

# Vegetation response to climate warming across the forest-tundra ecotone: species-dependent upward movement

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## Abstract

**Questions:** Rising temperatures are predicted to cause upward shifts and reorganisation of mountain vegetation. This study analyses how field layer vegetation across the forest-tundra ecotone has responded over a 22-year period. Main questions are: (a) have vegetation composition, richness and diversity changed; (b) have abundance of functional plant groups and individual species changed; and (c) which environmental factors regulate vegetation distribution and composition?

**Location:** Central Norway.

**Methods:** The study uses vascular plant species recordings and environmental data from permanent 1 m × 1 m quadrats ( $n = 266$ ), established in 1994 and revisited in 2016, along transects from forest to high alpine areas (750–1,500 m a.s.l.). Changes in vegetation composition (species and functional group levels) and influence of environmental factors are analysed using ordination and mixed-effect models.

**Results:** Ordination shows an overall upward vegetation movement corresponding to  $0.5 \pm 0.1$  m/y, and compositional homogenisation across the ecotone over time. Changes at species and functional group levels vary across the ecotone. Species richness and diversity increase over time due mainly to an increase of herbs and graminoids in the forested part of the ecotone. Evergreen woody species increase in abundance across the entire ecotone and most strongly above the forest. Deciduous woody species abundance is stable at group level but shows large variation at species level. Species-level responses deviate from group-level responses in all functional groups. Vegetation distribution and composition are environmentally explained by altitudinal distance to the treeline and microtopography.

**Conclusions:** Our results show how increased temperature impacts vegetation movements and reorganisation through mainly species-specific responses with low within-functional-group coherency. The apparent upward shift is moderate compared to the increase in temperature over the study period, but larger than in similar studies, although grazing pressure might co-control change rate. Species-specific responses and response rates highlight the need for detailed empirical data to predict and understand vegetation responses in a warming climate.

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## KEYWORDS

alpine vegetation, altitudinal gradients, climate warming, forest vegetation |resurvey, forest-tundra ecotone, species composition, species diversity, species-specific responses

## 1 | INTRODUCTION

During the last decades, global temperature has been rising and is predicted to continue to increase (IPCC, 2014). The temperature increase has been more pronounced at high latitudes and altitudes (ACIA, 2005; IPCC, 2014; Pepin et al., 2015). With higher temperatures, a northward and upward shift of vegetation is commonly predicted, as well as loss of resident species and a change in dominance between species (Elmendorf et al., 2012a; Bjorkman et al., 2018; Steinbauer et al., 2018).

The vegetation transition between boreal forest and the treeless tundra, the forest-tundra ecotone, is predicted to be sensitively responding to climate change with an upward shift in its location (ACIA, 2005; IPCC, 2014). Observed shifts are, however, spatiotemporally variable (Harsch et al., 2009), due to deviating main drivers of the ecotone (Holtmeier and Broll, 2005; Hofgaard et al., 2012).

The presence of a tree layer is important for the composition of the field layer (Hofgaard and Wilmann, 2002; Sundqvist et al., 2008). However, the field layer vegetation has been found to be less sensitive to air temperature than the tree layer (Scherrer and Körner, 2010; Lenoir et al., 2013). The field layer vegetation might therefore respond independently to a warming climate (Camarero et al., 2006; Battlori et al., 2009). Further, alpine vegetation is considered especially vulnerable in a warming climate, as alpine plant species are assumed to be weak in competition with potentially invading lower-altitude species (Körner, 2003).

Reported responses of field layer vegetation to warming in alpine areas include an increase in abundance of woody species and increased vegetation height (Myers-Smith et al., 2011; Elmendorf et al., 2012a; Bjorkman et al., 2018). However, many experimental and observational studies have reported modest vegetation responses to increased temperatures in arctic and alpine ecosystems in comparison to scenarios based on correlations with changes in biotic and abiotic factors alone (Vittoz et al., 2009; Wilson and Nilsson, 2009; Virtanen et al., 2010; Elmendorf et al., 2012a).

Further, studies show a large heterogeneity in observed vegetation responses to climate warming (Elmendorf et al., 2012a), suggesting that other factors inhibit or override the effects of increased temperatures, including both biotic factors such as herbivory (Hofgaard, 1997; Post and Pedersen, 2008; Speed et al., 2013), and abiotic factors such as topography, snow cover and soil conditions (Wipf and Rixen, 2010; Eskelinen et al., 2017; Graae et al., 2018).

A common approach to analysing complex vegetation responses is to categorise species into functional groups based on e.g. growth form or morphological characters. This approach is frequently used in studies of changes in alpine vegetation (cf. Wilson and Nilsson, 2009; Elmendorf et al., 2012a), often based on the functional groups defined in Chapin et al. (1996). However, several studies have found a lack of consistent species responses within functional groups

(Little et al., 2015; Saccone et al., 2017). Studies comparing the two approaches point to functional groups concealing species-specific responses, but also that species-level investigations can produce better understanding of the determinants for the functional groups (Little et al., 2015; Saccone et al., 2017).

Common methods to study the climate's effects on vegetation are gradient studies (space-for-time), experiments, and monitoring (Elmendorf et al., 2015). While gradient studies reflect the present environment, they tend to overestimate effects of climate change as a gradient reflects the average environment over a larger timespan and thus is an expression of site history rather than present climate (Elmendorf et al., 2015). Experiments, on the other hand, yield detailed control over some selected environmental factors, but are prone to artefacts especially when used over longer timespans (De Boeck et al., 2015; Ettinger et al., 2019; Løkken et al., 2019).

Monitoring, or resurveying of historic vegetation plots, has received renewed interest as a means to better understand vegetation changes over time (Kapfer et al., 2016), and avoids some of the disadvantages of space-for-time studies and experiments, particularly when plots are permanently marked (Verheyen et al., 2018). Resurvey of permanent plots located along altitudinal gradients can give particularly good insights as there is potential to detect shifts and altered dynamics in different vegetation zones (Wilson and Nilsson, 2009; Virtanen et al., 2010; Spasojevic and Suding, 2012; Gazol et al., 2017).

The present study analyses changes in field layer vegetation over a 22-year period by using recordings from permanent plots located along altitudinal gradients across the forest-tundra ecotone and adjacent sub-alpine forest and alpine tundra in Central Norway. The baseline data were recorded in 1994 (Hofgaard, 1997; Hofgaard and Wilmann, 2002) and the resurvey data in 2016. During this period, the study area experienced a 1.2°C increase in mean annual temperature. Three main questions are asked: (a) how has vegetation composition, richness and diversity changed in the 22-year period, and was the rate and direction of change sustained across the forest-tundra ecotone; (b) how has abundance of functional plant groups and individual plant species changed in the 22-year period, and how did these changes influence overall composition and diversity change; and (c) which environmental factors regulate vegetation distribution and composition across the forest-tundra ecotone overall, and has the importance of environmental factors changed in the 22-year period?

## 2 | METHODS

## 2.1 | Study area

The study area is located in Central Norway (Lat. 62°30'–62°36' N, Long. 8°50'–9°13' E), and is characterised by a rough topography with

large altitudinal differences within short distances. Most surrounding mountain peaks reach altitudes between 1,400 and 1,600 m a.s.l. The area is located in the transition between the northern boreal and the alpine vegetation zone and the climate is slightly continental (Moen, 1999). Due to a lack of nearby meteorological stations recording temperature, we used interpolated temperature data, with a spatial resolution of 1 km<sup>2</sup>, to investigate temperature trends over the study period (Norwegian Meteorological Institute, 2019). Mean annual and summer (June–August) temperature increased with 1.2 and 1.4°C respectively (from –0.6 to +0.6°C and from 7.6 to 9.0°C, respectively; Figure 1) when comparing the 15-year period predating the 1994 measurements (1979–1993) with the 15-year period predating the 2016 measurements (2001–2015). Precipitation data are available from the Hafsås meteorological station within the study area (operational 1978–present, 698 m a.s.l.). Mean annual precipitation did not change substantially over the study period (697 and 678 mm in the 15-year periods 1979–1993 and 2001–2015, respectively, see Appendix S1 for details).

The study area is used as grazing ground for domestic sheep during the summer season (June–September). There are no detailed annual records on the number of sheep using the study area, however, estimates based on numbers reported by the local association of sheep farmers (Sunndal beitelag, see Appendix S2), indicate that the number of released sheep has declined from 16.3 to 11.3 sheep/km<sup>2</sup> between 1994 and 2016.

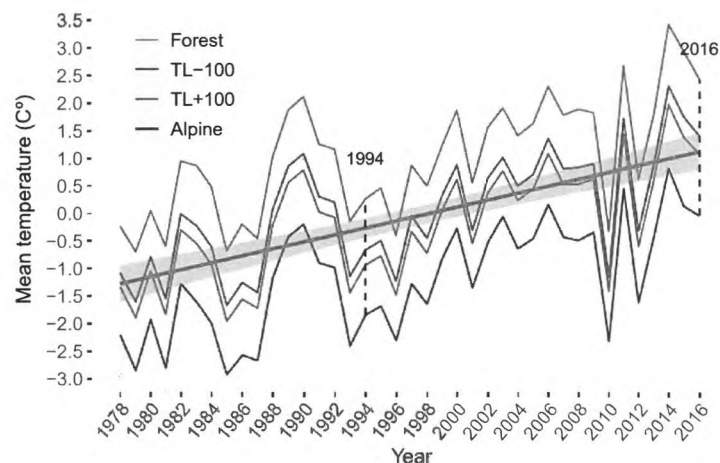
The typical bedrock in the area consists of gneiss, but a band of amphibolite schist runs southwest/northeast through parts of the area (Norwegian Geological Survey, 2019) and gives rise to richer soils locally (Table 1).

The forest in the study area is dominated by mountain birch (*Betula pubescens* spp. *tortuosa* (Ledeb.) Nyman), with few scattered individuals of *Pinus sylvestris* L., *Alnus incana* (L.) Moench, *Populus tremula* L. and *Sorbus aucuparia* L. The forest line, defined as the uppermost position of closed stands of birch trees at least 2 m in height, ranged from 940 m to 1,120 m a. s. l. in 1994, recorded using

an altimeter (Table 1). The treeline, i.e. the uppermost position of individual trees of at least 2 m in height, ranged from 980 m to 1,170 m a.s.l. There was no detectable altitudinal shift of either the forest line or the treeline between 1994 and 2016 (i.e. GPS recordings in 2016 were within the uncertainty estimates of the 1994 altimeter recordings) (J.O.Løkken, M. Evju, L. Söderström, & A. Hofgaard, unpubl). The field layer vegetation in the forest is dominated by herbs and graminoids such as *Trifolium europaeum* L. and *Avenella flexuosa* (L.) Drejer, respectively, and scattered dwarf shrubs such as *Vaccinium myrtillus* L. and *Empetrum nigrum* L. Between the forest line and the treeline the abundance of herbs and graminoids declines and the vegetation becomes dominated by alpine heath communities where dwarf shrubs such as *Empetrum nigrum*, *Vaccinium myrtillus* and *Vaccinium uliginosum* L. are the most common. Above the treeline and towards the mountain summits the vegetation becomes successively sparser with a higher dominance of low-statured alpine species such as *Salix herbacea* L. and *Carex bigelowii* Torr. ex Schwein. Further details on geographical location, geology, climate and vegetation are found in Hofgaard (1997) and Hofgaard and Wilmann (2002). Nomenclature follows the Norwegian Species Nomenclature Database (Norwegian Biodiversity Information Centre, 2019).

## 2.2 | Study design

The study consists of six transects including a total of 67 plots (10 m × 10 m, see Table 1 for transect details). The transects run from the closed forest to mountain summits and thus encompass the entire forest–tundra ecotone, including the forest, the forest line, treeline and tree species line (i.e. most advanced location of tree species specimens irrespective of size), and adjacent alpine areas. The lower end of the transects was determined by the valley bottom or by areas with intense human land use. The plots were placed along the transects at every 50 m a.s.l. interval (e.g. 750, 800, 850 m and so forth), mapped and permanently marked with plastic sticks and aluminium pipes. In the plots,



**FIGURE 1** Mean annual temperature for the different transect sections (forest, treeline ± 100 m, alpine), and a regression line with 95% confidence interval, for the overall trend 1978–2016, from interpolated temperature data (Source: Norwegian Meteorological Institute; www.met.no)

TABLE 1 Transect characteristics and distribution of analysed plots

Transect	Aspect	Geological substrate	Altitudinal range	Forest line position 1994	Treeline position 1994	Number of plots (quadrats) in 2016	Number of species 1994	Number of species 2016
A	E-NE	MGG	750–1,300	970	1,000	12 (47)	63	61
B	W-SW	MGG	750–1,400	940	980	13 (52)	65	68
C	NE	Mi	750–1,400	960	1,050	14 (56)	112	116
D	SW	Qu	850–1,400	1,060	1,130	12 (48)	83	86
E	S	Ag	850–1,150	1,120	1,170	5 (20)	34	38
F	SE	Mi, Qu	950–1,500	970	1,100	12 (48)	76	75

Abbreviations: Ag, augen gneiss; MGG, mylonitic gneiss; Mi, mica schist; Qu, quartzites and mylonitic gneiss, occasionally amphibolite.

the number of trees ( $\geq 2$  m), stand density, height of trees, and number of saplings ( $< 2$  m) were recorded and mapped at a  $5 \text{ m} \times 5 \text{ m}$  subplot level. For recording of field layer species four quadrats ( $1 \text{ m} \times 1 \text{ m}$ ) were located within each plot (one per subplot) according to a restricted random procedure (see Hofgaard [1997] for details). The quadrats were divided into 16 squares ( $0.25 \text{ m} \times 0.25 \text{ m}$ ) and presence/absence of all field layer species was recorded in each square, giving an abundance of each species per quadrat as the frequency of occurrence in squares. In 1994 a total of 74 plots and 295 quadrats were analysed. The transects were revisited in 2015, and 69 of the original 74 plots were located and registered by GPS. Two of the plots were rejected due to signs of intensified human land use. Thus, in 2016, 67 plots and 266 quadrats were reanalysed (see Table 1 for the distribution between transects).

Slope and aspect were recorded in 1994 for each quadrat. To avoid problems with the circularity of the aspect data (large values being very close to small values, i.e.  $0$  and  $360^\circ$  both represent north) we calculated the deviation in degrees from the optimal angle of aspect ( $205^\circ$ ) for solar radiation (Dargie, 1984), ranging from  $0$  to  $180^\circ$  (henceforward denoted devOpt). All plots were categorised according to bedrock type ('poorer'; plots on poor bedrock or 'richer'; plots on intermediately rich bedrock) determined by comparing the GPS position of each plot to a digital bedrock map available from NGU (Norwegian Geological Survey, 2019). Distance to the forest line and treeline was defined for each plot, based on the altitudinal distance between the plot and the respective line for each transect. Topographic Position Index (TPI) (Weiss, 2001) was assessed for each quadrat, surrounded by a continuous circle of  $250 \text{ m}^2$ . TPI is a measure of the difference in elevation of the central point from the average surrounding elevation, relative to the slope. Positive values indicate that the centre is higher than the surrounding (convex terrain), while negative values indicate a lower central altitude than the surrounding (concave). Further, we used the height of the trees and saplings to calculate the tree layer height in each subplot, as the mean height of the five tallest trees and/or saplings in each subplot.

### 2.3 | Data treatment and statistical analyses

To identify changes in field layer vegetation along the forest–tundra ecotone, we defined four transect sections along the ecotone, based on the grouping in Hofgaard and Wilmann (2002): Forest

(>100 m below treeline), TL–100 (plots from treeline to 100 altitudinal m below), TL+100 (treeline to 100 m above), alpine (>100 m above treeline).

Vegetation change was analysed both at species level and functional group level. Four functional groups were used: evergreen woody species, deciduous woody species, herbs, and graminoids. To examine changes at the species level, we selected the three most frequent species from each of the four functional groups (frequency recorded as the number of quadrats with the species' occurrence; see Appendix S3).

Due to a strong collinearity between environmental factors, especially those related to altitude, such as distance to treeline, and features of the tree layer, a combination of constrained ordination (CCA) and variance inflation factor (VIF) was used to determine the relative importance of the environmental variables as well as their collinearity, and subsequently to choose a statistically and ecologically useful set of environmental variables. A CCA analysis of the full vegetation matrix (species  $\times$  quadrat over both years) was used to determine which of the environmental variables had the strongest explanatory power on field layer composition. Correlation between variables (Appendix S4), their explanatory power (Appendix S5) and the VIF of each variable (Appendix S5) were used to guide variable removal. With the goal that no variable in the final set of environmental variables should have a higher VIF than 5 (cf. Zuur et al., 2007), the following set of environmental variables was included in further analyses: distance to treeline (treeline), height of tree layer (height), aspect (devOpt), bedrock, TPI, slope, number of saplings (saplings) and year (see Appendix S6 for how these variables varied with transect section).

To investigate patterns in field layer vegetation composition, the field layer data, combined over years, were subjected to a global two-dimensional non-metric multidimensional scaling (GNMDS). The GNMDS was run with the Bray–Curtis dissimilarity measure, 100 initial configurations, maximum 200 iterations and stress tolerance  $10^{-7}$  (Davey et al., 2013). Unreliable Bray–Curtis distances ( $> 0.8$ ) were replaced by geodesic distances, using the 'step-across' method (Williamson, 1978).

To assess the importance of the environmental variables on the species composition we used linear mixed-effect models (cf. Zuur et al., 2007) with quadrat axis score as response variable and environmental variables as predictors, using quadrat nested within plot nested within transect as random factor. This method accounts for

**TABLE 2** Parameter estimates for all environmental factors and associated *p*-value from the linear mixed-effects model of axis score on global two-dimensional non-metric multidimensional scaling (GNMDS) axes 1 and 2

Env. fact.	GNMDS1		GNMDS2	
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
(Intercept)	0.114	0.192	0.101	0.472
Year	0.041	<0.001	0.034	<0.001
Treeline	-0.003	<0.001	-0.001	0.074
Bedrock	0.061	0.506	-0.036	0.787
Slope	-0.001	0.501	0.001	0.596
TPI	0.004	0.190	-0.008	0.039
DevOpt	0.000	0.390	-0.001	0.053
Height	0.008	0.234	-0.006	0.478
Saplings	-0.004	0.228	0.002	0.601

Abbreviations: bedrock, bedrock quality; devOpt, deviation from optimal aspect; height, height of the tree layer; saplings, number of saplings; slope, slope of the quadrat in degrees; TPI, topographic position index; treeline, altitudinal distance to treeline; year, year of survey.

the spatial and temporal autocorrelation structure of the data. To investigate the vegetation distribution and composition across the forest-tundra ecotone and how this changed over the studied 22-year period, we constructed linear mixed-effects models including all environmental variables, transect section, year, and the two-way interaction between transect section and year. All models used the same random factor as the afore-mentioned model. A backward-selection procedure was used to simplify the models (cut-off:  $p = 0.05$ ), and only the most parsimonious models are presented.

We constructed separate mixed-effect models for the following response variables: (a) displacement of quadrat axis scores along each of the two axes in the GNMDS analysis; (b) species richness (number of species in each quadrat); (c) Shannon's diversity index; (d) the abundance of all four functional groups; and (e) the most frequently occurring species. As the quadrat displacement along the ordination axes was calculated as the difference in axis scores between years, this model did not include year and the interaction between year and transect section. Displacement of quadrat axis scores, richness, Shannon's diversity index and evergreen woody species were analysed with linear mixed-effects models. Abundance of the functional groups deciduous woody species, herbs and graminoids were run with generalised linear mixed-effects models, using a quasi-Poisson distribution with a log link. For the individual species abundance models, we used a binomial distribution with log link.

All statistical analyses were performed using the packages lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), MASS (Venables and Ripley, 2002) and vegan (Oksanen et al., 2018) in the R statistical environment (R Core Team, 2019).

### 3 | RESULTS

#### 3.1 | Species turnover and composition

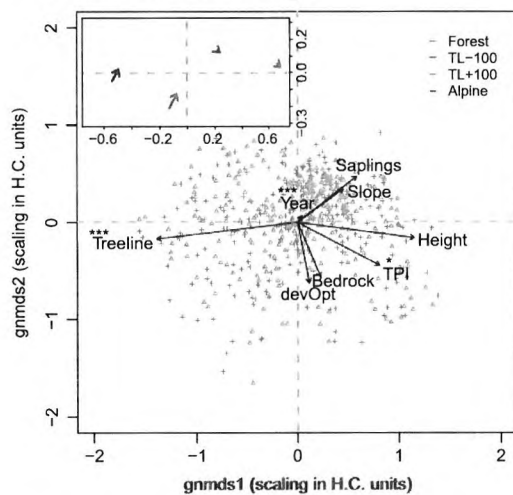
The total number of species recorded was 151 in 1994 and 150 in 2016, with a mean  $\pm$  SD of  $15.2 \pm 6.4$  species per quadrat in 1994,

and  $16.0 \pm 7.4$  species per quadrat in 2016. The number of species per quadrat (species richness) was highest in the forest section and declined with altitude (Appendix S7). In total ten species were lost between 1994 and 2016 (6.6%), and nine new species (6.0% of all species) were recorded in 2016 (Appendix S8). Lost species had low occurrence (present in 1–2 quadrats in 1994) and included six herbs and four graminoids. The new species in 2016 were found in 1–3 quadrats and included six herbs, two graminoids and one deciduous dwarf shrub.

The species composition GNMDS revealed variation in both the first (range  $-1.56$  to  $1.39$  half change units) and second ordination axes (range  $-1.65$  to  $0.92$  half change units). The variation along the first axis was significantly explained by distance to the treeline ( $p < 0.001$ , Table 2, Figure 2) with quadrats located in the alpine section on the negative end of the axis and forest quadrats towards the positive end. In addition, there was significant variation between years along the first axis ( $p < 0.001$ , Table 2). Variation along the second axis was best explained by TPI ( $p = 0.039$ , Table 2, Figure 2), and there were significant differences between years along this axis ( $p < 0.001$ , Table 2).

The change in species composition along the first axis (displacement of axis score) was significant ( $p < 0.001$ , Figure 2, Appendix S9), but was not explained by any of the environmental variables, i.e. the displacement was equal among quadrats. Species composition along the second axis changed significantly, and there was an effect of the height of the tree layer, where quadrats with low tree height had higher axis displacement ( $p < 0.001$ , Figure 2, Table 3a, Appendix S9). Thus, displacement along the second axis varied with quadrat location across the forest-tundra ecotone; quadrats below the treeline moved in a negative direction, while quadrats above the treeline moved in a positive direction (Figure 2), i.e. indicating a homogenisation of the species composition across the transect sections.

The overall change in species composition between 1994 and 2016, calculated as the average displacement of axis score per quadrat, was on average  $\pm$  SE  $0.04 \pm 0.01$  species and  $0.03 \pm 0.01$  species along the first and second axes, respectively. As the total length of



**FIGURE 2** Global two-dimensional non-metric multidimensional scaling (GNMDS) biplot of the field layer composition. Cyan crosses represent quadrats in 1994, while yellow triangles represent quadrats in 2016. Arrows in the main figure show the fitted environmental variables with stars indicating significant relationship with the ordination axes (See Table 2 for  $p$ -values). Arrows in the inset display the mean displacement of quadrat scores from 1994 to 2016 in the four transect sections Forest, TL-100, TL+100 and Alpine

the first axis (which mainly correlated with altitude) was 2.95 and the span of the altitudinal gradient was 750 m, the displacement along the first axis indicated approximately a  $10.5 \pm 1.7$  m upward shift of vegetation ( $750 \cdot [0.04/2.95]$ ).

### 3.2 | Species richness and diversity

There was a general increase in both species richness and Shannon's diversity index from 1994 to 2016 (Table 3b, Appendix S9), with a stronger increase in quadrats located in the forest and TL-100 compared with TL+100 and alpine sections (significant year  $\times$  section interaction; Table 3b, Appendix S9). Quadrats located in the alpine section only showed change in diversity (Table 3b, Figure 3). A general effect of bedrock was found, with the highest species richness on richer bedrock.

### 3.3 | Functional group and species-specific responses

The distribution across the ecotone and the abundance changes from 1994 to 2016 of the three most frequent species in each functional group showed a variety of coinciding and contradictory trends compared to the main trend of their respective functional group (Figure 4, Table 4).

#### 3.3.1 | Evergreen woody species

The mean abundance of the functional group evergreen woody species was negatively related to the height of the tree layer and distance to the treeline, and was positively related to the number of saplings (Figure 4, Table 3c, Appendix S9). The abundance of evergreen woody species increased overall from 1994 to 2016, but a significant year  $\times$  transect section interaction reveals a stronger response in the alpine section (Figure 4, Table 3c, Appendix S9). *Empetrum nigrum* was the dominant species in all transect sections above the forest with highest abundance in the sections around the treeline (Figure 4, Table 4, Appendix S9). The species showed a general abundance increase, with the strongest response in the alpine section (significant year  $\times$  transect section interaction). *Phylodoce caerulea* (L.) Bab. had significantly lower abundance in the forest than in the other transect sections and increased in overall abundance over time (Figure 4, Table 4, Appendix S9). *Vaccinium vitis-idaea* L. had its lowest abundance in TL+100 and no variation in abundance among other transect sections. There was no overall abundance change, but a significant year  $\times$  transect section interaction revealed that the abundance increased slightly in the alpine section and decreased in the three other transect sections (Figure 4, Table 4, Appendix S9).

#### 3.3.2 | Deciduous woody species

The abundance of the functional group deciduous woody species was positively related to the number of saplings, and negatively related to TPI, distance to the treeline and tree layer height, and consequently the abundance was lower in forest and alpine quadrats compared to TL-100 and TL+100 (Figure 4, Table 3d, Appendix S8). There was no significant change in the abundance of deciduous woody species from 1994 to 2016 (Figure 4). Of the three most frequent deciduous woody species, *Vaccinium myrtillus* was dominant at all transect sections below the alpine section. There was a significant overall abundance increase of the species, with strongest responses in sections above the forest (Figure 4, Table 4, Appendix S9). The abundance of *Salix herbacea* was highest in the TL+100 and alpine transect sections. The species had an overall abundance decrease over time, with the strongest decrease in the TL+100 and alpine sections (Figure 4, Table 4, Appendix S9). *Vaccinium myrtillus* had its highest abundance in the TL-100 transect section and showed an overall increase from 1994 to 2016. This increase was shown in all transect sections except the section with highest abundance (TL-100) where instead there was a slight decrease (Figure 4, Table 4, Appendix S9).

#### 3.3.3 | Herbs

Overall the herb abundance was positively related to TPI and tree height (Figure 4, Table 3d, Appendix S8). From 1994 to 2016 herb

**TABLE 3** ANOVA tables for the optimal models, found by backwards selection with an inclusion criterion of  $p < 0.05$ 

Response variable	Factor	F-value	p-value
(a)			
GNMDS axis 2	Height	17.4	<0.001
(b)			
Richness	Year	18.89	<0.001
	Bedrock	16.36	0.002
	Section	1.66	0.185
	Year × section	5.34	0.001
Shannon	Year	24.53	<0.001
	Bedrock	20.55	0.001
	Section	1.46	0.235
	Year × Section	2.97	0.033
(c)			
Evergreen	Year	22.96	<0.001
	Height	4.30	0.039
	Treeline	12.52	<0.001
	Saplings	7.14	0.008
	Section	6.65	<0.001
	Year × Section	4.83	<0.001
Response variable	Factor	Chi-Sqr	p-value
(d)			
Deciduous	TPI	3.97	0.046
	Height	3.98	0.046
	Treeline	8.14	0.004
	Saplings	6.13	0.013
	Section	37.31	<0.001
Herbs	Year	9.30	0.002
	Height	4.85	0.028
	TPI	7.23	0.007
	Section	8.65	0.034
	Year × Section	28.21	<0.001
Graminoids	Year	1.68	0.195
	Bedrock	10.47	0.001
	TPI	5.61	0.018
	Section	5.54	0.136
	Year × Section	8.40	0.038

Note: (a) Change in quadrat score along GNMDS axis 2 modelled by a linear mixed-effects model. (b) Species richness and Shannon diversity index modelled by linear mixed-effects models. (c) Abundance of evergreen species, modelled with linear mixed-effects model using the Satterthwaite method. (d) Abundance of deciduous woody species, graminoids and herbs modelled with generalized mixed-effects model using the Wald chi-square method. In all models, quadrat nested in plot nested in transect was used as random variable, except in (a) which used plot nested in transect

abundance increased in the forest section but not at higher altitudes (Figure 4, Table 3d, Appendix S8). The three most abundant herb species showed somewhat deviating distribution patterns across the forest–tundra ecotone. While *Bistorta vivipara* (L.) Delarbre was more abundant in the alpine transect section, *Solidago virgaurea* L. and *Trientalis europaea* were most abundant in the forest (Figure 4, Table 4, Appendix S9). There was no general change in abundance of *Bistorta vivipara* between 1994 and 2016, but a significant year × transect section interaction revealed a small abundance increase in the forest (Table 4, Appendix S9). In contrast, both *Solidago virgaurea* and *Trientalis europaea* increased in abundance between 1994 and 2016, *Solidago virgaurea* mainly in the forest, but *Trientalis europaea* along the entire gradient with emphasis on TL-100 and TL+100 (Figure 4, Table 4, Appendix S9).

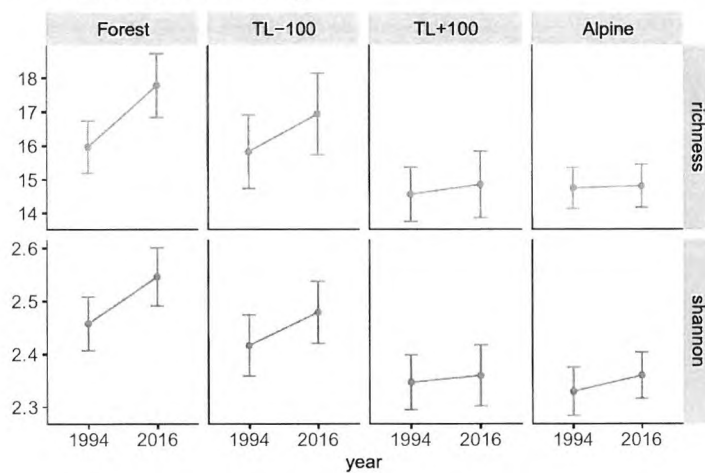
### 3.3.4 | Graminoids

The overall abundance of graminoids was positively related to bedrock richness and TPI (Figure 4, Table 3d, Appendix S8). Overall graminoid abundance did not change between 1994 and 2016, but a significant year × transect section interaction showed a slight increase in graminoid abundance over time in all sections except in TL+100, in which a slight decrease occurred (Figure 4, Table 3d, Appendix S8). The three most abundant graminoids showed deviating distribution patterns across the ecotone (Figure 4, Table 4, Appendix S9). The abundance of *Avenella flexuosa* was highest in the forest and decreased with increasing altitude whereas *Carex bigelowii* had its highest abundance in the alpine section and a decrease towards the forest. *Anthoxanthum odoratum* L. was distributed evenly across the ecotone (Figure 4, Table 4, Appendix S9). Regarding change in abundance from 1994 to 2016, *Anthoxanthum odoratum* showed an overall decrease, *Carex bigelowii* no overall change but a small increase in the forest section, and *Avenella flexuosa* showed no change (Figure 4, Table 4, Appendix S9).

## 4 | DISCUSSION

### 4.1 | Changes in species composition

The estimated upward shift of field layer vegetation of 10.5 m between 1994 and 2016, based on quadrat displacement along the first ordination axis, represents an overall vegetation movement of approximately 0.5 m/y. Even though 22 years is a relatively short time period to detect compositional vegetation changes, the experienced increase of 1.4°C in mean summer temperature represents an upward temperature shift of more than 200 altitudinal m (assuming a lapse rate of 0.6°C per 100 m of altitude; Wieser and Tausz, 2007). Accordingly, to keep track with the experienced warming an upward vegetation movement of approximately 10 m/y would have been needed. In light of this, the recorded upward shift of vegetation composition is moderate. However, it is



**FIGURE 3** Mean species richness and Shannon diversity index values in 1994 and 2016 in the four transect sections. Vertical bars show the standard error

of a similar order of magnitude as reported calculations for shift rates in species optima (i.e. ca. 1.1–3 m/y) (le Roux and McGeoch, 2008; Lenoir et al., 2008; Chen et al., 2011), but in contrast to other studies reporting minor or no signs of upward shifts (Vittoz et al., 2009; Wilson and Nilsson, 2009; Virtanen et al., 2010). Even though the estimated upward movement is statistically consistent, there is large variation among plots, and thus the rate of the upwards movement must be handled with care.

Our results of species composition above and below the treeline becoming more similar during the 22-year study period, is indicative of homogenisation of the vegetation. This is also reported for a variety of other alpine plant communities as a response to climate warming (Odland et al., 2010; Ross et al., 2012; Matteodo et al., 2016), and has been causally linked to invasion of widespread and generalist species and decline of rare or specialised species (Matteodo et al., 2016). Accordingly, analyses of the individual species show a distribution expansion and abundance increase of species with generally high presence throughout the ecotone, particularly in the area of the forest line and the treeline (e.g. *Empetrum nigrum*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*) and a parallel decline in specialist species like the alpine *Salix herbacea*.

#### 4.2 | Species richness and diversity

The observed overall increase in species richness is composed of an increase in the lower-elevation quadrats (where diversity was already high) and little to no increase in the upper parts. This is in line with results from the southern Scandes Mountains (Klanderud and Birks, 2003), but in contrast to results from the northern Scandes (Wilson and Nilsson, 2009) where a general decline in species richness was found over a similar time span (20 years). However, the area of the northern study (Wilson and Nilsson, 2009), although located at comparable altitudinal range as our study, is characterised by

moister climate conditions and without sheep grazing impact. These differences might thus explain the deviating results.

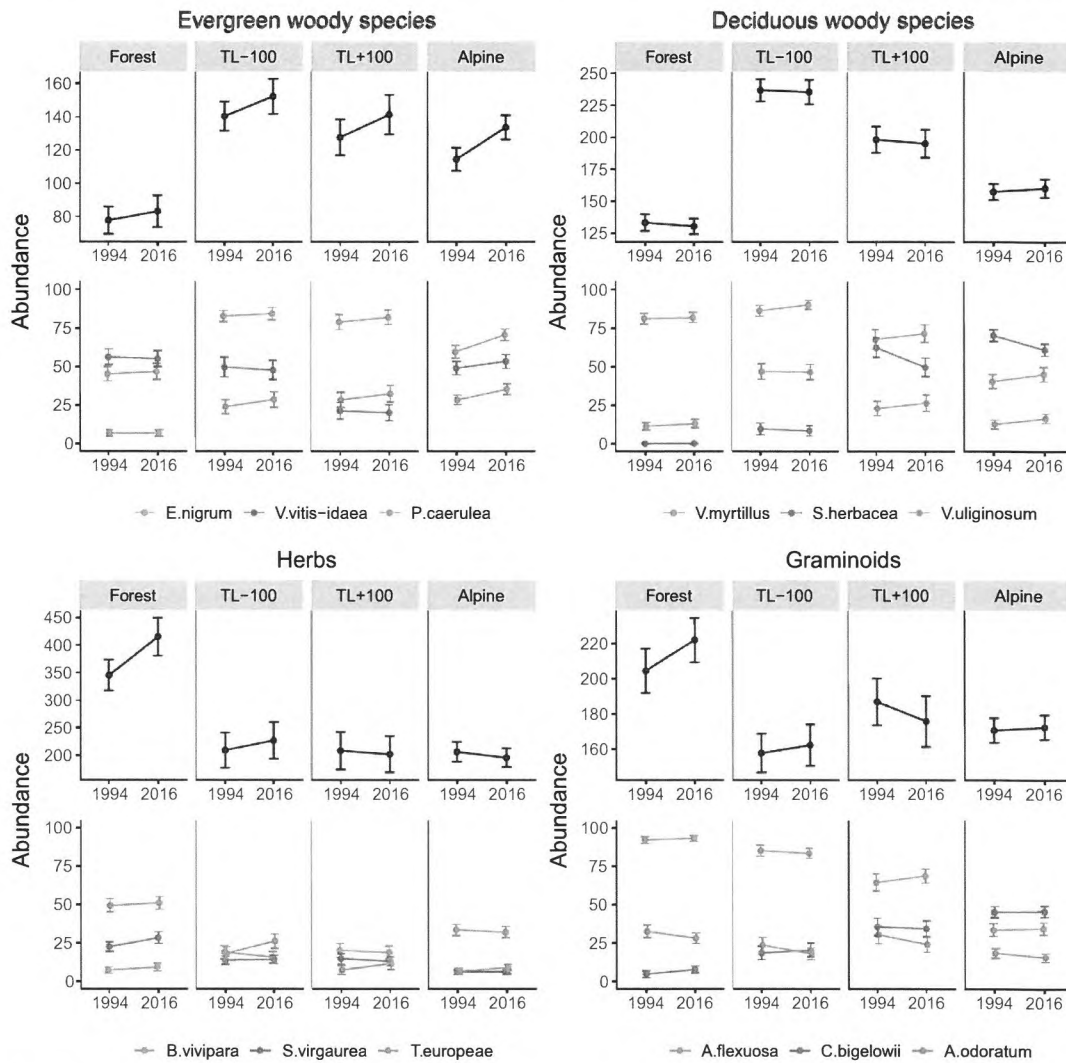
Further, our findings of a negligible increase in species richness in the alpine section stand in contrast to reports of a rapid increase in species richness at alpine summits due to climate warming (Pauli et al., 2012; Steinbauer et al., 2018). However, these studies are based upon large plots or entire summits, increasing the probability of recording rare species. Thus, the contrasting results may be due to study design (Wilson and Nilsson, 2009; Kullman, 2010).

The stronger increase in diversity in the parts of the ecotone with the highest initial diversity is in contrast to the classic diversity-invasibility hypothesis (Elton, 1958), that predicts species-rich communities to be more resistant to immigration by new species. However, contrasting results are reported, often referred to as the invasion paradox (cf. Fridley et al., 2007). This theory, however, places limited emphasis on abiotic constraints, and in alpine systems, abiotic factors such as wind and cold exposure are found to be able to dominate over competitive interactions (Spasojevic and Suding, 2012; Gazol et al., 2017). It has also been argued that invasiveness depends on the productivity of the area, and that low-productive areas experience less invasions (Davies et al., 2007), which agrees with our results and the results of Wilson and Nilsson (2009) who found stronger changes in the most productive, lower parts of the ecotone.

#### 4.3 | Individual species vs. functional groups

The results of analyses of individual species in our study underline the importance of a species approach, in addition to or instead of a functional group approach, when investigating vegetation dynamics. These mixed responses, with stronger species-specific responses, especially within the deciduous woody species group, underline how grouping species into traditional functional groups can be inadequate and even misleading to explain vegetation's responses to environmental change (Klanderud, 2008; Little et al., 2015; Saccone et al., 2017).





**FIGURE 4** Mean abundance of functional groups and individual species within each functional group in 1994 to 2016. The upper panels (black lines) in each figure part show the total sum of the abundance of all species within each functional group per transect section, and lower panels (coloured lines) show the three most abundant species per group and section. Error bars represent the standard error. Note difference in y-axis score for functional groups

Our results suggest that the decrease in sheep abundance in the study area from 1994 to 2016 might have given foraging-prone species improved resprouting and dispersal conditions. For example, the increase in *Solidago virgaurea* over time, a species which has been shown to respond positively to cessation of grazing (Evju et al., 2009), combined with the increase in *Vaccinium myrtillus* and a general decline in *Anthoxanthum odoratum*, indicate vegetation changes associated with a decreased grazing pressure over time (Pakeman et al., 2019).

Evergreen species, in particular *Empetrum nigrum*, have been found to increase in abundance in response to warming (Klanderud and Birks, 2003; Wilson and Nilsson, 2009; Vuorinen et al., 2017), suggesting that warming is a main driver of the observed increase also in our study area. Changes in tundra vegetation in response to climate warming are, however, regionally variable, in particular the response of deciduous woody species (Elmendorf et al., 2012a; Elmendorf et al., 2012b).

**TABLE 4** ANOVA table results of generalized linear mixed-effects models of abundance of individual species as a response of year, transect section and year  $\times$  section, chi-square showing results of model comparison by the Wald chi-square method, and stars denoting significance level of the ANOVA test: \*\*\*,  $p < 0.001$ ; \*\*,  $p < 0.01$ ; and \*,  $p < 0.05$ .

Response variable	Year	Transect section	Year $\times$ Section
<i>Empetrum nigrum</i>	67.11***	23.20***	38.65***
<i>Vaccinium vitis-idaea</i>	1.76	10.15*	25.15***
<i>Phyllodoce caerulea</i>	40.75***	18.41***	N/A
<i>Vaccinium myrtillus</i>	37.45***	27.70***	20.76***
<i>Salix herbacea</i>	128.90***	68.46***	9.14*
<i>Vaccinium uliginosum</i>	16.13***	24.73***	21.58***
<i>Bistorta vivipara</i>	2.43	18.22***	11.9**
<i>Solidago virgaurea</i>	4.27*	14.46**	12.92**
<i>Trientalis europaea</i>	34.10***	37.66***	25.69***
<i>Avenella flexuosa</i>	N/A	56.26***	N/A
<i>Carex bigelowii</i>	2.57	38.29***	13.44**
<i>Anthoxanthum odoratum</i>	51.60***	N/A	N/A

Note: N/A, response variables not included in the final model.

#### 4.4 | Environmental factors and drivers of change

Our analysis reveals distance to treeline as the strongest determinant of field layer vegetation composition. Although treeline and tree height are highly correlated with altitude, the results support that the presence of a tree layer exerts control over the field layer vegetation (Hofgaard and Wilmann, 2002). Further, the results suggest that vegetation changes above the treeline involve interactions with other drivers such as topography and substrate richness (i.e. displacement along the second ordination axis), which is in line with previously published findings (Hofgaard and Wilmann, 2002; Batllori et al., 2009; Scherrer and Körner, 2010; Lenoir et al., 2013). Even though the presence of a historic tree layer has lingering importance for current field layer vegetation composition (Hofgaard and Wilmann, 2002), the lack of treeline movement in the study area (Løkken, J.O., Evju, M., Söderström, L. & Hofgaard, A., unpubl.) combined with an upward shift of field layer vegetation suggest that the link with the tree layer might become weaker in a warming climate (Camarero et al., 2006; Batllori et al., 2009). These contrasting results suggest that vegetation in the forest-tundra ecotone responds in layer-specific manners to climate warming, possibly moderated by the presence of herbivores (Vuorinen et al., 2017; Løkken et al., 2019). In alpine and arctic tundra ecosystems, herbivory is a well-known driver counteracting effects of climate warming on vegetation (Olofsson et al., 2009; Speed et al., 2012; Eskelinen et al., 2017), that might inhibit the expansion of deciduous woody species, but with low effect on evergreen woody species (Ylänen et al., 2015; Vowles et al., 2017).

## 5 | CONCLUDING REMARKS

Our results on vegetation change over a 22-year period with substantial warming demonstrate how increased temperature impacts vegetation in complex species-specific manners, dependent on initial vegetation composition and local variability in biotic and abiotic factors such as the presence of a tree layer, microtopography, soil richness and grazing pressure. The estimated upward vegetation shift of 0.5 m/y, even though moderate in comparison with the temperature change in the area, is larger than what is found in most observational studies. In addition, the observed contrasting responses between the individual species, in particular within functional groups, underline the importance of considering the species level when studying climate change-related vegetation changes (Klanderud, 2008; Little et al., 2015; Saccone et al., 2017). Further, insights from a range of study approaches at local scales are important to feed realistic predictions of vegetation change, both reorganisation of species and rates, under climate warming (De Boeck et al., 2015).

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#### AUTHOR CONTRIBUTIONS


AH initiated and designed the study, and provided the 1994 data. JOL lead the field sampling in 2016. JOL performed the analyses with input from ME and AH. JOL drafted the paper in collaboration with all co-authors. The final version of the manuscript was read and approved by all co-authors.


#### DATA AVAILABILITY STATEMENT

The original data sets are stored in the NINA database (<https://doi.org/10.15468/kxvhzm>), and are available upon formal request addressed to the last author.

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#### SUPPORTING INFORMATION

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

- Appendix S1.** Precipitation statistics  
**Appendix S2.** Sheep density statistics  
**Appendix S3.** Individual species frequency  
**Appendix S4.** Correlation table for environmental variables

- Appendix S5.** CCA statistics and VIF for the environmental variables  
**Appendix S6.** Characteristics of the environmental factors  
**Appendix S7.** Diversity and richness summary statistics  
**Appendix S8.** Species turnover  
**Appendix S9.** Summary tables

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