

Effect of latitude and mountain height on the timberline (*Betula pubescens* ssp. *czerpanovii*) elevation along the central Scandinavian mountain range

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Previously published isoline maps of Fennoscandian timberlines show that their highest elevations lie in the high mountain areas in central south Norway and from there the limits decrease in all directions. These maps are assumed to show differences in “climatic forest limits”, but the isoline patterns indicate that factors other than climate may be decisive in most of the areas. Possibly the effects of ‘massenerhebung’ and the “summit syndrome” may locally have major effects on the timberline elevation. The main aim of the present study is to quantify the effect of latitude and mountain height on the regional variation of mountain birch timberline elevation. The study is a statistical analysis of previous published data on the timberline elevation and nearby mountain height. Selection of the study sites has been stratified to the Scandinavian mountain range (the Scandes) from 58 to 71° N where the timberlines reach their highest elevations. The data indicates that only the high mountain massifs in S Norway and N Sweden are sufficiently high to allow birch forests to reach their potential elevations. Stepwise regression shows that latitude explains 70.9% while both latitude and mountain explain together 89.0% of the timberline variation. Where the mountains are low (approximately 1000 m higher than the measured local timberlines) effects of the summit syndrome will lower the timberline elevation substantially and climatically determined timberlines will probably not have been reached. This indicates that models of future timberlines and thereby the alpine area extent in a warmer world may result in unrealistic conclusions without taking account of local mountain heights.

Keywords: Scandinavia, forest limit, multiple regression, ecology, global warming, Massenerhebung

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Introduction

The Scandinavian mountain range (the Scandes) stretches from 58 to 71° N. Along its central part, mountain height is highly variable with peaks higher than 2100 m only in south central Norway (ca. 69° N) and in northern Sweden (ca. 79° N). Mountain height is particularly low in the southernmost and northernmost parts, but also relatively low in the central parts (63–64° N). Published isoline timberline (forest limit) maps show major vari-

ations, with elevation limits from a maximum higher than 1200 m to sea level (Moen 1999; Heikkinen 2005).

It is well known that in terms of temperature, latitude compensates for altitude, and timberline elevation decreases generally toward north. As a rule of thumb, one degree increase in latitude is roughly equal to a 122 m decrease in elevation, and to a 0.55 °C temperature decrease (Lee 1969; Montgomery 2006). Also vegetation zones are often projected northwards, parallel with the timber-

line decrease. When viewed globally, timberline elevation decreases with latitude (Wieser & Tausz 2007; Berdanier 2010), but there are considerable variations. As shown by Körner (2012), the latitudinal decrease is not monotonic, and the highest timberlines are found in Tibet (30° N) where the mountains are highest. Consequently, it is obvious that factors other than latitude influence the position of the timberlines (e.g. Daubenmire 1954; Gorchakovsky 1989). The actual measured timberlines can, however, be limited by numerous other environmental factors (Holtmeier 2003; Wieser & Tausz 2007) but if no other factors are critical, the timberline elevation is assumed to be a response to summer temperature which is then defined as the climatic timberline.

It has long been recognized that large mountain systems create their own surrounding climate, influencing both temperatures and general climate character (the degree of continentality). The effects of mountain height on climate and timberline elevation were originally described as the *Massenerhebungseffekt* (or mass elevation effect) from the Alps, but have now also been applied globally to explain timberline variations (e.g. Dolukhanov 1978; Holtmeier 2003). In general, the larger the mountain mass, the more its climate will vary from the free atmosphere at any given altitude. The effect of low mountain height on the timberline elevation has been described as the mountain syndrome, and several hundred metres of mountain terrain above the measured timberline have to be available for the development of climatic timberlines (Körner 2012). Mountains serve as elevated heat islands where solar radiation is absorbed and transformed into long-wave heat energy, resulting in much higher temperatures than those found at similar altitudes in the free air (e.g. Barry 2008). It has been shown that timberlines in the middle parts of the Alps where the mountains are highest lie several hundred metres higher than in the southern and northern parts where the mountains are lower. Effect on timberline elevation is, however, not well known in other areas.

The most comprehensive work on alpine timberlines in Norway was performed by Aas (1964). He used both his own measurements and previously published data to develop timberline isoline maps for the whole of Norway. His original, unpublished map has later been extended to include also the northernmost parts of Sweden and Finland, and different versions have later been published. All maps show the same trends, but the

degree of smoothing of the isolines has varied. The timberlines decrease toward north, west, south and east from their maximum elevation in the Jotunheimen mountain range, central south Norway. An average decreasing trend of the timberlines from the Alps to North Scandinavia has previously been estimated to be 75.6 m per degree increase in latitude (Odland 2010). The isoline maps show, however, major regional deviations from this latitudinal trend. The timberlines in northernmost Scandinavia are particularly interesting because here both the northern (arctic) and the alpine timberlines intermingle at sea level and here the limits have been used to separate the arctic, alpine, and boreal biomes.

It is essential that possible factors limiting local timberline elevation are assessed. For any plant to reach its potential geographic distribution, suitable growth sites must be available, which is a basic assumption in all studies of causal autecology. In Fennoscandia there are several topographic and edaphic factors that can restrict the elevation and latitudinal distribution of trees. The ecological interpretation of local timberline measurements can be difficult, and the measured timberline distribution limits have probably far too often been classified as 'climatic'. The climatic limits of tree growth will occur only if no other factors, such as substrate, orography or human impact, prevent tree growth from reaching their climatically determined altitudinal or latitudinal limits (Holtmeier & Broll 2005). According to Dahl (1998) and Körner (2012), mountains need a certain height for true climatic treelines to be formed, and treelines on low mountain ranges have probably nothing to do with the climatic timberline. On the other hand, mountain height also influences air temperatures (Barry 2008), and timberlines may therefore reach their climatic (temperature) limit at lower elevations on low mountains. The alpine biome is by definition defined as areas above the climatic timberline. Grabherr et al. (2003) maintain that relatively low mountains may also have a timberline (topographic timberline) but their treeless vegetation was described as pseudo-alpine. An essential question is then if the published isoline maps show the climatic timberlines in Fennoscandia or not. The effects of mountain height on the elevation distribution of timberlines are also essential when future effects of global warming are modelled.

Some studies in different parts of the world have quantified the effects of latitude and mountain height on timberline elevations. In south-eastern

Eurasia (north of 32° N), Han et al. (2012) found that latitude, longitude and mountain height explained 49, 24 and 27% respectively of the timberline variation, and Zhao et al. (2014) found that latitude, continentality and mountain height explained ca. 45, 6, and 49% respectively of the timberline elevation in the Northern Hemisphere. In the Appalachian mountain range, western North America, Leffler (1981) found that only a few summits in the northern parts were assumed to exhibit true, temperature-controlled alpine timberlines. In the southern parts, the actual timberlines were situated several hundred metres below the theoretically estimated climatic timberline.

The main aims of this study are to 1) quantify the relative importance of mountain height and latitude on the variation of timberline elevation along the central part of the Scandinavian mountain range; 2) discuss the results in relation to possible explanatory variables and other timberline studies; and 3) discuss the significance of the results in relation to models on effects of global warming in the future.

Study area and methods

The study is based on previously published data on the timberlines along a latitudinal gradient from southern Norway to northernmost Scandinavia, sampled before the possible impacts of recent climate change. The study area has been stratified to the central part of the Scandinavian mountain range where the mountains and forest limits reach their highest elevations. The selected timberline measurements (Fig. 1, Table 1) lie within the geographic area where the highest timberlines have been found as shown by the isoline areas drawn by Heikkinen (2005).

Aas (1964) defined the timberline as the elevation where the distance between trees taller than 2.5 m became larger than 30 m, and only forest stands that were assumed to represent climatic limits were included. In addition to measurements given in Aas (1964), available data from Sweden have been included; mainly Arwidsson (1943), Åberg (1952), Kilander (1955), and Kullman (1979). Altitudes of the nearest highest mountains are given for all study sites. If data on mountain heights were not given in the studies, the altitudes were obtained from topographic maps. The term timberline is here used instead of the term “forest limit” which has mostly been used in previous Scandinavian studies.

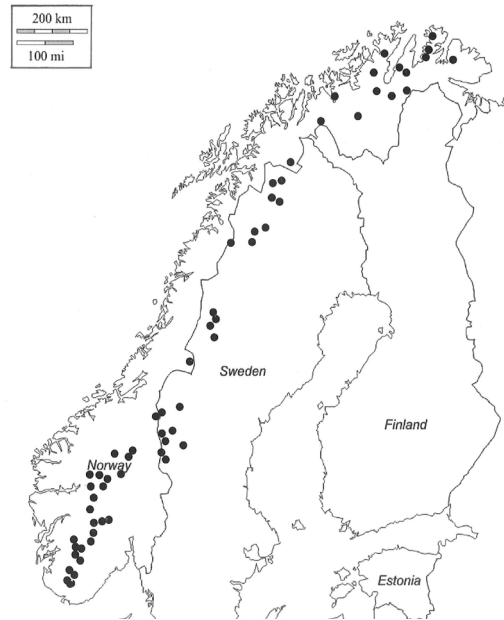


Fig. 1. Map showing the areas where data on timberlines and mountain heights were available.

West of the study area is a strong decrease in both mountain height, timberline elevation and a decrease in ‘continentality’ (e.g. Tuhkanen 1984; Moen 1999; Tikkanen 2005; Holten & Aune 2011). In the eastern parts, the mountains are mostly lower than 800 m (Corner 2005). As a quantification of continental versus maritime characteristics, the study can be allocated to different vegetation sections as defined by Moen (1999). Along the latitudinal gradient, the sites lie within three different sections: the slightly oceanic section (O1), the indifferent section (OC), and the slightly continental section (C1), and this stratification has excluded the most maritime parts from this data set.

Results

Variations in maximum timberline elevation and associated mountain heights from 58 to 71° N are shown in Figure 2 based on data shown in the Table 1. A linear trend line is drawn between the highest timberline elevations in S Norway and N Sweden

Table 1. Geographic location and measurements from the actual mountain areas (TE = timberline elevation, MH = mountain height, N = northing, E = easting, MH-TL = elevation difference between mountain height and timberline).

Mountain/Area	TE (m)	MH (m)	N	E	MH-TL	Mountain/Area	TE (m)	MH (m)	N	E	MH-TL	Mountain/Area	TE (m)	MH (m)	N	E	MH-TL
Lyngdal N	700	846	58.62	7.10	146	Selskampen	1223	1481	61.50	9.10	258	Stora söfallet	810	2001	67.28	18.25	1191
Knaben	754	971	58.70	6.99	217	Skogadalen	1210	2157	61.50	8.09	947	Ferras	740	1609	66.96	16.18	869
Åseral	810	1026	58.80	7.27	216	Tromfjell	996	1665	62.17	10.70	669	Tarrekajse	710	1800	67.03	17.37	1090
Ådneram	800	1198	58.99	6.99	398	Grimsdalen	1128	1511	62.05	9.47	383	Pårefjället	870	1700	67.20	17.58	830
Valle	1000	1161	59.21	7.59	161	Solnkleppen	1080	1827	62.00	10.29	747	Kebnekaise	800	2106	67.90	18.52	1306
Bykle	1095	1308	59.39	7.33	213	Nipfjället	920	1191	61.92	12.52	271	Tarfallatjället	800	1830	67.92	18.62	1030
Hovden	1030	1300	59.60	7.31	270	Sånfjället	905	1277	62.28	13.53	372	Nissonjärro	750	1804	68.25	18.90	1054
Haukelisæter	1070	1249	59.82	7.24	179	Jakobshøiden	925	1100	62.11	12.33	175	Pallemjället	750	1759	67.85	18.90	1009
Bjåen	1100	1303	59.62	7.58	203	Ormrøet	900	1100	62.58	12.58	200	Somaslakti	750	1744	68.23	18.70	994
Kalhovd	1110	1340	60.05	8.47	230	Brattriet	955	1121	62.43	12.37	166	Njunis	700	1717	68.60	19.50	1017
Mosvatn	1100	1431	59.76	8.27	331	Hamrafjället	975	1138	62.57	12.30	163	Raisduottarholti	600	1361	69.40	21.40	761
Vastulan	1116	1437	60.25	8.44	321	Helagsstøten	980	1796	62.54	12.28	816	Beskadas	500	649	69.50	23.50	149
Imingfjell	1135	1320	60.21	8.62	185	Anåfjället	1000	1332	62.60	12.75	332	Hållkavårri	375	1045	69.90	25.38	670
Tunhovd	1100	1314	60.34	8.92	214	Storsylen	920	1762	63.01	12.12	842	Beahcegeahaldi	580	1326	69.90	22.00	746
Geilo	1125	1859	60.59	8.10	734	Getryggen	830	1382	63.11	12.18	552	Stabbursdalen	400	1005	69.98	24.50	605
Hemsedal	1140	1399	60.88	8.38	259	Snasahøgane	800	1462	63.13	12.20	662	Råstiggåsa	330	1067	70.00	26.15	737
Flentspiken	1110	1239	60.37	9.17	129	Våstra bummersstøten	860	1554	63.07	12.30	694	Ralpesvarri	350	525	70.31	24.27	175
Visdalen	1117	1474	61.69	8.42	357	Gåsen	920	1462	63.21	13.28	542	Vieksa	250	369	70.37	25.83	119
Filefjell	1134	1780	61.20	8.16	646	Ottfjället	861	1265	63.21	13.28	404	Børselvfjellet	250	450	70.33	26.00	200
Bitrhorn	1100	1607	61.27	8.87	507	Gitesfjället	800	1062	64.87	15.25	262	Nordkinn	300	619	70.51	28.81	319
Gjendesheim	1170	1743	61.50	8.76	573	Marsfjällen	900	1564	65.13	15.12	664	Blåfjället	225	468	70.54	27.16	243
Gråhø	1130	1779	61.40	9.00	649	Sodra Gardfjället	800	1228	65.31	15.26	428	Gardevarri	200	633	70.61	24.93	433
Sikilsdalshe	1239	1778	61.50	8.90	539	Norra Gardfjället	800	1228	65.43	15.27	428	Nordkinn	200	338	70.67	27.33	138
Sikilsdalshorn	1281	1565	61.50	9.00	284	Jimjevaerie	900	1390	64.32	13.99	490	Nordkinn	100	269	70.96	27.60	169

(cf. Odland 2010). The Lowess smoother lines give trends in timberline elevation and mountain height along the latitudinal gradient. Figure 2 shows that there is not a monotonic timberline decrease from south to north, and in most of the mountain range the measured timberlines lie far below the linear trend line drawn between the highest mountains. The deviations are especially large in the southern and northern parts (cf. Fig. 1, Table 1).

The elevation of the highest mountains close to where the timberlines have been measured varies also strongly from south to north. The highest mountain massifs lie in central south Norway (Jotunheimen 61.5° N) with peaks up to 2469 m, and in north Sweden (Lule Lappmark ca. 67° N) with peaks up to 2012 m. In the central Scandes, the mountains are mostly lower than 1500 m, and in the northernmost areas the mountains rarely reach 500 m.

Relationship between the timberline elevation (TE in m), mountain height (MH in m) and latitude (L, ° N) was analysed by multiple linear regression with TE as the dependent variable. This gave the following equation (Eq. 1):

$$TE = 3710 + 0.315 * MH - 51.3 * L \quad (1)$$

where $n = 72$, $R^2 = 89.3$ and $p < 0.0001$. A stepwise regression showed that latitude explained 70.9% while both latitude and mountain height explained 89.0%.

Discussion

The present study area includes major variation in timberline elevation, and it is evident that latitude alone cannot explain this variation. A problem with the comparisons of timberline measurements from different sources may be associated with the vast number of forest- and tree limit definitions used both in Scandinavia and globally (e.g. Aas 1964; Holtmeier 2003; Walsh et al. 2003). One may, however, expect that 'errors' related to timberline measurement lie within the range of the treeline (tree limit) and the timberline (forest limit) i.e. within the timberline ecotone. Studies show that this difference is mostly smaller than 55 m (Kjällgren & Kullman 1998; Moen et al. 2004). Körner (2007) maintained that whoever looks for precision better than 50 m in elevation or 100 m on a slope, overlooks "the nature of the ecotone", and the debate becomes fruitless if greater precision is attempted. A 50 m difference in elevation corresponds to ca 0.3 °C difference in air temperature, which according to Körner (2007) is too small to permit meaningful biological interpretations.

The central parts of the Scandes include areas where the influence of a maritime climate upon mean air temperatures is relatively low (mostly less than 5 °C according to Tikkanen 2005), except in the northernmost coastal parts. The study areas lie

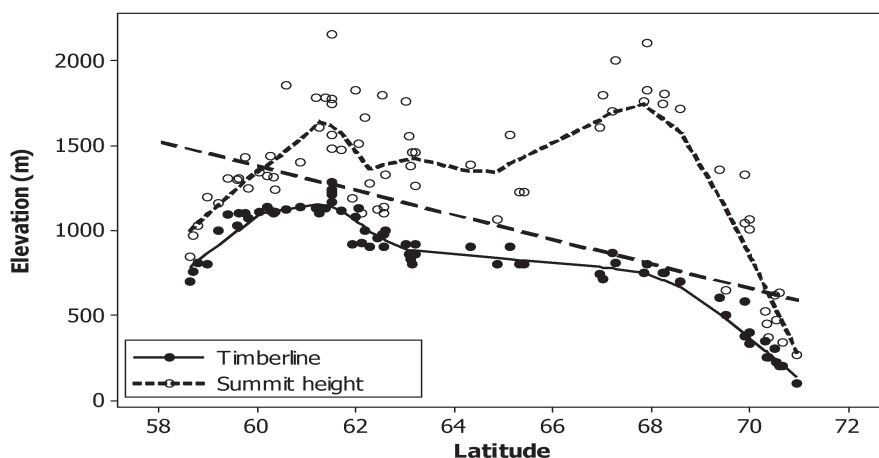


Fig. 2. Variation in measured forest limits and maximum mountain height from south to north Scandinavia with Lowess smoothers. A potential maximum timberline is drawn between the highest mountain areas in S Norway and N Sweden (cf. Odland 2010).

Table 2. Measured latitudinal timberline decreases in different study areas. Rate of elevational decrease is given in m latitude⁻¹.

Area and latitudinal span (° N)	Rate	Reference
N Europe, 46.5–61.5° N	75.6	Odland (2010)
Northern Asia	70–90	Malyshev (1993)
Northern Appalachian, USA, 44–55° N	83	Cogbill & White (1991)
Forest zone, N America, 49–57° N	75	Klinka et al. (1996)
N Canada, 55–60° N	60–65	Payette et al. (2001)
Central Sweden 62–68.5° N	75	Kullman & Hofgaard (1987)
Eastern Ural, 59–68° N	100	Shahgedanova et al. (2002)
Western Ural, 59–67° N	88	Shahgedanova et al. (2002)
N America, 35–70° N	110	Daubenmire (1954)
Appalachian, USA, 31–55° N	121	Leffler (1981)

mostly between the slightly oceanic and slightly continental vegetation sections according to Moen (1999). This indicates that the effect of a maritime climate on the actual timberlines is strongly reduced, but in some regions there may be an effect (cf. Kjällgren & Kullman 1998; Öberg & Kullman 2012). Effects of human influence were also reduced during timberline measurements (Aas 1964). Accordingly, most of the variation in timberline elevation may be assumed to reflect the effects of latitude (temperature) and mountain height. As a parallel, the explanatory effect of continentality was by Zhao et al. (2014) estimated to be 6% based on data from the whole Northern Hemisphere.

Effects of latitude and mountain height

The study shows that latitude explained approximately 71% of the timberline variation, but also mountain height contributed significantly with an explanatory rate of nearly 20%. The potential timberline drawn between areas (from 46.5 to 68.6° N) assumed to be high enough for trees to reach their potential climatic elevation, decreased approximately by 76 m latitude⁻¹ (Odland 2010). This result is surprisingly similar to trends found in other studies in the northern hemisphere (Table 2). Data sampled in 10 areas north of 45° N (Table 2) show an average decrease of 78 ± 10 m latitude⁻¹. This indicates that if the mountains were sufficiently high all along the studied latitudinal gradient,

the timberlines should follow a linear decreasing trend. Major deviations from this trend are particularly found in the southernmost and northernmost parts of the Scandes. In areas where the timberlines are highest, the mountains are 900–1300 m higher than the timberline, and where they are lower than the trend, the mountains are less than 600 m higher (cf. Table 1).

Also in some previous studies the effect of low mountain height on the timberline elevation has been shown, e.g. Perttu (1972), Leffler (1981), Han et al. (2012), and Zhao et al. (2014). A study of the maximum elevation limits of vascular plants in some Central Scandinavian mountains indicated that mountain heights were 200–600 m too low to allow vascular plants to reach their potential elevation (Odland 2010). Körner (2012) gives an example of the mountain syndrome from the Vosges mountains (France) where the actual timberline lay between 1300–1500 m, which was estimated to be 300–500 m below the expected climatic timberline. Leffler (1981) measured latitudinal variation in timberlines along the Appalachian Mountains, eastern USA. In the southern parts of this mountain range, the estimated climatic limit was assumed to lie some 1000 m above the actual measured timberline.

The present study therefore indicates that mountain height has a conclusive effect on the timberline elevation and that the Scandinavian mountains, with few exceptions, are too low to allow forests to reach their potential climatic limit.

Effects of climate

Previous studies have shown that there are significant linear decreases in air temperatures along the latitudinal gradient in the Northern Hemisphere (Table 3). It is generally assumed that the climatic timberlines are associated with a minimum heat requirement for tree growth for which the mean 10 °C July isotherm has frequently been used as proxy (e.g. Holtmeier 2003; Wieser & Tausz 2007). Studies have, however, found values varying between 9 and 12 °C (cf. Odland 1996; Körner 1998, 2003; MacDonald et al. 2008). Jobbagy and Jackson (2000) found that thermal variables explained 79% of the global variability of timberline.

Regional deviations from the 10 °C isotherm have often been related to the degree of continentality (Zhao et al. 2014). In maritime areas the mean July temperature at the timberlines lie mostly higher than in continental areas, and in Scandinavia the timberlines are strongly correlated with distance to the coast (e.g. Odland 1996; Kjällgren & Kullman 1998; Holten & Aune 2011). A major problem with this relationship is that both the degree of continentality and the general mountain height decrease toward coastal areas. In a regional study from Central Scandinavia (62° 25' N- 63° 20' N), Kjällgren and Kullman (1998) found that

latitude explained 66% and distance to the sea explained 52% of the timberline elevation. Also other climatic variables have been used to explain the timberlines, especially soil temperatures (Körner & Paulsen 2004), wind, and snow load (Autio & Colpaert 2005; Vajda et al. 2006).

The strong regional deviation in timberline elevation along the latitudinal gradient (Fig. 2) compared to the general linear decreasing temperature variables (Table 3) indicates that the studied timberlines in most parts of Fennoscandia should be described as 'observed' and not climatic. Only in the south central Norway and north Sweden are the mountains high enough to allow the forests to reach their potential climatic elevation limits.

The effect of mountain height (mass elevation effect) on both the timberline elevation and air temperatures have recently been demonstrated by Yao and Zhang (2014) from the Tibetan Plateau. They showed that the mass elevation effect of the central high mountain areas pushed the 10 °C isotherm upward in the warmest month up to elevations of 4600–4700 m, which enabled the treeline altitude to be situated 500–1000 m higher than along the eastern edge where the mountains reached only 1000 m a.s.l. This effect therefore contributes to the occurrence of the highest treeline in the Northern Hemisphere, which in the most favourable sites reached nearly 4900 m. At an elevation of 4500 m,

Table 3. Rate of change in average temperatures (°C) for each degree increase in latitude (MAAT = mean annual air temperature, MJuly = mean July temperature).

Variable	Rate	Area	Reference
MAAT	-0.49	Fennoscandia	Laaksonen (1976)
MAAT	-0.73	Northern extratropical hemisphere	De Frenne et al. (2013)
MAAT	-0.75	European alpine zone	Nagy & Grabherr (2009)
MAAT	-0.97	Northern Appalachian, USA, 44–55° N	Cogbill & White (1991)
MAAT	-0.72	North America, 40–60° N	Montgomery (2006)
MAAT	-0.57	W Europe, 42–62° N	Diaz & Bradley (1997)
MAAT	-0.25	North America and Greenland, 40–60° N	Montgomery (2006)
MJuly	-0.53	Northern Appalachian, USA, 44–55° N	Cogbill & White (1991)
MJuly	-0.37	Nordic countries	Tveito et al. (2000)
MJuly	-0.48	Northern extra-tropical hemisphere	De Frenne et al. (2013)

the monthly mean temperature differences between the high mountain area and the low mountain areas ranged from 1.6 °C (July) to 7.7 °C (March).

Implications for future effects of climate change

The strong effect of mountain height on the timberline elevation may also have major implication for evaluations of the possible effects of global warming. If a mountain height is low, an increase in temperature may result in no or small timberline uplift. Studies on the elevation changes of timberlines during the last decades have not been unambiguous despite the fact that the temperatures have increased, and there are different opinions also about the future effects of climate change. Timberline advance does not appear to be a worldwide phenomenon (Holtmeier & Broll 2007). A global study showed that only 52% of all 166 global tree line sites had advanced over the past 100 years despite documented amplified climate warming in high-elevation areas and northern latitudes (Harsch et al. 2009).

In Fennoscandia, temperatures have increased by 1–2 °C during the last decades. Estimated by temperatures only, nearly 300 m increases in timberline could be expected since the 1960s.

Recent studies have, however, found relatively low uplift rates. In an area with relatively low mountains (Hardangervidda, S Norway, e.g. Odland 2010), Rannow (2013) found a mean upslope migration of only 2.3 ± 1.6 m between 1965 and 2004 even though the temperatures had increased during this period. Similarly, Van Bogaert et al. (2011) found that the tree line in the Abisko area, N Sweden, had shifted only 24 m since 1912. Kullman (2010) maintained that it is unlikely that projected future climate warming would substantially threaten the continued existence of an extensive alpine zone in the Scandes because local topoclimatic constraints commonly prevent timberlines from obtaining their potential thermal limits.

Some recent studies emphasize that geomorphic and topographic factors may control the upward timberline shift more than the climatic input in the future, and so the use of climate models to predict the timberline uplift should take such factors into account (Autio & Colpaert 2005; Virtanen et al. 2010; Leonelli et al. 2011; Macias-Fauria & Johnson 2013). Donato (2013) suggested also that upward timberline shifts in a warming climate may

be heavily constrained by geologic factors that influence the availability of growing substrates at high elevations, leading to much less, or at least much slower, tree colonization into alpine areas than predicted by climate alone.

By a simple extrapolation of the relation between present climate and present plant distribution, an estimated 3–4 °C increase in mean annual temperature has been suggested to result in an uplift of 500–1000 m or a 300–400 km shift in latitude of the timberlines (Grace et al. 2002).

Similarly, Moen et al. (2004) estimated, on the basis of the modelled temperature increase and the general adiabatic temperature lapse rate, a forest uplift of several hundred metres and thereby projected a threat to the persistence of an extensive alpine zone in Scandinavia. According to Öberg and Kullman (2012) this is a quite unrealistic output. They found a treeline uplift of 3.0 m yr^{-1} in the maritime parts of the southern Swedish Scandes differed significantly from a retreat by 0.4 m yr^{-1} in the continental part. Palaeoecological studies also indicate that the upslope migration of treelines during the Holocene warm periods was much smaller than the estimated temperature increases would suggest (Paulsen et al. 2000). According to Öberg and Kullman (2011) as well as Kullman (2012) it is, however, documented that most of the mountains in the continental area have supported tree and forest growth virtually up to the highest peaks during periods with more favorable climates. It is therefore obvious, as maintained by Scheffer et al. (2012), that the way boreal forests respond to global warming is still poorly understood. Effects of mountain height appear to be very important, but also other factors such as differences in available substrate, historic and present cultural impacts, degree of a maritime influence, and effects of diverging timberline definitions should be considered.

Conclusions

The geographic variation of timberline elevation along the central mountain range of Scandinavia was mainly explained by latitude (71%) but it was also significantly influenced by the nearest mountain height, and together these factors explained 89% of the variation. In most parts of the Scandes, the mountains are assumed to be far too low to allow trees to reach their climatic limit. This is particularly evident in the northernmost and south-

ernmost parts where the mountain heights are low. The observed timberlines may be situated several hundred metres below the potential climatic timberline drawn between the highest mountain ranges in the Scandes, and the published timberline isoline maps from Fennoscandia therefore probably show mostly actual local timberlines and not the climatic distribution limits. Most recent timberline studies in Fennoscandia have found low uplift rates despite the fact that temperatures have increased by 1–2 °C during the last decades. One reason for this may be a consequence of low mountain heights. Modelling of future timberlines in a warmer world without taking account of the actual mountain heights may therefore result in unrealistic conclusions.

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