**RESEARCH ARTICLE**

# The relative role of climate and herbivory in driving treeline dynamics along a latitudinal gradient

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## Abstract

**Aim:** The treeline is an obvious ecotone between forest and tundra ecosystems. Climatic warming is expected to lead to the treeline advancing, although in many cases this has not been observed. This is most likely because other factors can also influence treeline dynamics, notably land use and herbivory in European treelines. In this study, the roles of climate and herbivory as determinants for change in stem number, growth and mortality responses of treeline ecotone trees were investigated.

**Location:** Thirty-six sites along a 1,000 km latitudinal gradient in the Scandes Mountains in Norway (60–69° N).

**Methods:** We recorded changes in stem numbers and height, and mortality between 2008 and 2012. A partial least-squares regression analysis (PLS) was carried out to find the relative importance of groups of variables representing climate, herbivory, site and tree properties for explaining the variation in these three response variables. We also fitted general additive models for each response with selected variables from the PLS analysis.

**Results:** We found an increase in number of stems and tree height for short and medium tall trees. The climatic variables explained the greatest proportion of the variation of the change in stem numbers, while tree height growth and mortality were best predicted by the growth stage of the tree and climate.

**Conclusions:** Our study shows that climate explains more of the variance in treeline performance than herbivory, tree properties or latitude. Relatively weak explanatory power of all variables suggests high context dependency of treeline dynamics between sites. It seems that at large scales, variables known to be important in regulating treeline dynamics within sites are poor predictors of treeline change in the short term.

**KEYWORDS**
climate change, herbivory, latitudinal gradient, Norway, treeline

# 1 | INTRODUCTION

In recent years, many studies have forecasted advances of the tree and forest lines towards higher elevations and latitudes due to global warming. For example, the dynamic global vegetation models predict that by the end of the 21st century, the area of the arctic tundra will be reduced by 40% (ACIA, 2005; Kaplan & New, 2006). On the other hand, analyses of historic data showing the development of the latitudinal forest- and treelines during the 20th century suggest this to be a huge overestimate (Hofgaard, Tømmervik, Rees, & Hanssen, 2013). Along the same line, a meta-analysis of 166 different sites worldwide showed that at 48% of these, the treelines had not advanced during the respective observation periods (Harsch, Hulme, McGlone, & Duncan, 2009). Tundra advance and southward shifts of forests in the northern hemisphere have also been observed (Crawford, Jeffree, & Rees, 2003; Harsch et al., 2009; Van Bogaert et al., 2011; Vlassova, 2002), even during periods with increased temperatures. Thus, these findings suggest that there are likely many other factors (e.g. Danby, 2011) potentially affecting the position of the treelines in addition to, or interacting with, temperature. This is also in line with meta-analyses suggesting that alpine and arctic vegetation responses to climate warming are context-dependent, i.e. dependent on site ambient temperature, moisture, and precipitation (Elmendorf et al., 2012; Grytnes et al., 2014). Precipitation is expected to increase by 5–30% in Northern Europe by 2100 (Hanssen-Bauer et al., 2009). Heavier snowfall during winter may result in shorter growing seasons in some areas, and more accumulated snow might affect tree recruitment, growth and mortality directly, but also affect herbivore forage availability (Mysterud & Austrheim, 2014). A longer duration of snow cover might also increase the probability of pine trees being infected with snow blight (*Phacidium infestans*) (Stöcklin & Körner, 1999). In other areas, on the other hand, winter precipitation may fall as rain in a warmer future, and the length of the growing season might increase (Hanssen-Bauer et al., 2009).

Temperature has direct effects on the establishment and growth of montane forest trees. At the treeline ecotone, defined as the transition zone between the continuous subalpine- and subarctic forest and the tundra, trees are at their temperature tolerance limit. A root zone average summer temperature of 6.7°C is suggested to be critical for trees to establish (Körner & Paulsen, 2004). Thus, minor changes in temperature may affect the position of treelines; in addition year-to-year variation in weather conditions may affect treelines locally. There is also evidence of treelines being more affected by short periods with extreme temperatures than mean temperatures (Gray, Betancourt, Jackson, & Eddy, 2006; Kitzberger, Steinaker, & Veblen, 2000). A single year of extreme low winter temperatures, coupled with a shallow snow cover giving little insulation, could set back many years of treeline ecotone advance from previous favourable years. Furthermore, Rupp, Chapin, and Starfield (2001) point out that treeline advances caused by increasing temperatures may be significantly lagged, and that responses depend on temperature to exceed a certain threshold before any observable change is seen.

Other important factors for treeline dynamics are herbivory and land use (Bryn & Hemsing, 2012; Gehrig-Fasel, Guisan, & Zimmermann, 2007; Speed, Austrheim, Hester, & Mysterud, 2010, 2011a, 2011b; Tasser, Walde, Tappeiner, Teutsch, & Noggler, 2007). Summer farms and grazing by domestic animals, such as cattle and sheep, have been common in many montane areas in Europe. Both the animals themselves and the human activity related to the summer farming, such as harvest of wood, have had large impacts on montane forest and treelines (Bryn & Hemsing, 2012; Solem et al., 2012). The animals may forage on seedlings and saplings in the treeline ecotone, limiting recruitment (Speed et al., 2010), height growth (Speed et al., 2011b) and radial growth (Speed et al., 2011a). Fertilization and disturbance in the top soil layer might also to some extent improve germination success for treeline trees (Tingstad, Olsen, Klanderud, Vandvik, & Ohlson, 2015) and tree recruitment is found to peak just after grazing cessation suggesting an important window of opportunity before the regrowth of other plant species limited by herbivory (Speed et al., 2011). Thus, in areas where summer farming and grazing animals have previously limited tree growth, treelines and montane forests may expand towards higher elevations when this activity is reduced. While herbivore densities have decreased in Norwegian lowland municipalities over the past few decades, municipalities dominated by alpine land have maintained their large herbivore pressure. There have been high regional variation and shifts between species from 1949 to 1999 (Austrheim, Solberg, & Mysterud, 2011) which are largely maintained until 2015 (Speed, Austrheim, Kolstad, & Solberg, 2019). However, due to a strong increase in the proportion of browsing cervids, herbivore pressure has shifted towards greater wood species foraging (from 15% to 38% in mountain municipalities from 1949 to 1999) (Austrheim et al., 2011). Distinguishing between such land-use effects and climatic effects on treeline dynamics, has so far proved difficult (but see Speed et al., 2010; Speed et al., 2011a; Speed et al., 2011b).

The current study sought to disentangle the effects of climate and herbivory on treelines by using field observations of mountain treeline trees at 36 different sites distributed along a 1,000 km latitudinal gradient in Norway. Since regional differences of changes in both precipitation and temperature have been observed in the past and are predicted for the future (Hanssen-Bauer et al., 2009), and because changes in herbivore pressure differ along the gradient, regional trends for the development of treelines were also expected. The latitudinal extent of the current study enabled us to examine the relative role of climate and herbivory for treeline dynamics, and whether the responses of treeline trees to these drivers were context-dependent, i.e. if they differ along this gradient. Tree recruitment was expected to increase with latitude in correspondence with a more pronounced latitudinal climate change (Stocker et al., 2013). The objectives were to examine: (a) if four-year changes in tree stem number, height growth, and mortality varied along the latitudinal gradient; and (b) the relative role of climate and herbivory in changes in tree performance.

## 2 | METHODS

### 2.1 | Study area

The field data used in this study were originally collected to serve as ground reference for tree detection by means of airborne laser scanning (ALS) along a transect (width ~200 m) from south (60°N) to north (69°N) in Norway (Figure 1) (Thieme, Bollandsås, Gobakken, & Næsset, 2011). The transect was planned to encompass as many alpine treeline ecotones as possible along the latitudinal gradient and follow the grid lines of the systematic design of Norwegian national forest inventory. The 36 selected sites along the transect had treeline ecotones that varied from being abrupt to gradual and patchy and the aspect of the slopes varied from site to site. Selection of sites was guided by information in the Norwegian M711 map series that comprise a rough indication of the treeline ecotone. The number of sites selected was constrained by budget, and furthermore, we aimed for a uniform distribution of sites along the latitudinal gradient. There were three tree species that dominated the treeline ecotones: the two most common conifer tree species in Norway, namely *Picea abies* and *Pinus sylvestris*, and *Betula pubescens* spp. *czerepanovii* which is the most common treeline-forming deciduous species. The vegetation varied between and within sites. Typical vegetation communities were species-poor sites dominated by lichens such as *Cladonia*

spp. and shrubs (e.g. *Betula nana* and *Vaccinium* spp.) (Figure 2a), and more species-rich sites dominated by graminoids and forbs (Figure 2b).

### 2.2 | Sampling design

At each of the 36 sites, sample plots with 25-m radii were established. The plot centres were located 50 m apart, on a line perpendicular to the treeline, so that they covered the elevational gradient, starting where distant trees with heights >2 m were found (Mork & Heiberg, 1937). Since the length of transition zones between the montane forest and the treeless areas varied, the number of plots on each site varied accordingly, and ranged between two and six. In total, 114 plots were established.

In each plot, trees (irrespective of species) from three different height classes (short trees: ≤ 1 m; medium height trees: 1–2 m; tall trees: ≥2m) were selected using truncated point-centred quarter (PCQ) sampling (Warde & Petranka, 1981). Following this procedure, the living tree closest to the plot centre for each of the four quadrants resulting from orthogonal division lines through the plot centre in the cardinal directions, was selected. The procedure was repeated for each height class, and the final sample included a maximum of 12 trees if there were no vacant quadrants for any of the height classes. Each selected tree was measured for height and
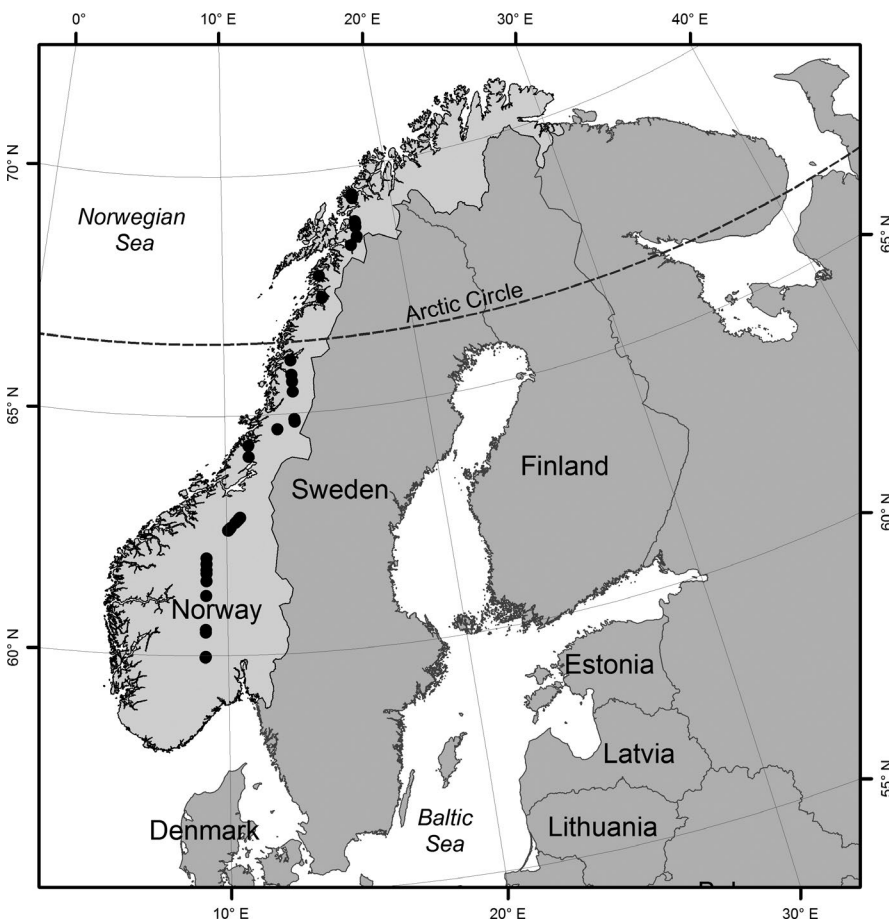


**FIGURE 1** Map showing the 36 different sampling sites as black dots along a 1,000 km latitudinal gradient in Norway

**FIGURE 2** Examples of typical vegetation communities at the sites. (a) Species-poor site with *Picea abies* as the dominating tree species. (b) Species rich site with *Betula pubescens* subsp. *czerepanovii* being the dominating tree species [Colour figure can be viewed at wileyonlinelibrary.com]
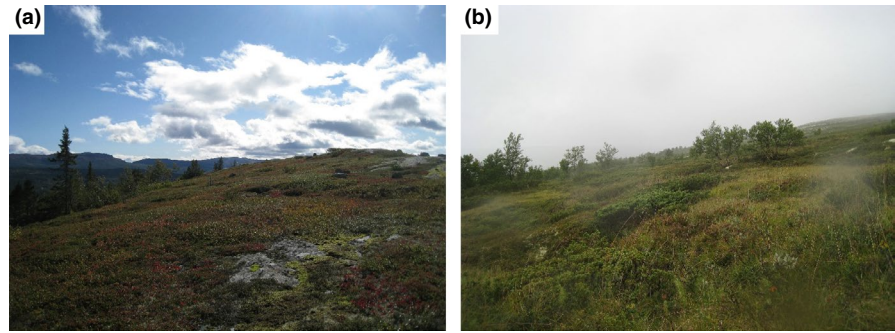
the tree species (denoted species id) was recorded. The dataset comprised *Picea abies*, *Pinus sylvestris* and *Betula pubescens* spp. *czerepanovii* (Table 1).

Tree variables from all plots were recorded in 2008 and in 2012. To ensure precise positioning of trees and plot centres, survey grade receivers (Legacy E+, Topcon, California, USA) were used in real-time kinetic (rtk) mode, receiving differential corrections of both the Global Navigation Satellite System (GLONASS) and the Global Positioning System (GPS). The precision of the coordinates is expected to be 3–4 cm. For more details on the sampling, see Thieme et al. (2011). Thus, both plot centres and each previously measured tree could be relocated using high-precision rtk-satellite positioning equipment. In 2012, all trees measured in 2008 were re-measured for height and in addition, we recorded if a previously measured tree had died. An updated PCQ sample for 2012 was acquired to enable an estimation of the number of living trees for the two sampling years.

## 2.3 | Calculation of number of stems, change in stem number, growth and mortality

The number of stems per unit area ($\lambda$) for each sampling site (comprising two to six plots) was estimated according to the estimator described by Cottam, Curtis, and Wilde Hale (1953) and Morisita (1954), as the inverse of the square, mean, tree-to-plot centre distance ($\bar{r}^2$):

$$\lambda = \frac{1}{\bar{r}^2} \qquad (1)$$

However, since the sampling was truncated and stopped at 25 m from the plot centre, there could be quadrants where no trees were

found (vacant quadrants), either for one, two or all height classes. In these cases, $\lambda$ was adjusted with a non-linear correction factor (CF) (see Warde & Petranka, 1981, Equation 2 and Table 1 for details) dependent on the ratio between vacant quadrants and the total number of quadrants, so that

$$\lambda = \frac{1}{\bar{r}^2} \times \mathrm{CF} \qquad (2)$$

The calculations were carried out separately for each tree height class, so that tree-size-specific number of stems was obtained for each site. Class-wise estimates of change in stem number were calculated as the difference between the stem number estimates of 2012 ($\lambda_{2012}$) and 2008 ($\lambda_{2008}$). In further analyses, the estimated change in number of stems relative to the observed number of stems in 2008 was used ($\Delta\lambda_{rel}$) rather than the absolute change, i.e.,

$$\Delta\lambda_{rel} = \frac{(\lambda_{2012} - \lambda_{2008})}{\lambda_{2008}} \times 100 \qquad (3)$$

Height growth (difference between height observations) was calculated for those trees that were measured in 2008 and that were still alive in 2012. Furthermore, mortality was recorded by assigning the value 0 to trees still alive at the second measurement, and the value 1 to those that were dead. As opposed to the number of stems and the corresponding change that was observed on site and tree size class level, mortality was observed on individual tree level.

## 2.4 | Herbivore data

To enable analyses that account for varying herbivore pressure, we used estimates of metabolic biomass (MBM) of all large herbivores,

**TABLE 1** Number of sample trees at first measurement (2008) divided into height classes and species. Percentages of total number of trees in brackets

| Height class | Total | *Picea abies* | *Pinus sylvestris* | *Betula pubescens* spp. *czerepanovii* |
|---|---|---|---|---|
| Short (≤1 m) | 361 (46) | 21 (3) | 33 (4) | 307 (39) |
| Medium height (1–2 m) | 249 (32) | 27 (3) | 12 (2) | 210 (27) |
| Tall (≥2 m) | 174 (22) | 24 (3) | 12 (2) | 138 (18) |
| Total | 784 | 72 (9) | 57 (7) | 655 (84) |

i.e. livestock and cervids, at a municipality scale ($n$ = 435). These estimates were available on animal-species level at 10-year intervals for the years between 1949 and 1999, and were based on different official statistics, such as hunting statistics (moose, red deer, roe deer, and wild reindeer), field counts (wild reindeer), and abundance reports from management of semi-domestic reindeer and livestock (sheep, cattle, goat, and horse). The estimates were means in kg MBM per square kilometre within each municipality encompassed by the transect. The average area of a Norwegian municipality is approximately 1,000 km$^2$. Detailed information about this data set can be found in Austrheim et al. (2011). From these species-wise numbers, we calculated short- (1989 to 1999) and long-term (1949 to 1999) change in total MBM. A summary of the herbivore data (all species together) by region is shown in the Supporting information, Appendix S1: Table S1.1. The regions were only used for an overview in the descriptive tables, and were constructed by distributing the 36 sites uniformly according to latitude. The southern region ranged between 60.00° and 62.65°, the middle one between 62.65° and 65.70°, and the northern region between 65.70° and 69.35°. Further analyses were carried out using latitude as a continuous variable (Universal Transverse Mercator projection, zone 32).

## 2.5 | Climate data

Climate data for each of the 36 sites included daily estimates of mean temperature, minimum temperature, maximum temperature, and total precipitation in the period between 1963 and 2012. To obtain these estimates, actual observations from the official weather stations in Norway were used to interpolate values valid for the exact coordinates of our sites. These calculations were carried out by the Norwegian Meteorological Institute (Tveito, Bjørdal, Skjevåg, & Aune, 2005). Similar to the processing of the herbivore data, we calculated both short-term and long-term change variables. First, we divided the data in 10-year periods, starting from the last sampling year. For each 10-year period, we calculated the summer temperature as the mean of the daily observations within the interval 1st of June to 30th of September. In addition, we registered the minimum temperature and the mean precipitation within the same interval. Furthermore, minimum temperature and mean precipitation were also calculated for the winter months (December, January, February and March). Then, from all these mean values, we calculated change. Short-term change was calculated as the difference between the means of the periods 2003 to 2012 and 1993 to 2002, and long-term change as the difference between the means of the periods 2003 to 2012 and 1963 to 1972. Table S1.2 in Appendix S1 shows a regionalized summary of the climate data.

## 2.6 | Statistical analyses

The statistical analyses were carried out in three separate steps. The first step sought to test if there were significant changes in stem numbers and tree heights between the two sampling years 2008 and 2012. The calculation of descriptive means and ranges was carried out on regional level to be able to perform simple assessments of potential differences between regions. For each region, we tested if there was a significant change in number of stems and tree height between 2008 and 2012 for each of the tree height classes by using generalized linear mixed-effect models (GLMMs). For the observed number of stems, we modelled the data as having a negative binomial distribution using the R-package *nlme* and the random factor was each site's unique id. For tree height, we modelled the data as having a Gaussian distribution using the R-package *lme4* and the random factor was sample plot nested in site.

The second step sought to identify the relative importance of the four variable categories through variable selection: (a) tree properties (species, height); (b) site (latitude); (c) herbivory (change in estimated number of sheep, reindeer, moose, and metabolic biomass of large herbivores between 1989 and 1999); and (d) climate (short and long-term change in mean temperature and mean precipitation in the summer months (June, July, August and September), short and long-term change in mean temperature in the winter months (December, January, February and March), mean summer temperature between 2002 and 2012). We used partial least-squares (PLS) regression to investigate the relative effect of environmental variables on the change in the number of stems, height growth and mortality (Proc Pls of the SAS/STAT® software, SAS Institute, Cary, NC, USA). PLS is a bilinear factor method that by linear combinations of all variables constructs principal components to explain the variation of a response variable (e.g. Martens & Martens, 2000; Wold, Sjøstrøm, & Eriksson, 2001). These principal components are in the case of PLS referred to as latent variables, variables that cannot be observed directly, but are the result of a mathematical model dependent on a set of observed variables. The latent variables are linear combinations of all observed variables, where a weight is given to each so that the explanatory power of the latent variable for the response is maximized. In the PLS modelling, we calculated four latent variables for each response, and calculated the proportion of explained variance by each of our observed explanatory variables aggregated to four categories (tree properties, site, herbivory, or climate). The change in stem number was calculated on the level of height class within sites. Consequently, the mean tree height within each class and site was used as explanatory variable instead of height of single trees. Furthermore, both height growth and mortality were analysed on the single-tree level. In all PLS analyses we calculated the Variable Importance for Projection (VIP) (Wold, 1994) to aid variable selection in the modelling step. The VIP-value indicates the relative contribution of a variable in the model.

The third step sought to explore the responses (relative change in number of stems, change in tree height, and mortality) of treeline dynamics to the variables identified in the second step. In order to understand how the response variables responded to environmental conditions, we fitted general additive models (GAMs) (Hastie & Tibshirani, 1990) using the *gam*-function (Wood, 2006) in R (R Foundation for Statistical Computing, Vienna, AT). GAM was chosen

**TABLE 2** Estimated mean numbers of stems per hectare at first measurement (2008), estimated change in number of stems and tree height, and mortality between 2008 and 2012

| Height class | n (sites) | Number of stems (ha⁻¹) | | Tree height (cm) | Mortality (%) |
| | | Mean ± SE | Change ± SE | Change ± SE | Mean (SD) |
| --- | --- | --- | --- | --- | --- |
| *Short trees* | | | | | |
| South | 12 | 3.78 ± 0.21*** (44.02) | 0.45 ± 0.12*** (25.12) | 12.67 ± 3.49*** | 9.0 (10.1) |
| Middle | 12 | 5.46 ± 0.01*** (234.40) | 0.06 ± 0.01*** (15.18) | 5.83 ± 3.01 | 4.5 (4.7) |
| North | 12 | 5.40 ± 0.43*** (222.40) | −0.01 ± 0.01 (−2.58) | 9.82 ± 2.31*** | 4.0 (7.5) |
| *Medium tall trees* | | | | | |
| South | 12 | 2.60 ± 0.18*** (13.50) | 0.24 ± 0.14 (3.61) | 9.54 ± 4.71* | 2.0 (7.2) |
| Middle | 12 | 3.95 ± 0.26*** (51.92) | 0.19 ± 0.07* (10.80) | 11.32 ± 3.40** | 3.1 (5.9) |
| North | 12 | 2.81 ± 0.59*** (16.59) | 0.51 ± 0.13*** (10.98) | 18.62 ± 3.62*** | 0.0 (0.0) |
| *Tall trees* | | | | | |
| South | 12 | 2.68 ± 0.20*** (14.65) | 0.04 ± 0.09 (0.57) | 15.71 ± 16.61 | 2.8 (9.6) |
| Middle | 12 | 2.89 ± 0.22*** (17.97) | 0.22 ± 0.08*** (4.51) | 11.18 ± 13.91 | 4.9 (8.3) |
| North | 12 | 1.30 ± 0.76 (3.66) | 0.30 ± 0.09*** (1.30) | 20.13 ± 20.11 | 0.0 (0.0) |

Level of significance: *,≤0.05; **, ≤0.01; ***, ≤0.001.

All numbers are distributed on height classes (short = 0–1 m, middle = 1–2 m, tall ≥ 2 m) and regions (South = 60.00°–62.65° N, Middle = 62.6–65.70° N, North = 65.70–69.35° N). Estimates of mean number of stems were fitted as a negative binomial distribution. Numbers in brackets for number of stems represent the back-transformed estimated means. Tree height was fitted with a Gaussian distribution.

as the appropriate modelling technique as we expected there to be a non-linear relationship between the response and explanatory variables. Explanatory variables were chosen based on the VIP-values obtained in the PLS analyses. The top-ranking variables from each variable category were first entered. If variables were statistically insignificant ($p > 0.05$), they were discarded. Alternative variables were then chosen according to their VIP-rank. We also allowed interaction terms to account for non-additive simultaneous influences on the responses. GAMs are similar to generalized linear models (GLMs). However, parameter estimates are replaced by smoothing functions, making GAM a non-parametric modelling technique. However, in this study, where candidate explanatory variables could be either continuous or class variables, we combined smoothing spline functions for the continuous variables and included the class variables parametrically. For the two continuous response variables, i.e., change in number of stems and tree height, we assumed a Gaussian distribution, whereas for mortality, which is a discrete event, we assumed a binomial distribution. To test if the smoothing terms were significant, we performed an analysis of deviance where chi-square tests were carried out to test if the deviance between the full model and models without each respective non-parametric components was significant. Visual inspections of model residuals were performed to assess if the assumption of normality was fulfilled.

## 3 | RESULTS

In general, there was a significant increase in number of stems from 2008 to 2012 irrespective of tree size (Table 2). Additionally, there were more short than medium and tall trees across all regions and

a larger change in number of stems was also observed for short trees.

For tree height, there was a significantly positive change between 2008 and 2012 for short and medium tall trees (Table 2). The change did not show any regional patterns. There was no significant change in tree height for tall trees. Mortality was higher for short trees than taller trees, at least in the southern and northern regions (Table 2).

The change in MBM for herbivores was in general positive for all regions and greatest in the south (Appendix S1: Table S1.1). For climate, there was in general a positive change for all variables except mean winter temperature and short-term change in winter temperature (Appendix S1: Table S1.2). The largest change in summer temperature (both short- and long-term) was observed for the middle region of Norway.

### 3.1 | Change in stem number

The screening of all explanatory variables using PLS regression showed that the first latent variable explained 5% of the variation in the relative change in stem number, and that an additional two percentage points were explained by the second latent variable. The inclusion of two additional latent variables had only a marginal effect on the explanatory power (Figure 3a). When the contributions of each observed variable to the total explained variance were summed by variable category for each latent variable (Figure 3a), it showed that the climatic variables were most important for the change in stem number between 2008 and 2012, as more than 90% of the variance explained by the first latent variable was related to climate. Climate was also most important in the other latent variables,
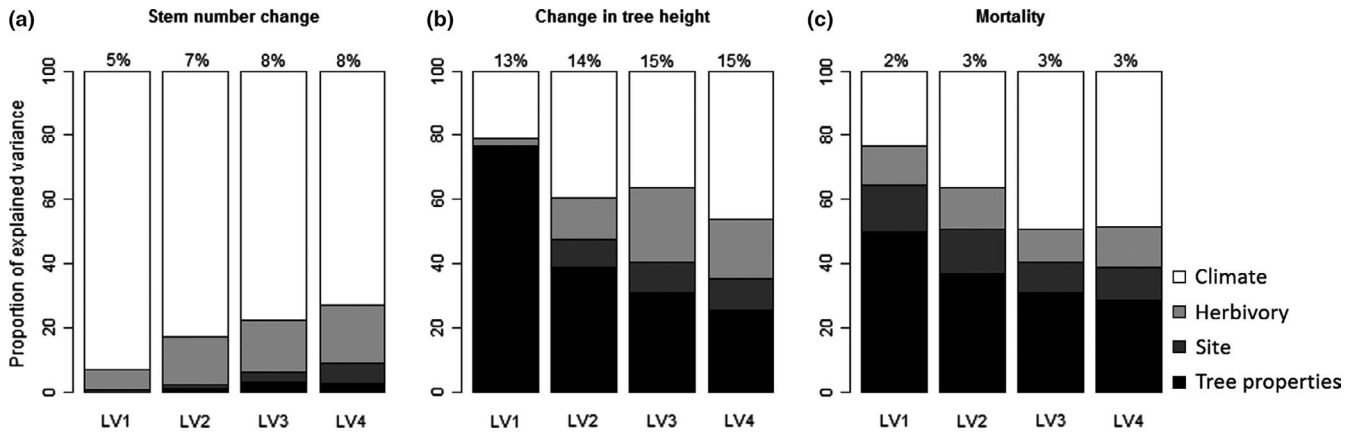
**FIGURE 3** Stacked plot of the contribution of four variable categories (climate, herbivory, site, and tree properties) to the variance explained by partial least-squares (PLS) models of (a) stem number change, (b) change in tree height, and (c) mortality, each with four latent variables (LV). The cumulative explained variance by each latent variable (LV1–LV4) appears at the top of each bar
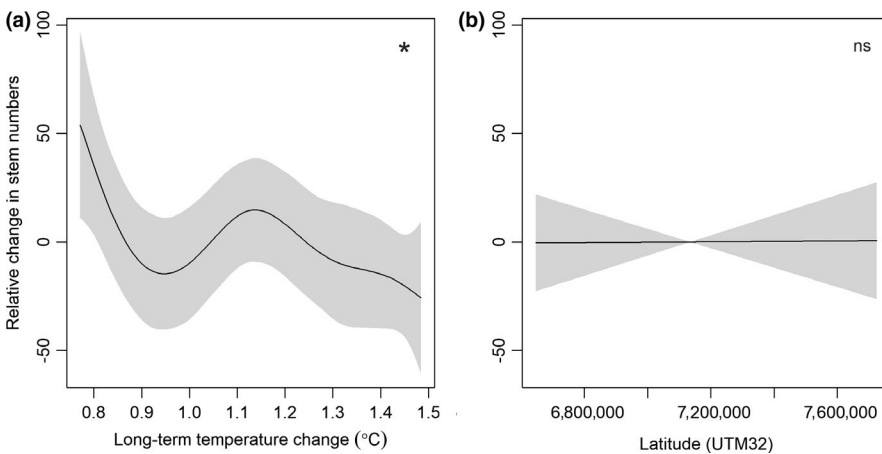


**FIGURE 4** Smooth components of the general additive model (GAM) for relative stem number change. On the *x*-axes are the observed values of the different variables: (a) long-term temperature change (difference in means between 2003 to 2012 and 1963 to 1972) and (b) latitude. The solid lines show the smoothed effect on a linear scale centred on zero. Grey areas are two times the standard deviation of the predictions. Level of significance: ns, not significant (>0.05); *, ≤0.05

even though the proportion of variance explained by site and herbivory increased somewhat as more latent variables were included (Figure 3a). However, the relationship between the change in stem number and the different explanatory variables was quite weak. Long-term temperature changes significantly affected the change in stem number and the relationship seemed to have a negative trend (Figure 4a). Latitude was not significant for the change in stem number (Figure 4b).

## 3.2 | Change in tree height

The screening showed that 13% of the variance of change in tree height was explained by the first latent variable in the PLS analysis (Figure 3b). The effects of additional latent variables on the total variance explained were marginal. Approximately 75% of the explained variance of the first latent variable could be attributed to the variables related to tree properties (tree height and species id), while approximately 20% was related to climatic variables (Figure 3b). Site and herbivory did not seem to be important for the first latent variable. In the next latent variables, however, both

site, herbivory, and climate explained more of the change in tree height, whereas the role of tree properties decreased (Figure 3b). Both tree height and short-term temperature change were significantly related with change in tree height (Figure 5). For tree height, growth seems to be asymptotic and levels out around tree heights of 200 cm (Figure 5a). Height growth seems to be faster at higher compared to lower latitudes (Figure 5b), but this is mainly for medium tall trees (Table 2). There was not seen any consistent trend in the relationship between temperature change and change in tree height (Figure 5c).

## 3.3 | Mortality

The first latent variable in the PLS screening explained only 2% of the variation in mortality (Figure 3c). Tree properties contributed by approximately 50% to the explained variance, climatic variables contributed more than 20%, while site and herbivory together explained about 25% (Figure 3c). There seems to be a tendency of increasing mortality with increasing temperature change (Figure 6a), whereas there is no relationship between latitude and mortality (Figure 6b).
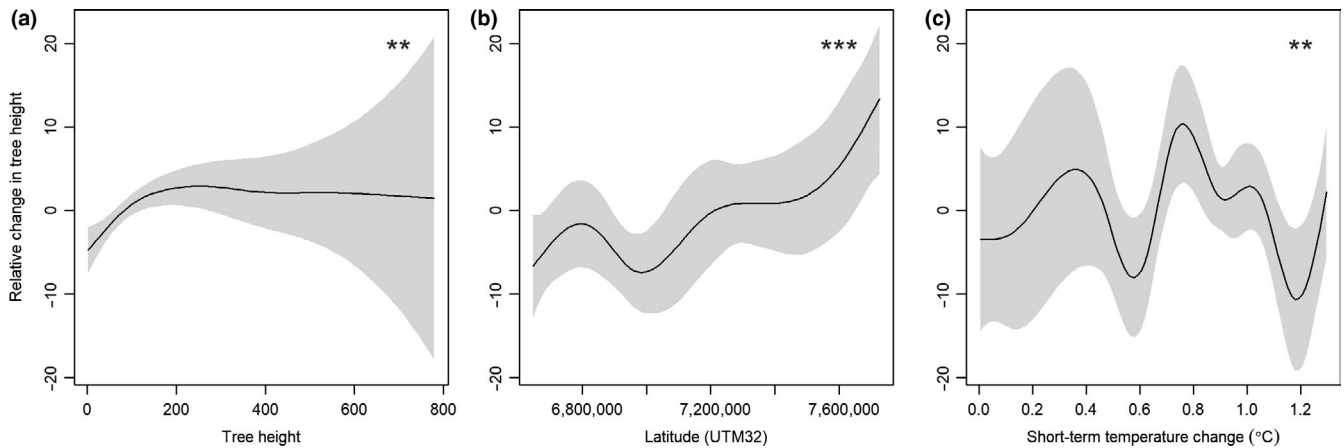
**FIGURE 5** Smooth components of the general additive model (GAM) for relative change in tree height. On the x-axes are the observed values of the different variables: (a) tree height (cm), (b) latitude, and (c) short-term temperature change (difference in means between 2003 to 2012 and 1993 to 2002). The solid lines are the predicted values on a linear scale centred on zero. Grey areas are two times the standard deviation of the predictions. Level of significance: **, ≤0.01; ***, ≤0.001

## 4 | DISCUSSION

In this short-term study, we investigated the role of climate and herbivory in determining stem number, growth and mortality responses of treeline ecotone trees along a 1,000-km latitudinal gradient. Climate seemed to be the strongest driver of change, although tree properties were important for height growth and mortality. However, our results show weak explanatory power of all variables, and hence suggest context dependency of treeline dynamics between sites.

A significant increase in tree height was observed for short and medium tall trees in the four-year period, and tree properties together with climate were found to explain most of the total variance in tree height change. Individual trees respond differently to climate depending on their growth stage (Smith, Germino, Johnson, & Reinhardt, 2009), and low temperatures are known to limit particularly tree height growth (Alvarez-Uria & Körner, 2007). At small spatial scales, the temperatures experienced by plants are very different from meteorologically measured conditions (Lenoir et al., 2013). However, as trees grow out of the field layer, they become more exposed to atmospheric conditions. As trees at the treeline

develop from seedlings to canopies, they are exposed to differing conditions. Seedlings often germinate within disturbed microsites and their growth is often facilitated by neighbouring vegetation (Tingstad et al., 2015). Taller individuals are more exposed to meso-scale climatic conditions such as wind, snow and other disturbance factors. Finally, canopy-forming trees are protected from abiotic conditions by surrounding canopy trees (Smith et al., 2009).

Although climate was the dominant explanatory factor in explaining treeline change in most of our models, the explanatory power was low. Moreover, the lack of a clear relationship between temperature change and treeline change in our study supports experimental and observational studies of alpine vegetation responses to warming suggesting that other factors likely interact with temperature at a local scale (Elmendorf et al., 2012; Grytnes et al., 2014). The lack of response of treelines to warming has previously been attributed to site or local level factors (Harsch et al., 2009). Herbivory is one such factor that has been linked to treeline limitation (Cairns & Moen, 2004; Speed et al., 2010). However, our study found that herbivory variables were less associated with treeline change than climatic variables. In contrast, Speed et al. (2010) found a clear relationship between densities of domestic sheep and treeline advance,

**FIGURE 6** Smooth components of the general additive model (GAM) for mortality. On the x-axes are the observed values of the different variables: (a) short-term temperature change (difference in means between 2003 to 2012 and 1993 to 2002) and (b) latitude. The solid lines are the predicted values on a linear scale centred on zero. Grey areas are two times the standard deviation of the predictions. Level of significance: ns, not significant (>0.05); *, ≤0.05
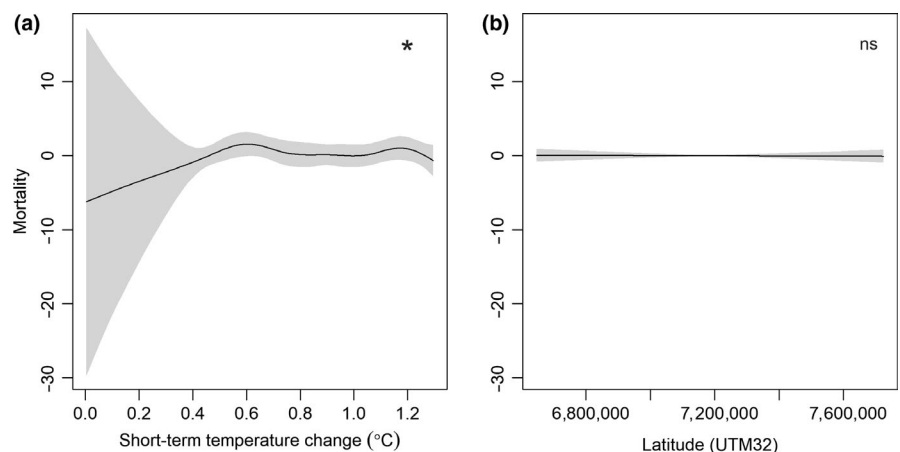
with even low densities of sheep being able to prevent forest succession. Very few regions of the Norwegian mountains are completely ungrazed, and this may explain the lack of short-term treeline response to herbivore variables along our gradient, also in municipalities with reduced herbivore pressure. The main change in herbivore communities across Norway has been a shift from livestock grazing to cervid browsing (Austrheim et al., 2011). Since cervids, the moose in particular, commonly browse within treeline ecotones (Molvar, Bowyer, & Van Ballenberghe, 1993), this change may have actually increased woody herbivory at treelines.

The difference in means for the four-year change in stem numbers, height and mortality, indicates that there are differences between regions (Table 2). However, the estimated means (Table 2) and GAMs for these response variables showed that the changes were quite uniformly distributed along the latitudinal gradient. Observed changes in number of stems and tree height seem to correlate with observed changes in short- and long-term changes of summer temperature in the middle region of Norway. However, a low proportion of variance in treeline performance across sites was explained by the explanatory variables included in the models. One possible explanation for this is that the study only looked at short-term treeline changes over a four-year period. Over such a short observation period, non-measured factors affecting treeline changes that are specific to the different sites become relatively more pronounced (Danby, 2011). It is likely that treeline dynamics are more strongly related to climate and herbivory processes at longer time scales, and that the low explanatory power of both the variables representing climate and herbivory in this particular study may be attributed to the short observation period.

In addition to climate and herbivory, the site dependency of treeline dynamics can be due to orographic factors (Holtmeier & Broll, 2005), such as steep rock walls and boulder screes, that may hamper trees from migrating into higher elevations. Furthermore, edaphic factors and soil conditions, such as the thickness of the humus layer, nutrients and soil moisture can also affect tree recruitment and growth (Tingstad et al., 2015). Whereas orographic factors are permanent, soil conditions may change over time being affected by temperature and precipitation that directly affect evapotranspiration. Other factors should therefore be investigated further to quantify their potential effects on the treeline dynamics.

Our study was designed to assess temporal shifts in treelines along a 1,000-km latitudinal gradient through the Scandes Mountains in Norway over a four-year period, and to partition shifts between different drivers. It thus benefits from a large spatial scale but a relatively short temporal scale. Different processes affect treeline dynamics at different spatial and temporal scales (Danby, 2011), and for Norway, the change in climate and herbivory varies with latitude. Our study represents an advance upon previous studies of treelines along latitudinal gradients (e.g. Lloyd, Bunn, & Berner, 2011) by including multiple drivers; namely climate and herbivory. However, our study found that these drivers explained a low proportion of the total variation in treeline performance along this gradient. Therefore, it seems that variables known to influence treeline dynamics over long periods are not good predictors of short-term change.

## AUTHOR CONTRIBUTIONS

IMM did statistical analyses, drafted the discussion and led the development of the manuscript. JDMS lead the interpretation of the results in addition to contributing to all other parts. KK contributed to the development of all parts of the manuscript. GA contributed to all parts of the manuscript and provided the herbivory data. EN designed the field data protocol and contributed to all parts of the manuscript. OMB was in charge of data collection, did the statistical analyses and drafted the Introduction, Methods and Results.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are stored at the Norwegian Centre for Research Data and are available upon request from https://dx.doi.org/10.18712/NSD-NSD2800-V1.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** Summary of herbivory and climatic data