DYNAMICS AND DRIVING FORCES OF TREELINE FLUCTUATION AND REGENERATION IN CENTRAL NORWAY DURING THE PAST DECADES

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With 3 figures, 2 tables, 5 photos, and 1 supplement
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Summary: The aim of this study was to analyse recent treeline fluctuations in central Norway to estimate the influence of land use change and climatic change during the past decades. Four study areas were chosen along steep oceanic-continental gradients in central Norway, representing different climatic regions. The analysis was performed using a combination of landscape-ecological, dendroecological, remote sensing and human-geographical methods. Treeline alterations were analysed by correlating climate change signals and spatial land use changes. All study sites showed a spatial expansion of forest fragments within the alpine treeline ecotone but little regeneration above the recent treeline. We found that intensive historical land use by logging and grazing had decreased the treeline at the beginning of the 20th century. Recent regeneration was found, mainly due to land use extensification. Climate analysis indicated warmer and moister conditions over the past decades. We found that these changes were restricted to the winter months, only. Furthermore, regeneration occurred on plots formerly disturbed by heavy grazing pressure or cryoturbation. Climatic change during the past decades had no effect on treeline fluctuations. The most decisive driving forces for treeline fluctuation and regeneration were changes of land use intensity. On the one hand, grazing pressure was the initial trigger for the expansion of forest fragments within the treeline ecotone. On the other, high grazing intensity combined with other land use practises caused stable stages of depressed treelines.

Zusammenfassung: Ziel der Studie war es, eine Analyse der aktuellen Fluktuationen der Baumgrenze in Mittelnorwegen vorzunehmen, um die Einflüsse von Landnutzungs- und Klimawandel auf die Baumgrenze in den letzten Jahrzehnten abzuschätzen. Vier Untersuchungsgebiete wurden entlang eines ozeanisch-kontinentalen Klimagradienten in Mittelnorwegen ausgewählt. Die Studie wurde mittels einer Kombination landschaftsökologischer, dendroökologischer, fernerkundlicher und humangeographischer Methoden durchgeführt. Die Veränderungen der Baumgrenze wurden mit Klimasignalen und Landnutzungsdaten korreliert. In allen Gebieten zeigte sich eine Ausdehnung bestehender Waldfragmente innerhalb des Baumgrenzökotons; eine Ausdehnung über den Bereich der bestehenden Baumgrenze hinaus war allerdings nicht festzustellen. Es zeigte sich, dass intensive Landnutzungsformen wie Holzeinschlag und Beweidung zu Beginn des 20. Jahrhunderts zu einer Absenkung der Waldgrenze geführt haben und dass die gegenwärtig zu beobachtende Ausdehnung der Waldbestände vorzugsweise auf eine Extensivierung der Landnutzung zurückzuführen ist. Eine Analyse vorliegender Klimadaten zeigte einen Trend zu insgesamt wärmeren und feuchteren Verhältnissen im jährlichen Mittel. Eine genauere Betrachtung erbrachte jedoch, dass diese Entwicklung lediglich auf Veränderungen in den Wintermonaten zurückzuführen war. Einen Einfluss der Klimaveränderung auf das Baumgrenzökoton konnte von uns nicht festgestellt werden. Die Regeneration der Baumbestände war nahezu ausschließlich auf Areale begrenzt, die vormals erheblichem Weidedruck ausgesetzt waren oder durch Kryoturbation eine Zerstörung der zusammenhängenden Vegetationsbedeckung aufwiesen. Folglich ist davon auszugehen, dass die Veränderungen in erster Linie mit veränderten Landnutzugsmustern zusammenhängen. Hat die Landnutzung in den vergangenen Jahrhunderten zu einer Depression der Waldgrenze geführt, so ist die intensive vormalige Landnutzung und die abnehmende Intensität der Nutzung in den vergangenen Jahrzehnten die Ursache für die Ausdehnung der Waldbestände.

Keywords: Norway, treeline, land use change, climatic change

1 Introduction

Due to their climatic limitation, treelines especially in the northern hemisphere are regarded as an important ecotone to investigate effects of global warming on terrestrial ecosystems (e.g. Rupp et al. 2000; Walther et al. 2002; Grace et al. 2002). Despite uncertainties in terms of a possible time delay of treeline responses to climate change, a climate-determined upward shift of the upper treeline was proven for the Swedish Scandes and the Urals (Kullman 2002; Moiseev and Shiyatov 2003). Although an almost global trend of increasing

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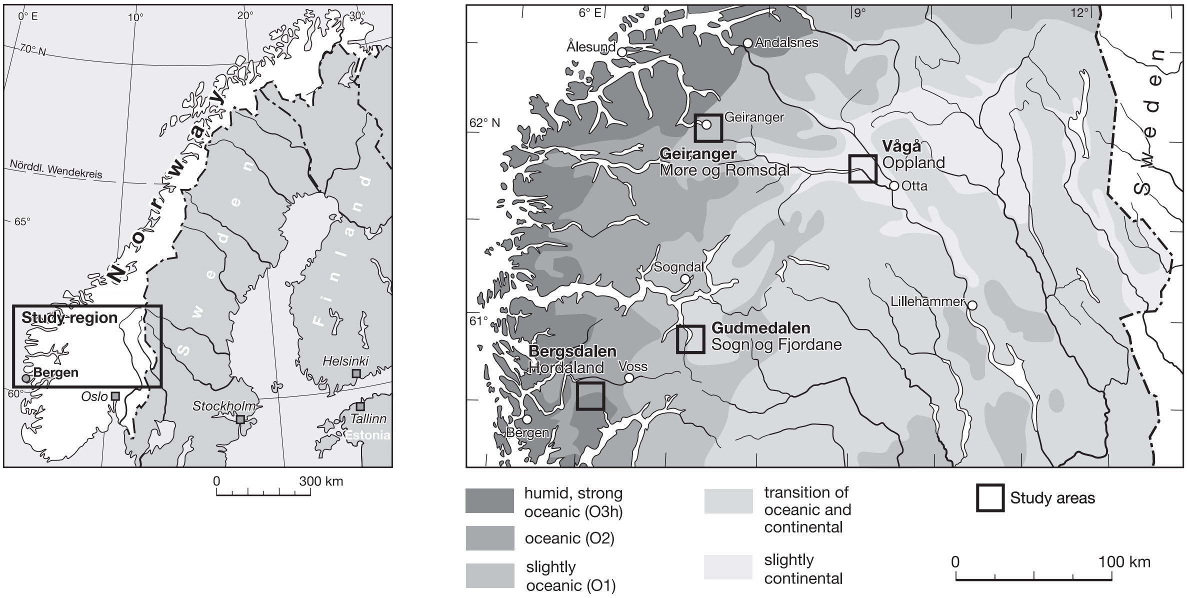


Fig. 1: Location of the study areas and the distribution of climatic regions (after Moen 1999).

temperature can be observed (Houghton et al. 2001; IPCC 2007), regional climate changes are much more relevant for ecological processes (Ostendorf et al. 1999) since climate change is expected to show different characteristics in different climatic regions (Sygna and O'Brien 2001). It is supposed that these regional differences cause ambiguous treeline responses (Dullinger et al. 2004). Beside the influence of climate, the role of human impact as a superior factor on the vegetation structure in many mountain regions of the world has been stressed repeatedly (e.g. Miehe and Miehe 2000). In many regions, anthropogenically delimited treelines show great elevational shifts after the cessation of a land use impact (Holtmeier and Broll 2005). For Norway, Hofgaard (1999) emphasised the long-term and strong influence of human activity on the alpine and subalpine belts. According to Hofgaard (1997), this influence might be misinterpreted as a response to climate change. Moreover, a lack of observable treeline response due to counteracting factors may lead to the conclusion of climatic insensitivity (Dalen and Hofgaard 2005). The importance of multiple factor constellations determining treeline distribution is stressed by Holtmeier (1974, 2003) and is expressed in many studies dealing with different treeline responses. Thus, we analysed the Norwegian treeline fluctuations during the past five decades in different climatic regimes with respect to the multiple factor constellation by incorporating numerous parameters. The compilation of a comprehensive dataset is key to analyse which of these parameters was responsible for the observed changes in forest cover and treeline fluctuations. Treeline nomenclature within this study accords with Holtmeier (1974) who applied the term treeline to the transition zone from closed forests to the most advanced individuals of the forest-forming tree species within the alpine belt, disregarding the absolute height of trees but their relation to the average depth of winter snow pack.

In our study we investigate central Norwegian treeline fluctuations during the past five decades in different climatic regimes. We analyse the influence of land use change and climatic change on the dynamics of treeline fluctuation and mountain forest regeneration.

2 Materials and methods

Within the central Norwegian study region, four study areas were selected along an oceanic-continental climatic gradient (Löffler et al. 2006). Figure 1 presents the location of the study areas and their allocation to different climatic regions (Moen 1999).

Table 1 shows the characteristics of the four study areas. According to the oceanic-continental climate differentiation and a subsidiary mountain mass elevation effect, *Betula pubescens* spp. *czerepanovii* dominated treelines rise from app. 700 m at Bergsdalen in the western part to app. 1,050 m a.s.l. at Vågå in the eastern part of the study region. Local parent rock materials differ in origin but show similar acid-silicate chemistry. Slope angles and expositions vary regionally. A comparison between the potential forest limit

Table 1: Characteristics of the four study areas. The mean annual temperatures according to DNMI (2004) were converted to sea level by applying a temperature lapse rate of 0.6 K/100 m; annual precipitation according to Aune (1993) and parent rock material according to Sigmond et al. (1984); climatic forest limit according to Aas and Faarlund (2000)

Location	Position [lat./ long.]	Mean annual temperature [°C]	Annual precipitation [mm]	Altitude of treeline position [m a.s.l.]	Potential climatic forest limits [m a.s.l.]	Slope angle of location [°]	Exposition	Parent rock
Vågå	N 61° 53' E 9° 15'	5.5	300 – 500	925 – 1,050	1,125	9	S	Phyllite
Geiranger	N 62° 03' E 7° 15'	7.0	1,500 – 2,000	750 – 880	900	39	SE	Gneiss
Gudmedalen	N 60° 45' E 7° 5'	6.1	1,500 – 2,000	950 – 1,030	1,050	17	W	Manganite
Bergsdalen	N 60° 30' E 5° 50'	5.65	3,500 – 4,000	600 – 730	700	16	N	Granite

that is based on the assumption of a climatic limitation (Aas and Faarlund 2000) and recent treeline positions show that all studied treelines are suppressed in altitude. Photos 1 to 4 give an impression of the recent situation and characteristics of the investigated treeline ecotones in the four study areas.

The analysis of treeline fluctuations during the past decades comprised a bitemporal aerial photo interpretation that was completed by dendroecological investigation about the age structure of the forest stands. We reconstructed and analysed climate variations as well as current and past land use and land cover changes. Vegetation mapping and statistical analysis of plant species and underlying environmental parameters served for an evaluation of ecological properties that are necessary for the regeneration of the Scandinavian mountain birch *Betula pubescens* ssp. *czerepanovii* (hereafter referred to as *Betula pubescens*). The analysis of the regeneration potential under local ecological properties is essential to determine the potential for changes of treeline distribution. In this study we used ordination techniques that are established and effective to evaluate these ecological properties considering multiple factor constellations along gradients and are useful to illustrate differences among species.

2.1 Bitemporal aerial photo interpretation

Treeline fluctuations were delineated using bitemporal aerial photo processing. Limited by the availability of aerial photos of the study areas, latest photos of 1992 to 1994 were compared with earliest photos existing (Vågå 1964, Geiranger 1976, Gudmedalen 1969, Bergsdalen 1972). Scales of aerial photos differed from 1:15,000 to 1:40,000. Aerial photos were transformed into orthophotos using a digital elevation model with a resolution of 25 m. Forest fragments, solitary trees and woodless areas were categorised. A threshold of 100 m^2 was used to distinguish between an accumulation of solitary trees and forest fragments.

2.2 Climate data analysis

Long-term meteorological data for the different study areas were provided by the Norwegian Meteorological Institute (DNMI 2004). The nearest meteorological stations were selected with maximum distances of app. 50 km to the study areas. Except for the easternmost climate station, all other stations are located in valley floors. Due to limited operating time of these stations, the analysed period only covers 31 years (1966–1996). To analyse the magnitude of climatic trends we used Sen's slope equation (Sen 1968) and tested significances by applying the non-parametrical Mann-Kendall-Test (Mann 1945; Kendall 1970). Calculations of precipitation and temperature trends are based on monthly means using MAKESENS (Salmi et al. 2002).

2.3 Investigations of land use changes

To obtain data about land use changes in the four study areas, inquiries and interviews were accomplished according to Löffler et al. (2004). Inquiries resulted in information about type and intensity of past and present land use. Official statistics provided quantitative data about past and present numbers of grazing animals and numbers of mountain summer farms. Additionally, local farmers and landowners were questioned about land use changes, using a qualitative, informal and semi-structured approach (Lundberg 2002).

Table 2: Significant environmental parameters used to analyse species distribution patterns in the ordination analysis. Abbreviations (abbrev.), type of parameter (metric or ordinal) as well as the minimum and maximum values are summarized

	parameters	abbrev.	type	min.	max.
topography					
	exposure	EXP	metric	-1	1
	relative altitude	ELEV	metric	-130	347
vegetation structure					
	forest	F	ordinal		
	sigle tree	ST	ordinal		
soil parameters					
	soil moisture	SM	metric	15	80
climatic parameters					
	annual mean temperature	T_Ymid	metric	1.3	6.65
	mean of three warmest month	JJA	metric	10.9	14.08
	annual precipitation sum	PRECIP	metric	548	1280

2.4 Dendroecological methods

Tree rings provide information about age structure and succession dynamics of a forest site and can be used to reconstruct long-term climate changes as well as short-term stand disturbances (Schweingruber 1996). In each study area wood core samples were collected from *Betula pubescens* trees of different age classes to analyse the distribution characteristics along an elevation gradient. Trees with a trunk diameter above 5 cm were cored at the trunk basis. Trees were drilled twice, parallel and perpendicular to the slope. The length of the aslope trunk from the root to the drill-point was recorded. From trees with a diameter below 5 cm stem disks were taken at the trunk basis. The samples were fixed and polished in the laboratory before tree rings were counted using a stereo-microscope. In cases when the corer had not hit the pith, the number of missing rings was estimated – based on the width and the curvature of the innermost rings of the core.

2.5 Ecological mapping

In each study area representative sites were selected comprehending a gradient from arboreous to non-arboreous areas. Ecotopes were delineated within each site and characterized following the concept of the *landscape-ecological complex analysis* (Mosimann 1985; Löffler 2002). These ecotopes served as homogeneous strata in a stratified sampling design. The nomenclature of plant species was based on Lid and Lid (1994). Abundance of plant species was estimated using a percentage scale of coverage. *Betula pubescens* individuals were divided into juvenile trees/saplings (< 50 cm height) and mature trees (> 50 cm height). The coverage of plant layers was estimated as to tree-, shrub-, grass-, herb-, moss-, and lichen-layers. Moreover, soil profiles were dug out and soil horizon thicknesses and combinations were documented. The pH-value was measured in H_2O and $CaCl_2$ in the field using a volumetric sample-liquid proportion of 1:2.5. Soil moisture (0–15 cm depth) was measured with a TDR-sensor (uncalibrated). The height of the winter snow cover was estimated using the occurrence of snow lichen *Pamelia oliviana* (Holtmeier 1974) on the tree stems.

2.6 Statistical analysis

Direct ordination analysis was used to correlate species abundances with environmental parameters to define ecological niches of vegetation types and plant species. The environmental parameters and their underlying ecological gradients were weighted according to their importance in explaining species dispersion using canonical coefficients. To estimate the variance of the data set a detrended correspondence analysis (DCA) was calculated. Due to a variance of more than two standard deviations, a canonical correspondence analysis (CCA) was performed. Results were graphed in an ordination diagram presenting important types of information: position of species (triangles) and sites (squares), nominal environmental parameters (circles), and length and direction of quantitative determinant vectors (arrows).

The position of a species was arranged according to the inter-species relationship and its relations to ecological gradients involved (Ter Braak 1986, 1994; Jongman et al. 1997). 218 species in 106 plots and 10 additional environmental parameters were used. In total 14 parameters were analysed, 10 significant parameters were used (Tab. 2). Expositions values were *cosinus*-transformed. Land use intensity (LUI) was assessed by means of land use data of the area, excrement frequency of grazing animals at the plot scale, and further marks of grazing pressure (e.g. trampling pits). Due to climate differences between the study areas a relative altitude (ELEV) had to be used instead of the absolute altitude. Relative altitudes resulted from the difference between current and potential climatic treeline, which was determined according to Aas and Faarlund (2000). A Monte Carlo permutation test was run with 499 permutations to select significant environmental parameters ($p \leq 0.05$). We focussed on inter-species-distances and used a biplot scaling. The statistical analyses were realized using Canoco 4.5 (Ter Braak and Šmilauer 2002). Moreover, the distribution of *Betula pubescens* juveniles was analysed using plant layer coverage. We tested the significance applying a T-test of means with SPSS-software (SPSS Inc, Chicago, Illinois).

3 Results

3.1 Vågå

The bitemporal aerial photo interpretation (1964–1992) shows a slight increase of forest fragments. They are concentrated in formerly open areas within the existing forests, along the road and near a former summer farm (Suppl. I, upper left). Only a few newly established solitary trees can be traced above the former treeline. The age structure of the trees includes all age classes and does not show any trend with altitude. The mean tree age is 69 years. The study area Vågå was extensively grazed by sheep (21–25 animals per km²) and a few cattle (15 in total) during the past approx. 20 years at least. Sheep and cattle grazing were only practised as sideline farming for cultural reasons. In contrast, heterogeneous livestock patterns occurred in the beginning of the 20th century when the total number of sheep was five times lower than recently, but the numbers of cattle and goats were much higher. In addition, the practises of pollarding, foliage harvesting and cutting of wood in an 'incorrect' and 'careless' way caused a higher impact of man on the treeline at that time. The climate data show positive trends of annual mean temperature (+0.03 K/y, $p > 0.1$) and

Photo 1: Impression of the treeline in the study area Vågå, characterized by gentle slopes and a wide treeline ecotone at around 1,050 m a.s.l. (August 2002)

Photo 2: Single standing mature trees are predominant at the recent treeline at the study area Gudmedalen at 1,050 m a.s.l. (August 2003)

precipitation (+4.02 mm/y, p = 0.05) during the last decades. The analysis of monthly climate data reveals that these positive trends are mainly the result of increasing winter temperatures and increasing winter to spring precipitation (Suppl. I, upper left).

3.2 Gudmedalen

The comparison of the aerial photos (1976–1992) reveals differences in tree coverage between the northern and the southern slopes (Suppl. I, lower left). The northern slope remained almost unchanged. In contrast, the southern slope experienced remarkable treeline fluctuations characterised by extensive propagation of trees. Tree recruitment on the south slopes occurred almost exclusively between formerly isolated individuals. Two age classes can be distinguished, consisting of old trees (mean age 127 years) and young trees (max. 47 years), respectively. As found by enquiries both sides were cultivated differently. The northern part of the Gudmedalen valley was grazed continuously by approx. 300 goats. In contrast, the southern part was affected by a clear-cut in the 1930s with exception of some isolated trees. Moreover, approx. 80 sheep were pastured on the southern slope until abandonment of the summer farm in the 1960s. Climate trend analyses indicate an increase of annual mean temperature (+0.03 K/y, p = 0.5) and precipitation sum (+5.28 mm/y, p = 0.05). Again, intra-seasonal temperature and precipitation trends only show a significant increase during the winter months.

3.3 Geiranger

Results from aerial photo processing (1972–1993) show an increase in the number of forest fragments and solitary trees (Suppl. I, upper right). Little treeline change happened in this study site. Clearly visible changes occurred mostly in the lower parts of the treeline ecotone that have been formerly used as grassland and the establishment of many solitary trees in the surrounding of the summer farm. The mean age (46 years) of all sampled trees is significantly younger than in the other study areas. The mean and maximum tree ages in formerly cultivated areas are 27 and 34 years respectively. No age trend with altitude is visible. Rivers and topography isolate the grazing area from other grazing grounds within the valley. Before the 1960s, the study site was continuously used as summer grazing ground. The farm consisted of a main building in the valley floor at 430 m a.s.l., while the summer farm was situated at 630 m a.s.l. in an avalanche-sheltered position. As found by questioning approx. 25 dairy cattle were kept throughout the summer. After the 1960s a shift to sheep keeping with approx. 120 animals led to an abandonment of the summer farm. Since 2000, the

Photo 3: The treeline in the study area Geiranger at approx. 900 m a.s.l. is shown in the front view (July 2003)

main farm is not used any more in the traditional way, but serves as a camping ground. Climatic trends show an increase of annual mean temperature (+0.01 K/y, $p = 0.01$) and annual precipitation sum (+4.19 mm/y, $p = 0.05$). The monthly climate data indicate that both trends are caused by rising temperature and precipitation during the winter months only (Suppl. I, upper right).

3.4 Bergsdalen

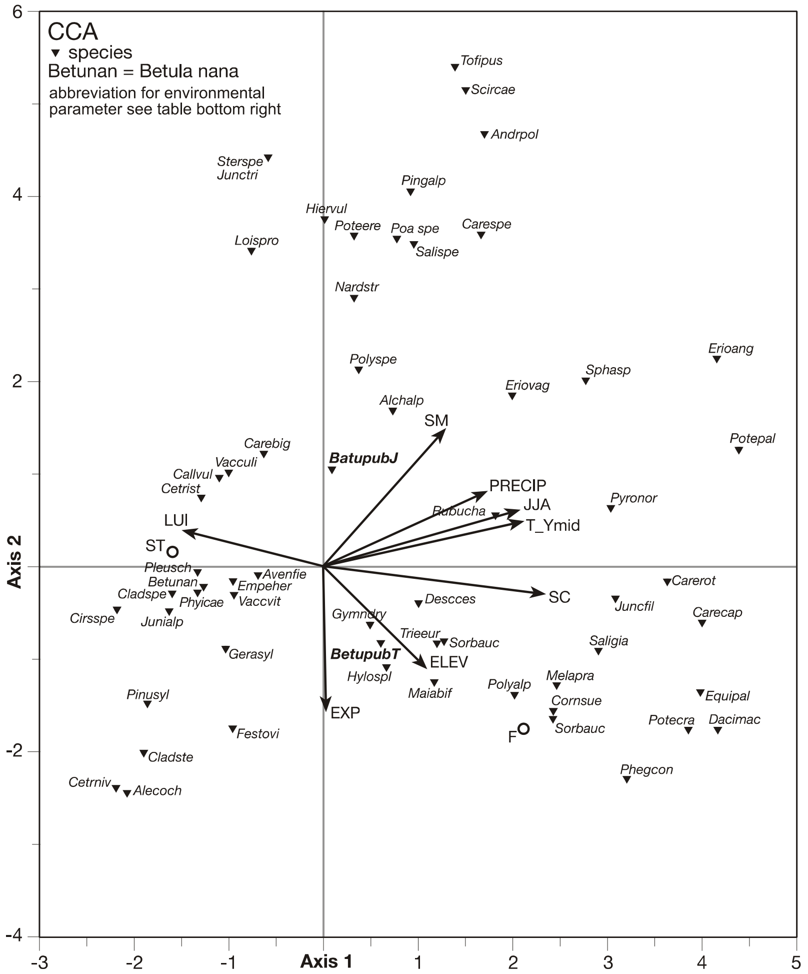
Little differences between 1974 and 1993 are displayed by the comparison of the aerial photos (Suppl. I, lower right). These differences are restricted to areas within the treeline ecotone and along linear structures of pre-existing forest fragments. These are located parallel to the slope and along rock outcrops, whereas plain areas are devoid of trees. The ecotone is characterised by relatively old trees (mean age 84 years) that show stunted growth forms and very small annual increment rates.

The study area has been used since the beginning of the past century. Exact data are available since 1965. The development of livestock numbers in the study area is reconstructed on annual data based on the farm level (Suppl. I, lower right). Numbers of sheep and cattle increased slightly since the 1960s. Unfortunately, it is not possible to estimate the current number of livestock in the study area. As an adaptation to insufficient grazing ground, a specific form of land use developed in this region: during summers, sheep are brought from farms along the near coast to the study area in the Scandes Mountains. The number of these sheep exceeds the number of local sheep by up to three times but fluctuated from year to year (Suppl. I, lower right). According to a local administrator these numbers have to be considered as minimum numbers. The analysis of climate data showed the same patterns as in all other study areas. We found an annual increase of temperature (+0.02 K/y, $p < 0.1$) and precipitation (+7.97 mm/y, $p = 0.1$). Seasonal temperature and precipitation trends showed a significant increase only during the winter months.

Photo 4: Polychromic *Betula pubescens* individuals at 700 m a.s.l. form a shrublike cover in the extremely oceanic study area Bergsdalen (August 2003)

3.5 Spatial distribution of vegetation with special emphasis on birch regeneration

A direct gradient analysis of 106 vegetation plots and 218 plant species was performed with all environmental parameters exceeding a significance level of 0.05 (Fig. 2). Due to the unimodal distribution with an intra-set inertia of 10.782, a canonical correspondence analysis was conducted. Eigenvalues of the first four axes explained 12.4% of the species data (2). Figure 2 presents an ordination diagram with 95% of species best correlated due to graphical reasons. The results of the permutation test showed a strong correlation of species distribution with climatic conditions (temperature: T_Ymid, JJA; and precipitation: PRECIP). As indicated by the length of the explanatory vectors, snow coverage, soil moisture, land use intensity, and relative altitude are important as to the total inertia, too. LUI is positively correlated with altitude, expressing a similar effect of grazing and altitude. SM and EXP are statistically important vectors and have explanatory power for a few species. SC is important concerning the differentiation of chionophilous and chionophobous species. Alpine lichen species are characterised by lower soil moisture and very thin snow cover (Fig. 2, lower left corner), lowest annual mean temperature and lowest precipitation sum, as well as higher LUI. Subalpine plant species are characterised by medium soil moisture, thick snow cover, oceanic climate, low altitudes, as well as low LUI (Fig. 2, lower right corner). Mire plant species are characterised by higher soil moisture, oceanic climate, lower altitudes and intermediate LUI (Fig. 2, upper right). Focussing on the distribution of *Betula pubescens* in the ordination diagram, both juvenile and mature trees (boxes) are assigned to different parameter combinations. Mature *Betula pubescens* trees correlate with decreasing altitude, low land use intensity and forest. In contrast, the occurrence of *Betula pubescens* juveniles is positively correlated with high land use intensity



Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.498	0.339	0.259	0.246	10.782
Species-environment correlations	:	0.910	0.856	0.808	0.790	
Cumulative percentage variance						
of species data	:	4.6	7.8	10.2	12.4	
of species-environment relation	:	24.2	40.6	53.2	65.2	
Sum of all eigenvalues	:					10.782
Sum of all canonical eigenvalues	:					2.060

Parameter	abbr.	F-value	p-value
normal annual mean	T_Ymid	3.708	0.001
snow cover	SC	2.677	0.001
mean temperature JJA	JJA	2.479	0.001
precipitation	PRECIP	2.595	0.001
soil moisture	SM	2.002	0.001
land use intensity	LUI	1.840	0.001
forest	F	1.803	0.002
exposition	EXP	1.512	0.032
relative altitude	ELEV	1.354	0.036
single tree	ST	1.325	0.057

Fig: 2: Ordination diagram of a canonical correspondence analysis (CCA) using all 106 plots, 218 plant species and 8 significant ($p \leq 0.05$) environmental parameters (bottom right). Due to the focus on species-environmental relations and graph visibility, only the 95 % best correlated species and the 8 significant environmental parameters are graphed. Statistical report of the performed CCA (bottom left) and significance levels of environmental parameters used (bottom right) are provided

and wet conditions. In summary, both age classes show similar ecological distributions but differences concerning the dominant forcing factors for their occurrence.

Detailed mapping of vegetation reveals that the current regeneration of *Betula pubescens* is restricted to wet depressions and micro-relief upper slopes. Nearly no regeneration occurs within the forests and we found most *Betula pubescens* juveniles on heavily disturbed sites (Photo 5). Statistical analyses revealed that the abundance of *Betula pubescens* juveniles showed a significant reduction beneath trees and an increase of open ground plots simultaneously (all $p \leq 0.05$, Fig. 3). Moreover, the occurrence of the juveniles tends to lower density of shrub layers. *Betula pubescens* regeneration occurs mainly on bare ground or wet plots with light conditions.

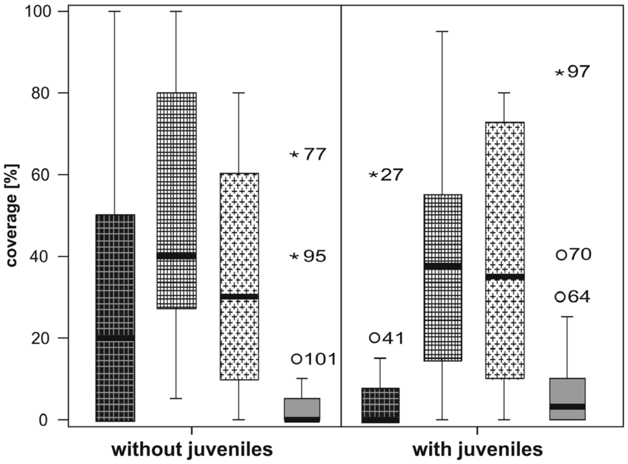
Photo 5: Typical situations for *Betula pubescens* regeneration. Left: boggy micro-mount. Centre: disturbance due to trampling on an upper slope. Right: trampling pit in a wet depression (August 2003)

4 Discussion

Our results show that the treeline ecotone in central Norway is characterised by an increase in forest fragments and solitary tress during the past decades. During this period, annual mean temperature increased in all study areas investigated. Considering the postulated effects of global warming on treeline fluctuations in general, such forest expansions have often been interpreted as direct effects of increasing annual temperatures (e.g. Rochefort et al. 1994; Grace et al. 2002; Kullman 2002). Our analysis of monthly climate data shows that positive temperature trends are restricted to the winter months. A more detailed description is given by Rössler and Löffler (2007). Førland et al. (2000) found similar results regarding the climatic trend since 1876. A wealth of studies provides evidence that at the treeline, *Betula pubescens* is mainly influenced by summer air temperatures (i.e. Aas 1964; Tuhkanen 1980; Odland 1996). Recent studies emphasise the determination of alpine treelines by low soil temperatures (Körner 1999; Körner and Paulsen 2004), which most likely influence birch regeneration via the limitation of nitrogen uptake (Karlsson and Weih 2001). In our study regions, summer temperatures did not change significantly over the last decades. On the other hand, the rising winter temperatures did not prolong the vegetation period during the same period. Thus, the observed treeline fluctuations cannot be interpreted as a consequence of climatic change.

The studied alpine treelines in central Norway are heavily influenced by human activity. Land use change results either in a suppression or a rise of treelines. These results correspond to findings reported in the literature (Aas and Faarlund 1995; Hofgaard 1997, 1999; Olsson et al. 2000; Bryn and Daugstad 2001; Löffler et al. 2004). Except for the Bergsdalen study area, the detected land use changes follow a general trend found in Norway. In the beginning of the past century, land use intensity was higher than today due to summer farming, firewood collecting and grazing. This resulted in a high but spatially heterogeneous pressure on the treeline ecotone (Aas and Faarlund 1995). Because of the introduction of modern forest management concepts and the cessation of summer farming, this pressure decreased during the past decades and enabled the regeneration of birch. Aas and Faarlund (1995) described a rapid dispersion of *Betula pubescens* into former summer farm areas as a response to land use changes. This behaviour is also typical for the investigated areas in our study. Moreover, our results reveal that the local treelines investigated never exceeded the potential climatic treeline during the past century, although mature trees assuring seed dispersal existed during the past decades. The recent development at the central Norwegian treeline has to be mostly interpreted as an extensive infilling-effect resulting from land use abandonment. This effect is reported recently to be one major dynamic present at the treelines in the Swiss alps (Gehrig-Fasel et al. 2007).

According to Arno (1984) an upward shift of depressed treelines depends on a series of beneficial factors: the production of fertile seeds, suitable micro-climatic conditions for seedling establishment and sufficient numbers of suitable sites for germination. Tree establishment rates depend mainly on the number of suitable germination plots (Holtmeier et al. 2003) or on browsing intensity (Löffler et al. 2004). *Betula pubescens* as a pioneer species germinates quickly and colonises open ground successfully (Kinnaird 1974). Moss cushions and short grasslands are suitable for birch regeneration, due to sufficient light benefit (Kinnaird 1968; Miles and Kinnaird 1979a, b), whereas forests and dense



	a) mean coverage without juveniles (n = 78) [%]	b) mean coverage with juveniles (n = 28) [%]	statistics of difference a - b t-value	p-value
▦ tree layer	26.05	5.89	3.571	0.01
⊞ shrub layer	52.17	39.29	1.973	0.051
▨ grass layer	32.83	40.82	-1.344	0.182
▩ open ground	3.53	9.43	-2.260	0.026

Fig. 3: The boxplot-diagram illustrates the influence of the mean coverage of different vegetation layers and open ground areas of all 106 investigated plots on the occurrence of *Betula pubescens* juveniles

dwarf-shrub heaths hinder regeneration due to insufficient light conditions (Kinnaird 1974; Holtmeier 1974) and heavy competition (Berkowitz et al. 1995; Hobbie and Chapin 1998). Our results confirm these former studies by ordination of ecological niches of birches and correlation with the coverage of plant layers.

Available sites for birch regeneration provide suboptimal growth conditions, since upper slopes and ridges are characterised by harsh snow-free winter conditions where birch seedlings struggle to survive (Holtmeier 1974). Moreover, seedlings in wet depressions suffer from a deficit in nutrient supply and from high soil moisture (Miles and Kinnaird 1979a). Hence, optimal ecological niches of *Betula pubescens* are situated on the slopes where most of the mature trees presently grow. But these niches are also favoured by dwarf-shrubs which hamper the regeneration of *Betula pubescens*. Thus, we argue that the disturbance of the dense dwarf-shrub vegetation by trampling and browsing of grazing livestock is a necessity for fast regeneration of the treeline. Finally, grazing pressure has to be interpreted as an ambivalent parameter enabling the regeneration of birch on the one hand and suppression of juvenile trees by browsing on the other hand.

5 Conclusions

Coming back to the initial focus of this study, whether climate change or land use changes can be assigned as the superior driving force explaining the observed alpine treeline changes in central Norway, we conclude that land use changes during the past decades were of far greater importance for treeline alternations than climate change. Our regional findings are in accordance with results of comparable studies in other mountain regions of the world that proved the superior impact of human activity on treeline changes (Messerli and Ives 1984; Wardle 1991; Messerli and Winiger 1992; Hofgaard 1999; Theurillat and Guisan 2001; Schickhoff 2005). Finally, we conclude that high grazing intensity combined with other land use practises caused stable stages of depressed treelines. Changes in grazing pressure were the initial trigger for the expansion of forest fragments within the treeline ecotone in all our study areas. During the past decades, climate change had no obvious effect on treeline fluctuations. This conclusion is in line with a recent study by Dalen and Hofgaard (2005) from other parts of Norway. So, claims that research on climatic change response including field monitoring and satellite image analysis should focus on undisturbed treelines (Holtmeier and Broll 2005) seem difficult to be conducted in mountain regions that have experienced a long history of human land use, because this accounts for almost all mountain systems of the old world. The identification of "natural" treelines would have to include careful investigation concerning the local land use history in the treeline ecotone.

References

Aas, B. (1964): Björke–og barskoggrenser i Norge: En undersøkelse av de øvre kimatiske skoggrenser. Hovedfagsoppgave i Naturgeografi. Oslo.

Aas, B. and Faarlund, T. (1995): Skoggrenseutviklingen i Norge, særlig i det 20. århundre. In: AmS-Varia 24, 89–100.

– (2000): Forest limits and the subalpine birch belt in north Europe with a focus on Norway. In: AmS-Varia 37, 103–147.

Arno, S. F. (1984): Timberline: mountain and arctic forest frontiers. Washington.

Aune, B. (1993): National atlas of Norway: climate. Hønefoss.

Berkowitz, A. L.; Canham, C. D. and Kelly, V. R. (1995): Competition vs. facilitation of tree seedling growth and survival in early successional communities. In: Ecology 76, 1156–1168.

Byrn, A. and Daugstad, K. (2001): Summer farming in the subalpine birch forest. In: Wielgolaski, F. E. (ed.): Nordic mountain birch ecosystems. Man and Biosphere Series 27. London, 179–315.

Dalen, L. and Hofgaard, A. (2005): Differential regional treeline dynamics in the Scandes Mountains. In: Arctic, Antarctic, and Alpine Research 37, 284–296.

DNMI (2004): Norwegian Meteorological Institute 1966–1996. Yearly rapports – daily values. Oslo.

Dullinger, S.; Dirnböck, T. and Grabherr, G. (2004): Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. In: Journal of Ecology 92, 241–252.

Førland, E.; Roald, L. A.; Tveito, O. E. and Hanssen-Bauer, I. (2000): Past and future variations in climate and runoff in Norway. DNMI-Report 19/00 KLIMA. Oslo.

Gehrig-Fasel, J.; Guisan, A. and Zimmermann, N. E. (2007): Tree line shifts in the Swiss Alps: climate change or land abandonment? In: Journal of Vegetation Science 18, 571– 582.

Grace, J.; Berninger, F. and Nagy, L. (2002): Impacts of climate change on the treeline. In: Annals of Botany 90, 537–544.

Hobbie, S. E. and Chapin, F. S. III (1998): An experimental test of limits to tree establishment in Arctic tundra. In: Journal of Ecology 86, 449–461.

Hofgaard, A. (1997): Inter-relationship between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. In: Global Ecology and Biogeography Letters 6, 419–429.

– (1999): The role of "natural" landscapes influenced by man in predicting responses to climate change. In: Ecological Bulletins 47, 160–167.

Holtmeier, F.-K. (1974): Geoökologische Beobachtungen und Studien an der subarktischen und alpinen Waldgrenze in vergleichender Sicht (nördliches Fennoskandien/Zentralalpen). Erdwissenschaftliche Forschung 8. Wiesbaden.

– (2003): Mountain timberlines. Dordrecht.

Holtmeier, F.-K. and Broll, G. (2005): Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. In: Global Ecology and Biogeography 14, 395–410.

Holtmeier, F.-K.; Broll, G.; Müterthies, A. and Anschlag, K. (2003): Regeneration of trees in the treeline ecotone: northern Finnish Lapland. In: Fennia 181, 103–128.

Houghton, J. T.; Ding, Y.; Griggs, D. J.; Noguer, M.; van der Linden, P. J.; Dai, X.; Maskell, K. and Johnson, C. A. (2001): IPCC – The scientific basis. Contribution of working group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge.

IPCC (2007): Climate change 2007: the physical science basis, summary for policymakers. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. http://www.ipcc.ch/SPM2feb07.pdf (12. 03.2007)

Jongman, R. H. G.; Ter Braak, C. J. F. and Van Tongeren, O. F. R. (1997): Data analysis in community and landscape ecology. Cambridge.

Karlsson, P. S. and Weih, M. (2001): Soil temperatures near distribution limit of the mountain birch (*Betula pubescens* ssp. *czerepanovii*): implications for seedling nitrogen economy and survival. In: Artic, Antarctic and Alpine Research 33, 88–92.

Kendall, M. G. (1970): Rank correlation methods. London.

Kinnaird, J. W. (1968): Ecology of birch woods. In: Proc. Bot. Soc. Br. Isl. 7, 181–182.

– (1974): Effect of site conditions on the regeneration of birch (*Betula pendula* roth. and *Betula pubescens ehrh.*). In: Journal of Ecology 62, 467–474.

Körner, C. (1999): Alpine plant life: functional plant ecology of high mountain ecosystems. Berlin.

Körner, C. and Paulsen, J. (2004): A world wide study of high altitude treeline temperatures. In: Journal of Biogeography 31, 713–732.

Kullman, L. (2002): Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. In: Journal of Ecology 90, 68–77.

Lid, J. and Lid, D. T. (1994): Norsk flora. Oslo.

Löffler, J. (2002): Altitudinal changes of ecosystem dynamics in the central Norwegian high mountains. In: Die Erde 133, 155–186.

Löffler, J.; Lundberg, A.; Rössler, O.; Bräuning, A.; Jung, G.; Pape, R. and Wundram, D. (2004): The central Norwegian alpine tree line under a changing climate and changing land use. In: Norwegian Journal of Geography 58, 183–193.

Löffler, J., R. Pape & D. Wundram (2006): The Climatologic Significance of Topography, Altitude and Region in High Mountains. A Survey of Oceanic-Continental Differentiations of the Scandes. Erdkunde 60: 15–24.

Lundberg, A. (2002): The interpretation of culture in nature: landscape transformation and vegetation change during two centuries at Hystad, SW Norway. In: Norwegian Journal of Geography 56, 246–256.

Mann, H. B. (1945): Nonparametric tests against trend. In: Ecometrica 13, 245–259.

Messerli, B. and Ives, J. D. (1984): Gongga Shan (7556 m) and Yulongxue Shan (5596 m). Geographical observations in the Hengduan Mountains of Southwestern China. In: Lauer, W. (ed.): Natural environment and man in tropical mountain ecosystems. Erdwissenschaftliche Forschung 18. Stuttgart, 55–77.

Messerli, B. and Winiger, M. (1992): Climate, environmental change, and resources of the African mountains from the Mediterranean to the equator. In: Mountain Research and Development 12, 315–336.

Miehe, G. and Miehe, S. (2000): Comparative high mountain research on the treeline ecotone under human impact. In: Erdkunde 54, 315–336.

Miles, J. and Kinnaird, J. W. (1979a): The establishment and regeneration of birch, juniper and scots pine in the Scottish Highlands. In: Scottish Forestry 33*,* 102–119.

– (1979b): Grazing: with particular reference to birch, juniper and scots pine in the Scottish Highlands. In: Scottish Forestry 33, 280–289.

Moen, A. (1999): National atlas of Norway: vegetation. Hønefoss.

Moiseev, P. A. and Shiyatov, S. G. (2003): Vegetation dynamics at the treeline ecotone in the Ural highlands. In: Nagy, L.; Grabherr, G.; Körner, C. and Thompson, D. B. A. (eds.).: Alpine biodiversity in Europe. Berlin, Heidelberg, New York, 423–433.

Mosimann, T. (1985): Untersuchungen zur Funktion subarktischer und alpiner Geoökosysteme (Finnmark [Norwegen] und Schweizer Alpen). Physiogeographica 7, Basel.

Odland, A. (1996): Differences in the vertical distribution pattern of *Betula pubescens* in Norway and its ecological significance. In: Paleoclimate Research 20, 42–59.

Olsson, E. G. A.; Austrheim, G. and Grenne, S. N. (2000): Landscape change patterns in mountains, land use and environmental diversity, Mid–Norway 1960–1993. In: Landscape Ecology 15, 155–170.

Ostendorf, B.; Hilbert, D. W.; Köstner, B.; Tappeiner, U. and Tasser, E. (1999): Toward a predictive understanding of ecosystem processes at the scale of landscapes. In: Oxley, L.; Scrimgeour, F. and McAleer, M. (eds.): International Congress on Modelling and Simulation. Proceedings 3, 685–690.

Rochefort, R. M.; Little, R. L.; Woodward, A. and Peterson, D. L. (1994): Changes in sub-alpine tree distribution in western North America: a review of climatic and other causal factors. In: The Holocene 4, 89–100.

Rössler, O. and Löffler, J. (2007): Uncertainties of treeline alterations due to climatic change during the past century in the central Norwegian Scandes. In: Geoöko 28, 104–114.

Rupp, T. S.; Chapin, F. S. III and Starfield, A. M. (2000): Response of subarctic vegetation to transient climate change on the Seward Peninsula in north-west Alaska. In: Global Change Biology 6, 541–555.

Salmi, T.; Määttä, A.; Anttila, P.; Ruoho-Airola, T. and Amnell, T. (2002): Detecting trends of annual values of atmospheric pollutants by the Mann-Kendall test and Sen's slope estimates. The excel template application MAKESENS. Publication on Air Quality 31. Helsinki.

Schickhoff, U. (2005): The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and ecological aspects. In: Broll, G. and Keplin, B. (eds.): Mountain ecosystems: studies in treeline ecology. Berlin, 275–354.

Schweingruber, F. H. (1996): Tree-rings and environment. Dendroecology. Vienna.

Sen, P. K. (1968): Estimates of the regression coefficient based on Kendall's tau. In: Journal of the American Statistical Association 63, 1375–1389.

Sigmond, E.; Gustavson, M. and Roberts, D. (1984): Berggrunnskart over Norge. M. 1: 1.000.000. Trondheim.

Sygna, L. and O'Brien, K. (2001): Virkninger av klimaendringer i Norge. Cicero Report 1. Oslo.

Ter Braak, C. J. F. (1986): Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. In: Ecology 67, 1167–1179.

– (1994): Canonical community ordination. Part I: Basic theory and linear methods. In: Ecoscience 1, 127–140.

Ter Braak, C. J. F. and Šmilauer, P. (2002): CANOCO Reference Manual and CanoDraw for Windows User's Guide. Software for Canonical Community Ordination (Version 4.5). New York.

Theurillat, J.-P. and Guisan, A. (2001): Potential impact of climate change on vegetation in the European Alps: a review. In: Climatic Change 50, 77–109.

Tuhkanen, S. (1980): Climatic parameters and indices in plant geography. In: Acta Phytogeographica Suecica 67, 1–110.

Walther, G.-R.; Post, E.; Convey, P.; Menzel, A.; Parmesan, C.; Beebee, T. J. C.; Fromentin, J.-M.; Hoegh-Guldberg, O. and Bairlein, F. (2002): Ecological responses to recent climate change. In: Nature 416, 389–395.

Wardle, P. (1991): Vegetation of New Zealand, New York.

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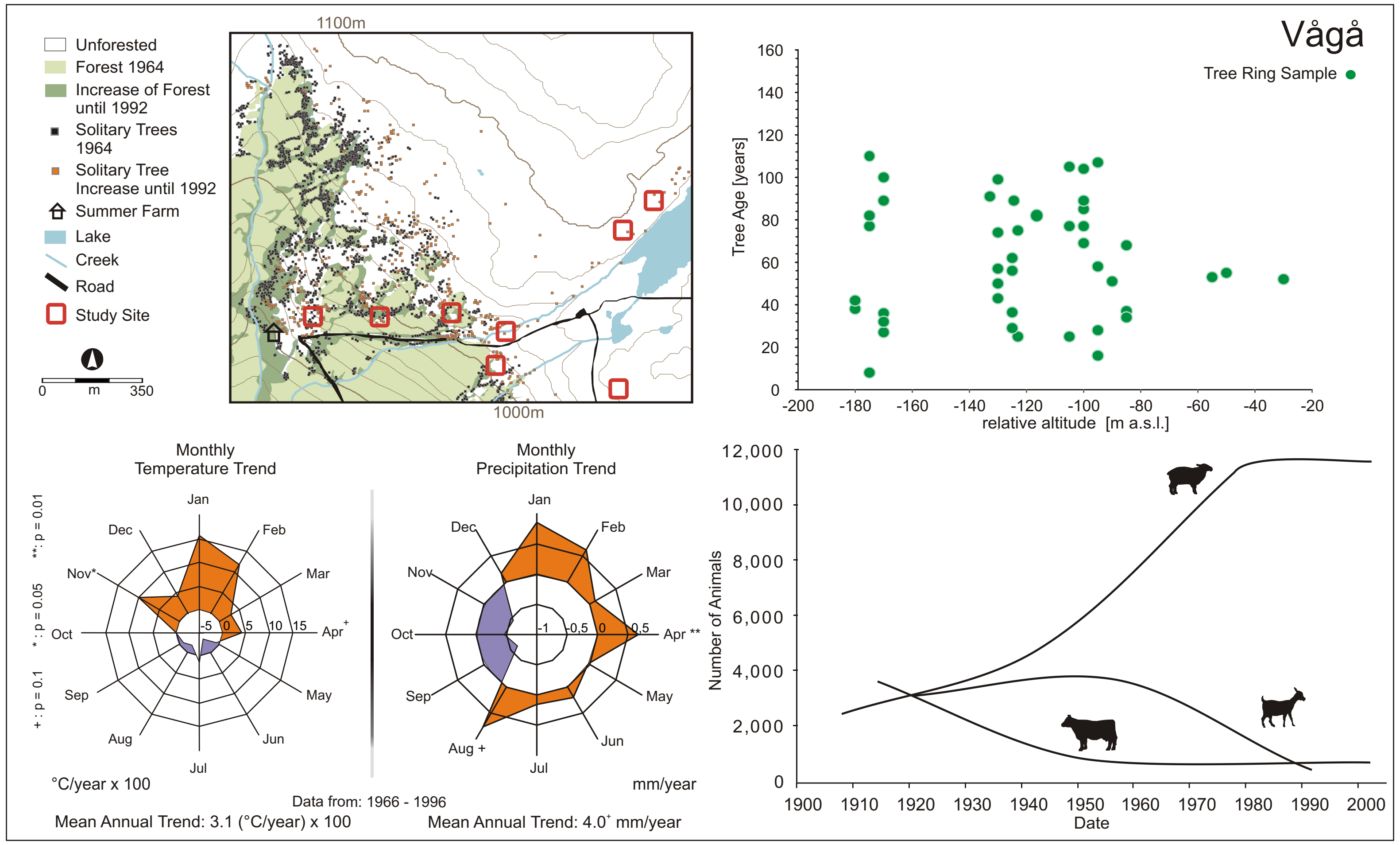

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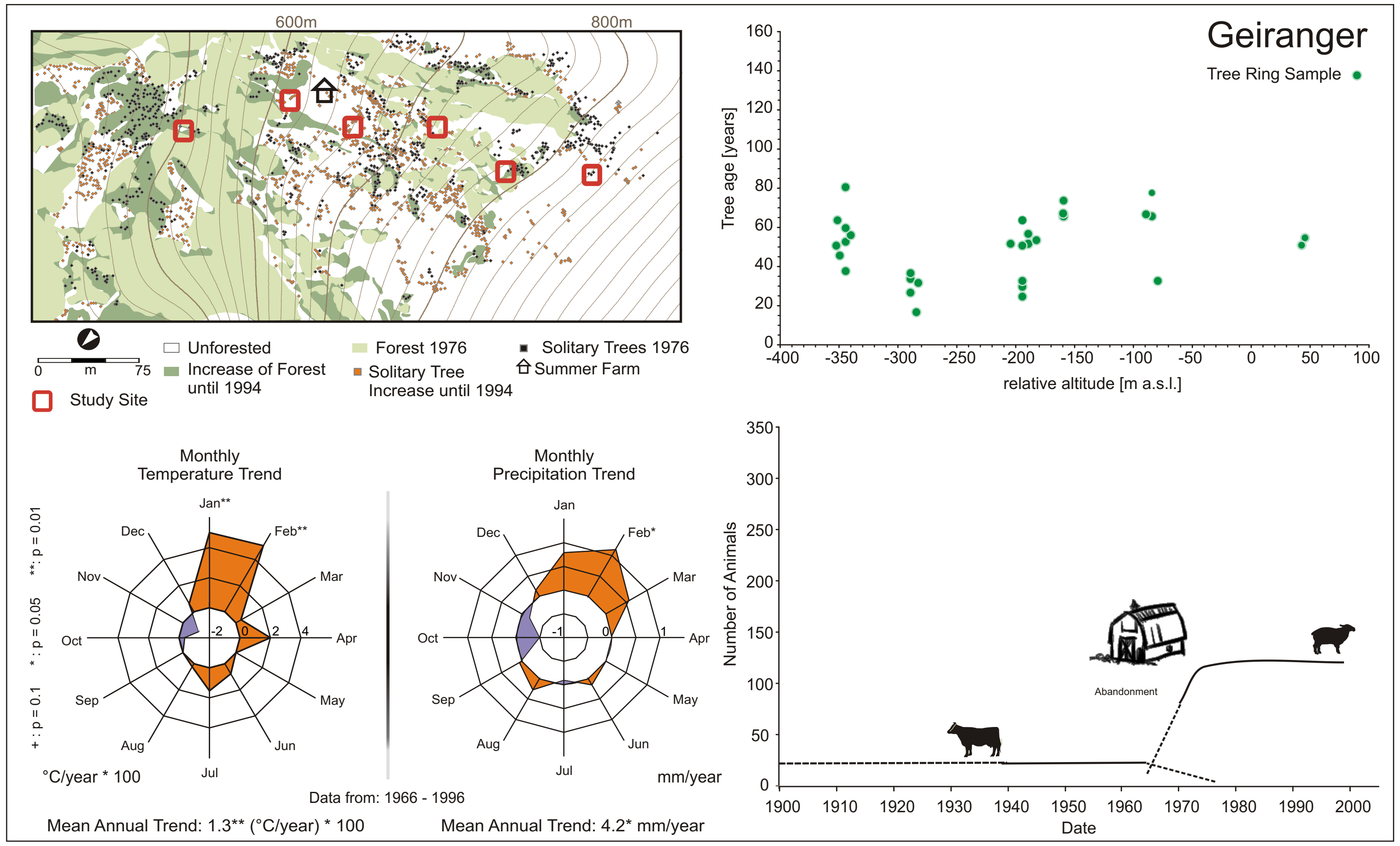

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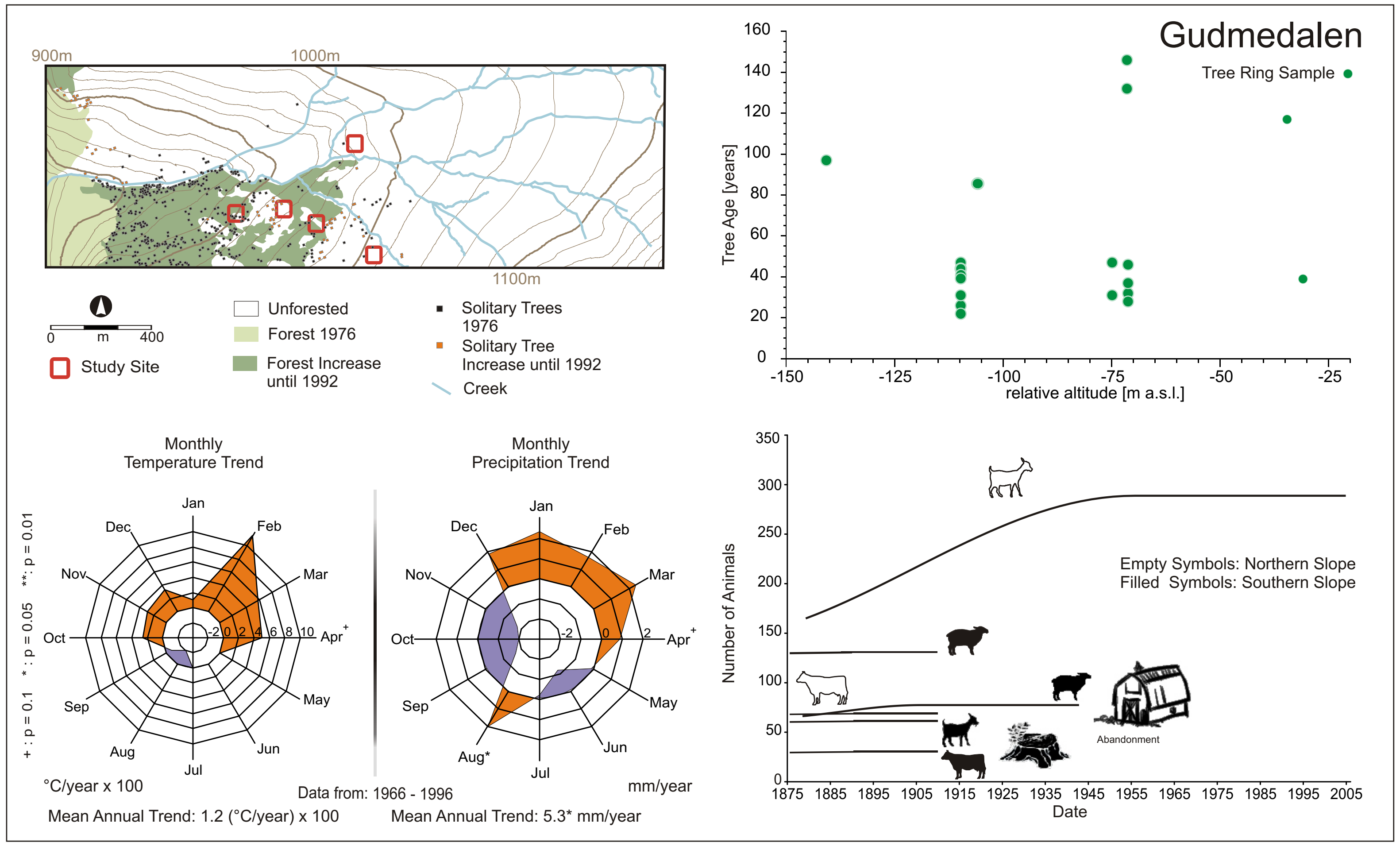

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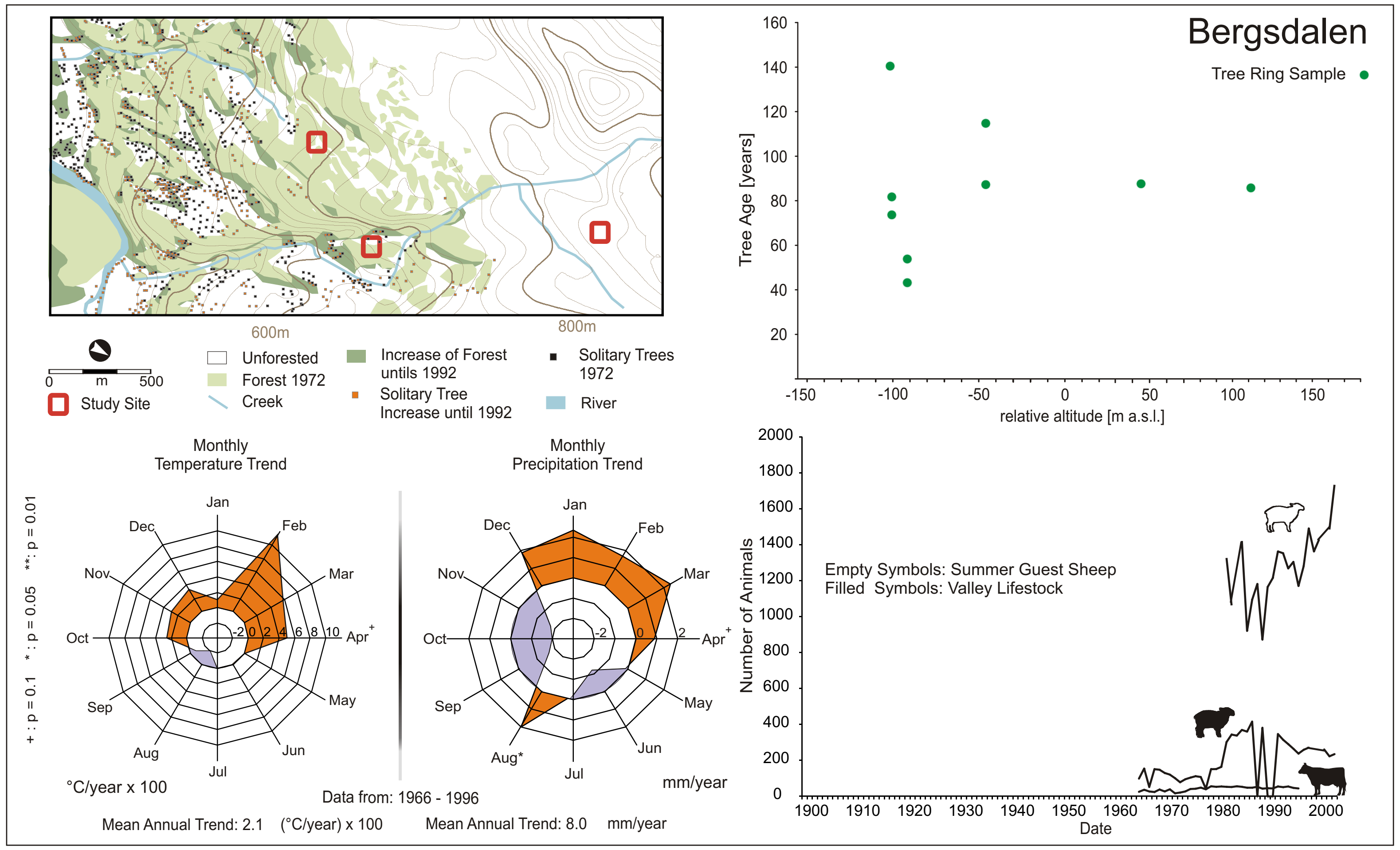

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