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In: *Journal of Biogeography*, 38 (5), 907-921, 2011.

doi: 10.1111/j.1365-2699.2010.02453.x

To refer to or to cite this work, please use the citation to the published version:

Van Bogaert, R.; Haneca, K.; Hoogesteger, J.; Jonasson, C.; De Dapper, M.; Callaghan, T.V. (2011). A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography* 38 (5), 907-921. doi: 10.1111/j.1365-2699.2010.02453.x

A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming

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Running head: Twentieth century tree line changes in Swedish sub-Arctic

1 **Abstract**

2 Models project that climate warming will cause the treeline to move to higher
3 elevations in alpine areas and more northerly latitudes in Arctic environments. We
4 aimed to document changes or stability of the treeline in a sub-Arctic model area at
5 different temporal and spatial scales, and particularly to clarify the ambiguity that
6 currently exists about treeline dynamics and their causes. The study was conducted in
7 the Torneträsk area in northern Sweden where climate warmed by 2.5 °C between
8 1913 and 2006. Mountain birch (*Betula pubescens* ssp. *czerepanovii*) sets the alpine
9 treeline. We used repeat photography, dendrochronological analysis, field
10 observations along elevational transects and historical documents to study treeline
11 dynamics. Since 1912, only four out of eight treeline sites had advanced: on average
12 the treeline had shifted 24 m upslope (+0.2 m year⁻¹ assuming linear shifts).
13 Maximum treeline advance was +145 m (+1.5 m year⁻¹ in elevation and +2.7 m year⁻¹
14 in actual distance), whereas maximum retreat was 120 m downslope. Counter-
15 intuitively, treeline advance was most pronounced during the cooler late 1960s and
16 1970s. Tree establishment and treeline advance were significantly correlated with
17 periods of low reindeer (*Rangifer tarandus*) population numbers. A decreased
18 anthropozoogenic impact since the early 20th century was found to be the main factor
19 shaping the current treeline ecotone and its dynamics. In addition, episodic
20 disturbances by moth outbreaks and geomorphological processes resulted in descent
21 and long-term stability of the treeline position, respectively. In contrast to what is
22 generally stated in the literature, this study shows that in a period of climate warming,
23 disturbance may not only determine when treeline advance will occur but if treeline
24 advance will occur at all. In the case of non-climatic climax treelines, such as those in
25 our study area, both climate-driven model projections of future treeline positions and

26 the use of the treeline position for bioclimatic monitoring should be used with caution.

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29 Key words: climate warming, dendrochronology, herbivory, human impact, mountain

30 birch, reindeer, sub-Arctic, Sweden, tree line, tree line causes

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47 **Introduction**

48 Mean annual temperatures have risen globally over the past century, with the most
49 pronounced and rapid changes at high elevations and latitudes (ACIA, 2005). As the
50 location of elevational and polar treelines is mainly caused by heat deficiency, in the
51 Northern Hemisphere climate warming is expected to cause treelines to advance to
52 higher elevations and more northerly latitudes (Harsch et al., 2009). Indeed, modern
53 evidence for such relocations exists and these have been explicitly or implicitly
54 related to recent climate warming (Shiyatov et al., 2007; Kullman and Öberg, 2009).
55 However, in many circumpolar and high-elevational areas the position of the treeline
56 has not changed (Masek, 2001; Holtmeier et al., 2003; Payette, 2007; Van Bogaert et
57 al., 2007) or has even retreated (Vlassova, 2002; Dalen and Hofgaard, 2005; Kullman,
58 2005; Cherosov et al., 2010).

59 Treeline heterogeneity increases from global to regional, to landscape and to local
60 scales of analysis (Callaghan et al., 2002). Moreover, the factors controlling the
61 position and structure of the treeline are highly scale-dependent and vary from place
62 to place (Sveinbjörnsson et al., 2002). Individual trees and the forest system may
63 respond differently to change; warming may increase tree growth, while at the same
64 time seedling survival may be reduced because of water stress brought about by
65 greater evapotranspiration and drying of the uppermost soil. Furthermore, the time-
66 scale of a study influences outcomes because it determines the processes and
67 responses that can be studied. There are short-term responses (defined as a year or
68 less and reflected in individual tree growth), medium-term responses (some years to a
69 few decades and reflected in changing survival rates of seedlings and altered tree
70 physiognomy) and long-term responses (several decades to centuries and reflected in
71 a general treeline advance or retreat) (Holtmeier and Broll, 2005).

72 Both experimental and field studies have shown that climate warming might not be
73 the only mechanism leading to recently observed northward and upward movement of
74 vegetation. Changes in disturbance regimes (Holtmeier and Broll, 2010), land use
75 (Hofgaard, 1997), plant–plant interactions (Van Bogaert et al., 2009) and herbivory
76 (Hoogesteger and Karlsson, 1992; Speed et al., 2010; Van Bogaert et al., 2010) may
77 easily override the effect of increasing mean annual temperatures.

78 On a global scale, heat deficiency may be the dominant factor controlling treeline
79 dynamics, but regional studies have shown that treeline position rarely changes in
80 parallel with the shift of any isotherm (Holtmeier and Broll, 2007). At present, one of
81 the most important gaps and uncertainties in treeline research appears on intermediate
82 (10–10,000 km²) spatial scales (Holtmeier and Broll, 2007; Kullman and Öberg,
83 2009) at which feedbacks to the climate system are significant (Harding et al., 2002),
84 yet studies on the causes of treeline dynamics that also consider site history are very
85 rare (Payette et al., 2002).

86 The main goal of this paper was to identify and explain recent changes in the
87 position and structure of this vegetation boundary. By confronting long-term climatic
88 and environmental records with new dendrochronological measurements, field
89 observations and analysis of repeat photography, we expected to provide new insights
90 into the driving forces behind current treeline dynamics in northern regions. We
91 focused on a Swedish sub-Arctic study area for which multiple previous treeline
92 studies exist. However, these studies presented contradictory results in terms of both
93 the directions and causes of treeline shifts (Table 1). Furthermore, the suggested
94 causal mechanisms behind reported treeline shifts were not supported by convincing
95 evidence. This study differs from previous ones by providing ample evidence of
96 recent treeline dynamics and their causal mechanisms. Here, we focused on different

97 spatial scales, ranging from an individual mountain (*c.* 20 km²) to an entire landscape
98 area (*c.* 1000 km²), and different temporal scales, ranging from a 30-year to a 100-
99 year time period.

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122 **Material and methods**

123

124 *Study area*

125 The Torneträsk area is located at the eastern fringe of the Scandes Mountains in
126 sub-Arctic Sweden (68°25' N, 19°00' E) (Fig. 1). The mean annual temperature for
127 Abisko (388 m a.s.l.), located at the south-western end of Lake Torneträsk (Fig. 1), is
128 -1.0 °C and mean annual precipitation amounts to 310 mm for the normal period
129 1961–90 (Alexandersson et al., 1991). However, climate has recently changed: mean
130 annual temperature and precipitation increased from -1.2 °C and 301 mm,
131 respectively, during the first instrumental decade (1913–22) to +0.6 °C and 342 mm
132 for the 10-year period 2000–09 (Abisko Scientific Research Station meteorological
133 records 1913–2009). Moreover, statistically smoothed trends showed a 2.5 °C
134 increase in temperature over the period 1913–2006 (Callaghan et al., 2010). Lake
135 Torneträsk is surrounded by 1200 km² of subalpine forests dominated by mountain
136 birch (*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti), the species
137 that sets the treeline in Fennoscandia. The position of the alpine treeline varies around
138 700 m a.s.l. (Dalen and Hofgaard, 2005). Local variability in precipitation,
139 topography, geology and land-use history is substantial (Hofgaard, 1999). Polycormic
140 (multi-stemmed) types of birch forest are found in dry areas with poor soils, whereas
141 monocormic (single-stemmed) birch forests can be found in areas with a deeper snow
142 cover and a more calcareous soil (Sonesson and Hoogesteger, 1983). The dominant
143 agents of disturbance to the birch forest are the more or less cyclic pest outbreaks of
144 the autumnal moth (*Epirrita autumnata* Bkh.) and the winter moth (*Operophtera*
145 *brumata* L.) (Tenow, 1972). At the treeline, disturbance by reindeer (*Rangifer*
146 *tarandus* L.) may be significant (Cairns and Moen, 2004).

147

148 *Definitions and approach*

149 In the present paper the term ‘treeline’ refers to the transition zone extending from
150 the upper limit of the closed subalpine forest to the uppermost birch individual. In
151 repeat photography analysis, we used the lower boundary of this ecotone as a main
152 reference as it is more distinct than the upper boundary. This boundary was set to 30%
153 tree-cover in a convention used by most other treeline studies (Rees et al., 2002).
154 Time series of photographs were scanned at identical resolution, so that individual
155 pixels could be compared. A pixel was classified as forested or non-forested. The
156 30% tree-cover isoline was statistically plotted using ARCGIS SPATIAL ANALYST 9.2
157 (ESRI, Redlands, CA, USA) (Fig. 2).

158 The boundary line was visited *in situ* at locations where the 30% tree-cover isoline
159 crossed an easily identifiable landmark such as a big boulder (Fig. 2). Field
160 measurements showed that the individual trees at the treeline detectable on the
161 photographs had a mean canopy size of 3.5 m diameter, implying that a 30% tree-
162 cover corresponded to a distance interval of 2.2 m in any direction between the
163 canopy boundaries of different individuals trees. In the field we could now delimit
164 both the upper and lower boundary of the treeline ecotone. Note that the outcome of
165 this study did not depend on the definition setting. A 10% tree-cover analysis (7.0 m
166 between different tree canopy boundaries) produced similar results.

167

168 *Repeat photographic analysis*

169 Seven ground photographs taken between 1912 and 1952 from different mountain
170 slopes in the Torneträsk area were successfully repeated (Fig. 1). Prominent
171 landmarks were found in the direct vicinity of the historical treeline (Fig. 2). The

172 actual shift in elevational position of the treeline could then be estimated by
173 comparing the old and recent photographs and by recording the elevational difference
174 between the landmark and the present treeline position with a calibrated aneroid
175 altimeter in the field.

176 Furthermore, repeat aerial photographs from the period 1959–2000 were studied to
177 quantify recent elevational shifts in the boundaries of the treeline ecotone of Mount
178 Nuolja (M_{S3} in Fig. 1). The images were scanned at 1600 dots per inch (d.p.i.)
179 implying a resolution of 0.3 m and were then georeferenced and rectified in the
180 program ORBIT GIS 4.4 (Eurotronics, 2009, Lokeren, Belgium). Maximal geometric
181 distortion between the two photographs amounted to 5 m. To study the driving forces
182 behind treeline dynamics, we looked for contrasting results from the analyses of the
183 aerial photographs. Two areas were selected for further analysis in the field: (1) an
184 area on the east slope of Mount Nuolja characterized by a significant upslope shift of
185 the treeline, and (2) an area on the south slope with no significant change in the
186 position of the treeline.

187

188 *Repeat transect analysis and field measurements*

189 To study the causal mechanisms and timing of treeline advance, tree sampling and
190 field measurements were carried out at five sites in the wider Torneträsk area in 2006.
191 We sampled treeline individuals at the two contrasting sites of Mount Nuolja and at
192 the three Sonesson and Hoogesteger transect sites N1, N2 and S1 (Fig. 1). In 1977,
193 these transect sites were randomly selected in treeline areas that differed in climate
194 (dry versus wet), soil (calcareous rich versus poor) and tree growth form (mono-
195 versus polycormic birch forest) (Sonesson and Hoogesteger, 1983). In 2006, we
196 established nine transects through the birch forest: three at sites N1, N2 and S1

197 corresponding to the original transects of Sonesson and Hoogesteger, and six on
198 Mount Nuolja (three on the east and three on the south slope). The Sonesson and
199 Hoogesteger transects were *c.* 1200 m long and crossed several contours running from
200 the lake level (341 m a.s.l.) up to the alpine area (*c.* 700 m a.s.l.). At the upper end of
201 these transects, 40 treeline birches were randomly sampled over a width of 500 m. For
202 Mount Nuolja, a transect set-up of higher resolution was designed to identify the
203 causes of the contrasting treeline dynamics that were found by repeat photographic
204 analysis. The transects were 200 m long and ran along different contours equally
205 spread over the treeline ecotone (see Appendix 1). All six transects contained seven
206 plots measuring 10 x 10 m, in which all birch individuals were sampled. The birches
207 were cut off at the root collar (individuals <2 m) or cored as low as possible
208 (individuals >2 m) with an increment corer according standard methods (Fritts, 1976).
209 Twenty-five monocormic erect birch individuals were cored 40 m downslope of all
210 five treeline sites to serve as a reference for the treeline samples. However, because
211 ring growth of these reference individuals may also have been affected by ubiquitous
212 moth herbivory, 30 non-browsed pine (*Pinus sylvestris* L.) individuals were sampled
213 in the Abisko area to construct a birch-minus-pine ring-width chronology that serves
214 as a reference for moth herbivory on birch (Eckstein et al., 1991; Van Bogaert et al.,
215 2009). (For more methodological detail, see Van Bogaert et al., 2009.)

216 To study the mechanisms behind treeline shifts, the following variables were
217 recorded for all sampled birch individuals: tree height, stem diameter at breast height
218 (130 cm; DBH), growth form (mono- or polycormic), herbivory damage, elevation (m
219 a.s.l.), inclination, aspect and snow depth. Herbivory damage was classified visually
220 as browsed or not browsed, but also statistically by constructing a birch-minus-pine
221 ring-width chronology and anatomically by studying features of wood anatomy

222 (Appendix 2). The mean height limit of the epiphytic lichen *Melanelia olivacea* (L.)
223 Essl. on adult birch stems was used as a proxy for mean snow depth (Sonesson et al.,
224 1994). All measurements and dendrochronological analyses have been made with
225 identical methods applied in the original study by Sonesson and Hoogesteger (1983)
226 and with field assistance by one of the original researchers.

227 Altogether, we studied changes in the elevational position of the treeline ecotone
228 for 10 sites spread over the Torneträsk area (Mount Nuolja M_{S3} had two sites; Fig. 1).
229 In total, 678 tree cores and 188 stem discs of mountain birch and 30 tree cores of pine
230 were analysed to study site history. (For a detailed description of the
231 dendrochronological analysis, see Appendix 2.) The samples were also used to cross-
232 reference with the estimated treeline dynamics that we obtained from repeat
233 photography and repeat transect analysis.

234

235 *Analysis of tree establishment*

236 The year of tree (>2 m) establishment was determined by exact tree-ring dating of
237 the innermost growth ring surrounding the pith. However, the year of establishment is
238 hard to determine when the individual is not cored at the stem–root intersection or the
239 pith is not perfectly hit. Therefore, estimated establishment data were derived from
240 the tree cores after grouping them into 10-year age classes. Tree cores of treeline
241 birches with rotten pith (13%) or with a substantial number of rings missing due to
242 failure to hit the pith (22%) were omitted from this analysis. An annual recruitment
243 analysis was made for the saplings (<2 m) that were cut off at the root collar ($n = 188$)
244 to allow for a more accurate determination of the year of establishment. The presumed
245 annual number of birch recruits was correlated with climatic and biotic factors using
246 Spearman's rank correlation coefficients (r_s).

247

248 *Historical anthropozoogenic impact*

249 Emanuelsson (1987) produced a map with the locations of the traditional reindeer
250 migration routes and the reindeer herder camps near the treeline (Appendix 3). These
251 points of relatively intense previous human impact were located in the field and
252 distances to our study sites were recorded by a GARMIN GPSMAP60CSX device.

253

254 *Long-term records as validation*

255 The Torneträsk area has an exceptionally long-term record of climatic and other
256 environmental data offering a powerful instrument for validation of measurements
257 (Callaghan et al., 2010). Daily temperature and precipitation measurements are
258 available since 1913 (Callaghan et al., 2010), human impact has been described in
259 detail since 1600 (Emanuelsson, 1987), reindeer population numbers since 1750
260 (Emanuelsson, 1987) and moth outbreaks on birch have been reported since 1862
261 (Tenow, 1972).

262

263 *Statistical analyses*

264 Regression analyses with forward selection were used to test which of the
265 environmental and anthropogenic variables best explained the elevational shifts of the
266 treeline ecotone. The sign of relationships and relative importance of the variables
267 that corresponded to elevational shifts in the treeline position were studied using
268 Pearson correlation coefficients. For further information on the technical details of the
269 correlation of treeline dynamics and compass direction see Dalen and Hofgaard
270 (2005). All statistical analyses were conducted in the program SPSS v. 15.0 (SPSS
271 INC., 2006, Chicago, IL, USA).

272 **Results**

273

274 *Treeline dynamics*

275 At the scale of an individual mountain, analysis of repeat aerial photographs of
276 Mount Nuolja for the period 1959–2000 showed that the upper limit of the closed
277 forest, representing the lower boundary of the treeline ecotone, had increased in
278 elevation by 25 m (rate of +0.6 m year⁻¹ assuming linear advances). However, site
279 variability was high: on the eastfacing slope an area was found where this boundary
280 had increased in elevation by 45 m (+1.1 m year⁻¹) as a result of a dramatic
281 densification of the uppermost tree patches (Fig. 3). In contrast, on the south-facing
282 slope a significant area was found where the boundary had remained stationary (Fig.
283 3). These trends were persistent over a longer period (1912–2009). On the east-facing
284 site, repeat landscape photography showed that the treeline ecotone had advanced 60
285 m in elevation since 1912 (+0.6 m year⁻¹; Table 2). On the south-facing site,
286 dendrochronological analysis showed long-term immobility: at the upper and lower
287 boundary of the treeline ecotone 8% and 28%, respectively, of the treeline birches had
288 established before 1900 (Table 3).

289 At the landscape scale, repeat photography and dendrochronological analysis
290 showed that the lower boundary of the treeline ecotone in the Torneträsk area had on
291 average advanced 24 m in elevation over the period 1912–2009 (+0.2 m year⁻¹) (Table
292 2). However, at this scale also, spatial variability was high: at four out of the eight
293 remaining treeline sites the treeline had moved upslope, at three others it had
294 remained stationary, and at one site the treeline had significantly descended (Table 2).

295 The treeline ecotone of site S4, located along the reindeer migration route
296 (Appendix 3), had shifted 145 m upslope (+1.5 m year⁻¹) or 260 m in actual distance

297 (+2.7 m year⁻¹) over the period 1912–2009 (Fig. 2, Table 2). Moreover, significant
298 forest densification was observed at the treeline and in the lowland (Fig. 2). In sharp
299 contrast, the continuous treeline boundary of site N1 was 120 m lower in elevation in
300 2009 compared with the years 1912 and 1952 (Fig. 4, Table 2). The retreat was
301 caused by a severe outbreak of the winter moth (*O. brumata*) in 1964–65 and
302 extended over a distance of more than 10 km (Fig. 4). Although in 1977 two young
303 birches were documented at site N1 in the recently created forest gap, these
304 individuals had perished by 2006 (Fig. 5). At treeline site N2 and the area up to 7 km
305 eastwards of this site, both the lower and upper boundaries of the treeline ecotone had
306 remained stationary since at least 1912 (Table 3). The uppermost birch trees (>2 m)
307 were between 110 and 258 years old with little or no recruitment of new trees (>2 m)
308 in the last 100 years (Fig. 5). Most of the smaller birches (DBH < 2.5 cm) recorded at
309 site N2 in 1977 had perished by 2006 (Fig. 5). At site S1 on the southern side of Lake
310 Torneträsk, potential treeline advance was seen (Fig. 5). In contrast, at sites N4 and
311 S5, which were characterized by slope angles >35, immobility of the position of the
312 treeline was documented for the past 60 to 100 years (Fig. 6).

313

314 *Presumed drivers of treeline dynamics*

315 Sites that were located in the vicinity of previous human activity showed a
316 pronounced advance of the treeline. This was indicated by the significant negative
317 correlation found between the elevational shift of the treeline and the distance to
318 previous campsites of reindeer herders or the railway that was constructed in 1898–
319 1902 ($r = -0.46$; $P = 0.04$; Table 2, Appendix 3). Previous anthropogenic impact
320 explained 35% of the variance in documented treeline dynamics (measured by R^2)
321 since 1912. When adding snow depth to the regression, R^2 increased to 59% (Table

322 2). Visually identified browsing damage of the seedlings was not correlated with
323 documented shifts of the position of the treeline ($r = 0.24$; $P = 0.48$; Table 2).
324 However, browsing damage to both seedlings and trees (>2 m) identified by
325 dendrochronological analysis showed a significant correlation with documented
326 treeline shifts ($r = -0.82$; $P = 0.03$; Table 2, values in brackets). Adding this
327 parameter to the regression increased R^2 to 68% for these five sites. Polycormicity of
328 treeline birches was positively correlated with advance of the treeline (Table 2). In
329 contrast, aspect and inclination showed no overall correlation with recorded treeline
330 shifts since 1912.

331 Annual recruitment of birch saplings (<2 m) at the treeline of Mount Nuolja was
332 not correlated with summer (June–August) or winter (December–February)
333 temperature for the period of measurement 1964–2006 ($r_s = 0.14$, $P = 0.74$ and $r_s = -$
334 0.08 , $P = 0.88$, respectively) (Fig. 7). Neither was annual birch recruitment correlated
335 with summer or winter precipitation ($r_s = 0.12$, $P = 0.66$ and $r_s = -0.14$, $P = 0.76$,
336 respectively). Also, no positive correlation ($r_s = -0.21$, $P = 0.20$) was found between
337 summer temperature and tree (>2 m) establishment for the long-term period 1800–
338 2000 (Fig. 8). In contrast, disturbance at the treeline, expressed by the negative
339 birchtreeline-minus-pinesubalpine and birchtreeline-minusbirchsubalpine ring-width
340 indices, was positively correlated with annual birch (<2 m) recruitment ($r_s = 0.54$, $P =$
341 0.06 and $r_s = 0.47$, $P = 0.10$ respectively) (Fig. 7). Furthermore, a significant negative
342 correlation was found between tree (>2 m) establishment at the treeline and reindeer
343 population numbers for the period 1800–2000 ($r_s = -0.69$; $P = 0.03$). Comparatively
344 low tree establishment numbers were recorded for the warmer 1850s and 1920–30s,
345 when reindeer population numbers were high, whereas high tree establishment
346 numbers were found for the cool late 19th century and particularly during the cooler

347 late 1960s and 1970s when reindeer population numbers were low (Fig. 8). Even
348 when saplings (<2 m) were included in the analysis, birch establishment at the treeline
349 was highest during the late 1960s and 1970s.

350

351 Nevertheless, climate highly determined birch growth at the treeline. Exceptionally
352 cool summers caused significantly ($P < 0.05$) reduced radial growth for 1 year in the
353 subalpine birches, but for 2 years in the birches at the treeline (e.g. 1900–01 and
354 1975–76, Table 4).

355 The main biotic disturbance events during the period 1800–2006 that significantly
356 ($P < 0.05$) reduced radial growth in the treeline individuals were, in order of
357 importance, reindeer browsing and moth herbivory (Table 4). Reindeer browsing
358 damage showed local variability, both in timing and intensity. For example, greater
359 damage was seen on the south slope of Mount Nuolja than on the east slope (Table 4).
360 However, if reindeer population numbers were high, browsing damage was ubiquitous
361 on all sites studied: for the years 1863, 1911, 1929, 1979 and 1985 the treeline birches
362 showed browsing scars together with significant growth reductions (Table 4). The
363 most severe and ubiquitous damage in the 20th century caused by browsing was found
364 in the year 1929, when reindeer population numbers reached an absolute peak (Fig.
365 8). During that year more than 50% of the treeline birches in the Torneträsk area
366 showed a significant growth reduction (Table 4).

367 Invertebrate herbivory also affected the treeline. During the summers of 1902–03,
368 1964–65, and to a lesser extent in 1955 and 1994, moth herbivory caused significant
369 growth reductions and, in 1964–65 large-scale mortality (Fig. 4) in the birches
370 constituting the treeline ecotone (Table 4). Local variability in the impact of
371 disturbance was again substantial (Table 4).

372

373 **Discussion**

374

375 *Trends and presumed causes of treeline dynamics*

376 This study aimed to document changes or stability in the treeline ecotone in the
377 Torneträsk area at different temporal and spatial scales, and particularly to clarify the
378 ambiguity that currently exists about treeline dynamics and the driving processes
379 behind them (Table 1).

380 In contrast to one of the most widely held expectations of vegetation responses to
381 warming, i.e. that Arctic treelines will move northwards and elevational treelines
382 upslope (Harsch et al., 2009), this study documented highly varying treeline dynamics
383 for the Torneträsk area in sub-Arctic Sweden during a period of multi-decadal climate
384 warming (Callaghan et al., 2010). Contrasting treeline dynamics were recorded at
385 spatial scales ranging from an individual mountain to an entire landscape and at
386 temporal scales ranging from three decades to more than a century (Figs 3 and 5,
387 Table 2). This is surprising because temperature and precipitation, the climatic
388 parameters generally accepted to limit recruitment and growth at the mountain birch
389 treeline (Kullman and Öberg, 2009), both significantly increased since 1913 (see
390 ‘Study area’).

391 Moreover, dendrochronological analysis indicated that treeline advance in the past
392 two centuries was most pronounced during the cooler late 1960s and 1970s (Fig. 8),
393 contradicting the interpretations of previous studies in the area (Table 1). During this
394 period, reindeer population numbers in the Torneträsk area reached a record low
395 following some severe winters. By the late 1960s the total herd had become three
396 times smaller than in the period 1850–60 when all reindeer were gathered around the

397 treeline by the nomadic herders (Fig. 8; Emanuelsson, 1987). Although reindeer have
398 always been part of the birch ecosystem, their impact on the vegetation should be
399 evaluated in terms of population densities (Helle, 2001). Fenced pastures near the
400 treeline in the 19th and early 20th centuries resulted in higher reindeer population
401 densities in the treeline ecotone than in both earlier and more recent times
402 (Emanuelsson, 1987). Dendrochronological analysis for the five transect sites N1, N2,
403 S1, S3_E and S3_S showed that the impact of reindeer browsing at the treeline gradually
404 decreased after the 1930s (Table 4). From the 1920s onwards, the campsites and
405 pastures have been gradually abandoned, synchronously with most other heavily
406 grazed out-farms in Fennoscandia (Bryn and Daugstad, 2001; Lundh, 2001).

407 A similar process of reduced human impact was identified at site S2. Repeat
408 landscape photography and dendrochronological analysis showed a remarkable
409 densification and an upslope shift by 50 m of the lower boundary of the treeline
410 ecotone for the period 1912–2009 (Table 2). However, historical reports documented
411 the local clearance of the birch forest at this site between 1898 and 1902, thereby
412 lowering the treeline ecotone by 70 m (Emanuelsson, 1987). Extending the period by
413 15 years would result in a net balance of a 20 m descent of the treeline for the period
414 1897–2009. This shows the importance of the temporal scale in treeline research and
415 suggests caution with far-reaching conclusions based on findings such as apparent
416 correlations between temperature and treeline advance obtained from short-term
417 studies.

418 Reduced anthropozoogenic disturbance (Ellenberg, 1988) compared with the early
419 20th century best explained the varying treeline shifts recorded in our study area
420 (Table 2). We confirmed the hypothesis of Emanuelsson (1987) and Cairns and Moen
421 (2004) that the impacts of humans and semidomesticated herbivores have

422 significantly determined the elevational shifts of the treeline boundary (Table 1).
423 Distinguishing human impact from natural factors is, however, one of the most
424 difficult tasks in treeline research (Ellenberg, 1988; Hofgaard, 1997). Only accurate
425 historical reports of the anthropozoogenic impact on northern vegetation make a
426 proper evaluation of this factor possible. Unfortunately, this information is often not
427 available (Moen et al., 2008) and is a major weakness in studies dealing with range
428 migrations of plant species. The Torneträsk area has a long history of human
429 occupation, but human impact was presumably not higher than in other areas of
430 northern Eurasia (Von Middendorf, 1864; Veijola, 1998; Hofgaard, 1999; Lundh,
431 2001; Vlassova, 2002). The major difference from other regions is rather that its
432 anthropozoogenic impact has been well documented since *c.* 1600 (Emanuelsson,
433 1987).

434 In addition to reindeer grazing, the mountain birch treeline also suffers from
435 episodic outbreaks of the autumnal and winter moth (Kallio and Lehtonen, 1973).
436 Several studies have shown that the lack of recovery of forests defoliated by moths is
437 the product of an interaction between damage due to moth outbreaks and reindeer
438 grazing (Kallio and Lehtonen, 1973; Helle, 2001; Tenow et al., 2005). In the mid
439 1960s, caterpillars of the autumnal moth defoliated the birch treeline ecotone in
440 northern Finland over an area of *c.* 5000 km², of which 1200 km² of birch forest did
441 not recover (Seppälä and Rastas, 1980). Exclosure experiments showed that reindeer
442 grazing of birch seedlings was the cause of the lack of forest recovery (Lehtonen and
443 Heikkinen, 1995). This interaction between moth and reindeer herbivory forms the
444 greatest threat to the mountain birch forest, and devastated areas may remain treeless
445 for decades to centuries irrespective of prevailing climatic conditions (Seppälä and
446 Rastas, 1980). At treeline sites N1 and N2 we documented this process. The lack of

447 recent tree (>2 m) establishment and the browsing scars documented in the tree rings
448 indicated that, in addition to moth herbivory, reindeer browsing is still a controlling
449 factor at these sites (Fig. 5, Table 4). This example further stresses the importance of
450 disturbance in regulating recruitment and mortality at the treeline and masking or
451 even nullifying any beneficial effects of recent climate warming on tree recruitment
452 and treeline shifts (see Fig. 7).

453

454 *Other factors affecting treeline dynamics*

455 A multitude of environmental conditions affect tree establishment and survival and
456 these factors may differ in space and time (Sveinbjörnsson et al., 2002). Besides
457 anthropozoogenic impacts, snow depth significantly increased the proportion of
458 explained variance in documented treeline dynamics (R^2 increased from 0.35 to 0.59;
459 Table 2). The importance of an ample snow cover for mountain birch, providing
460 insulation in winter and moisture in spring, has been elucidated in previous treeline
461 studies (Dalen and Hofgaard, 2005; Kullman and Öberg, 2009). Nevertheless, winter
462 precipitation was not correlated with tree establishment at the treeline, suggesting that
463 local snow distribution is a more complex factor than just the sum of amounts of
464 winter precipitation (Holtmeier and Broll, 2010).

465 In contrast to other studies (Danby and Hik, 2007; Kullman and Öberg, 2009),
466 slope aspect and inclination were not correlated with elevational shifts of the treeline
467 ecotone. Possibly, local site conditions and various historical disturbances were of
468 greater importance than relative solar radiation and regional wind exposure. The lack
469 of correlation between inclination and documented treeline shifts resulted from the
470 fact that both flat and very steep slopes experienced immobility of the treeline (Table
471 2), possibly because of high wind exposure and geomorphological activity,

472 respectively (Holtmeier and Broll, 2010). Polycormicity of treeline birches was
473 positively correlated with documented elevational shifts of the position of the treeline
474 (Table 2). Polycormic birch forests are less prone to disturbance than monocormic
475 forests as they do not rely on hazardous seedling establishment (Tenow et al., 2005).
476 At the polycormic treeline of Mount Nuolja we recorded high birch recruitment
477 during years with increased disturbance (Fig. 7).

478

479 *Projecting future treeline dynamics*

480 The extreme discrepancy that exists between model projections of the treeline
481 position and *in situ* observations is a world-wide phenomenon (Holtmeier and Broll,
482 2007; Van Bogaert et al., 2007). In the next 100 years, alpine and polar treelines are
483 projected to shift upslope by 2 to 6 m year⁻¹ (Moen et al., 2004) and northwards by
484 7.4–20 km year⁻¹ (Kaplan and New, 2006) if climate warming continues. However,
485 the fastest upslope shifts of treelines recorded during 20th century warming are in the
486 range of 1 to 2 m year⁻¹ (Shiyatov et al., 2007; Kullman and Öberg, 2009). Moreover,
487 the fastest northward-migrating treeline replaces tundra by taiga at a rate of 3–10 m
488 year⁻¹ (Kharuk et al., 2006); i.e. 2000 times slower than model projections. For
489 comparison, the fastest upward and lateral (actual distance) displacements of the
490 treeline in the Torneträsk area were respectively +1.5 m year⁻¹ and +2.7 m year⁻¹. A
491 global study by Harsch et al. (2009) showed that only 52% of all 166 global treeline
492 sites had advanced over the past 100 years despite documented amplified climate
493 warming at high-elevation areas and northern latitudes (ACIA, 2005).

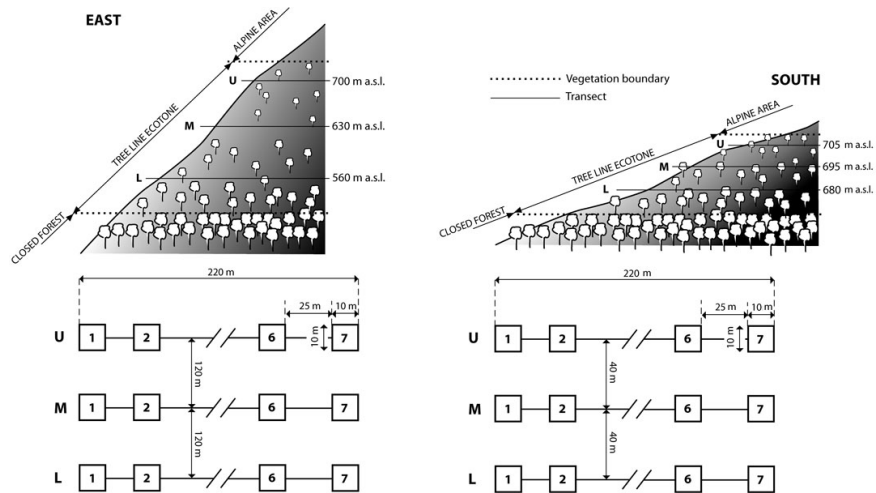
494 Climate scenarios for our study area in northern Fennoscandia project an increase
495 in mean annual temperature of 3.5 °C by the year 2080 compared to the reference
496 period 1980–2000 (Saelthun and Barkved, 2003) and an upslope shift of the treeline

497 by 233–667 m for the next 100 years (Moen et al., 2004). In such scenarios, mountain
498 birch would be largely replaced by conifer tree species (Wolf et al., 2008a). However,
499 these models almost exclusively operate with positive growth responses, and new
500 findings such as likely increases in birch herbivory in a warming sub-Arctic (Ims et
501 al., 2007; Wolf et al., 2008b) and negative growth responses to increased temperatures
502 (Kirchhefer, 1996) suggest that the modelled treeline advances are unlikely to be fully
503 realized. Indeed, Van Bogaert et al. (2010) showed that not a conifer but deciduous
504 European aspen (*Populus tremula* L.) recently colonized the birch treeline ecotone in
505 our study area. Moreover, topography, being the only relatively constant factor
506 through time, will prevent an upslope shift of orographically controlled treeline areas
507 (inclination $>35^\circ$) such as sites N4 and S5 (Fig. 6).

508 In conclusion, in areas where the number of domesticated herbivores has decreased
509 over the past century, rapid vegetation changes and advances in the treeline may be
510 expected. However, in treeline areas controlled by severe disturbance by moth
511 herbivory or slope processes, treeline advance may not occur. In contrast to Harsch et
512 al. (2009) who concluded that the role of disturbance during recent climate warming
513 is restricted to determining *when* treeline advance will occur, this study shows that
514 disturbance and its after-effects may equally well determine *if* treeline advance will
515 occur at all.

SUPPORTING INFORMATION

Appendix S1 High-resolution transect design for Mount Nuolja. Each transect line had seven plots, numbered from left to right. The spatial intervals refer to actual distances in metres. Abbreviations used: U: Upper transect line; M: Middle transect line; L: Lower transect line.



Appendix S2 Dendrochronological analysis.

Tree sampling

Tree cores were taken as low as possible (at *c.* 20 cm stem height), so that the presumed year of establishment could be determined by subsequent tree-ring counting. The mean difference in the number of annual rings counted at the root collar and at 20 cm stem height of the saplings was added to the number of tree-rings counted on the tree cores to make a better estimate of the year of tree establishment. Cores taken at 20 cm stem height or higher are more suitable for the identification of disturbance events (Schweingruber, 2007). Stunted and older individuals were also cored at breast height to avoid tension wood and reduce the number of missing rings that are common at lower stem height (Sonesson & Hoogesteger, 1983).

Ring-width chronology construction

Ring-widths were measured up to 0.01 mm precision using a LINTAB™ measuring stage and the dendro software package TSAPWin™ v. 0.53 (Rinn, 2003, Heidelberg, Germany). Ring-width chronologies were built for the reference birches sampled below the tree line ecotone of the five tree line sites located at Mount Nuolja (S3_{East} and S3_{South}) and at the Sonesson and Hoogesteger transects (N1, N2, and S1; Fig. 1). These five birch chronologies, in addition to the pine chronology, served as a ring-width reference for the tree line birches. Chronology building was done in TSAPWin™ using both visual comparisons and well-established statistical parameters. Values of t_{BP} greater than 4.0 and of GLK% ('Gleichläufigkeit'; the degree that trees react with a similar growth increase or decrease compared to the previous growing

season) greater than 65% were considered significant in analogy with previous studies (Levanič & Eggertsson, 2008). In this way, missing rings were generally easily identified. Individual ring-width series were standardised in the program ARSTAN (Cook, 1985) using regional curve standardisation (Briffa *et al.*, 1992).

Interpretations of stem cross section anatomy (Fig. S1)

In addition to a statistical ring-width approach, we performed a meticulous study of the wood anatomical features of the tree line birches. This analysis generally provides more information about the disturbance event than do statistics of differences in ring-widths (Levanič & Eggertsson, 2008). Frost rings, white rings, browsing scars and callus tissue all point to specific damage patterns (Fig. S1).

Narrow rings can be the result of e.g. a cool summer, reindeer (or other mammal) browsing, or moth herbivory. If only young and small (<2 m) tree line individuals show a narrow ring in year 'x', a cool summer is less likely to be the cause of the growth reduction. In this case reindeer browsing is more likely since the browse height of reach for reindeer is limited to *c.* 1.5 m and will therefore mainly affect saplings (Helle, 2001). This hypothesis may later be confirmed if one or more young individuals are found that show a browsing scar for year 'x' (Fig. S1c). If only older individuals (>60 years) show a narrow ring for year 'y', a cool summer is less likely, but defoliation by the autumnal or winter moth, who select for older individuals (Bylund, 1995), is more likely. This hypothesis may later be confirmed if one or more older individuals show a 'white' ring for year 'y', pointing to a defoliation event by an invertebrate (Schweingruber, 2007) (Fig. S1d).

Reindeer mainly strip off the birch leaves, rather than gnawing on the twigs and

stems (Haukioja & Heino, 1974). Therefore, a part of the browsing scars observed in the tree-rings may be attributed to moose, voles, and particularly to mountain hare (*Lepidus timidus* L.) that also feed on birch, although predominantly in winter (Danell & Huss-Danell, 1985). However, the most ubiquitous growth reductions accompanied by several small browsing scars were identified for the summer of 1929, the year when reindeer population numbers reached an absolute peak (Fig. 8 and Table 4). Therefore, we assumed throughout the study that the browsing scars documented in the growing season were attributed to reindeer.

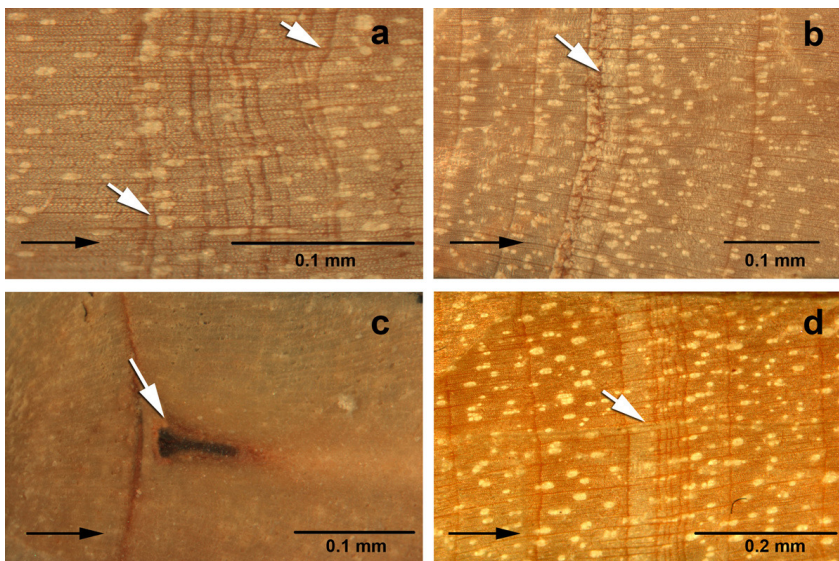


Figure S1 Study of wood anatomical features in mountain birch. The white arrows point to the area of interest, whereas the black arrows show the direction of growth. Birch individuals subjected to biotic or climatic stress regularly show wedging rings (a) that may result in erroneous dating. Pointer years such as the frost ring of 1984 shown in (b) can help in tracing these partly or completely missing rings. A typical frost ring (b) showing damage to the cambium. In June 1984, a 27-day period of

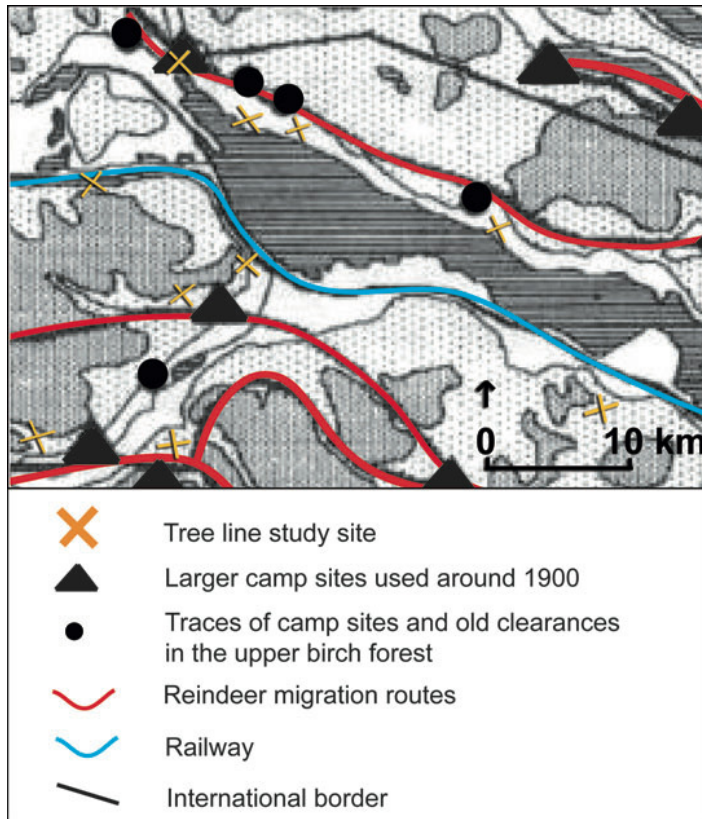
warm spring weather with minimum temperatures up to +11.9 °C was suddenly interrupted by three days of -1.3 °C, recorded at the Abisko meteorological station located 300 m below the tree line. A small scar (c) at 110 cm stem height presumably caused by reindeer browsing in the early summer of 1929. A bright coloured ring followed by four exceptionally narrow rings (d) points to complete tree defoliation by an insect.

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Appendix S3 Historical anthropozoogenic impact in the Torneträsk area. The points of relatively intense historical impact identified by Emanuelsson (1987) were relocated in the field and the distances between these points and the studied tree line sites were recorded by a GPS (see Table 2).



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Tables

Table 1. Previous field studies on observed treeline shifts and their presumed causes in the Torneträsk area of sub-Arctic Sweden.

Author	Year	Area	Methods	Results	Presumed attribution
Sandberg	1940	Mount Nuolja	Repeat Observation	Establishment of 0.5 m tall birch saplings during warm 1930s up to 200 m above the upper limit of the closed forest	Climate warming
Persson	1952	North-Torneträsk	Observations; elevational measurements of tree line ecotone	Contrasting tree line types and age structure	Contrasting site history, climate, geomorphological and biotic processes
Sandberg	1963	Mount Nuolja	Repeat observations; repeat photography	Forest densification at lower boundary of tree line ecotone. No increased abundance of birch at upper boundary.	Climate warming
Sonesson & Hoogesteger	1983	West- Torneträsk	Elevational transects; dendrochronology	Elevational advance of tree line ecotone by 20-50 m between 1937-1977	Climate warming
Emanuelsson	1987	Whole Torneträsk	Ethnographical historical research; aerial and ground observations; interviewing local people; repeat photography	Elevational advance and densification of tree line ecotone since 1900. Significant anthropozoogenic impact on the tree line in period 1600-1920	Recent decrease in anthropo-zoogenic impact
Holmgren & Tjus	1996	Mount Nuolja	Field observations; literature review; climate analysis	Elevational advance of the tree line ecotone by c. 40 m between 1930-1996	Climate warming
Lundgren	1999	Mount Nuolja	Repeat tree line measurements 1971-1998	Elevational advance of upper limit of tree-sized birches (>2 m) by 22-46 m	Climate warming
Hällmarker	2002	Mount Nuolja	Remote sensing; repeat photography	Elevational advance of lower boundary of tree line ecotone by c. 20 m between 1959-2000	Climate warming, reduced anthropo-zoogenic impact, moth outbreaks, geomorphology
Cairns & Moen	2004	Southwest-Torneträsk	Field measurements; herbivory analysis	Differential reindeer grazing impacts cause differential tree line shifts and structure	Differential reindeer grazing pressure
Dalen & Hofgaard	2005	Southwest-Torneträsk	Dendrochronology; field measurements	Major recruitment phase at upper boundary of tree line ecotone in 1960s; possibly advancing tree line	Moth outbreak of 1955, herbivory, climate warming
Truong <i>et al</i>	2006	Southwest-Torneträsk	Field observations; genetic study	Birch seedlings found up to 500 m above the upper limit of the closed forest	Climate warming

Table 2. Documented treeline shifts and site conditions for 10 sites studied in the Torneträsk area of sub-Arctic Sweden for the period 1912–2009 (see Fig. 1). Independently obtained results from repeat photography, repeat transect measurements and dendrochronological analysis were cross-referenced to determine the shift of the lower boundary of the treeline ecotone. Browsing damage was classified visually and for five sites also by dendrochronological analysis (the values listed in brackets). So as not to bias the results, Mount Nuolja (site S3), for which the two treeline sites were not randomly selected, was not included in the calculation of the mean elevational shift of the treeline in the Torneträsk area. Pearson correlation coefficients and R^2 -values (the proportion of explained variance in documented treeline shifts) obtained by forward selection of the different variables are listed at the bottom of the table.

Site	Elevational shift of tree line ecotone (m)	Aspect (°)	Inclination (°)	Anthropozoo-genic impact (distance in m from previous camp or railway)	Snow depth (m)	Browsed tree line birches (%)	Polycormic tree line birches (%)
N1	-120 ± 20	220	29	1210	0.5	47 (81)	42
N2	0 ± 10	205	17	720	0.7	35 (73)	24
N3	+50 ± 5	220	26	180	1.2	42	66
N4	0 ± 10	180	41	910	0.3	29	63
S1	+40 ± 15	155	0	490	1.0	51 (64)	52
S2	+50 ± 5	15	27	190	0.9	39	58
S3-East	+60 ± 5	80	26	220	1.2	43 (53)	60
S3-South	0 ± 10	170	10	800	0.3	29 (72)	43
S4	+145 ± 10	200	26	210	1.2	32	68
S5	0 ± 5	50	40	960	0.5	16	74
All except S3	+24 ± 2						
r (P)	All	-0.24 (0.45)	-0.06 (0.87)	-0.46 (0.03)	0.44 (0.04)	0.24 (0.48)	0.44 (0.17)
R^2	All	0	0	0.35	0.59	0.59	0.59

Table 3. Treeline shifts in the Swedish Torneträsk area identified by repeat photography analysis (upper part) and compared with dendrochronological analysis (bottom part) for the elevational transects. The geographical scale of the study ranged from an individual mountain (Mount Nuolja, site M_{S3}) to the landscape scale (sites N1, N2 and S1). Trees were grouped into three establishment periods: individuals established (1) before 1900; during the peak of intensive reindeer management practices, (2) in the period 1900–63; before the reindeer population reached its long-term minimum, and (3) in the period 1964–2006; the most recent period during which reindeer population numbers were initially very low and subsequently increased again.

		Scale				
		Individual mountain (M _{S3})		Torneträsk landscape area		
		East Slope	South Slope	N1	N2	S1
Dynamics of tree line ecotone	Elevational shift (m) of the tree line ecotone for the period 1912-2009	+60 ± 5	0 ± 5	-120 ± 5	0 ± 5	+40 ± 5
Age structure of tree line ecotone	Upper transect:	Number of individuals (%)	Number of individuals (%)	Number of individuals (%)	Number of individuals (%)	Number of individuals (%)
	>1900	0 ± 0 (0 ± 0%)	3 ± 1 (8 ± 3%)	0 ± 0 (0 ± 0%)	16 ± 1 (66 ± 4%)	0 ± 0 (0 ± 0%)
	1900-1963	0 ± 1 (0 ± 4%)	0 ± 1 (0 ± 3%)	5 ± 1 (25 ± 5%)	4 ± 1 (17 ± 4%)	11 ± 1 (42 ± 4%)
	1964-2006	23 ± 1 (100 ± 4%)	33 ± 1 (92 ± 3%)	15 ± 1 (75 ± 5%)	4 ± 1 (17 ± 4%)	15 ± 1 (58 ± 4%)
	Middle transect:					
	>1900	0 ± 0 (0 ± 0%)	2 ± 1 (10 ± 5%)	-	-	-
	1900-1963	1 ± 1 (5 ± 5%)	1 ± 1 (5 ± 5%)	-	-	-
	1964-2006	19 ± 1 (95 ± 5%)	17 ± 1 (85 ± 5%)	-	-	-
	Lower transect:					
	>1900	2 ± 1 (6 ± 3%)	36 ± 3 (28 ± 3%)	-	-	-
	1900-1963	1 ± 1 (3 ± 3%)	0 ± 3 (0 ± 3%)	-	-	-
	1964-2006	30 ± 1 (90 ± 3%)	94 ± 3 (72 ± 3%)	-	-	-

Table 4. Significant ($P < 0.05$) disturbance events at the tree line in the Swedish Torneträsk area for the period 1800–2006. The geographical scale of the study ranged from an individual mountain (Mount Nuolja, site M_{S3}) to the landscape scale (sites N1, N2 and S1). Ring-width chronologies of birch and pine individuals sampled below the tree line ecotone were used as a reference. Major disturbance events are given in bold and were defined as events that affected 50% or more of the tree line individuals in two or more different sites. The number of replicates is given in brackets. Note that the list of disturbance events is not exhaustive, particularly for the period 1800–1900 for which fewer replicates were available.

Growth Reduction Period	Individual mountain (M_{S3})		Scale Torneträsk landscape			Presumed Event	Tree-ring anatomical wood features	Validation
	East Slope	South Slope	N1	N2	S1			
	1801-11	-	-	-	100% (3)			
1853-59	-	-	-	67% (6)	-	Reindeer browsing 1853, 1857	Browsing scars 1853, 1857	Peaking reindeer population
1863-64	0% (2)	50% (2)	-	50% (6)	-	Reindeer browsing 1863	Browsing scars 1863	Peaking reindeer population
1900-01	50% (2)	50% (2)	-	33% (6)	-	After-effect cold summer 1900	Small ring in old and young individuals 1901	1900:exceptionally cold: 4 °C below long-term mean
1902-04	25% (8)	100% (4)	-	71% (14)	-	-Moth defoliation old birches 1902- 1903 (N2) -Reindeer browsing young birches 1903 (M_{S3})	-White ring 1902- 1903 (N2); -Browsing scars 1903 (M_{S3})	-Reported moth outbreak in N-Fennoscandia (Tenow, 1972) -Average reindeer population
1909-11	33% (12)	25% (4)	-	71% (14)	-	Reindeer browsing 1909, 1911	Browsing scars 1909, 1911	Peaking reindeer population
1919	50% (12)	0% (10)	-	13% (16)	-	Reindeer browsing 1919	Browsing scars 1919	Average reindeer population
1925	17% (12)	10% (10)	-	13% (16)	0% (2)	Reindeer browsing 1925	Browsing scars 1925	High reindeer population
1929	50% (12)	60% (10)	100% (2)	50% (24)	67% (3)	Reindeer browsing 1929	Browsing scars 1929	Peaking reindeer population
1934-35	14% (14)	10% (10)	100% (2)	0% (24)	25% (4)	Reindeer browsing 1934	Browsing scars 1934	High reindeer population
1955-58	33% (10)	50% (10)	0% (5)	13% (30)	60% (5)	Moth defoliation 1955	White ring 1955	<i>E. autumnata</i> outbreak 1955
1964-68	50% (12)	83% (12)	20% (5)	63% (30)	0% (5)	Moth defoliation 1964 (M_{S3}) Moth defoliation 1965 (N1-N2)	White ring 1964 (M_{S3}) White ring 1965 (N1-N2)	<i>E. autumnata</i> peak 1964 (M_{S3}) <i>O. brumata</i> outbreak 1965 (N1-N2)
1975-76	33% (18)	18% (18)	10% (20)	15% (32)	10% (10)	After-effect cold summer 1975	Small ring in old and young individuals 1976	1975:exceptionally cold: 3 °C below long-term mean
1979	35% (34)	45% (22)	6% (32)	30% (32)	50% (12)	Reindeer browsing 1979	Browsing scars 1979	High reindeer population
1984	17% (46)	21% (33)	26% (38)	30% (34)	25% (16)	Frost damage	Frost ring 1984	May: 27 days +12°C June: 3 days -1.3°C
1985	9% (46)	21% (33)	21% (38)	30% (36)	29% (14)	Reindeer browsing 1985	Browsing scars 1985	Peaking reindeer population
1991-92	23% (46)	28% (49)	11% (38)	18% (36)	11% (18)	Reindeer browsing 1991-1992	Browsing scars 1991-1992	High reindeer population
1994-96	37% (62)	59% (56)	21% (38)	23% (37)	11% (18)	-Moth defoliation 1994 (old birches) -Reindeer browsing 1994 (young birches)	-White ring 1994 -Browsing scars 1994	- <i>E. autumnata</i> peak 1994 -Average reindeer population
1997-98	8% (62)	11% (56)	5% (38)	15% (37)	31% (26)	Reindeer browsing 1997-1998	Browsing scars 1997-1998	Average reindeer population
2005-06	4% (101)	7% (97)	8% (43)	20% (38)	15% (30)	Reindeer browsing 2005-2006	Browsing scars 2005-2006	High reindeer population

Figure legends

Fig. 1. The Torneträsk study area in sub-Arctic Sweden. The locations of the historical transects and photo points that have been revisited to study changes in the tree line ecotone are indicated.

Fig. 2. Tree line site S4 on the south side of Lake Torneträsk in 1912 and 2009. The yellow lines denote the 30%-tree-cover isolines (statistically determined by using the software ArcGIS Spatial Analyst 9.2). The process of identifying the elevational position of this isoline in the old photographs is illustrated here: in the centre of the inset, a rock outcrop attached to the bedrock can be seen that was positioned near the upper limit of the isoline of 1912. The same landmark is seen on the 2009 photograph and could be recorded in the field with a GPS-device with an aneroid altimeter. As a reference, elevation in metres above sea level is indicated. Upper photo: B. Mesch, lower photo: R. Van Bogaert.

Fig. 3. Repeat aerial photograph analysis on Mount Nuolja in sub-Arctic Sweden. Contrasting tree line dynamics are seen for the east- and south-facing slope for the period 1959-2000. The statistically-determined 30%-tree cover isoline is plotted in yellow. Note that due to different camera filters, trees are plotted as white dots in the images on the left, but rather as dark reddish dots on the infrared-images on the right.

Fig. 4. The tree line ecotone near transect N1 on the northern side of Lake Torneträsk in 1952 and 2009. The statistically-determined 30%-tree cover isoline is plotted in

yellow. Although the 2009 photograph is taken in winter causing a reduced tree-cover, large forest gaps are seen as a result of a severe moth outbreak in 1964-1965. Upper photo: E. Persson, lower photo: S. Johnsson.

Fig. 5. Comparison of the tree line transects N1, N2, and S1 visited in 1977 and 2006. The colours of the bars represent different d.b.h. or age classes. Black bars denote birch trees that established before 1900, dark grey bars birches with a d.b.h. >7.5 cm that established after 1900, light grey bars birches with a d.b.h. between 2.5 and 7.5 cm, and white bars birch saplings with a d.b.h. <2.5 cm. Note the different scaling of the vertical axis of site S1. (NB: the gap between c. 520 and 640 m a.s.l. at site N1 is due to forest defoliation by invertebrates, see Fig. 4.)

Fig. 6. Orographic tree line sites with an inclination >35° showed long-term stability. The statistically-determined 30%-tree cover isoline is plotted in yellow. Upper photo on the left: E. Persson, bottom left: B. Mesch; upper and bottom right: R. Van Bogaert.

Fig. 7. Estimated annual birch recruitment at the tree line of Mount Nuolja (a) in relation to disturbance (b) and summer temperature (c) for the period 1964-2006. Note that birch-minus-pine indices were plotted as such that positive values point to increased moth damage. See text for correlations.

Fig. 8. Tree (>2 m) establishment at the Torneträsk tree line versus summer (June-August) temperature and reindeer population numbers for the period 1800-2000. A second-degree polynomial function shows the long-term summer temperature trend.

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Figures

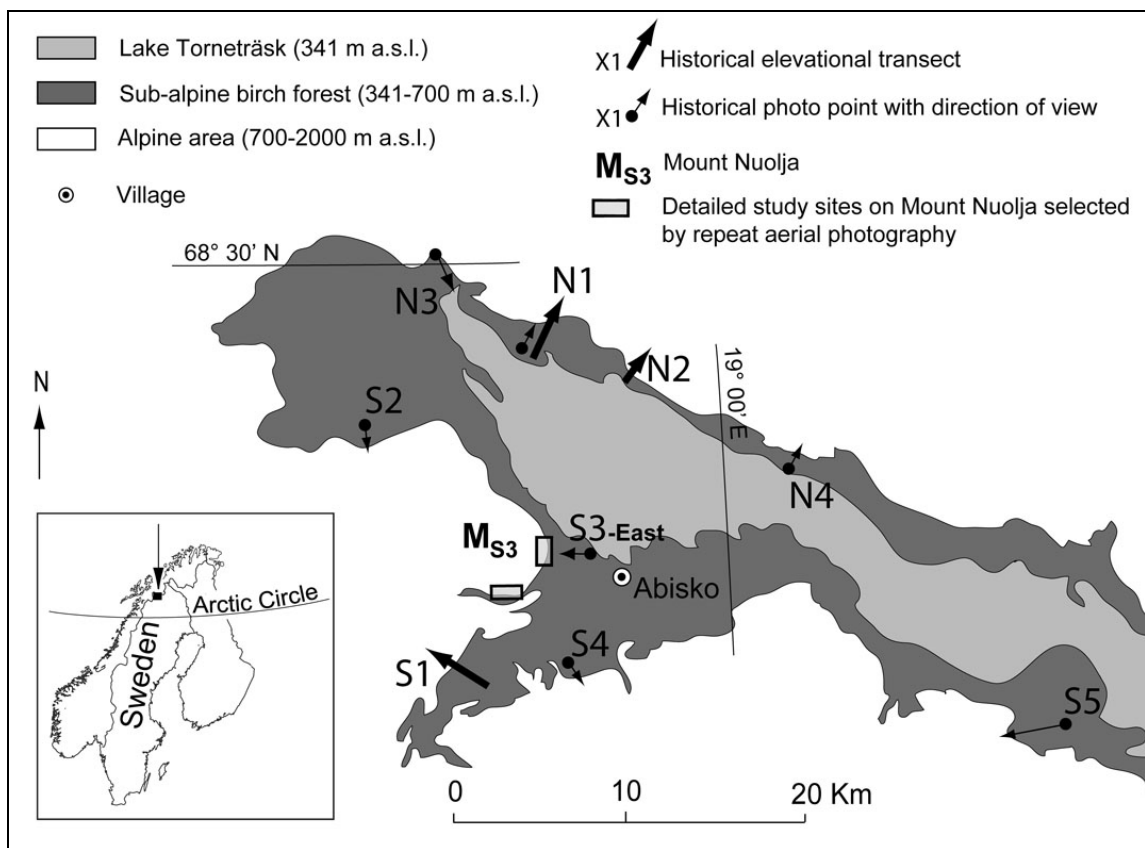


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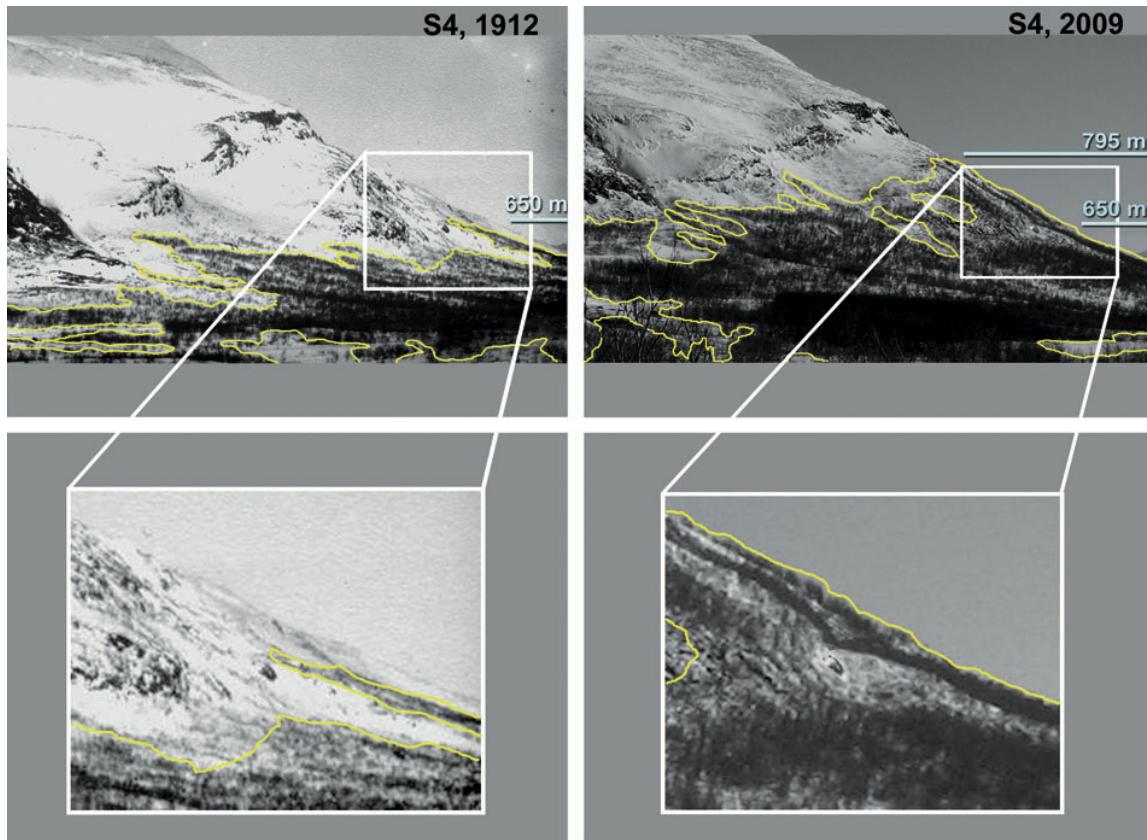


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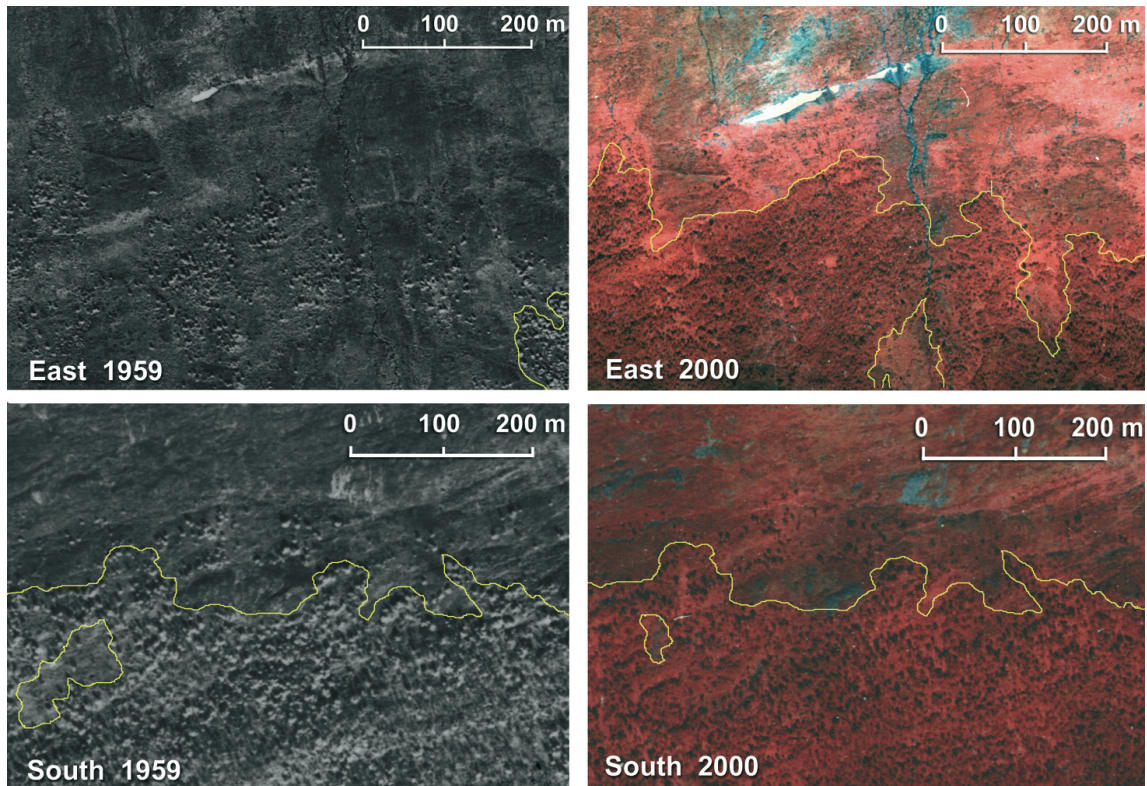


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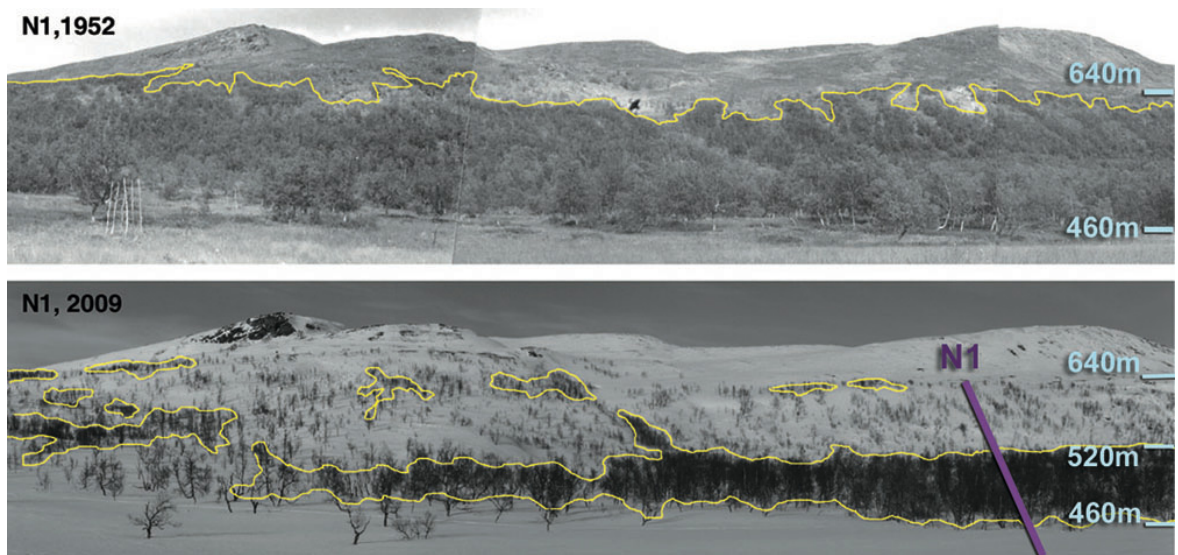


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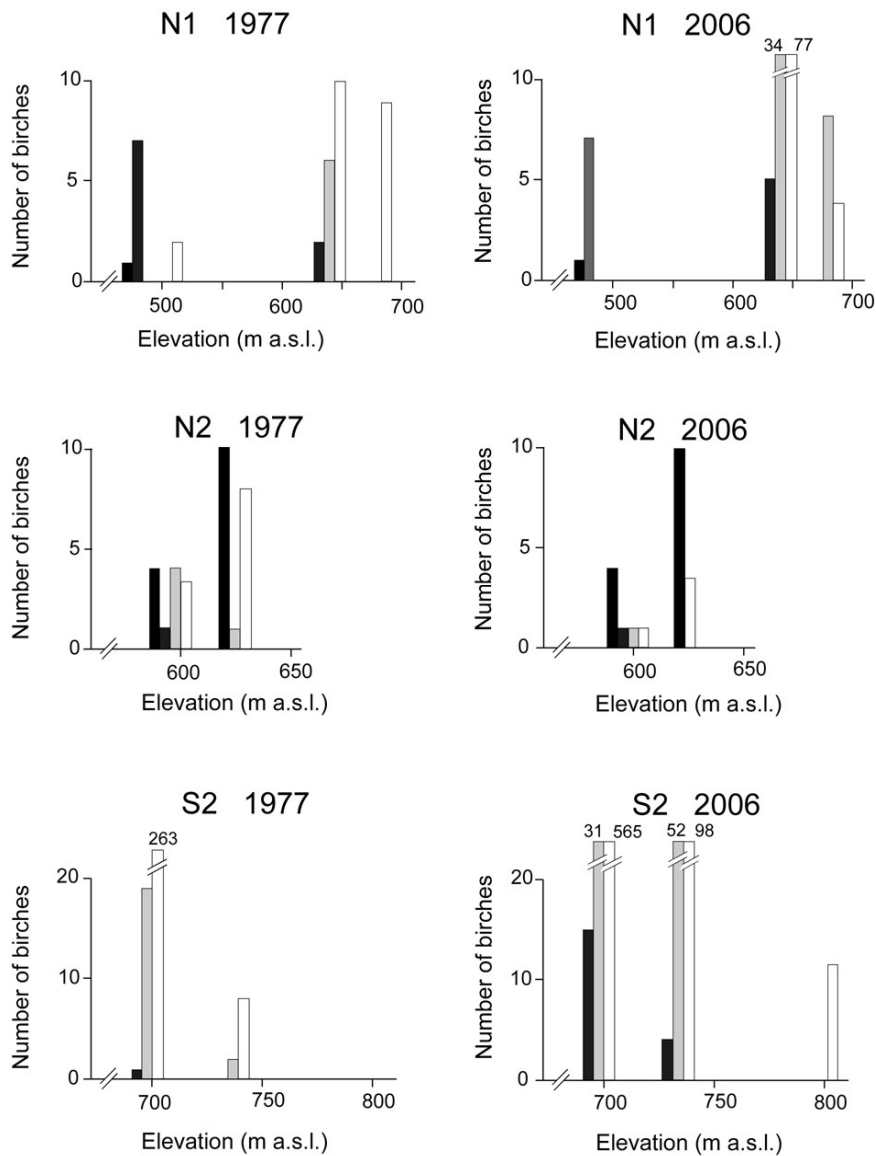


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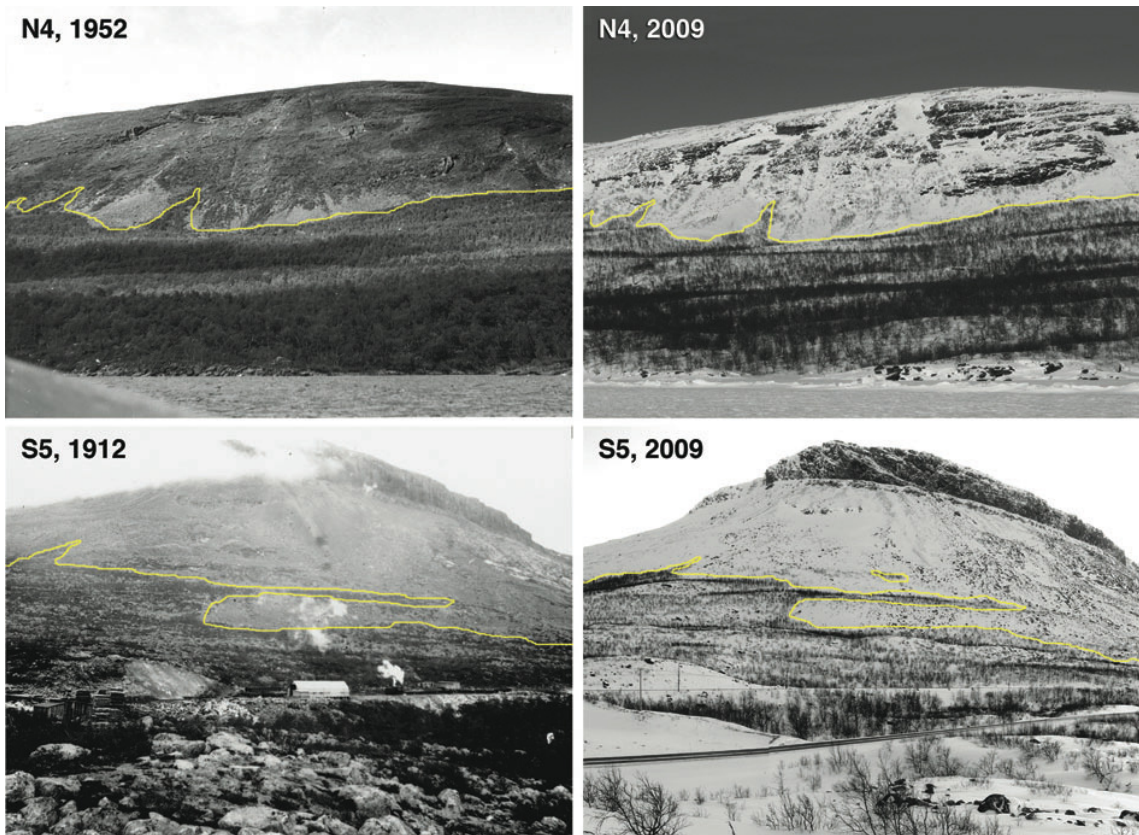


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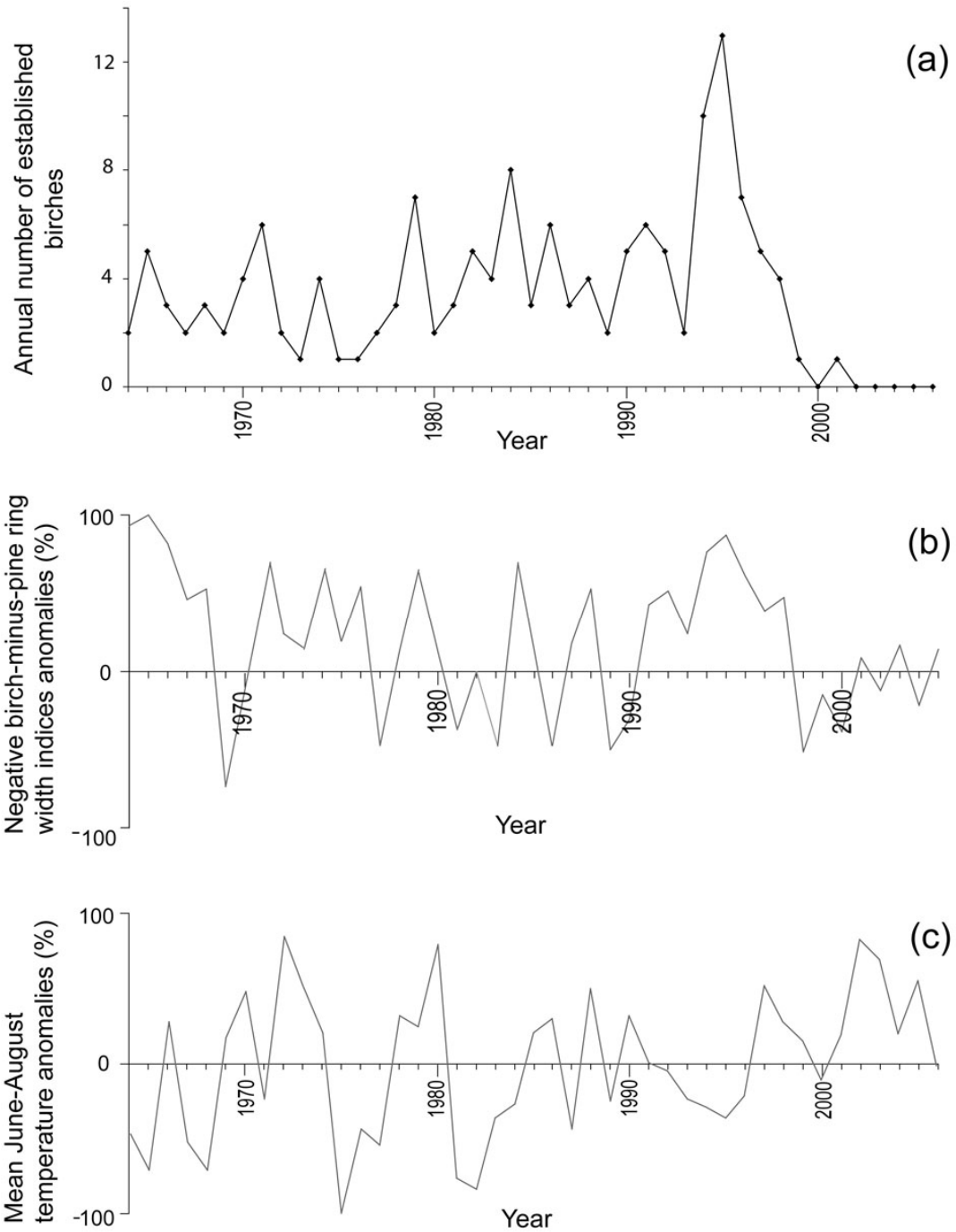


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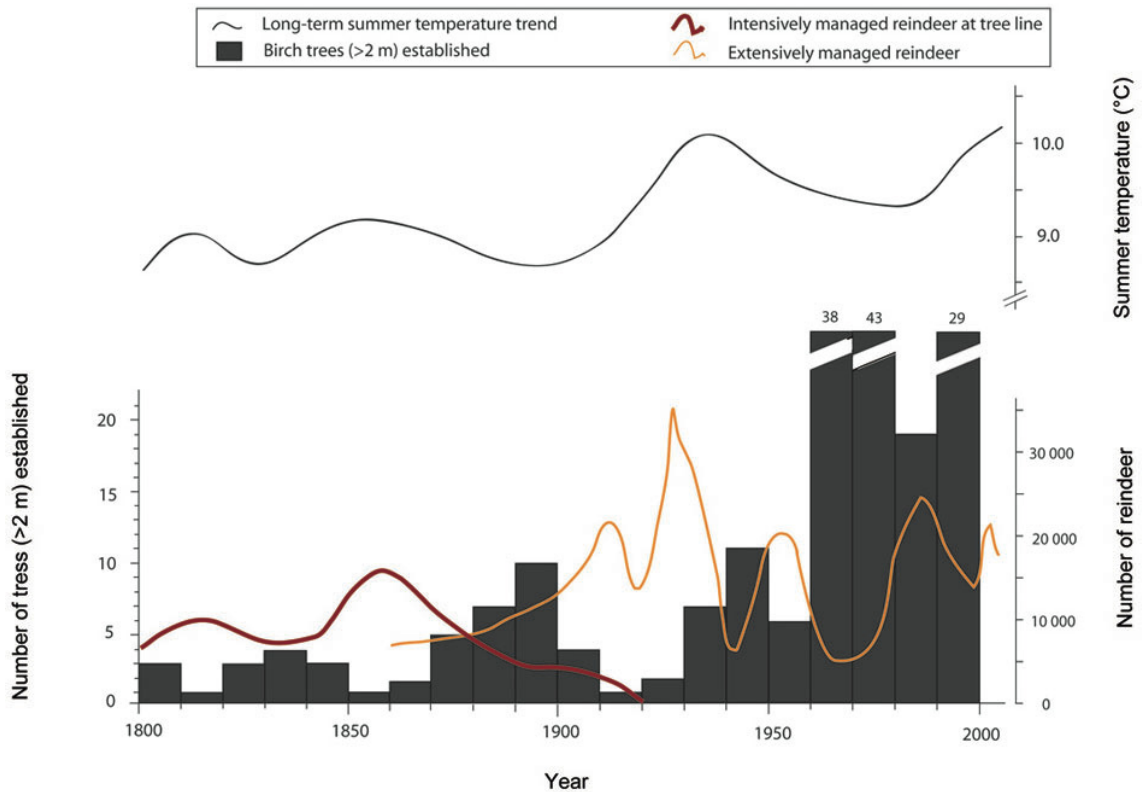


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