisture through snow melt, soil temperature or wind exposure. It also affects the risk of disturbances like snow breakage, snow avalanches snow fungi infections, and grazing (Holtmeier 2009). As forest line trees are less exposed to local climatic conditions than treeline trees, they are less dependent on snow cover for establishment in favourable microclimates (Holtmeier and Broll 2005), possibly explaining the absence of snow predictors in the forest line model. However, most of the snow-related factors that might affect treeline distribution would more likely be captured by the topographic variables, which are upscaled and not downscaled, like snow water equivalent in March. An additional explanation for why snow water equivalent in March predicts treeline distribution is that there are no presence observations in both treeline evaluation and training data sets from the area around Jostedalsbreen, which might cause this variable to gain additional explaining power by predicting absences in areas with known presence and reward the resulting models with inflated AUC scores. At Jostedalsbreen however, the amounts of snow are limiting to treelines, but absence in this area is also predicted by temperature predictors, and geographically speaking, snow water equivalent in March is therefore probably redundant for predictions at Jostedalsbreen.

Potential causes for TFL advance

In Norway, the observed movement of TFLs in the last century is thought to primarily be a result of regrowth in abandoned agricultural land, and not climate change (Bryn 2008, Rössler *et al.* 2008, Wehn *et al.* 2012). Summer farming, which includes grazing from livestock, logging and fodder collection, was extensive in the middle of the 19th century and large areas of subalpine birch forest were removed as a consequence. Since then, the intensity has decreased steadily (Bryn and Daugstad 2001) but still large parts of the study area had been affected by human land use in 1917, according to Resvoll-Holmsen (1918). From 1949 to 1974 the grazing period in the mountains for sheep, cow, cattle, horse and goat decreased with altogether 33% (Austrheim *et al.* 2008). From 1939 to 1995 numbers of sheep grazing outfield increased with 23%, while goats and cattle numbers decreased with 46% and 76%, respectively (Drabløs 1997). Forest lines in Jotunheimen, earlier suppressed by goats and cattle, advanced in response to similar changes in the composition of outfield grazers from 1960 to 2002 (Wehn *et al.* 2011). Our data indicated that TFLs did not rise significantly on average from 1917 to 1967 with about half of both individual TFLs advancing and declining. At many of the sampling sites land use changes had probably occurred too late for TFLs to respond by 1967 as Aas (1969) attributed observations of decline and stability of TFLs between 1917 and 1967 to grazing, clearing of forests, in addition to TFLs already being positioned close to the summit. He concluded that all climatically determined TFLs were stable or had risen as a response to improved climate in the 1930s to 1940s, which we did not detect in our results, because we included all his observations. Annual temperature in the study area increased slightly (0.3-0.6 degrees) from 1900-1935, followed by a decrease (0.5-1.0 degrees) from 1935-1970 and a strong increase (1.1-1.2 degrees) from 1970-2004 (Hanssen-Bauer *et al.* 2006). Almost exclusive advance of TFLs and higher movement rates from 1967 to 2017 is therefore probably a combination of higher increases of temperature and reduced domestic outfield grazing in the last half of the century. However, to separate the influence of changes in climate and land use on the last century's TFL dynamics is hard, as in other studies (Bryn and Potthoff 2018) because the study area has been subjected to changes in both processes simultaneously.

Model reliability and potential improvements

The present TFL models, modelled without topographic variables and used for estimation of changes in area, obtained AUC-ROC values of 0.788 and 0.768, respectively, which according to Araújo *et al.* (2005) indicates "fair" model performances in geographical space. The model selection emphasizes the temperature dependence of TFL distribution, although it might be somewhat influenced by modelling constraints. Model selection is influenced by the choice of pseudo-absences, because by choosing pseudo-absences with a broad environmental range compared to the environmental range of the presences the AUC-ROC gets inflated due to the improvement of the model's ability to predict "true" absences (Stokland *et al.* 2011). Temperature variables can easily sort out pseudo-absences far above and far below TFLs, which might have increased their chance of being selected. Therefore, the models might be good at predicting TFL distributions on a large scale, but less so at smaller scales, where for example topography is considered important (Holtmeier and Broll 2005). Because choosing pseudo-absences with a narrower environmental range might be worse for investigation of large-scale patterns, the choice of pseudo-absences is a matter of modelling purpose (Stokland *et al.* 2011).

In all models, the magnitude of predictions was concentrated in certain parts of the study area, most notably with higher values in a transect from south-west to north-east where sampling density was high, compared to areas with no sampling, in north-west. Increased sampling in areas with low sampling size would potentially improve the model in areas where relative probabilities of presence were low. These inabilities to extrapolate into areas with low sampling size might be a result of modelling with explanatory variables that do not affect TFL distributions directly. Microtopography and landforms are important for site conditions (e.g., wind, snow relocation and solar radiation), but interactions with other factors may alter the suitability of a topographic position. For example, differences in amount of radiation due to topography are ameliorated in oceanic relative to continental climates due to increased wind and cloudiness (Holtmeier and Broll 2012). In this hypothetical example topography is a proxy for the amount of radiation, and the optimal topographical position changes with continentality, whereas the optimal amount of radiation does not. Here, using explanatory variables that affect TFL distribution more directly instead of proxies might improve the extrapolation ability of the model in space, but also in time (Guisan and Zimmermann 2000, Dormann *et al.* 2012).

Ideally, distribution modelling is carried out with explanatory variables that are measured at the relevant temporal and spatial scale and are causally related to the distribution of the modelled target (Araújo *et al.* 2019). Some, or possibly all distribution models fall short of these assumptions (Barry and Elith 2006), including ours. TFLs in Fennoscandia are most likely influenced by a complex assemblage of factors like soil temperature, snow distribution patterns, nutrient and moisture availability, herbivory, competition, wind exposure and former land use (Moen *et al.* 2008). Proxies for biotic interactions are hard to obtain at all, while some of the other factors were accounted for indirectly by the explanatory variables in this study, although they might have been more appropriate at smaller scales.

Delayed responses to climate change

That distribution modelling is performed with explanatory variables measured at the relevant temporal scale necessitates that the modelled TFLs are in equilibrium with the environment, which is less likely in a rapidly changing climate (Guisan and Thuiller 2005). Historical disturbances also cause disequilibrium (Barry and Elith 2006), and the impact on the modelled response of TFLs to summer and autumn temperature is that they do not represent the TFLs true response to the explanatory variables, and the models represent empirical rather than climatic TFLs (Guisan and Thuiller 2005). The climatic and snow variables used for modelling represent the period 2004 to 2014 and the models therefore assume that TFLs respond within about a decade to changes in the environment, represented by the predictors.

Time lags in mountain forest development varies considerably in space and may take anywhere from a few decades to at least more than a century (Bugmann and Pfister 2000, Lloyd and Fastie 2003). Forest development and expansion depends on positive feedbacks with establishment of trees initially, giving shelter, absorbing heat and trapping snow and seeds (Kullman 2010a), and forest lines are therefore expected to respond considerably slower than treelines to changes in the environment (Rannow 2013). As some of the factors responsible for time lags involved in treeline advance Körner (2012) acknowledges competition with alpine plants, short periods with cold temperature leading to decline, and the time needed for a young individual to become a tree according to definitions. Several studies on TFL dynamics the last century in the northern Hemisphere have reported that TFLs are moving slower than expected from changes in summer temperature (Harsch *et al.* 2009, Rannow 2013, Dial *et al.* 2016, Rees *et al.* 2020, Lu *et al.* 2021). Assuming TFLs move exclusively with increases in summer temperature, which increased with approximately 0.2-0.5°C in the study region between 1900 and 2004 (Hanssen-Bauer *et al.* 2006), our observed TFLs would rise with about 35-85 m, assuming an adiabatic lapse rate of 0.6 degrees per 100 m (as in Kullman and Öberg (2009)). Our analysis of elevational changes showed that TFLs on average and several individual TFLs advanced substantially higher than this. Moreover, the current mean temperature of the warmest quarter in areas where past treelines were georeferenced are 1.1°C higher than in the locations they are today, whereas for forest lines their past georeferenced locations are 0.3°C higher than in the present locations at the current conditions. If the summer temperature changed more from 1917 to 2017 at TFL locations compared to other areas, we would also observe larger differences in the current summer temperature between the past and present georeferenced locations than what occurred elsewhere. However, changes in summer temperature have been rather uniform across the study area the last century (Hanssen-Bauer 2005), which might reflect a change in the distribution of forest lines that are within what is expected from changes in summer temperature, and a substantially larger expected change in the treeline distribution. The higher difference in current summer temperature between past and present georeferenced locations for treelines compared to forest lines, in addition to the higher elevational changes might therefore indicate the higher time lag for forest line than treeline movement. That treelines moved much quicker than expected from changes in summer temperature might seem like time lags are absent, although it is more likely an indication of the decreasing intensity of summer farming in the region the last century. Kullman and Öberg (2009) also observed treelines moving faster than expected from changes in temperature, although they attributed it to absence of climatic time lags. They suggest that smaller shifts are recorded in other studies due to the commonly low precision of TFL observations from the early part of the century and few sites with observations, which may explain why relatively high maximum shifts of individual TFLs were recorded in this study.

Uncertainties in estimation of distributional changes

The method of parameterizing past and present TFLs with different presence data but the same explanatory data is erroneous because it is equivalent to changing the ecological response of the modelled target between the models. However, it is analogous to modelling of past TFLs with explanatory variables that have changed uniformly across the study area, which is a more reasonable assumption indicated by climate analyses for the last century (Hanssen-Bauer 2005, Hanssen-Bauer *et al.* 2006). Still, temperature has increased less in the lowlands and oceanic areas in Norway, compared to the mountains and continental areas (Tveito 2014). In modelling of past TFLs explanatory variables representative for the relevant period would of course be preferred, but such downscaled climate projections do not exist. Estimation of parameters for past TFL models might therefore be affected by the use of inaccurate explanatory data.

Due to the geometric shape of mountains, equivalent advances in elevation of treelines and forest lines leads to higher increases in land cover of forest lines, although the percentage of area reduced above lines will be higher for treelines (Körner 2007). Our estimation of changes in TFL distributions indicated that increases in land cover of treelines was much higher than they were for forest lines. Although a quicker response of treelines compared to forest lines in a changing environment is expected (Rannow 2013), this might seem contradictory, considering that the TFLs responded with similar elevational changes in the same period. The differences between changes in elevation and distribution may be attributed to the use of different samples and lack of observations from certain areas in the past TFL training data, affecting the estimates of past TFL distributions. Observations of past treelines were more easterly distributed relative to past forest line observations, which may have caused the current mean temperature of the warmest quarter in georeferenced locations of past treelines to be higher than they were in those of past forest lines, since in south Norway, TFLs are generally situated at a higher summer temperature in the west than in the east (Aas 1964, Aas and Faarlund 1996). Assuming that the differences in temperature between these locations were the same in 1917 (Hanssen-Bauer 2005), this indicates that treelines were situated at a higher summer temperature than forest lines in 1917, which would be remarkable. This error might also have been caused by high spatial uncertainty of the georeferenced past TFL observations, which was on average 2,3 km for treelines and 2 km for forest lines. This has further propagated into the area estimates, which show that the treeline land cover was smaller than the forest line land cover in 1917. However, we do not know if it is the changes in treeline or forest line distribution, or both that is over- or underestimated.

The models estimate smaller changes in steep relative to gentle mountain slopes, which may be an effect of extrapolating with primarily temperature variables as predictors. Temperature increases more slowly with distance on gentle compared to steep slopes and consequently changes in parameter estimations between different models have larger effects on predictions in such areas. Still, it is in accordance with predictions since greater expansion of TFLs is expected at gentle relative to steep slopes This expectation is not entirely due to temperature increasing more slowly with distance at gentle slopes, but also because TFLs in many locations are limited at steep slopes by mass wasting and avalanches (Holtmeier and Broll 2012). Although predicting changes in TFLs almost exclusively with temperature variables has been regarded as too simplistic (Kullman 2010b), some confidence might be given to our estimates because TFLs correlated strongly with the mean of the warmest quarter in the 1910s (Helland 1912), while our models indicate that they still do so.

Implications of TFL expansions

TFL dynamics affects biodiversity and climate, although altitudinal relative to latitudinal TFL advance is expected to have greater impact on biodiversity, and smaller impact on climate in a global context. This is because alpine areas store less soil carbon and harbours more species per unit area than arctic areas (Walker *et al.* 2001). Regarding climate feedbacks initial altitudinal TFL advances have the most impact because the available land area of mountains shrinks with elevation (Körner 2007). The most important climatic consequences of advancing boreal forests are expected to arise from associated increases in evapotranspiration, carbon flux and uptake, reduction in surface albedo and increased release of biogenic volatile organic compounds (Bonan 2008). Increased evapotranspiration enhances snow and cloud cover, which generally have a stronger cooling effect on temperature than warming from the increased latent heat flux (Rydsaa *et al.* 2017). Enhanced carbon uptake cools the temperature, while reduced surface albedo contributes to warming, especially in areas with seasonal snow cover (de Wit *et al.* 2014). The effect of surface albedo is clearly dominating at higher latitudes, suggesting that boreal forest advance represents a net positive climate feedback (de Wit *et al.* 2014, Rydsaa *et al.* 2017). Due to shedding of leaves in autumn, the influence of albedo is less in boreal forests dominated by deciduous compared to evergreen trees (Rydsaa *et al.* 2017). Although several studies from Norway have investigated climate feedbacks from advance of boreal forests, no studies so far have considered the most important feedbacks simultaneously. Quantification of the radiative forcing from advance of TFLs is crucial to improve climate models and the understanding of TFL dynamics.

The high diversity of habitats in mountain ecosystems, which inhabit approximately 21% of the flowering plant species worldwide, is mainly attributed to rapid elevational changes over short distances and high topographic variation (Körner 2004). Changes in TFL distributions are assumed to be indicators of distributional changes of subalpine and alpine species as they are directly affected by trees and forests which alter site conditions (Holtmeier and Broll 2017). Moreover, ordination analysis has shown that species composition varies with distance from TFLs (Hofgaard and Wilmann 2002). Initial TFL rise are expected to increase species richness through advances of lowland species, but as alpine areas gradually shrink, the probability of extinction of alpine species are expected to increase (Moen *et al.* 2004). Klanderud and Birks (2003) observed increasing species richness and expansion of elevational limits of vascular plants in Jotunheimen from 1930 to 1998. They also found out that species with wide ecological and elevational range increased most in abundance and elevational extent, while species with narrow ecological range, such as snow bed species, declined in abundance. Similar trends with elevational advances of vascular plants at the cost of snow bed communities have also been observed in Swedish Scandes (Kullman 2010b). In addition to the uncertainty of future changes of TFLs, the impact further TFL rise will potentially have for alpine biodiversity is highly unpredictable, especially since alpine plant species were able to survive periods of TFL elevation peaks of the Holocene, primarily in steep slopes and high-altitude mountains (Bruun and Moen 2003).

Further research on TFL dynamics

To improve the understanding of TFL dynamics, more focus is needed on the functional mechanisms limiting TFLs (Holtmeier and Broll 2020). Although correlation studies are unable to prove causation, they are useful for generating hypotheses, and our results indicated that the mean temperature of the warmest quarter, maximum and minimum temperature in November, snow water equivalent in March and slope inclination might serve as proxies for functional mechanisms limiting TFLs in the region. Identification of the responsible functional mechanisms might be better answered by experimental field and laboratory studies because variables that affect targets distributions more directly are often harder to obtain or less precise, and thus less appropriate for modelling studies (Guisan and Zimmermann 2000).

As already discussed, the assumption that the modelled target is in equilibrium with the environment can cause problems for modelling of TFLs. Process-based distribution models should also be developed for TFLs as they have the advantage of being dynamic and as a consequence, they do not carry this assumption (Dormann *et al.* 2012). Another difference is that they commonly operate with parameters that affect distributions more directly than correlative distribution models (Beale and Lennon 2012).

More research is also needed on delayed responses of TFLs to changes in climate. Mountain ecosystems were less impacted by humans further back in time, and palaeoecological and modelling studies are therefore suitable for detecting climatic lags on longer time scales (Körner 2012). Short-term delays might be identified by field studies with more frequent revisitations, which would also make it easier to identify the relative importance of drivers of TFL dynamics.

Conclusions

We observed and estimated large TFL elevational and distributional changes in south Norway the last century. Old, high-resolution data sets, like Resvoll-Holmsen's, used in this study are essential for detection of changes in the distribution of TFLs, as they respond slowly to changes in the environment (Körner 2012). The results in this study were solely based on data collected in the field and only consist of locally uppermost TFLs, less likely to have been impacted by human land use (Körner 2012), which makes the data more appropriate for detecting changes in the distribution of climatically determined TFLs.

The current distribution of treelines was predicted by mean temperature of the warmest quarter, maximum temperature in November, snow water equivalent in March and slope inclination, while mean temperature of the warmest quarter, slope inclination and minimum temperature in November predicted the forest line distribution. During the last century, treelines moved on average 0.53 m/year and the estimated increase in land cover was 6 688 km^2, corresponding to a decline of areas above the treeline with 27.6%. In the same period, forest lines moved with on average with 0.36 m/year and expanded their land cover with 1 137 km^2, a 5.3% reduction of areas above the forest line. Estimations of past TFL land cover might have been affected by lack of observations in certain areas, especially west in the region. Climate and land use changes are most likely the main drivers of the observed TFL dynamics, but it is hard to separate the relative influences of these factors on the observed changes in the study. Overall, the performance of the TFL distribution models is fair but at smaller scales and in areas outside a transect from south-west to north-east in the study region, where samples were lacking, they should be interpreted with more caution.

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Appendices

Table S1. Explanatory variables, their transformations, estimated coefficients and fraction of total variation accounted for (FTVA) for all present treeline models, modelled with topographic variables. Model 5 was chosen as the best model (details in Results: Table 1). L = linear, M = monotonous, D = deviation (D1, D2 or D05)

Present treelines with topographic variables (model 1)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.4021	0.1402	-
Mean temperature of warmest quarter	D2	-18.0449	3.2529	0.7
Max temperature in November	D2	-35.6984	9.418	0.191
Relative Slope Position	D2	-1.4887	0.3927	0.109
Present treelines with topographic variables (model 2)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.615	0.1282	-
Mean temperature of warmest quarter	D2	-11.81	3.1799	0.736
Max temperature in November	D2	-25.7207	6.7755	0.179
Max temperature in February	D2	-29.0646	9.0445	0.085
Present treelines with topographic variables (model 3)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-5.8773	0.362	-
Mean temperature of warmest quarter	D2	-11.897	3.0847	0.627
Max temperature in November	D2	-15.0989	4.4619	0.191
Slope inclination	M	1.9873	0.4757	0.109
Snow water equivalent in March	D2	-36.4191	15.5912	0.073
Present treelines with topographic variables (model 4)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.245	0.1473	-
Mean temperature of warmest quarter	D2	-12.2395	2.8818	0.67
Min temperature in November	D2	-6.9891	1.9449	0.161
Slope inclination	D2	-1.5618	0.4288	0.098
Max temperature in November	D2	-15.8574	5.9738	0.071
Present treelines with topographic variables (model 5)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.027	0.1659	-
Mean temperature of warmest quarter	D2	-18.2672	3.8813	0.648
Max temperature in November	D2	-22.3564	6.6365	0.192
Snow water equivalent in March	D2	-39.2789	12.4535	0.096
Slope inclination	D2	-1.3524	0.3867	0.064

Table S2. Deviance residuals for all present treeline models, modelled with topographic variables. Model 5 was chosen as the best model (details in Results: Table 1).

Present treelines modelled with topographic variables (model 1)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.5419	-0.7608	-0.2269	-0.0002	3.7276
Present treelines modelled with topographic variables (model 2)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.3968	-0.8326	-0.223	-0.0001	3.9077
Present treelines modelled with topographic variables (model 3)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.7792	-0.7654	-0.2558	-0.0019	3.7657
Present treelines modelled with topographic variables (model 4)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.6432	-0.7386	-0.2566	-0.0015	3.8215
Present treelines modelled with topographic variables (model 5)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.7405	-0.7562	-0.1801	-0.0001	3.7465

Table S3. Model properties for all present treeline models, modelled with topographic variables (see details in Table S1). Model 5 was chosen as the best model (details in Results: Table 1).

Present treelines modelled with topographic variables (model 1)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1432	571
AIC	1440	
Fisher scoring iterations	9	
Present treelines modelled with topographic variables (model 2)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1438.1	571
AIC	1446.1	
Fisher scoring iterations	9	
Present treelines modelled with topographic variables (model 3)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1431.2	570
AIC	1441.2	
Fisher scoring iterations	9	
Present treelines modelled with topographic variables (model 4)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1427.9	570
AIC	1437.9	
Fisher scoring iterations	9	
Present treelines modelled with topographic variables (model 5)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1407.1	570
AIC	1417.1	
Fisher scoring iterations	9	

Table S4. Single, mean and standard AUC-ROC and AUC-PR for all present treeline models, modelled with topographic variables (see details in Table S1), evaluated by each treeline evaluation data set. Model 5 was chosen as the best model (details in Results: Table 1).

	Present treelines modelled with topographic variables									
	Model 1		Model 2		Model 3		Model 4		Model 5	
	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR
Evaluation 1	0.725	0.433	0.742	0.486	0.786	0.560	0.746	0.510	0.798	0.580
Evaluation 2	0.724	0.430	0.723	0.408	0.777	0.505	0.739	0.468	0.787	0.532
Evaluation 3	0.758	0.475	0.757	0.489	0.799	0.564	0.760	0.520	0.808	0.590
Evaluation 4	0.723	0.416	0.726	0.429	0.782	0.559	0.730	0.475	0.792	0.560
Evaluation 5	0.749	0.433	0.765	0.463	0.807	0.550	0.767	0.496	0.813	0.548
Mean	0.736	0.437	0.743	0.455	0.790	0.548	0.748	0.494	0.800	0.562
SD	0.016	0.022	0.018	0.036	0.013	0.024	0.015	0.022	0.011	0.023

Table S5. Explanatory variables, their transformations, estimated coefficients and fraction of total variation accounted for (FTVA) for all present forest line models, modelled with topographic variables. Model 5 was chosen as the best model (details in Results: Table 1). L = linear, M = monotonous, D = deviation (D1, D2 or D05)

Present forest lines modelled with topographic variables (model 1)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.3762	0.1491	-
Mean temperature of warmest quarter	D2	-16.8693	3.9514	0.703
Slope inclination	D2	-1.6239	0.3761	0.178
Max temperature in November	D2	-15.7683	4.8436	0.119
Present forest lines modelled with topographic variables (model 2)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-5.929	0.3532	-
Mean temperature of warmest quarter	D2	-18.6059	3.7826	0.712
Max temperature in November	D2	-19.88	5.5592	0.198
Slope inclination	M	2.0327	0.5208	0.09
Present forest lines modelled with topographic variables (model 3)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.4214	0.147	-
Mean temperature of warmest quarter	D2	-16.5243	3.5921	0.767
Max temperature in November	D2	-17.0688	5.0696	0.155
Slope inclination	D2	-1.3426	0.3896	0.078
Present forest lines modelled with topographic variables (model 4)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-6.5059	0.5916	-
Mean temperature of warmest quarter	D2	-17.1384	3.7924	0.68
Max temperature in November	D2	-18.0936	4.435	0.223
Slope inclination	M	4.7243	1.9033	0.097
Slope inclination	L	-3.1875	1.9097	^
Present forest lines modelled with topographic variables (model 5)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.3579	0.1526	-
Mean temperature of warmest quarter	D2	-17.6087	3.4663	0.81
Slope inclination	D2	-1.6018	0.3905	0.1
Min temperature in November	D2	-6.9019	2.3524	0.09

Table S6. Deviance residuals for all present forest line models, modelled with topographic variables (see details in Table S5). Model 5 was chosen as the best model (details in Results: Table 1).

Present forest lines modelled with topographic variables (model 1)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.5696	-0.7793	-0.3212	-0.0026	3.9038
Present forest lines modelled with topographic variables (model 2)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.7973	-0.7879	-0.2337	-0.0006	3.8533
Present forest lines modelled with topographic variables (model 3)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.5392	-0.758	-0.3042	-0.0032	3.879
Present forest lines modelled with topographic variables (model 4)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.4969	-0.7668	-0.2894	-0.0007	3.9196
Present forest lines modelled with topographic variables (model 5)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.584	-0.7744	-0.3034	-0.0039	3.9784

Table S7. Model properties for all present forest line models, modelled with topographic variables (see details in Table S5). Model 5 was chosen as the best model (details in Results: Table 1).

Present forest lines modelled with topographic variables (model 1)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1370.6	541
AIC	1378.6	
Fisher scoring iterations	8	
Present forest lines modelled with topographic variables (model 2)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1354.6	541
AIC	1362.6	
Fisher scoring iterations	9	
Present forest lines modelled with topographic variables (model 3)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1366.9	541
AIC	1374.9	
Fisher scoring iterations	8	
Present forest lines modelled with topographic variables (model 4)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1366.8	540
AIC	1376.8	
Fisher scoring iterations	8	
Present forest lines modelled with topographic variables (model 5)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1371.2	541
AIC	1379.2	
Fisher scoring iterations	8	

Table S8. Single, mean and standard AUC-ROC and AUC-PR for all present forest line models, modelled with topographic variables (see details in Table S5), evaluated by each forest line evaluation data set. Model 5 was chosen as the best model (details in Results: Table 1).

	Present forest lines modelled with topographic variables									
	Model 1		Model 2		Model 3		Model 4		Model 5	
	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR
Evaluation 1	0.782	0.562	0.796	0.598	0.763	0.526	0.776	0.553	0.795	0.523
Evaluation 2	0.764	0.483	0.772	0.516	0.741	0.451	0.752	0.474	0.790	0.494
Evaluation 3	0.783	0.527	0.797	0.557	0.765	0.506	0.777	0.521	0.785	0.444
Evaluation 4	0.776	0.524	0.786	0.541	0.760	0.501	0.770	0.511	0.791	0.507
Evaluation 5	0.783	0.521	0.790	0.545	0.774	0.521	0.783	0.528	0.794	0.496
Mean	0.778	0.523	0.788	0.551	0.761	0.501	0.771	0.517	0.791	0.493
SD	0.008	0.028	0.010	0.030	0.012	0.030	0.012	0.029	0.004	0.030

Table S9. Explanatory variables, their transformations, estimated coefficients and fraction of total variation accounted for (FTVA) for all present treeline models, modelled without topographic variables. Model 5 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area. L = linear, M = monotonous, D = deviation (D1, D2 or D05)

Present treelines modelled without topographic variables (model 1)				
	Transformation	Estimate	Standard error	FTVA
Intercept	-	-4.7153	0.1247	-
Mean temperature of warmest quarter	D2	-18.1494	3.2167	0.786
Max temperature in November	D2	-36.7703	9.3258	0.214
Present treelines modelled without topographic variables (model 2)				
	Transformation	Estimate	Standard error	FTVA
Intercept	-	-4.615	0.1282	-
Mean temperature of warmest quarter	D2	-11.81	3.1799	0.736
Max temperature in November	D2	-25.7207	6.7755	0.179
Max temperature in February	D2	-29.0646	9.0445	0.085
Present treelines modelled without topographic variables (model 3)				
	Transformation	Estimate	Standard error	FTVA
Intercept	-	-4.5606	0.1448	-
Mean temperature of warmest quarter	D2	-15.5902	3.0518	0.704
Max temperature in November	D2	-17.2076	4.6399	0.214
Snow water equivalent in March	D2	-41.8961	15.5031	0.082
Present treelines modelled without topographic variables (model 4)				
	Transformation	Estimate	Standard error	FTVA
Intercept	-	-4.5546	0.1316	-
Mean temperature of warmest quarter	D2	-15.2167	2.9137	0.728
Min temperature in November	D2	-7.1245	1.961	0.175
Max temperature in November	D2	-18.4761	6.1046	0.097
Present treelines modelled without topographic variables (model 5)				
	Transformation	Estimate	Standard error	FTVA
Intercept	-	-4.3446	0.1493	-
Mean temperature of warmest quarter	D2	-22.173	3.8465	0.692
Max temperature in November	D2	-25.0438	6.7889	0.205
Snow water equivalent in March	D2	-37.4189	12.4658	0.103

Table S10. Deviance residuals for all present treeline models, modelled without topographic variables. Model 5 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Present treelines modelled without topographic variables (model 1)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.3285	-0.8421	-0.2608	-0.0002	3.8135
Present treelines modelled without topographic variables (model 2)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.3968	-0.8326	-0.223	-0.0001	3.9077
Present treelines modelled without topographic variables (model 3)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.3917	-0.8346	-0.2425	-0.0006	3.6972
Present treelines modelled without topographic variables (model 4)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.4349	-0.7996	-0.2686	-0.0006	3.7144
Present treelines modelled without topographic variables (model 5)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.551	-0.7954	-0.1717	0	3.7193

Table S11. Model properties for all present treeline models, modelled without topographic variables. Model 5 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Present treelines modelled without topographic variables (model 1)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1450.2	572
AIC	1456.2	
Fisher scoring iterations	9	
Present treelines modelled without topographic variables (model 2)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1438.1	571
AIC	1446.1	
Fisher scoring iterations	9	
Present treelines modelled without topographic variables (model 3)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1450.2	571
AIC	1458.2	
Fisher scoring iterations	8	
Present treelines modelled without topographic variables (model 4)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1442.7	571
AIC	1450.7	
Fisher scoring iterations	9	
Present treelines modelled without topographic variables (model 5)		
	Value	**Degrees of freedom**
Null deviance	1608.3	574
Residual deviance	1420.5	571
AIC	1428.5	
Fisher scoring iterations	9	

Table S12. Single, mean and standard AUC-ROC and AUC-PR for all present treeline models, modelled without topographic variables, evaluated by each treeline evaluation data set. Model 5 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

	Present treelines modelled without topographic variables									
	Model 1		Model 2		Model 3		Model 4		Model 5	
	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR	AUC-ROC	AUC-PR
Evaluation 1	0.740	0.486	0.742	0.486	0.776	0.495	0.735	0.497	0.784	0.508
Evaluation 2	0.732	0.445	0.723	0.408	0.764	0.496	0.731	0.437	0.776	0.533
Evaluation 3	0.759	0.501	0.757	0.489	0.786	0.534	0.755	0.494	0.796	0.551
Evaluation 4	0.735	0.452	0.726	0.429	0.768	0.503	0.717	0.426	0.778	0.506
Evaluation 5	0.763	0.475	0.765	0.463	0.799	0.539	0.763	0.484	0.805	0.550
Mean	0.746	0.472	0.743	0.455	0.778	0.514	0.740	0.467	0.788	0.530
SD	0.014	0.024	0.018	0.036	0.014	0.021	0.019	0.034	0.012	0.022

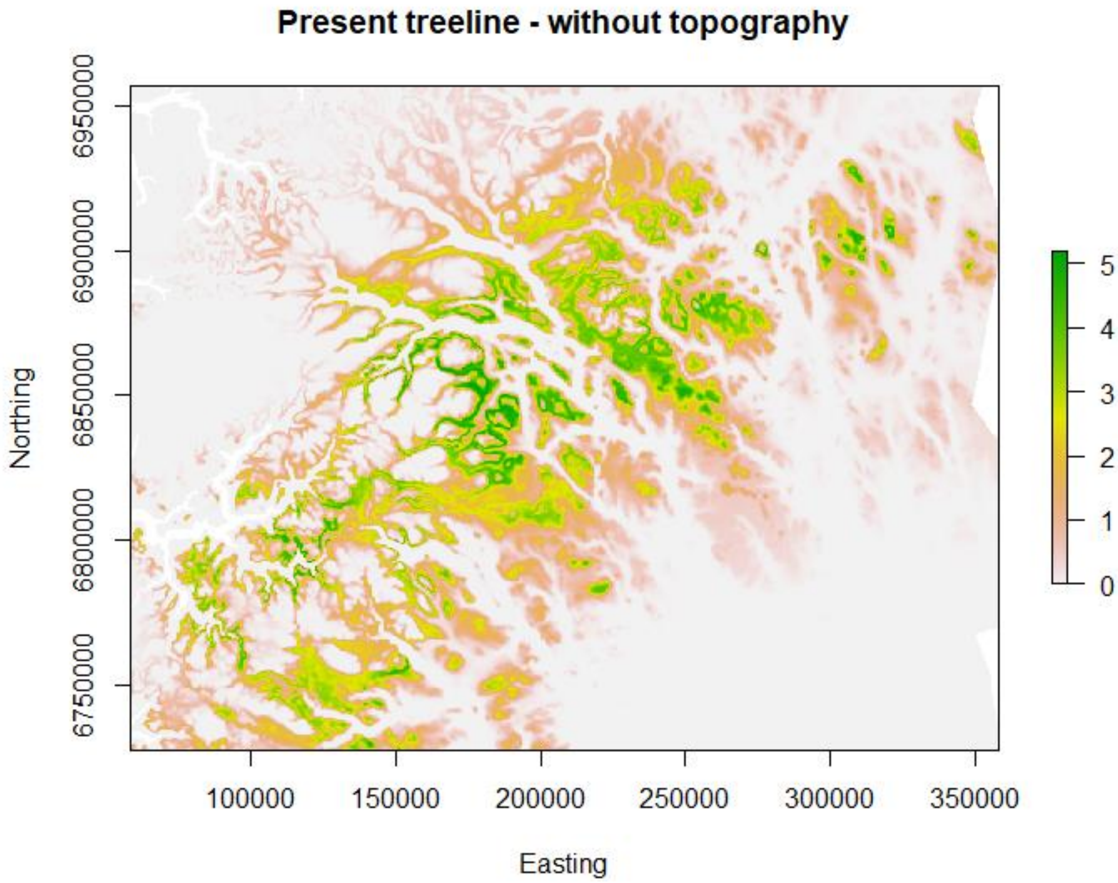

Figure S1. Modelled distribution of present treelines without topographic variables (model 5 in Table S9-12; see Figure S2 for modelled response of the predictors) in south Norway with probability ratio output (PRO) values indicated on a continuous scale, where white indicates low relative probability of presence and green indicates high. Because the values are relative, a given value in this model may not correspond to the same value from another model, and area estimates are made under the assumption that the highest local predictions indicate areas with local maximum elevation of the model object. Coordinate reference system: WGS 84/UTM zone 33N.

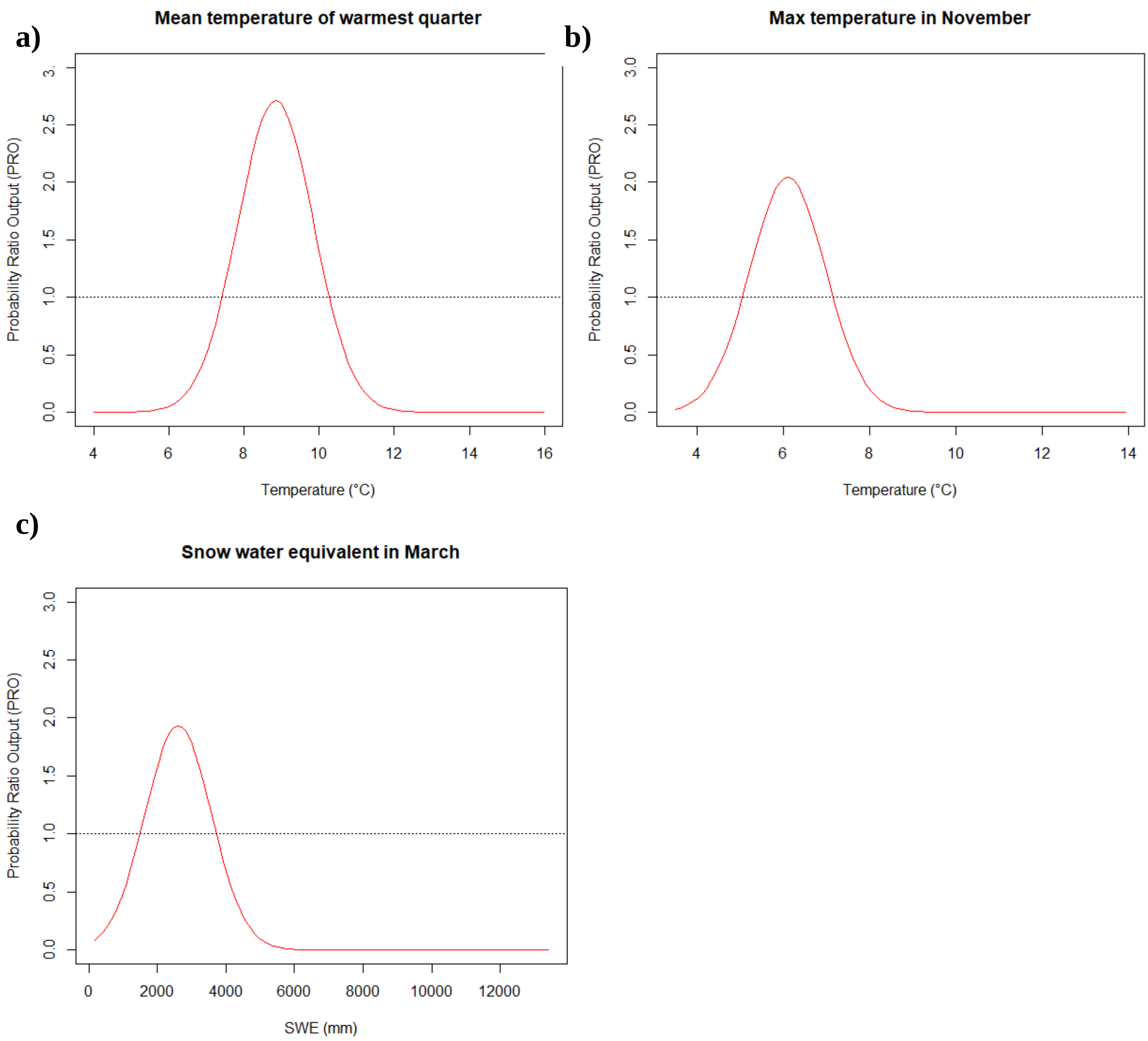

Figure S2. Response plots showing probability ratio output (PRO) values as a red line for the **(a)** mean temperature of the warmest quarter, **(b)** maximum temperature in November and **(c)** snow water equivalent in March in the model of present treelines, modelled without topographic variables (see Table S9-12 model 5 for details, and Figure S3 for frequency of observed presence (FOP) plots).

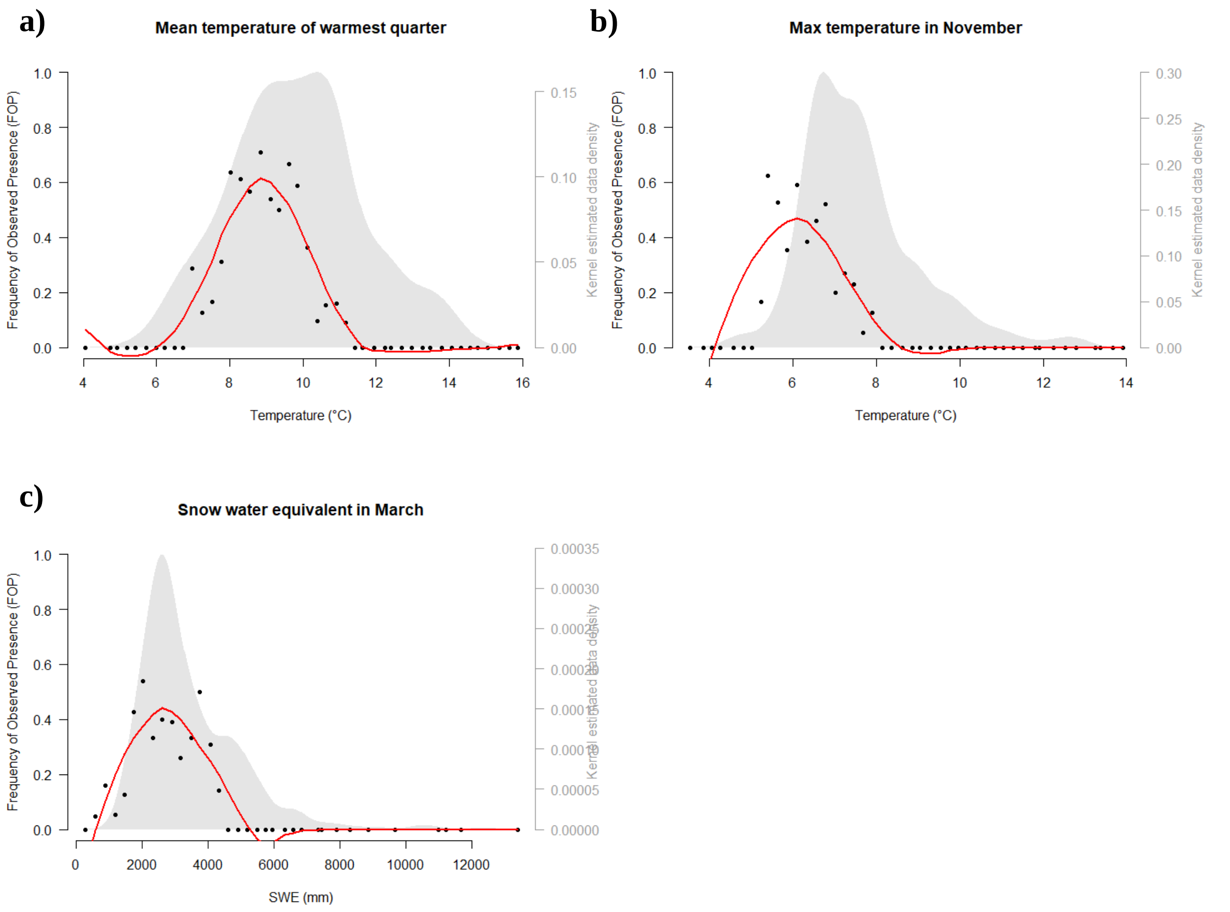

Figure S3. Frequency of observed presence (FOP) plots of present treelines modelled without topographic variables (see model 5 Table S9-12 for details, and Figure S2 for modelled response of the predictors) for the **(a)** mean temperature of the warmest quarter, **(b)** maximum temperature in November and **(c)** snow water equivalent in March presented as black dots. The red line is fitted to the points by a local regression with the MIAmaxent package and the density of values for each explanatory variable in the data set is presented in grey.

Table S13. Explanatory variables, their transformations, estimated coefficients and fraction of total variation accounted for (FTVA) for all present forest line models, modelled without topographic variables. Model 2 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area. L = linear, M = monotonous, D = deviation (D1, D2 or D05)

Present forest lines modelled without topographic variables (model 1)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.8009	0.1292	-
Mean temperature of warmest quarter	D2	-22.1883	4.1372	0.816
Max temperature in November	D2	-18.313	4.9166	0.184
Present forest lines modelled without topographic variables (model 2)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.7093	0.1263	-
Mean temperature of warmest quarter	D2	-21.5286	3.7799	0.782
Max temperature in November	D2	-22.6393	5.8582	0.218
Present forest lines modelled without topographic variables (model 3)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.746	0.126	-
Mean temperature of warmest quarter	D2	-21.204	3.605	0.832
Max temperature in November	D2	-19.198	5.208	0.168
Present forest lines modelled without topographic variables (model 4)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.7293	0.1273	-
Mean temperature of warmest quarter	D2	-21.5119	3.7602	0.753
Max temperature in November	D2	-19.214	4.5448	0.247
Present forest lines modelled without topographic variables (model 5)				
	Transformation	**Estimate**	**Standard error**	**FTVA**
Intercept	-	-4.798	0.126	-
Mean temperature of warmest quarter	D2	-21.03	3.581	0.9
Max temperature in November	D2	-15.865	5.441	0.1

Table S14. Deviance residuals for all present forest line models, modelled without topographic variables. Model 2 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Present forest lines without topographic variables (model 1)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.2793	-0.8588	-0.334	-0.0008	3.8301
Present forest lines without topographic variables (model 2)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.3393	-0.8704	-0.2408	-0.0002	3.7364
Present forest lines without topographic variables (model 3)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.3143	-0.8334	-0.2804	-0.0008	3.8286
Present forest lines without topographic variables (model 4)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.325	-0.8133	-0.3225	-0.0003	3.8193
Present forest lines without topographic variables (model 5)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.281	-0.8512	-0.2999	-0.001	3.878

Table S15. Model properties for all present forest line models, modelled without topographic variables. Model 2 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Present forest lines modelled without topographic variables (model 1)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1391	542
AIC	1397	
Fisher scoring iterations	8	
Present forest lines modelled without topographic variables (model 2)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1371.2	542
AIC	1377.2	
Fisher scoring iterations	8	
Present forest lines modelled without topographic variables (model 3)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1379.7	542
AIC	1385.7	
Fisher scoring iterations	8	
Present forest lines modelled without topographic variables (model 4)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1382.2	542
AIC	1388.2	
Fisher scoring iterations	8	
Present forest lines modelled without topographic variables (model 5)		
	Value	**Degrees of freedom**
Null deviance	1524.4	544
Residual deviance	1387.9	542
AIC	1393.9	
Fisher scoring iterations	8	

Table S16. Single, mean and standard AUC-ROC and AUC-PR for all present forest line models, modelled without topographic variables, evaluated by each forest line evaluation data set. Model 2 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

	Present forest lines modelled without topographic variables									
	Model 1		**Model 2**		**Model 3**		**Model 4**		**Model 5**	
	AUC-ROC	**AUC-PR**	**AUC-ROC**	**AUC-PR**	**AUC-ROC**	**AUC-PR**	**AUC-ROC**	**AUC-PR**	**AUC-ROC**	**AUC-PR**
Evaluation 1	0.766	0.458	0.774	0.477	0.746	0.434	0.756	0.462	0.736	0.404
Evaluation 2	0.731	0.389	0.741	0.404	0.714	0.370	0.722	0.386	0.710	0.367
Evaluation 3	0.782	0.490	0.794	0.544	0.763	0.481	0.774	0.528	0.753	0.446
Evaluation 4	0.758	0.432	0.762	0.441	0.744	0.424	0.749	0.446	0.741	0.416
Evaluation 5	0.768	0.437	0.770	0.443	0.756	0.433	0.760	0.442	0.752	0.426
Mean	0.761	0.441	0.768	0.462	0.745	0.428	0.752	0.453	0.738	0.412
SD	0.019	0.037	0.019	0.053	0.019	0.039	0.019	0.051	0.017	0.029

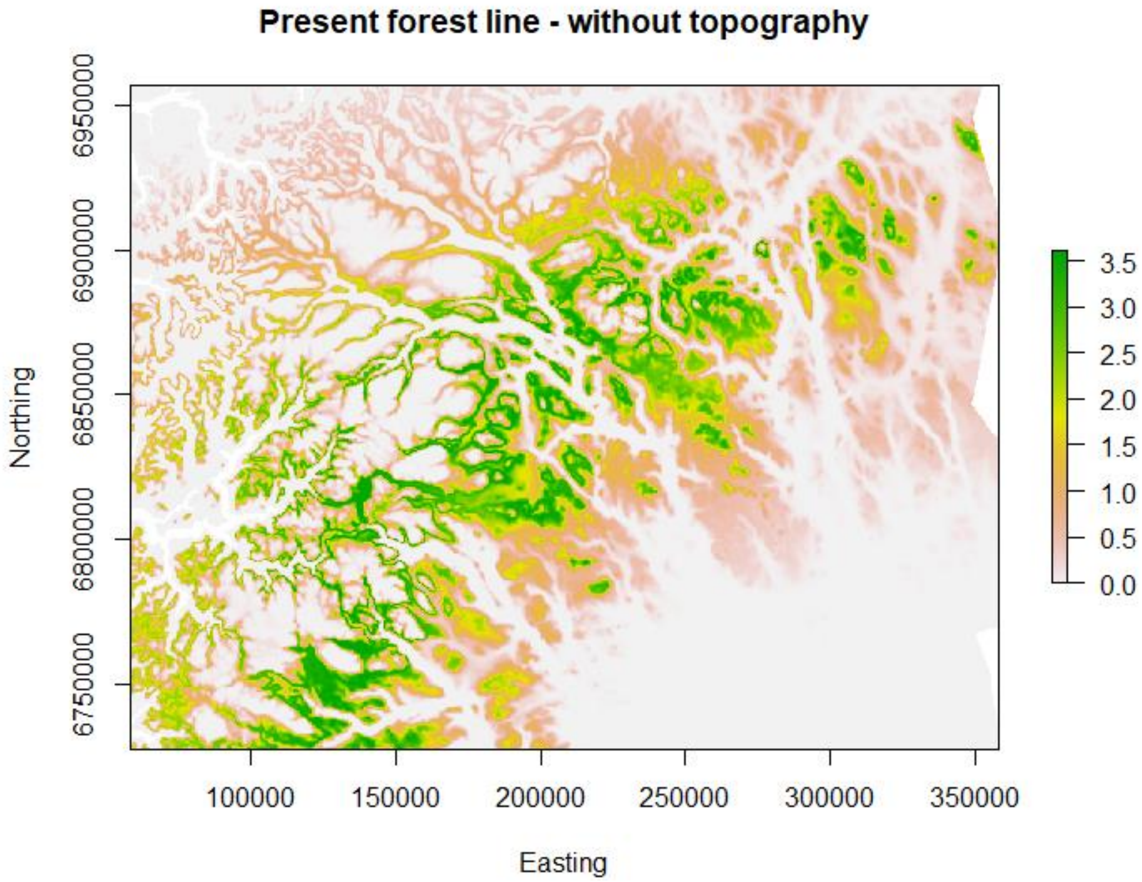

Figure S4. Modelled distribution of present forest lines without topographic variables (model 2 in Table S13-16; see Figure S5 for modelled response of the predictors) in south Norway with probability ratio output (PRO) values indicated on a continuous scale, where white indicates low relative probability of presence and green indicates high. Because the values are relative, a given value in this model may not correspond to the same value from another model, and area estimates are made under the assumption that the highest local predictions indicate areas with local maximum elevation of the model object. Coordinate reference system: WGS 84/UTM zone 33N.

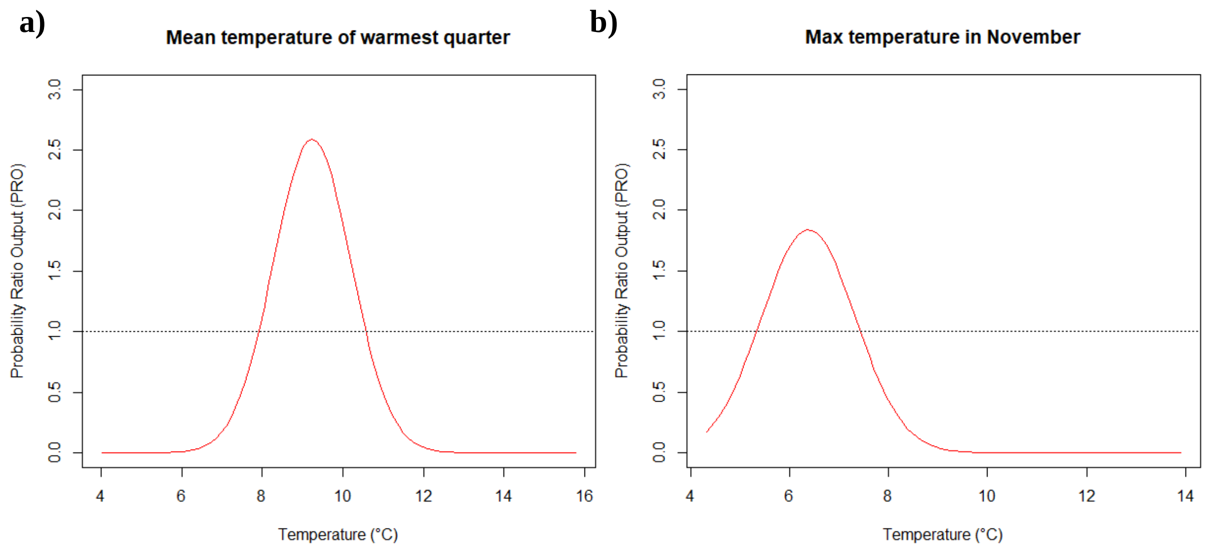

Figure S5. Response plots showing probability ratio output (PRO) values as a red line for the **(a)** mean temperature of the warmest quarter and **(b)** maximum temperature in November in the model of present forest lines, modelled without topographic variables (see Table S13-16 model 2 for details, and Figure S6 for frequency of observed presence (FOP) plots).

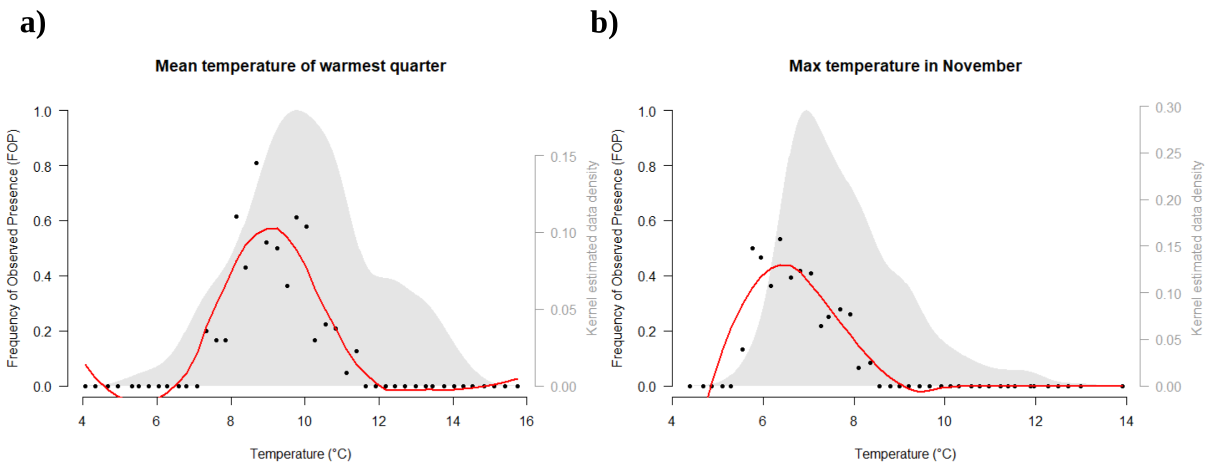

Figure S6. Frequency of observed presence (FOP) plots of present forest lines modelled without topographic variables (see model 2 Table S13-16 for details, and Figure S5 for modelled response of the predictors) for the **(a)** mean temperature of the warmest quarter and **(b)** maximum temperature in November presented as black dots. The red line is fitted to the points by a local regression with the MIAmaxent package and the density of values for each explanatory variable in the data set is presented in grey.

Table S17. Explanatory variables, their transformations and estimated coefficients for all past treeline models. Model 4 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area. L = linear, M = monotonous, D = deviation (D1, D2 or D05)

Past treelines modelled without topographic variables (model 1)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.3491	0.2325
Mean temperature of warmest quarter	D2	-20.2307	7.3478
Max temperature in November	D2	-25.9687	9.7014
Snow water equivalent in March	D2	-66.5156	34.0216
Past treelines modelled without topographic variables (model 2)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.2285	0.2543
Mean temperature of warmest quarter	D2	-17.1175	5.0247
Max temperature in November	D2	-16.8251	7.6661
Snow water equivalent in March	D2	-8.8255	4.0394
Past treelines modelled without topographic variables (model 3)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.3834	0.2153
Mean temperature of warmest quarter	D2	-21.9316	6.3196
Max temperature in November	D2	-15.6402	6.9251
Snow water equivalent in March	D2	-29.6239	14.6817
Past treelines modelled without topographic variables (model 4)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.5857	0.2161
Mean temperature of warmest quarter	D2	-24.0823	9.2003
Max temperature in November	D2	-9.3026	4.4229
Snow water equivalent in March	D2	-21.1228	12.2045
Past treelines modelled without topographic variables (model 5)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-3.8309	0.3905
Mean temperature of warmest quarter	D2	-32.4935	9.417
Max temperature in November	D2	-20.8872	8.634
Snow water equivalent in March	D2	-130.0242	61.428

Table S18. Deviance residuals for all past treeline models, modelled without topographic variables. Model 4 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Past treelines modelled without topographic variables (model 1)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.5583	-0.8246	-0.0743	0	3.513
Past treelines modelled without topographic variables (model 2)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.6491	-0.7573	-0.1457	-0.0001	3.62
Past treelines modelled without topographic variables (model 3)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.5652	-0.6593	-0.1684	0	3.6131
Past treelines modelled without topographic variables (model 4)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.42	-0.7954	-0.1218	-0.0001	3.5721
Past treelines modelled without topographic variables (model 5)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.6358	-0.844	-0.1212	0	3.6658

Table S19. Model properties for all past treeline models, modelled without topographic variables. Model 4 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Past treelines modelled without topographic variables (model 1)		
	Value	**Degrees of freedom**
Null deviance	559.42	199
Residual deviance	487.94	196
AIC	495.94	
Fisher scoring iterations	9	
Past treelines modelled without topographic variables (model 2)		
	Value	**Degrees of freedom**
Null deviance	559.42	199
Residual deviance	488.61	196
AIC	496.61	
Fisher scoring iterations	9	
Past treelines modelled without topographic variables (model 3)		
	Value	**Degrees of freedom**
Null deviance	559.42	199
Residual deviance	486.85	196
AIC	494.85	
Fisher scoring iterations	9	
Past treelines modelled without topographic variables (model 4)		
	Value	**Degrees of freedom**
Null deviance	559.42	199
Residual deviance	495.77	196
AIC	503.77	
Fisher scoring iterations	9	
Past treelines modelled without topographic variables (model 5)		
	Value	**Degrees of freedom**
Null deviance	559.42	199
Residual deviance	492.12	196
AIC	500.12	
Fisher scoring iterations	10	

Table S20. Total prediction error for all past treeline models, modelled without topographic variables, evaluated by 4-fold cross-validation. Model 4 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

	Past treelines modelled without topographic variables				
	Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**
Total prediction error	120.17	123.50	127.42	99.28	140.97

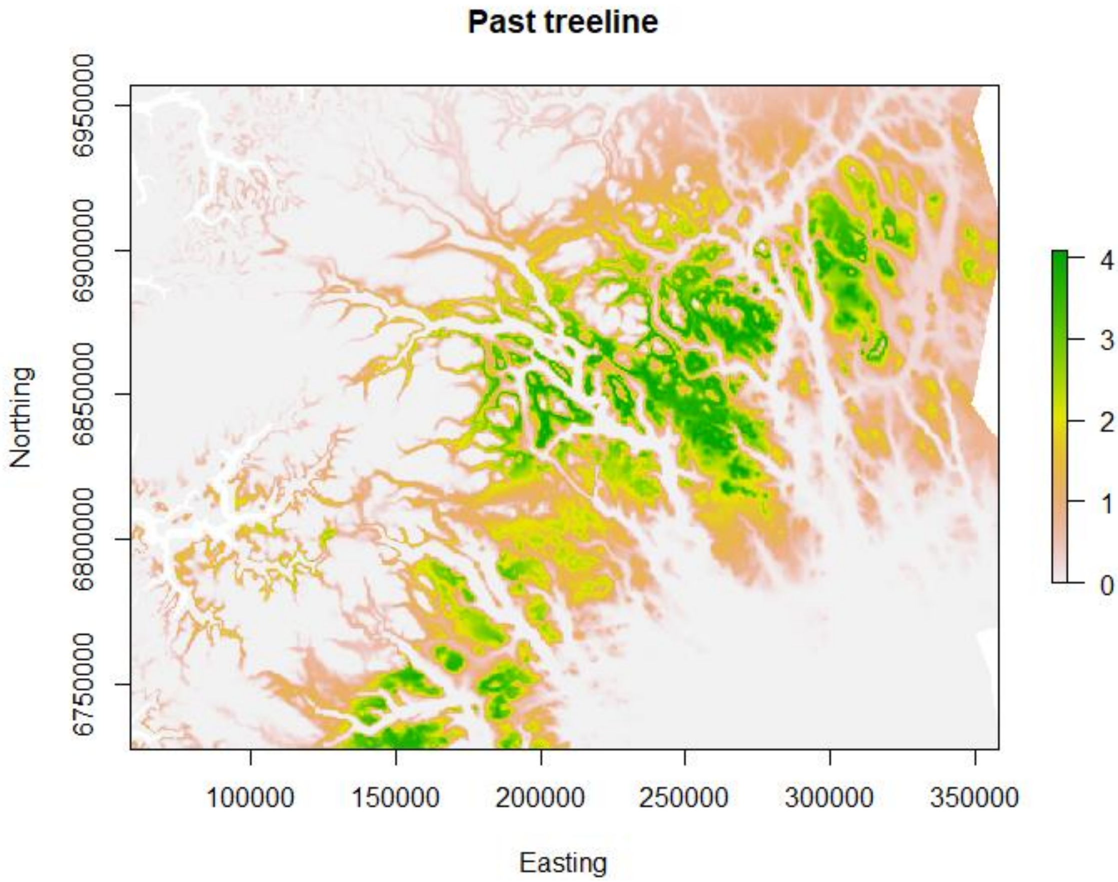

Figure S7. Modelled distribution of past treelines without topographic variables (model 4 in Table S17-20; see Figure S8 for modelled response of the predictors) in south Norway with probability ratio output (PRO) values indicated on a continuous scale, where white indicates low relative probability of presence and green indicates high. Because the values are relative, a given value in this model may not correspond to the same value from another model, and area estimates are made under the assumption that the highest local predictions indicate areas with local maximum elevation of the model object. Coordinate reference system: WGS 84/UTM zone 33N.

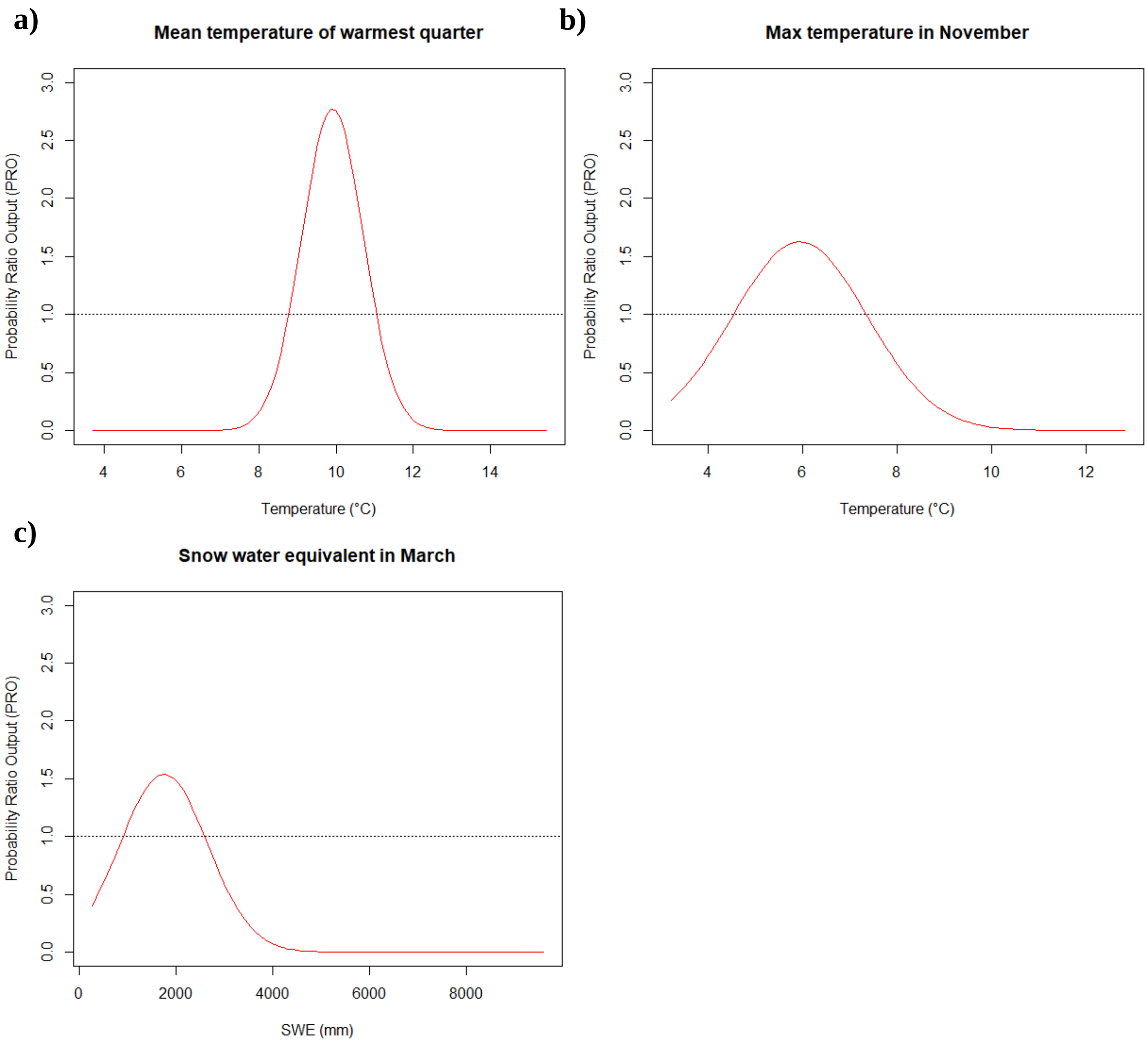

Figure S8. Response plots showing probability ratio output (PRO) values as a red line for the **(a)** mean temperature of the warmest quarter, **(b)** maximum temperature in November and **(c)** snow water equivalent in March in the model of past treelines, modelled without topographic variables (see Table S17-20 model 4 for details, and Figure S9 for frequency of observed presence (FOP) plots).

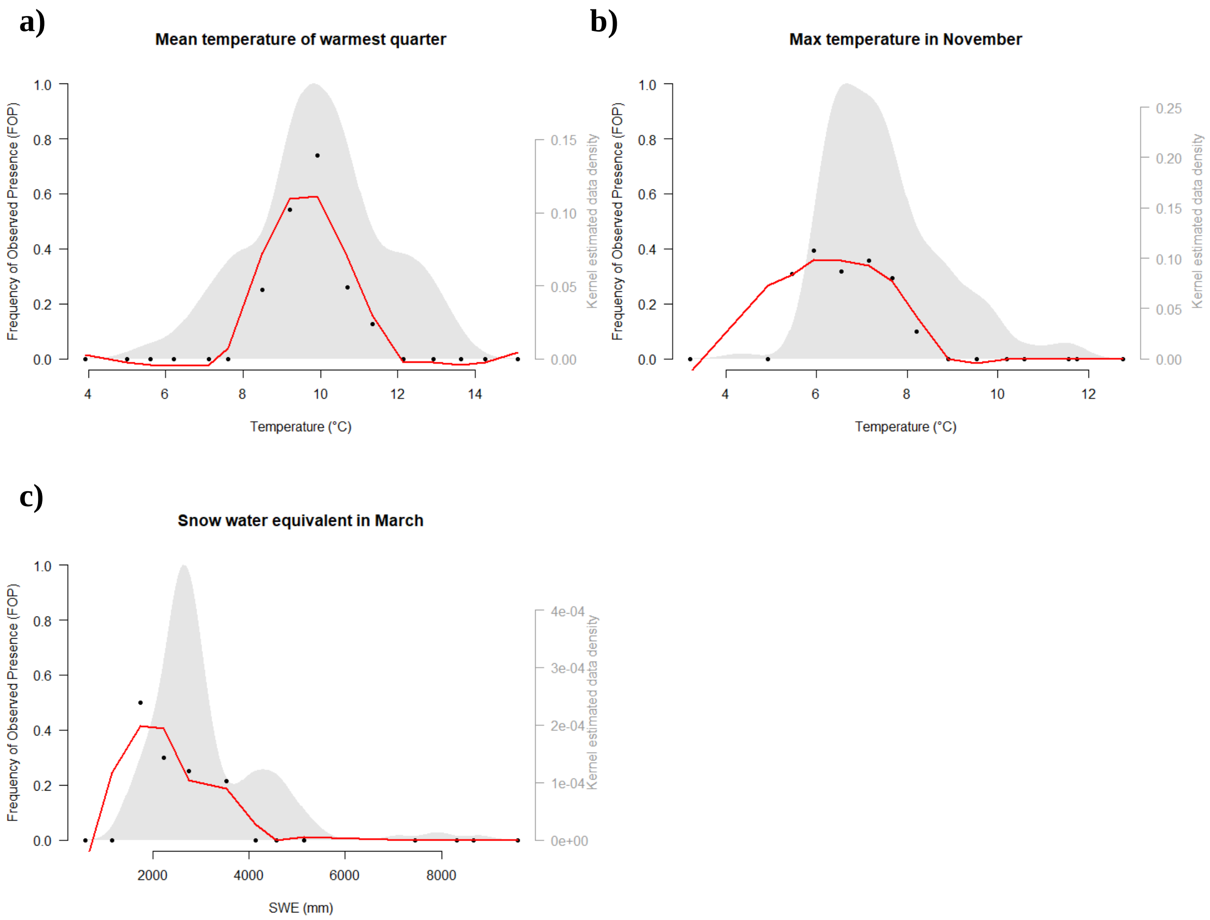

Figure S9. Frequency of observed presence (FOP) plots of past treelines modelled without topographic variables (see model 4 Table S17-20 for details, and Figure S8 for modelled response of the predictors) for the **(a)** mean temperature of the warmest quarter, **(b)** maximum temperature in November and **(c)** snow water equivalent in March presented as black dots. The red line is fitted to the points by a local regression with the MIAmaxent package and the density of values for each explanatory variable in the data set is presented in grey.

Table S21. Explanatory variables, their transformations and estimated coefficients for all past forest line models, modelled without topographic variables. Model 1 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area. L = linear, M = monotonous, D = deviation (D1, D2 or D05)

Past forest lines modelled without topographic variables (model 1)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.5702	0.2133
Mean temperature of warmest quarter	D2	-36.3087	12.1306
Max temperature in November	D2	-28.06	12.9777
Past forest lines modelled without topographic variables (model 2)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.4832	0.2176
Mean temperature of warmest quarter	D2	-35.3791	10.8754
Max temperature in November	D2	-15.5606	8.5136
Past forest lines modelled without topographic variables (model 3)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.4893	0.2024
Mean temperature of warmest quarter	D2	-34.8612	10.3549
Max temperature in November	D2	-25.4277	11.1068
Past forest lines modelled without topographic variables (model 4)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.5452	0.2077
Mean temperature of warmest quarter	D2	-44.4331	13.1415
Max temperature in November	D2	-19.4759	9.6964
Past forest lines modelled without topographic variables (model 5)			
	Transformation	**Estimate**	**Standard error**
Intercept	-	-4.6388	0.2087
Mean temperature of warmest quarter	D2	-45.1153	14.2037
Max temperature in November	D2	-12.7324	5.8861

Table S22. Deviance residuals for all past forest line models, modelled without topographic variables. Model 1 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Past forest lines modelled without topographic variables (model 1)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.4221	-0.7988	-0.1016	0	3.6883
Past forest lines modelled without topographic variables (model 2)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.4989	-0.7448	-0.0636	0	3.5688
Past forest lines modelled without topographic variables (model 3)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.4918	-0.6134	-0.0693	0	3.5215
Past forest lines modelled without topographic variables (model 4)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.4516	-0.7185	-0.0539	0	3.6039
Past forest lines modelled without topographic variables (model 5)				
Min	**1st quartile**	**Median**	**3rd quartile**	**Max**
-1.3809	-0.7864	-0.1026	0	3.7354

Table S23. Model properties for all past forest line models, modelled without topographic variables. Model 1 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

Past forest lines modelled without topographic variables (model 1)		
	Value	**Degrees of freedom**
Null deviance	503.48	179
Residual deviance	437.42	177
AIC	443.42	
Fisher scoring iterations	9	
Past forest lines modelled without topographic variables (model 2)		
	Value	**Degrees of freedom**
Null deviance	503.48	179
Residual deviance	434.33	177
AIC	440.33	
Fisher scoring iterations	9	
Past forest lines modelled without topographic variables (model 3)		
	Value	**Degrees of freedom**
Null deviance	503.48	179
Residual deviance	431.74	177
AIC	437.74	
Fisher scoring iterations	9	
Past forest lines modelled without topographic variables (model 4)		
	Value	**Degrees of freedom**
Null deviance	503.48	179
Residual deviance	435.24	177
AIC	441.24	
Fisher scoring iterations	10	
Past forest lines modelled without topographic variables (model 5)		
	Value	**Degrees of freedom**
Null deviance	503.48	179
Residual deviance	441.98	177
AIC	447.98	
Fisher scoring iterations	9	

Table S24. Total prediction error for all past forest line models, modelled without topographic variables, evaluated by 4-fold cross-validation. Model 1 was chosen as the best model (details in Results: Table 1) and used for estimation of changes in area.

	Past forest lines modelled without topographic variables				
	Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**
Total prediction error	109.406	112.0539	118.0767	111.6726	110.0859

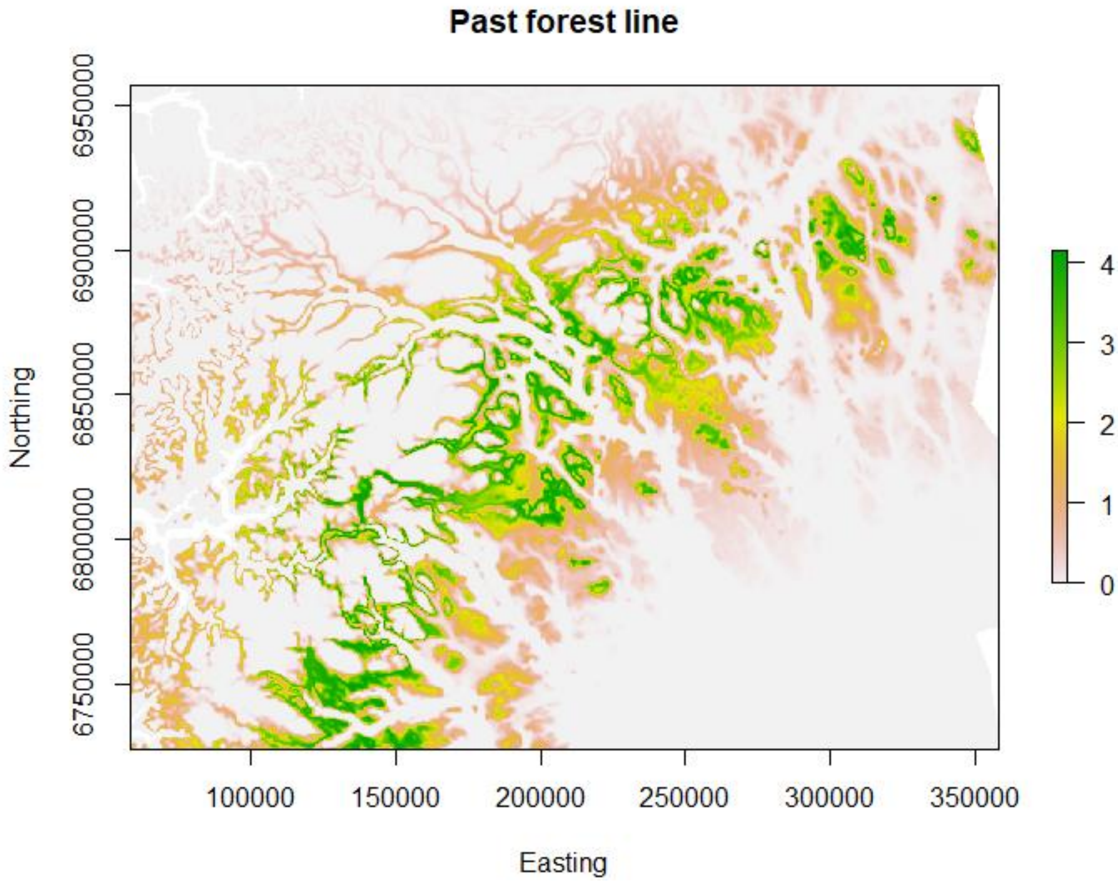

Figure S10. Modelled distribution of past treelines without topographic variables (model 1 in Table S21-24; see Figure S12 for modelled response of the predictors) in south Norway with probability ratio output (PRO) values indicated on a continuous scale, where white indicates low relative probability of presence and green indicates high. Because the values are relative, a given value in this model may not correspond to the same value from another model, and area estimates are made under the assumption that the highest local predictions indicate areas with local maximum elevation of the model object. Coordinate reference system: WGS 84/UTM zone 33N.

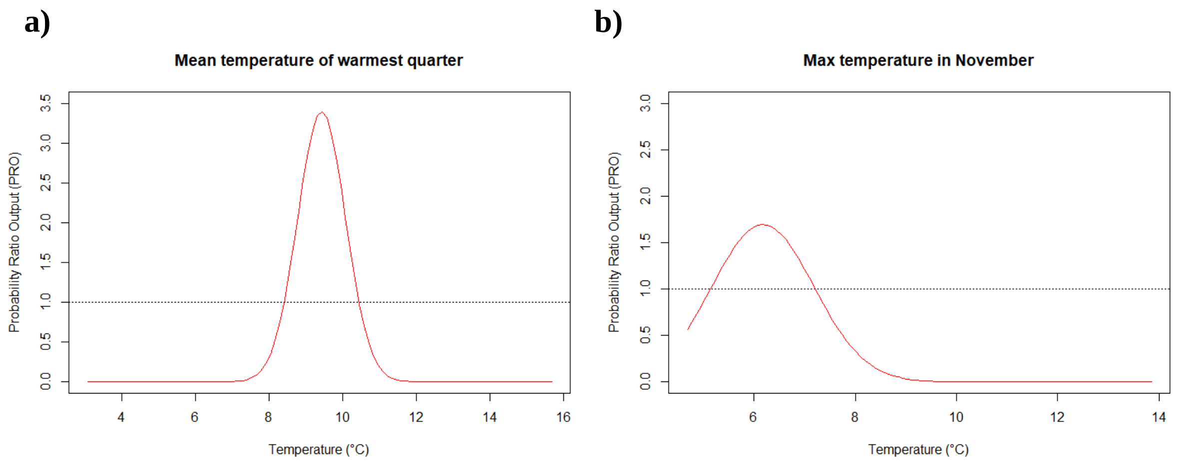

Figure S11. Response plots showing probability ratio output (PRO) values as a red line for the **(a)** mean temperature of the warmest quarter and **(b)** maximum temperature in November in the model of past forest lines, modelled without topographic variables (see Table S21-24 model 1 for details, and Figure S12 for frequency of observed presence (FOP) plots).

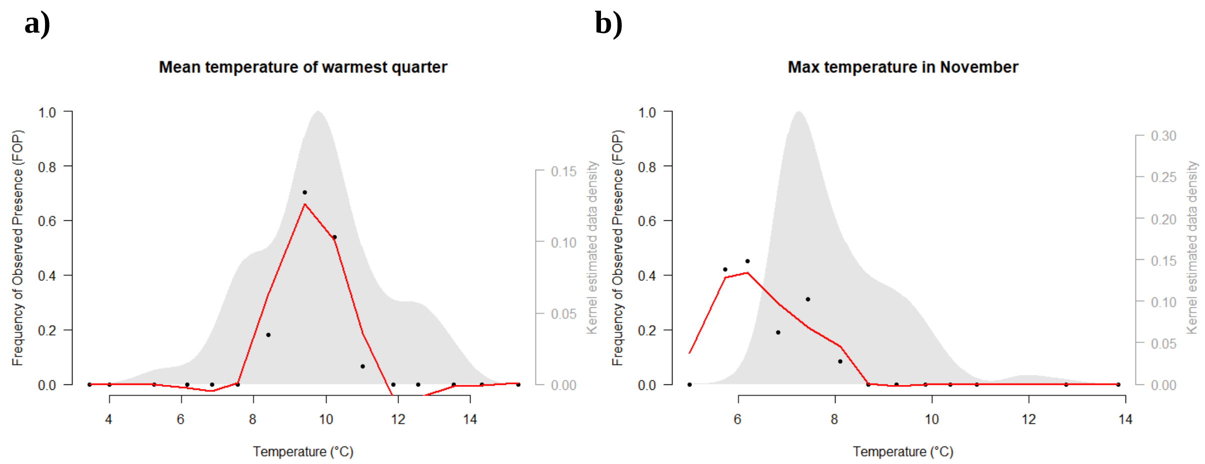

Figure S12. Frequency of observed presence (FOP) plots of past forest lines modelled without topographic variables (see model 1 Table S21-24 for details, and Figure S11 for modelled response of the predictors) for the **(a)** mean temperature of the warmest quarter and **(b)** maximum temperature in November presented as black dots. The red line is fitted to the points by a local regression with the MIAmaxent package and the density of values for each explanatory variable in the data set is presented in grey.

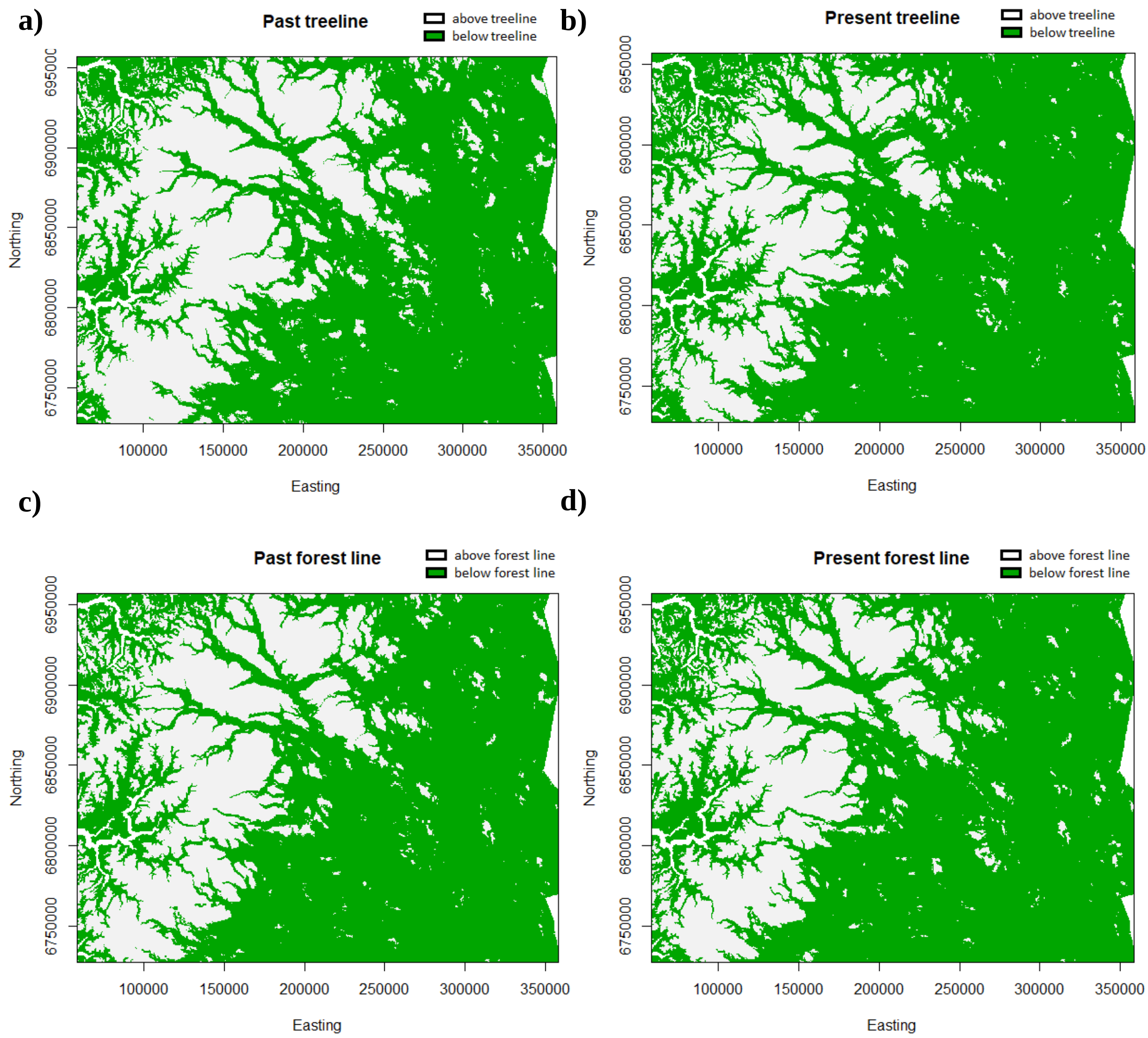

Figure S13. Binary maps of **(a)** past treelines, **(b)** present treelines, **(c)** past forest lines and **(d)** present forest lines in south Norway made by transformation of continuous probability ratio output into a binary scale where areas above the tree- and forest lines are indicated in white, and areas below are indicated in white. The maps are based on past and present tree- and forest line models, modelled without topographic variables (see Figure S1, S4, S7 and S10), where values are relative. Thus, the models are not comparable, but the maps are, under the assumption that the highest local prediction values in each model represent the most likely elevation of tree- and forest lines locally. Coordinate reference system: WGS 84/UTM zone 33N.

Veileder for kartlegging av tre- og skoggrenser

Anders Bryn 2013-2020

Litt om å hva som menes med tre, og da med fokus på fjellbjørk:

Et tre er en fysiognomisk enhet – ikke en artsenhet eller tilsvarende. Det vil alltids finnes individer høyere opp enn de vi skal måle inn. Det er derfor viktig å tenke på hvorfor vi måler akkurat trær, og hva det da vil si å være et tre i grenseområdene mot fjellet.

- De skal stikke opp over snøen om vinteren og utsettes for klimatiske prosesser hele året – inkludert vinteren.
- De skal utsettes for atmosfærisk klima – ikke bakkenært klima. Normalt ligger meteorologiske stasjoner i Norge 2 m over bakken, men da på lokaliteter uten vegetasjon (eller med krypende vegetasjon under 10 cm). Normalt vil vegetasjonen i tre- og skoggrensa være på omkring 30 - 70 cm eller noe mer. Derfor bruker nesten alle forskere definisjoner på trær som > 2.5 m (mange 3 m og noen 3.5 m). Det er avstanden fra øvre tette vegetasjonsdekke som gjelder for å unngå bakkenært klima.
- I gjentaksstudier kan man også argumentere for at de skal oppleves som trær, ettersom definisjonene ser ut til å være rimelig subjektive.

I gamle studier brukes ofte lengdemålet «mannshøyde», og dette er ikke entydig definert. Fram mot 1900-tallet regnes en mannshøyde til 170-175 cm, mens den etter 1900 øker gradvis mot 180 cm. Følger man favnen fram til 1887, blir høyden omkring 180 cm.

Ifølge Børre Aas ble dette tolket som et høydekrav til 2 m, men da som fast stamme i 2 meters høyde. Den totale høyden vil da i nesten alle tilfeller være høyere. Min erfaring er at trær som regel er høyere 2.5 m, og at det ikke er en gradvis nedgang i trærnes høyde som funksjon av meter over havet. Det som avgjør er om trærne har kommet seg over snødekket og etablert seg «der» med en tydelig krone – og da er de som regel høyere enn 2 m.

Min erfaring er helt parallell til det Søren Ve skriver i 1940, og som de fleste andre som jobber med tre- og skoggrenser erfarer:

«*Normann (1895-1901) definerte slik: «- den øverste høide over havet, hvor der forekommer oprette i regelen enstammede og mer end mandshøie birker». Tengwall (1920, s. 319) segjer at ein må ha inngåande kjennskap til korleis dei økologiske faktorar utformar bjørki i kvart einskilt tilfelle for å kunna avgjera um ei bjørk skal reknast for tre eller buske. Men etter mi røynsle er det sjeldan at ein på desse kantar råkar meir enn mannshøge bjørker som ikkje kan reknast for tre. Dei aller fleste som ikkje har karakteren av tre – tunne skot med fåe sidegreiner -, vil som regel vera mindre enn mannshøge. Det er difor nærmast Normann sin definisjon eg har halde meg til.*»

Formål:

Formålet i denne fasen er å forstå **regional** variasjon, ikke lokal variasjon. Lokal variasjon vil registreres systematisk etter at den regionale variasjonen er registrert og undersøkt.

- Gjenta registreringer for å studere endringer, med særlig vekt på å tall-feste endringshastigheter
- Separere tre- fra skoggrenser, slik at endringshastighetene kan beskrives for henholdsvis den fysiognomiske enheten tre og for økosystemet skog (slik skog er definert her)
- Etablere nye registreringer for klimatiske tre- og skoggrenser, slik at vi kan studere koblingene mellom klima og tre- og skoggrenser
- Etablere nye registreringer for klimatiske tre- og skoggrenser, slik at andre kan bruke våre registreringer til gjentak om «noen» år (sannsynligvis 25 eller 50 år)
- Etablere et grunnlag for systematisk overvåking av tre- og skoggrenser. Vi skal **ikke** starte overvåkingen i denne fasen, men skaffe data for å kunne etablere en overvåking

Normalt vil det måtte registreres fra 5 – 15 trær per tregrenselokalitet, og tilsvarende per skoggrenselokalitet. Jeg har registrert opp til 50 punkter på en lokalitet(et fjell – et stedsnavn hos Aas) – hvor alle ulike eksposisjoner kommer i spill, og da ble det likevel bare ett gjentaks-punkt registrert. Dette gjør at mengden variabler som registreres i hvert punkt, må holdes på et absolutt minimum, men fange opp det som er nødvendig for å forstå regional variasjon.

I denne første fasen var det viktigere å gjennomføre alle gjentak, heller enn å registrere nye lokaliteter eller nye eksposisjoner. Nå som mange av studielokalitetene er gjentatt, er det viktigere å registrere nye lokaliteter, dvs tre- og skoggrenser på nye fjell. Det er derfor viktig å se på klokka og framdriftsbehovet underveis i sesongen, og beregne hvor mye tid du kan gjøre per lokalitet (fjell). Normalt bør en klare en til to lokaliteter (fjell, eller stedsnavn) per dag, noen ganger flere, men innimellom bare en lokalitet.

Det er ikke om å gjøre å bekrefte endringer eller stillstand. Det er om å gjøre å dokumentere hvilke endringer som har skjedd. Se på hver lokalitet (fjell) med nye øyne. Avvik fra egne forventninger må påregnes.

- Inger har i tillegg formål om å dokumentere NiN-typene ved klimatiske tre- og skoggrenser. Dette bikker over mot lokal variasjon, og kan være en god test for overgang til overvåking (fra regional til lokal)
- Anders registrerer tre- og skoggrenser på Sunnmøre for både fjellbjørk, gran og furu.
- Adam leter konsekvent etter de høyeste tre- og skoggrensene på nye fjell, fjell som Hanna Resvoll-Holmsen og Børre Aas ikke har registrert på. Dette skyldes at de høyeste tre- og skoggrensene nå kan ligge andre steder enn de gjorde for 100 år siden.

Det som er avgjørende er å prøve å forstå hva Resvoll-Holmsen, Aas, og Ve har definert som et tre og skog, for å re-kartlegge dette. Samtidig bør vi legge igjen en mer objektiv definisjon for våre data, slik at det blir lettere å avgjøre hva et tre er for de som kommer etter oss. Det er dette kompromisset dere finner igjen i min definisjon av hva et tre er.

Alle registrerer med appen Natur i endring, i tillegg til vanlige registreringer med skjema, GPS og kamera (m GPS). Dette sikrer data, og gir oss mulighet til å publisere bedre på Natur i endring dataene.

Litt om det å gjenfinne en lokalitet:

Det er vanskelig å vite nøyaktig hvor de har registrert tidligere. Prøv å tenke på tilgang, topografi m.m. når dere leter opp lokaliteter. Et godt utgangspunkt kan være å lese seg fram til hvor de har gått fra, eller tenke seg fram til beste sted å gå fra (på den tiden de registrerte). Dette er og blir en subjektiv øvelse.

Dersom du mener at det er nødvendig å justere høydene til Ve, Resvoll-Holmsen eller Aas, så skal dette kun gjøres dersom du er helt sikker på at tidligere målinger er feil. Ulike tilfeller:

- Gamle målinger går høyere enn selve topp-punktet på fjellet, hvilket er umulig. Da må man inn å justere innlesingspunkt / kalibreringspunkt fra gamle gradteigskart. Slike lokaliteter må beskrives i kommentarfeltet. Høyden reduseres tilsvarende feilen i opprinnelig gradteigskart.
- Gamle og vitale trær som er eldre enn de tidligere registreringene, og som finnes høyere opp enn det som Ve, Resvoll-Holmsen eller Aas har angitt. Bruk trebor for å forsikre deg om at treet er minst 20 år eldre enn forrige registreringstidspunkt i brysthøyde. For Aas er dette mulig, men det er trolig vanskelig for Resvoll-Holmsen og Ve, ettersom trærne i de tilfellene vil måtte være svært gamle.
- Bjørk brytes normalt ned rimelig raskt (sammenliknet med f. eks furu). Likevel har jeg funnet døde trær på bakken over tidligere registrerte tregrenser. Da bør lokalitet registreres fullt ut, og så kan vi vurdere om tregrensemålingene fra gammelt av skal heves.
- Du står på en lokalitet som Ve, Resvoll-Holmsen eller Aas ikke oppdaget, men som er betraktelig høyere. Dette er vanskelig å vurdere, og her må en være konservativ.
    - Ligger lokaliteten slik til i terrenget at den er lett å overse?
    - Ligger lokaliteten bak en rygg / kam i terrenget f. eks?
    - Er det store gamle trær på lokaliteten? Bruk treboret ved behov….
    - Er det fysiske barriærer bort til lokaliteten som gjør at den kanskje ikke ble besøkt?

Tredefinisjon:

- Normalt skal de være enkelt stammet / en-stammet, men dersom fler-stammet – da bør den sentrale stammen være > 2.5 m høy (total lengde er ikke interessant)
- Trærne bør være opprette, men nederste del kan være krypende / bøyd før den strekker seg
- Stammen i brysthøyde (1.3 – 1.5 m over bakken) skal ikke være for fleksibel eller bøyelig (ikke tynn)
- Trærne bør ikke være buskformet:
    - dette er en variabel fysiognomisk gruppe som kan ta mange former

    - oftest < 2.5 m i tregrensenivå, men særlig vier kan få høye former
- Trærne skal stikke opp over snøen om vinteren og ha etablert en «krone» over snøen.
    - Krona trenger ikke å være bred. Tvert imot er den ofte smal, og det er ok
    - Hvis krona ender i «pisk» uten grønne blader, skal den helst ikke telle med (med mindre alle andre kriterier er tilfredsstilt).
    - Dersom «pisken» henger, skal den ikke strekkes ved lengdemåling
- Toppen skal / bør ikke være buskformet
- Stammen skal / bør ikke ha mange sidegreiner
- Fast enkeltstamme skal være «mannshøy», før den går over i ett eller flere fleksible toppskudd;
    - total høyde normalt > 2.5 m høy, men ikke alltid
    - diameter i brysthøyde normalt > 5 cm, men mindre (3 cm) kan aksepteres dersom alle andre kriterier er tilfredsstilt
- Men trehøyde måles, og trær under 2.5 måles også inn – så langt ned som de oppfattes som trær:
    - 10 cm nøyaktighet under 2.5 m,
    - 50 cm nøyaktighet over 2.5 m høye trær.
- Det er høyden treet har over bakkeplanet som teller – ikke lengden på krypende stammer. Når høyden måles, måles den fra bakken hvor rota er festet, også når treet er krypende. Dette er spesielt viktig i bratt terreng og der det er store snømengder.
- Det er høyeste lokalitet som leses inn, stratifisert på 8 ulike hellingsretninger. Hellingsretning leses **ikke** av fra kart eller GPS, men fra kompass
- Rotskudd fra basis kan aksepteres som tre når alle andre kriterier er tilfredsstilt.

Skogdefinsjon

Alle trær som inngår skal tilfredsstille kravet til å være trær (se over). Det er de absolutt høyest voksende skogteiger eller skogtunger som skal registreres. Det er det øverste treet (i m o.h.) i skogteigen som skal registreres.

Det skal ikke være mer enn 15 meter avstand mellom trærne målt fra stammen, med mindre trærne har store trekroner – da måles avstand fra ytterste kant av trekronene. Høyde inngår ikke i avstandsmålet, så i bratt terreng kan det godt være noe lenger målt ved bakken (opp mot 20-25 meter). Avstand anslås – det måles ikke. Det tar for lang tid!

Skogteiger over sammenhengende skog skal registreres, men da skal det minst være 15 individuelle trær i populasjonen som utgjør skogen. Alle de 15 individene skal klart holde definisjonen til å være et tre (se over). De kan godt stå tett (og ha felles vegetativt opphav for lenge siden), men de bør kunne oppfattes som individer.

Registreringer av tregrense

1. Øverste tre av fjellbjørk, på hver tidligere registrerte hellingsretning, skal <u>alltid</u> registreres.

Dersom det finnes andre treslag som vokser høyere enn fjellbjørka, og som holder alle krav til å være et tre, så skal det høyest voksende individet av hvert treslag også registreres. Andre parametere registreres som for fjellbjørka. Treslag som kan forekomme høyere enn bjørka er fremst gran og rogn, men også furu, osp og gråor er i sjeldne tilfeller observert høyt.

2. I tillegg skal det registreres øverste tre av fjellbjørk på andre hellingsretninger (nye) som er tilgjengelige m.h.t. gåavstand. Dette er for å etablere et bedre datasett, og å fylle inn de lokalt høyeste trærne.

3. Dersom det er mulig, bør en også forsøke å registrere øverste tre av fjellbjørk på fjell i regionen som antakeligvis er høyere enn der det tidligere er registrert av Resvoll-Holmsen, Aas eller Ve. Dette må imidlertid vurderes av hver enkelt ved å se på kart, bruke kikkert osv. Det er viktigere å repetere målingene til de andre, enn å etablere nye (gjelder ikke Adam – han finner nye lokaliteter). Men for å legge igjen et bra utgangspunkt for andre, samt å finne klimatiske tre- og skoggrensenes, bør nye lokaliteter leses inn. Vi kan ikke ta for gitt av Resvoll-Holmsen, Ve og Aas leste inn kun klimatiske grenser (selv om de registrerte de høyeste i sin tid).

4. Følgende variabler registreres ved hvert tre:
   a. **<u>Stedsnavn (lokalitetsnavn), dato for registrering og registratornavn</u>**
   b. **<u>Kode for punktet du leser inn</u>**
      i. Det kan bli mange trær per lokalitet med samme hellingsretning.
      ii. Lag et enkelt kodesystem med en meget kort tekststreng som lett tastes inn på GPS
   c. **<u>Treslag</u>**
   d. **<u>Altitude:</u>** Høyde (meter o.h.) som leses av fra GPS **<u>og</u>** fra aneroid barometer (husk å kalibrere barometer hver dag på morgenen). Barometer kalibreres kun ved kjente høyder. La GPS stå på hele tiden fra du går fra bilen / hytta. Høyde interpoleres i tillegg fra kartbasen i etterkant.
   e. **<u>Treets høyde:</u>** Total høyde på treet (men ikke lengde) – måles fra bakken der rota er festet uten å strekke ut toppen. Trær >2.5 m måles i 50 cm intervaller, trær <2.5 m måles i 10 cm intervaller. Ved bøyde eller krypende trær, måles høyden vertikalt fra toppen og ned til bakken.
   f. **<u>GPS usikkerhet i ± meter</u>**
   g. **<u>Koordinater:</u>** Lokalitetens koordinater og koordinatsystem brukt av GPS på punktet
   h. **<u>Hellingsretning</u>** (bruk kompass – ikke GPS eller kart – se lenger ned)
   i. **<u>Vegetasjonstyper:</u>** Alle registrerer vegetasjonstype etter Rekdal & Larsson (2005), inkludert alle tilgjengelige variabler.
      i. Det er treets økologi som er poenget. Står f. eks treet på en rygg med rabbevegetasjon, men med tydelige røtter i næringsrikt vann, da registreres både 2c (rabbe) og 3b (høgstaudeeng).
      ii. Poenget er å registrere det som i hovedsak påvirker individet. Normalt vil det holde med å registrere en vegetasjonstype m variabler, men enkelte ganger er det nødvendig med 2.

iii. Variablene er viktige å registrere og følger standard instruks fra Rekdal & Larsson (2005)
iv. Tregrenser registreres som åpne vegetasjonstyper (i gruppe 1, 2, 3, 9 eller 12)
v. Skoggrenser registreres som skogdefinerte typer (i gruppe 4, 6, 7 eller 8)

j. **NiN-typer:** Inger skal i tillegg registrere NiN-typer fra 1:5.000 målestokkområdet.
   i. Vi kan diskutere i felt hvilke eventuelle uLKM'er og variabler som kan registreres ved henholdsvis tregrensa og skoggrensa

k. Ta **foto av tre med GPS**. Foto taes fra siden, ikke ovenfra eller nedenfra. Ta foto slik at lokaltopografi og vegetasjon blir tydelig i foto. Ikke stå for langt unna treet ved tregrenser, men ha større avstand ved skog, slik at hele øvre skogteigen kommer fram.

l. **Utvikling:** Registrer om populasjon er i:
   i. **Framgang (+):** mange nye saplings (over 15 cm) på vei opp i umiddelbar nærhet eller over dagens grense. Årets nye individer teller ikke (germlings), og heller ikke individer under 15 cm høyde (seedlings). Disse kan ikke registreres systematisk i denne fasen. Nye individer bør være minst 15 cm høye (dvs saplings). Rotskudd fra det målte individet teller ikke, med mindre de er i ferd med å etablere seg som nye trær litt unna mor-individet. Er det helt «vill» spredning, dvs hundrevis av nye saplings på vei opp, så registreres dette som (++).
   ii. **Tilbakegang (-):** Bestand bestående av bare gamle trær, ingen rekruttering i umiddelbar nærhet. Tydelig tegn til sykdom, alderdom, skader, toppbrekk, døde trær på bakken, naturlige stubber m.m. Midlertidige skader gir ikke tilbakegang, men varig svekking av individ gir tilbakegang (tenk målerangrep, rustsopp m.m.)
   iii. **Stillstand (0):** ingen nye individer på vei opp i umiddelbar nærhet, men for øvrig friske og sunne trær uten synlige tegn til skader, sykdom m.m.

m. **Alder:** Anslå treets alder subjektivt i 4 klasser etter beste evne (bruk trehøyde, diameter, barkstruktur, kronestruktur, forgreining m.m., men **ikke** bor for telling av vekstringer uten at dette er nødvendig for å endre tidligere høyde. Minimer bruken av trebor – det tar for lang tid):
   i. < 25 år
   ii. 25 – 50 år
   iii. 50 – 100 år
   iv. > 100 år

n. **Diameter i brysthøye:** Mål diameter på stammen på det øverste treet ved brysthøye (1.3-1.5 m over bakken) i cm

o. **Kommentarer:**
   i. Tydelig og omfattende beiting på øvre individer noteres. Legg særlig merke til sau og elg. Normal småbeiting kan tas for gitt og skal ikke registreres.
   ii. Tydelig og omfattende soppangrep (rustsopper) og bjørkemålerangrep noteres (skill tidligere målerangrep fra dagens). Normale småskader kan tas for gitt og skal ikke registreres.
   iii. Dersom lokaliteten er usikker m.h.t. tidligere registrering, skal dette registreres.

Normale definisjoner ved tregrensa / skoggrensa

- **Germlings:** årets nye spirer – dvs årets nye etableringsforsøk. Ikke mulig å observere systematisk i vår tilnærming. Alt fra 0 til 15 cm store, normalt mindre ved tregrensen.
- **Seedlings:** de første åra rett etter etablering. Normalt ikke mulig å observere systematisk i vår tilnærming. Som oftest registrert som individer opp til 15 cm høye.
- **Saplings:** buskforma individer over 15 cm, men under 2.5 meter (som oftest 3 eller 3.5 meter). Holder ikke definisjonen av å være et tre (se over). Som oftest settes et krav om at hovedstamme skal være under 10 cm diameter i brysthøyde, men dette er for strengt for fjellbjørk i henhold til Resvoll-Holmsen, Ve og Aas sin definisjon. Jeg har brukt opp til 5 cm diameter i brysthøyde.
- **Trees:** se definisjon over. Bør normalt ha >5 cm diameter i brysthøyde (dvs stiv stamme i brysthøyde), være > 2.5 m høyt, være rimelig rettvokst, være en-stammet eller med en klar sentral-stamme, ha en mer eller mindre etablert og tydelig krone, mangle tette smågreiner på stammen, mangle den lange topp-pisken osv osv

Registreringer av skoggrense

Alt det som registreres for trær skal også registreres for skogen. Alle tre-variablene registreres for det øverste treet i populasjonen.

Vegetasjonstypene og variablene registreres som dominerende for de 5-10 øverste trærne. Dersom det varierer, så bruk vegetasjonstypen ved det øverste treet. Det er også her det vurderes om populasjonen er i framgang, stillstand eller tilbakegang.

Vær oppmerksomme på skogens omtrentlige alder.

Hellingsretning

Både Resvoll-Holmsen, Aas og Ve har lest inn lokalitetenes hellingsretning, og det har de fleste andre som har gjennomført slike målinger også gjort. Dette skyldes antakelsen om at hellingsretning er viktig for tre- og skoggrensenes høyde. Jeg har fortsatt denne registreringen, men ikke registrert hvor bratt hellingen er. Bratthet vil avleses med hjelp av GIS fra høydemodeller i etterkant. Bratthet og hellingsretning kan kombineres til eksposisjon i GIS, samt innstråling (både diffus og direkte stråling).

Alle, inkludert jeg, har delt hellingsretning inn i 8 klasser – de eksakte hellingsretningene avleder vi fra GIS i etterkant, slik at variabelen blir kontinuerlig:

Kategori	Fra	Til	Senter
Nord	337.5	22.5	360 / 0
Nord-øst	22.5	67.5	45
Øst	67.5	112.5	90
Sør-øst	112.5	157.5	135
Sør	157.5	202.5	180
Sør-vest	202.5	247.5	225
Vest	247.5	292.5	270
Nord-vest	292.5	337.5	315

Småtopografiske variasjoner teller ikke – det er dominerende hellingsretning som skal registreres. Trøbbelet består i hva småtopografisk variasjon er – den har særdeles mange former – og det går ikke an å beskrive alle. Her er noen utfordringer:

- I nederoderte bekkedaler er dette vanskelig. Nederoderte bekkedaler med tydelig hellingspåvirkning gir opphav til endringer i hellingsretning.
- I nedløpende slukeskere, morenerygger og berghammere er dette også vanskelig. Blir disse store og gir tydelig opphav til endrede vekstforhold for trærne, så skal hellingsretning registreres der treet står.
- Små topografiske forsenkninger som gir lokal leside og jordfuktighet, og hvor trærne alltid står rotfesta i nedkant av forsenkningen. Disse følger ofte normal hellingsretning, men kan avvike

Praktiske råd

- Ta alltid back-up av GPS, helst som avskrifter direkte i felt, og som avskrifter på kvelden. Det er fort gjort å miste GPS'en, og da må alle registreringer være sikret med back-up.
- Last opp foto fra kamera ofte. Det er fort gjort å miste kamera også.
- Legg alltid inn bilen som waypoint i GPS, og track hele tiden. Dette er viktig i tilfelle det blir tåke, og veien hjem er bratt. Da kan du følge ditt eget spor (track) tilbake med GPS'en. Ha alltid med ett ekstra sett med batterier til GPS.
- La GPS stå på hele tiden fra du kjører eller går fra telt el. hytte. Presisjonen øker når GPS står på hele tiden. Ved foto, må du vente til GPS-koordinater er inne på kamera, og dette tar

noe tid. Mitt kamera angir GPS presisjon kontinuerlig, slik at jeg ser når jeg tar foto med gode koordinater. Ikke alle kameraer har dette, og da bør du skru på kamera i det du kommer fram, gjøre registreringene, og så ta foto. Da er GPS i kamera ok.

- Ha alltid noe ekstra mat og drikke liggende i bilen, samt tørre klær og ekstra sko m.m. Jeg pleier å ha en pose med epler i bilen hele tiden, samt ei full vannflaske. Ikke fyll vann fra bekker i områder med mye sau eller død lemen, og ikke fra breelver (grått vann).
- Det er særdeles sjelden at den raskeste veien mellom to punkter er den rette linje. Prøv å følge stier og veier fram til du er i nærheten av dit du skal, før du bykser ut av stien.
- Hold høyden mellom de ulike trærne. Jeg pleier å kartlegge tregrenser innover, og skoggrenser tilbake, så blir det mindre opp-og-ned gange.
- Det er utfordrende å finne de øverste uteliggerne av trær. Bruk kikkert. Uteliggerne av tregrensa kan ligge et par hundre meter høyere enn skoggrensen. Spesielt vanskelig kan dette være i nesten flatt terreng. Da kan tregrensa ligge flere kilometer unna skoggrensa!
- Snakk med lokalbefolkninga om følgende (dersom du treffer noen av dem):
  - Gamle stier og veier opp til fjells, dersom terrenget er krevende
  - Når setra og beitinga opphørte dersom lokalitet er nær setrer
  - Hvor mye sau (beitedyr) som går i fjellområdet hvor tre- og skoggrenser skal registreres
  - Hvilke områder som var avskoget tidligere, og når gjengroinga startet
  - Bygdelitteratur, gamle kart, tidligere registreringer m.m.
  - Men, ta alle svar med en forvissning om at «manns minne er kort», og at informasjonen ikke nødvendigvis er gjeldende for akkurat de områdene som Resvoll-Holsem, Ve og Aas gikk i.