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1 **North Fennoscandian mountain forests: History, composition, disturbance**
2 **dynamics and the unpredictable future**

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25 ABSTRACT

26 North Fennoscandian mountain forests are distributed along the Scandes Mountains
27 between Sweden and Norway, and the low-mountain regions of northern Norway, Sweden
28 and Finland, and the adjacent northwestern Russia. Regionally, these forests are
29 differentiated into spruce, pine or birch dominance due to climatic differences. Variation in
30 tree species dominance within these regions is generally caused by a combination of
31 historical and prevailing disturbance regimes, including both chronic and episodic
32 disturbances, their magnitude and frequency, as well as differences in edaphic conditions
33 and topography. Because of their remoteness, slow growth and restrictions of use, these
34 mountain forests are generally less affected by human utilization than more productive and
35 easily utilizable forests at lower elevations and/or latitudes. As a consequence, these
36 northern forests of Europe are often referred to as “Europe’s last wilderness”, even if human
37 influence of varying intensity has been ubiquitous through historical time. Because of their
38 naturalness, the North Fennoscandian mountain forests are of paramount importance for
39 biodiversity conservation, monitoring of ecosystem change and for their sociocultural values.
40 As such, they also provide unique reference areas for basic and applied research, and for
41 developing methods of forest conservation, restoration and ecosystem-based management
42 for the entire Fennoscandia. However, the current rapid change in climate is predicted to
43 profoundly affect the ecology and dynamics of these forests in the future.

44

45 1. Introduction

46

47 North Fennoscandian mountain forests are distributed along the remains of ancient
48 mountain ranges, most notably the Scandes mountain range along the border between
49 Sweden and Norway, and the low-mountain regions of northern and northeastern Finland,
50 and the adjacent northwestern Russia (Fig. 1). These regions harbor both northern boreal
51 forests and subarctic/subalpine birch forests, which are collectively henceforward referred
52 to as *northern mountain forests*. Because of remoteness, low productivity and restrictions of
53 use, the overall human impact on these forests has generally remained significantly lower
54 compared with more southern boreal forests at lower latitudes and/or elevations (Veijola,
55 1998). However, over the entire region, some low-intensity human use of the forest has
56 occurred for millennia, such as the influence of the Sápmi people and their reindeer herding
57 culture (Josefsson et al., 2009). Reindeer herding continues to be a culturally important land
58 use, which has recently also generated conflicts with other land uses like forestry (Helle and
59 Jaakkola, 2008; Berg et al., 2008).

60 The exact degree of human impact, i.e. the extent to which the current forests
61 deviate from a natural state, varies strongly across forest types and landscapes, from
62 negligible to local deforestation (Östlund et al., 2015). Nevertheless, these mountain forests
63 still harbor some of the largest areas of relatively natural boreal forest in Northwestern
64 Europe (Aksenov et al., 2014). By natural forest we mean a forest which structure, species
65 composition and processes have not been significantly altered by human activities (Brumelis
66 et al. 2011). Much of our current understanding of natural forest disturbance and
67 successional dynamics and their impact on biodiversity in Fennoscandian conditions is
68 derived from these forests (Kuuluvainen and Aakala, 2011). The ongoing climate change,

69 with a predicted mean annual increase of mean annual temperature by 4°C and precipitation
70 by 20% by the end of the 21st century (IPCC, 2013), is likely to profoundly affect the ecology,
71 dynamics and productivity of these forests in the future (Kellomäki et al., 2008; IPCC, 2013;
72 Gauthier et al., 2015).

73 The ecological character and biological diversity of northern mountain forests reflect
74 to a large extent their Holocene climate and vegetation history. Because of their northern
75 position, continental ice retreated from these areas as late as around 15-10000 years before
76 present (Parducci et al., 2012). Tree species colonized the region from different directions,
77 following the course of retreat of the ice sheet. The developing early Holocene tree
78 communities were accordingly characterized by the forests surviving the glaciation period
79 and surrounding the retreating ice to the west, south and east (Kullman, 2008; Paus et al.,
80 2011; Parducci et al., 2012). Current dominant boreal tree species, pine (*Pinus sylvestris* L.),
81 spruce (*Picea abies* (L.)Karst.) and birch (*Betula pubescens* Ehrh.), all arrived in early
82 Holocene 14-11 kyr B.P in the first de-glaciated areas of western Fennoscandia (Kullman,
83 2008). During the mid-Holocene climatic optimum, thermophilous deciduous tree species
84 like elm and oak occurred in the region.

85 The historic timing of formation of boreal tree species dominance at stand or regional
86 scales differs between species, with birch and pine predating spruce (Kullman, 2008). The
87 spread and development of regional dominance of spruce has occurred in the last ca. 3000
88 years, in parallel with long-term climate changes favoring spruce but disfavoring
89 thermophilous tree species (Kullman, 2001; Giesecke and Bennett, 2004; Bradshaw and
90 Lindbladh, 2005). Concurrently with increasing spruce dominance, high elevation and high
91 latitude forests retreated downhill and southwards (Payette and Lavoie, 1994; Kullman,
92 1995). This process was reversed after the termination of the Little Ice Age (Grove, 1988) in

93 late 19th century. The rate of this recent regain of forest area differs somewhat between
94 geographical regions and between tree species, but has generally accounted for ca. 0.6
95 vertical meters per year in the northeastern part of the mountain forest region (Aakala et al.,
96 2014; Mathisen et al., 2014) and 0.9 vertical meters per year in the southern part (Kullman
97 and Öberg, 2009). Latitudinal advance has occurred with ca. 150 m per year for birch forest
98 and ca. 70 m per year for pine forests (Hofgaard et al., 2013).

99 The impact of climate change on forests close to their bioclimatic range limits entail a
100 complex web of both gradual and episodic abiotic and biotic processes (Hofgaard, 1997;
101 Scheffer et al., 2012). The warming climate changes ecosystem structure and composition
102 through changing competitive relationships among the constituent tree species (Kellomäki et
103 al., 2008). Climatic conditions are changing too fast for long-lived plant species such as trees
104 to respond through natural migration, and this is predicted to increase the probability and
105 severity of disturbance events. In addition other change rate-related developments, such as
106 extreme weather events and insect outbreaks are likely to become more common (IPCC,
107 2013; Gauthier et al., 2015). These perturbations could counteract or reinforce climate-
108 driven changes of the northern mountain forest ecosystems (Hofgaard, 1997; Koven, 2013;
109 Bright et al., 2014). There are historical and modern examples where perturbations, such as
110 cuttings, forest fires or insect outbreaks have pushed northern mountain forest ecosystems
111 to an alternative, non-forested stable state (e.g. Neuvonen et al., 2005; Karlsson et al., 2009;
112 Östlund et al., 2015).

113 A large share of the remaining natural Fennoscandian mountain forests are
114 protected. These forests together with other forests with long history of low human
115 interference and restrictions of utilization, have provided unique possibilities for
116 fundamental research on the ecology of primeval forests at various scales (Kuuluvainen and

117 Aakala, 2011). Thus, much of our current understanding of natural forest disturbance and
118 successional dynamics, and biodiversity concerning Fennoscandian boreal forests as a whole
119 is derived from these northern mountain forests.

120 The main purpose of this paper is to review the current understanding of the
121 dynamics and disturbance ecology of North Fennoscandian mountain forests and to discuss
122 the implications of this knowledge on forest conservation, restoration and ecosystem-based
123 management in the context of ongoing climate change. Specifically, we asked: 1) What is the
124 value of understanding of past ecosystem dynamics considering future conditions? 2) How resilient
125 are the mountain forests in a changing environment? 3) What are the main shortcomings of
126 knowledge concerning the ecology of mountain forests? 4) What are the main lessons learned from
127 ecological research concerning conservation and ecosystem based management?

128

129 **2. Definition, geographic distribution, environmental conditions and forest communities**

130 Due to the location of the region at high latitudes, forests considered as mountain forests
131 are growing at lower elevations than elsewhere in Europe. Hence, we loosely define
132 northern mountain forests as those prevailing in the mountainous region and growing close
133 to the elevational and latitudinal limit of forest distribution. However, tree line areas are
134 excluded from this review. Forest is defined as a tree community with minimum tree height
135 of 5 m and at least 10% of canopy cover (FAO, 2010).

136 In this paper North Fennoscandian mountain forests are defined to stretch
137 latitudinally from southern Swedish Lapland at 64°N to 69°N in northern Norway, and
138 longitudinally from 14°E in Norway to 34°E in the Kola Peninsula, Russia (Fig. 1). In the west,
139 the Scandes Mountains rise to height of 1000-2100 m above sea level (a.s.l.). The area east
140 of the northern Scandes Mountains through northern Finland and to Kola Peninsula is

141 characterized by gently rolling hills (fells), which rarely reach heights above 1000 m a.s.l.. The
142 bedrock in the area is mostly composed of ancient Precambrian granites and gneisses,
143 covered by Quaternary and younger Holocene sediments, mainly podzolized moraines
144 (Lidmar-Bergström and Näslund, 2005).

145 North Fennoscandian mountain forests are unique in that, due to the warming effect of the
146 golf-stream, they grow further north than any other mountain forests. Compared to more
147 southern mountain forests, the light climate is characterized by stronger seasonal changes,
148 with long days in the summer and several months of short days in the winter. The extreme
149 annual variation in solar radiation is reflected in below-zero temperatures and snow cover
150 which prevail for 7-8 months. Also, low sun angles are prevalent for part of the growing
151 season, which emphasizes the effect of topography on the distribution of solar energy, e.g.
152 on south vs. north facing slopes.

153 The climatic differences within the region are further shaped by the location between
154 the Atlantic and Arctic oceans, and the Eurasian continent. The climate ranges from
155 markedly or slightly oceanic close to the Norwegian coast (Moen, 1999), to variably
156 continental in different areas of central and eastern parts of northern Fennoscandia. This
157 gives rise to large differences in precipitation, which varies from 1000 mm in the western
158 part to 450-500 mm in northern Finnish Lapland and 300-400 mm in more continental parts
159 of northern Norway and Sweden (Moen, 1999; Tikkanen, 2005). A considerable share of the
160 precipitation falls as snow during the winter months.

161 Although mixed stands also occur, forests are regionally differentiated into spruce,
162 pine or birch dominance due to topography and edaphic conditions and climate regimes. In
163 general, xeric sites are dominated by pine, while mesic sites follow a post-disturbance
164 successional trajectory from birch as a pioneer species, to the dominance of spruce. At

165 smaller-scales and on sites capable of supporting any of the three main species, tree species
166 dominance is influenced by within-region characteristics and variation in the disturbance
167 regimes.

168 In general, North Fennoscandian mountain forests can be considered as among the
169 last remnants of natural forests in Europe. Here we adopt the view of naturalness described
170 by Brumelis et al., (2011) which puts focus on structures, species and processes as the three
171 core dimensions of forest naturalness. For a large part of the Fennoscandian mountain
172 forests, trees of all species and wide age ranges occur, volumes of dead wood, species
173 richness among plants, fungi and animals are high and natural disturbance processes are still
174 active. As a large fraction of boreal forest species in general are dependent on dead wood
175 (Stokland et al., 2012), the mountains forests represent important core area for many
176 species declining elsewhere in Fennoscandian boreal forests.

177

178 *2.1. Scots pine dominated forests*

179

180 Scots pine dominated forests in North Fennoscandia often occur on rocky or dry
181 sandy and moraine soils, on glaciofluvial soils, on eskers and on delta formations (Raunio et
182 al., 2008). These forests are generally open and exhibit significant variability in structure and
183 successional stages as well as small-scale spatial heterogeneity (Aaltonen, 1919). In spite of
184 their openness, belowground competition plays a major role in tree regeneration and stand
185 dynamics (Kuuluvainen and Ylläsjärvi, 2011). Mixed-severity fires have historically been one
186 driver of forest dynamics (Aaltonen, 1917; Hesselman, 1917), although fire cycles have been
187 longer than previously assumed, up to hundreds of years (Wallenius et al., 2010). Even non-
188 pyrogenic pine dominated forests exist, but at a low frequency (Zackrisson et al., 1995).

189 Species dominating the forest floor include dwarf shrubs *Calluna vulgaris*, *Vaccinium vitis-*
190 *idaea* and *Empetrum hermaphroditum*, and in the bottom layer mosses and lichens such as
191 *Pleurozium schreberi*, *Cladonia arbuscula* and *C. rangiferina*.

192 The degree of naturalness has been declining during recent decades particularly in
193 the pine dominated lichen-rich forests in many regions of the mountain forests. For
194 example, in northern Finland, this is associated with factors such as reduction of old forests
195 due to forestry, and increasing trampling and grazing by reindeer which accelerate nutrient
196 cycling (Raunio et al., 2008). In addition, although fire cycles tend to be long in these
197 northern pine forests (see below), the century long fire suppression represent loss of
198 naturalness (Drobyshev et al., 2014). These factors are also likely future threats to this
199 habitat type, in addition to effects of climate change (Gauthier et al., 2015).

200 A prominent feature in natural pine forests is the presence of large standing dead
201 and bark-less snags, so called kelo trees (*sensu* Niemelä et al., 2002, Fig. 2a). These trees
202 have commonly survived a history of repeated surface fires, and hence their wood has a
203 characteristic high resin content, and are thus highly resistant to decay (Niemelä et al.,
204 2002). As such they represent in some cases a forest structure developing over millennia – as
205 living trees for more than 500 years, and as snags for up to several centuries, before finally
206 falling to the ground and slowly decomposing.

207

208 2.2. Norway spruce dominated forests

209

210 Norway spruce dominated forests cover extensive areas in North Fennoscandian
211 Mountains. These forests are found on mesic to moist sites with varying fertility from
212 productive herb-rich sites to poorer site where mosses and dwarf shrubs (predominantly

213 *Vaccinium myrtillus* L.) dominate the forest floor, and accumulation of poorly decomposed
214 raw humus is prominent (Fig. 2b, Arnborg, 1943; Havas and Kubin, 1981). As fire is rare in
215 Norway spruce dominated forests (Hörnberg et al. 2011; Ohlson et al. 2011), late
216 successional forest dynamics is characterized by gap or patch scale disturbances and
217 regeneration (Hofgaard 1993 a, b; Edman et al., 2007; Aakala and Keto-Tokoi, 2011).
218 Disturbance agents often include wind in combination with fungal infections, insects and
219 snow (Edman et al., 2007; Länneppää et al., 2008). A prominent feature among dying spruce
220 is a general senescence prior to mortality, with either persistent slow growth or steadily
221 declining growth in the decades preceding their deaths (Fraver et al. 2008; Länneppää et al.,
222 2008).

223 In the spruce dominated forests the establishment of tree seedlings is often
224 physically impeded by the ubiquitous mat of dwarf shrubs, grasses, mosses and a layer of
225 poorly decomposed humus, which decreases nutrient availability (Arnborg, 1943; Sirén,
226 1955). Hence regeneration is strongly dependent on the availability of suitable substrates
227 created by local gap or patch disturbances, such as mineral soil exposed by tree falls and
228 uprootings, and decaying logs on the forest floor (Hofgaard, 1993a, b; Hörnberg et al. 1997;
229 Caron et al., 2009; Grenfell et al., 2011). For spruce, individual decaying logs may remain
230 important regeneration substrate for as long as 150 years (Hofgaard, 1993a). This long-term
231 suitability of logs as regeneration substrate counter balance the low frequency production of
232 viable seeds, with good seed years occurring typically many years apart (Hofgaard, 1993c).
233 Spruce may also reproduce vegetatively through layering and form long-lasting clones
234 (Öberg and Kullman, 2011). This is in particular a characteristic in abiotic harsh environments
235 such as the forest-tundra transition and in coastal areas. Overall, the diversity of microsites

236 created by tree falls provide opportunities for recruitment of other tree species in addition
237 to spruce.

238 Accordingly, late successional spruce forest generally maintain some proportion of birch
239 admixture (Steijlen and Zackrisson, 1987).

240 Forest fires are rare in spruce-dominated forests (Ohlson et al. 2011), due to the low
241 flammability of the thick humus layer, which retains moisture for extended periods of time
242 (Tanskanen et al., 2005). However, when conditions are beneficial for forest fires to occur,
243 their impact on forest is usually drastic (Wallenius et al., 2005). This is due to the
244 combination of thin poorly insulating bark and low-hanging branches that create ladder-fuels
245 and promote crown scorching and even crown fires. As a result, spruce trees are easily killed
246 by fire creating a huge amount of dead wood. The post-fire succession usually starts with
247 dominance of deciduous species, mainly birch but also aspen (*Populus tremuloides*) and goat
248 willow (*Salix caprea* L.) (Sirén, 1955). Hence, similar to wind-throws, forest fire support the
249 presence of deciduous species as an important tree component in otherwise spruce
250 dominated landscape.

251

252 *2.3. Mountain birch dominated forests*

253

254 At sites edaphically and climatically suitable for the two conifers, abundance of birch
255 is a characteristic of a transient early-successional stage. However, elsewhere mountain
256 birch dominated forests cover large areas of Northern Fennoscandia (Fig. 2c). The main part
257 of this ecoregion is mainly located in Norway, followed by Sweden and to a lesser extent in
258 Finland and the Kola Peninsula in Russia. These forests characterize the landscape both in
259 coastal and inland areas at elevations and latitudes above and beyond the coniferous boreal

260 forest. In birch-dominated subalpine and subarctic areas, mountain birch is usually referred
261 to at subspecies-level (*B.p. ssp. tortuosa* Ledeb. or *B.p. ssp. czerepanovii* (Orlova) Hämet-Ahti
262 are most common in the literature). When it occurs in other areas in mixture with the
263 coniferous boreal trees, it is generally referred to at species-level, i.e. *B. pubescens*.

264 The mountain birch has a wide bioclimatic range, and species composition of the
265 forest floor varies accordingly. Dwarf shrubs (*Vaccinium* spp., *Empetrum* sp.) are generally
266 most abundant, but herb-rich communities prevail in humid nutrient-rich areas and lichen
267 dominated communities in dry areas. In Norway and Sweden, where reindeer herding is
268 associated with rotation of grazing areas, lichen dominated inland areas are commonly used
269 as winter grazing lands for semi-domesticated reindeer, while herb-rich birch forests are
270 used as summer grazing lands. During the last decades the lichen biomass has decreased due
271 to intense grazing practice, and is being replaced by moss-rich communities (Tømmervik et
272 al., 2009).

273 Natural birch forest dynamics is driven by cyclic and abrupt population increases of
274 defoliating insects, such as the autumnal moth (*Epirrita autumnata*) and winter moth
275 (*Operophtera brumata*) (Tenow, 1972; Tenow et al., 2007). The frequency and intensity of
276 these insect outbreaks are linked to climate at local to regional scales, and can cause large
277 scale stand mortality (Fig. 2d, Tenow and Nilssen; 1990; Neuvonen et al., 2005; Tenow et al.,
278 2007). Following the defoliation and subsequent stem mortality, the birch forest will slowly
279 recover its density through mainly growth of basal sprouts (Tenow, 1996; Tenow and Bylund,
280 2000). Mountain birch has both frequent and high quality seed production throughout its
281 range, as opposed to spruce and pine, and recruitment is not seed limited. However, grazing
282 and browsing animals such as sheep in Norway, and reindeer throughout the region might
283 hinder tree recruitment and maintain open woodland areas (Aune et al., 2011).

284

285 3. Disturbance and successional dynamics

286

287 The accumulated body of information challenges the conventional view that North
288 Fennoscandian mountain forests mostly represent homogeneous and static communities of
289 the 'climax type'. The development of forests is slow indeed, because they grow in harsh
290 climatic conditions in the proximity of the range limits of the constituent tree species.
291 However, these forest ecosystems are in a state of constant change even in the absence of
292 major disturbances (Lilja et al., 2006; Edman et al., 2007; Caron et al., 2009; Aakala et al.,
293 2009).

294 The disturbance agents in mountain forest landscapes vary greatly in their type,
295 severity and spatio-temporal characteristics. Some disturbance factors, such as fires
296 (Kauhanen, 2002; Vajda et al., 2006), storms (Aakala et al., 2009), snow load (Hesselman,
297 1912; Hofgaard et al., 1991) and insect outbreaks (Tenow et al., 2013), are occasionally
298 capable of causing widespread mortality, whereas some operate at smaller scale but more
299 frequently such as pathogenic fungi and browsing/grazing mammals (e.g. moose and
300 reindeer) (Edman et al., 2007; Länneppää et al., 2008), and sometimes snow and slush
301 avalanches, which occasionally reach into forested areas (Fig. 2e). Taken together these
302 multi-cause disturbances act as diversity drivers at a wide range of spatial and temporal
303 scales.

304 At stand scale three basic types of forest dynamics have been suggested to occur
305 (Kuuluvainen, 2009). Two of them are classical modes of forest dynamics: even-aged stand
306 dynamics driven by stand-replacing disturbance, and gap or patch phase dynamics driven by
307 small scale tree mortality mostly in old forests. However, as the review of Kuuluvainen and

308 Aakala (2011) highlights, intermediate severity disturbances, causing partial tree mortality
309 and leading to complex stands structures consisting of multiple tree age cohorts, are also
310 common (Lassila, 1921; Hofgaard, 1993a). In reality, these types of forest dynamics can be
311 mixed in space and time and are thus not easily separable even at stand scale.

312 At landscape scale, these different disturbance factors and the associated dynamics
313 often operate in a mixed or nested manner in space and time. More or less continuously
314 occurring deaths of individual or small groups of trees (gap dynamics) (Kuuluvainen, 1994)
315 often appear superimposed on the more infrequent but larger scale partial disturbance
316 events due to insects, wind or fire (Fraver et al., 2008). This kind of disturbance regime that
317 operates at multiple spatial and temporal scales typically creates variable and complex forest
318 structures (Caron et al., 2009).

319 In the boreal forest, fire is traditionally considered as the dominating disturbance
320 agent (Sirén, 1955; Zackrisson, 1977). In Fennoscandian mountain forests, however, fire has
321 played a smaller role compared to boreal forest at lower elevations and latitudes. This is due
322 to both natural and anthropogenic reasons: these areas show a short fire season due to high
323 precipitation and late snow melt, and the decreasing lightning frequency towards north
324 translate into reduced natural ignitions (Granström, 1993; Larjavaara et al., 2005). In
325 addition, the formerly important anthropogenic driver of ignitions has generally become
326 weaker, especially during the 20th century (Wallenius, 2011). Accordingly, fire history studies
327 using tree rings or cores from peatlands and lake sediments, have shown that prior to
328 significant human influence the fire cycles were in the range of several hundred years
329 (Carcaillet et al., 2007; Wallenius et al., 2010). However, despite fires being rarer than in the
330 southern parts of the boreal forests (Granström, 1993; Larjavaara et al., 2005; Drobyshev et
331 al., 2014), their influence is readily apparent in the age structure and species composition at

332 xeric sites (Lassila, 1921), and in many places these sites still display structures typical for
333 surface-fire driven dynamics (Kuuluvainen and Aakala, 2011).

334 Compared with xeric pine dominated forests, the fire cycles have been longer in
335 moister *Picea abies* dominated forests, and it is possible that parts of northern mountain
336 forests have not burned since the last glaciation (Hyvärinen and Sepponen 1988; Steijlen and
337 Zackrisson, 1987; Fraver et al., 2008). The intrinsically long fire cycles in the spruce-
338 dominated Fennoscandian mountain forests indicate that other disturbance agents than fire
339 play an important role in forest dynamics (Norokorpi, 1979; Hofgaard, 1993; Kuuluvainen
340 and Aakala, 2011). In the absence of fire, tree mortality is caused by wind, competition,
341 fungi, insects and stem breakage due snow loads (Hofgaard et al., 1991; Länneppää et al.,
342 2008), disturbances which are often related to old age and senescence of trees (Fraver et al.,
343 2008). This type of tree mortality agents drive gap phase dynamics resulting in small-scale
344 heterogeneity of forest structure, characterizing both age- and physiognomic structure, in
345 these old growth spruce forests (Hofgaard 1993a,b, Caron et al. 2009). These small-scale gap
346 dynamics result in a fairly constant background mortality that is then occasionally
347 punctuated with episodic larger scale disturbances, especially storms (Jonsson and Dynesius,
348 1993; Kuuluvainen, 1994; Fraver et al., 2008; Aakala et al., 2009). Disturbances such as wind
349 throws expose mineral soil promoting regeneration, and allowing deciduous trees to
350 maintain their presence in otherwise conifer-dominated stands over the longer term in
351 particular (Kuuluvainen, 1994; Grenfell et al., 2011), as well as supporting diversity in the
352 ground vegetation (Jonsson and Esseen, 1990).

353 Forest fires are relatively rare in mesic sites in northern mountain forests, but under
354 favourable conditions, they can be severe and affect large areas (Kauhanen, 2002; Aakala et
355 al., 2009). An example is provided by the northern spruce forest studied by Aakala et al.

356 (2009) which was still dominated by the post-fire tree cohort regenerated following a fire
357 317 years earlier. Such stand-replacing fire events have a significant and long lasting impacts
358 on forest landscape structure, composition and biodiversity (Yli-Sirniö et al., 2012). Stand-
359 replacing fires create open sunny habitats with large amounts of charred dead wood, which
360 harbour a high number of saproxylic species, many of which were earlier thought to be
361 confined to shady and moist old-growth forests (Martikainen, 2000). On fertile soils and
362 mesic conditions the successions following fire are first dominated by deciduous species,
363 such as *Betula* spp., *Populus tremula* and *Salix caprea* (Sirén, 1955; Lilja et al., 2006). Later in
364 succession deciduous tree species give way to *Picea abies* which gains increasing dominance.
365 However, *Betula*, *Populus* and *Salix* trees may remain as a component of the forest for long
366 time periods due to their ability to produce asexual sprouts from the base (*Betula* and *Salix*)
367 and the roots (*Populus*). In particular, this asexual reproduction ability is essential to birch
368 forest recovery after both stand-level and landscape-level insect outbreaks (Tenow, 1996;
369 Tenow and Bylund, 2000). Seed-based recruitment is prohibited or delayed by grazing and
370 field layer competition (Tenow, 1996). The presence of *Populus* and *Salix* have important
371 biodiversity consequences since they host a large number of specialized species (e.g.
372 Martikainen, 2000; Kuusinen, 1996).

373 Although the effect of competition on forest dynamics may be less pronounced than
374 in more productive forests at lower latitudes (Hyttborn et al., 1987) due to the open
375 structure of mountain forests (see Fig. 2), competition may still be a factor regulating tree
376 growth and mortality (Kuuluvainen and Ylläsjärvi 2011). For instance, Aakala et al. (2016)
377 showed that competition clearly influenced the asymmetry of tree crowns, and Fraver et al.
378 (2013) showed that the spatial arrangement of trees within stands regulated inter-tree
379 competition and tree growth in old-growth mountain spruce forest. This latter is further

380 exemplified by distinct growth releases of neighboring trees when single trees die (Dynesius
381 and Jonsson, 1991; Caron et al., 2009).

382 In the big picture of spatio-temporal forest dynamics, different variations of uneven-
383 aged (or cohort-aged) dynamics appear to play a dominant role in Fennoscandian mountain
384 forest dynamics. In *Picea* dominated stands occurring on moist sites this is due to absence of
385 fire and thus inherently long fire rotations (Wallenius et al., 2010) and the predominance of
386 gap or patch dynamics. In dry *Pinus* dominated sites, where fires may be more common, tree
387 mortality is often partial or patchy as large *Pinus* trees with their thick heat-insulating bark
388 often survive surface fires. This, and the post-fire regeneration, result over time in forest
389 with several age cohorts of trees (Lassila 1921; Engelmark et al., 1998). In *Betula* dominated
390 forests insect outbreaks are, in the absence of fire, the main driver of stand dynamics.

391

392 **4. Discussion**

393

394 Research carried out during the past decades has greatly advanced our
395 understanding of the history, ecology, biodiversity and dynamics of North Fennoscandian
396 mountain forest ecosystems, and the varying but ubiquitous long-term influence of humans
397 on these seemingly natural forest ecosystems (Fraver et al., 2008; Josefsson et al., 2009;
398 Kuuluvainen and Aakala, 2011). It is clear that the predicted rapid changes in climate will
399 greatly influence many key biological processes controlling the dynamics of these forests
400 growing close to their northern distribution range. Some of the changes are gradual but also
401 episodic more drastic disturbances will become more likely (Gauthier et al. 2015). As a
402 consequence, the ongoing climate change will exert unprecedented pressures to the
403 “health” of these forests, which are of paramount importance as biodiversity hotspots and

404 as the core of the forest protection area network in the whole of Fennoscandia. Critical
405 components of ecosystem health can be defined as the biodiversity, resilience and adaptive
406 capacity of the constituent ecosystems (Gauthier et al., 2015). These ecosystem properties
407 are the crucial components of forest health and should form the basis of conservation and
408 management actions.

409 Our understanding of the ecology and dynamics of these forests is based on past
410 conditions. A relevant question then is how relevant and useful this knowledge is in the
411 future climatic conditions that will significantly differ from past conditions (Sprugel, 1991;
412 Keane et al., 2009; IPCC, 2013). However, we can identify several important roles that
413 research on past disturbance dynamics can play in forest protection and sustainable
414 ecosystem-based management. First, an often-invoked role is the establishment of baseline
415 or reference information on ecosystem properties and dynamics (e.g. natural range of
416 variability, Willis and Birks, 2006; Keane et al. 2009). Detecting changes is possible only if we
417 have a sufficient understanding of the baseline conditions and their variability. Second, we
418 need knowledge on past forest dynamics to understand how the baseline conditions have
419 historically formed and, for example, what has been the role of human activities in this
420 process (Hofgaard, 1999; Josefsson et al. 2009).

421 Given that humans have lived in the Fennoscandian mountain forests for millennia
422 we can assume that they to some extent have influenced forest structure and dynamics (e.g.
423 Östlund et al. 2004). Prior to colonization by mainly farmers from the south during the 17th
424 and 18th centuries, only indigenous Sami groups lived in these forests. Sami people have
425 traditionally been viewed as finding subsistence from hunting and gathering and relatively
426 late in history becoming dependent on reindeer herding (see Sommerseth 2010). However,
427 the traditional view is being challenged and no consensus on the onset of reindeer herding

428 seems to exist. Also recent studies suggest that Sami land-use was more complex than
429 assumed and may have included small scale shifting cultivation (Östlund et al. 2015). The
430 land use pattern is evident in pollen profiles from local settlements and provide together
431 with archeological evidence an insight in to Sami subsistence patterns (Sommerseth 2010). It
432 is suggested that in some place forest resources may have been overexploited near the tree
433 line, resulting in ecosystem degradation and subsequent shift in land use (Bergman et al.
434 2013). However, in general it is difficult to translate the impact of Sami land use into a
435 broader impact on the forest landscape.

436 Understanding the historical processes is a pre-requisite for appropriate use of the
437 past baseline information. For example, in research on forest change over larger spatial
438 scales, using satellite images and forest inventories, past forest dynamics need to be
439 understood to attribute detected changes to effective drivers. This is necessary to discern
440 the influences of past disturbances from the direct influences of climate change due to
441 warming temperatures, increasing CO₂ concentration or nitrogen deposition (Myneni et al.
442 2001). Another prerequisite for effective monitoring is looking at deviations from baseline
443 conditions at multiple spatial scales.

444 North Fennoscandian mountain forests are occasionally considered to be resilient
445 against adverse changes, particularly because a large part of them is protected (Aksenov et
446 al. 2014). This view may also gain support from the slow growth and sometimes quasi-
447 equilibrium dynamics of late-successional forests (e.g. Caron et al., 2009; Aakala et al., 2009).
448 However, we have learned that these forests are not as stable as was perhaps once assumed
449 and ecological theory predicts that ecosystems close to their distribution range are most
450 vulnerable to sudden state shifts (Atkinson, 1992; Scheffer et al., 2012). For instance, the

451 Holocene history tells us that major changes in altitudinal positions in the treeline ecotone
452 may occur as a result of the predicted changes in future climate (Aakala et al. 2014).

453 It is generally acknowledged that climate change will strongly affect the future
454 development of forests and the predicted temperature increase (IPCC 2013) suggest that the
455 climate conditions in mountain forests will be displaced towards conditions resembling
456 forests at lower altitudes. It is also clear that disturbance is central in vegetation dynamics
457 and in translating climate change into vegetation response (Overpeck et al., 1990). There is a
458 risk that with accumulating environmental stressors in the rapidly warming climate, critical
459 thresholds are surpassed and abrupt changes in ecosystem conditions can become a reality
460 (Gauthier et al. 2015). Old spruce forests are perhaps most vulnerable to the effects of
461 warming climatic conditions and associated disturbances such as droughts, insect outbreaks,
462 and perhaps also fire (Kellomäki et al., 2008; Kuuluvainen et al. 2014).

463 However, we lack understanding of the changing role of disturbances, and especially
464 that of fire in mountain forest ecosystems. In the past centuries, the occurrence of fire has
465 to a great extent been determined by human influences in interaction with those of climatic
466 fluctuations (Drobyshev et al., 2014). First, settlement activities until late 20th century
467 increased fires due to human-caused ignitions. Since forests became a valuable resource, fire
468 was handled more carefully and fire suppression was developed, which resulted in an
469 almost-complete elimination of forest fires over the entire Fennoscandia (Wallenius, 2011;
470 Drobyshev et al., 2014). This was true also in xeric sites where fires have historically been
471 most prevalent. As trees are long-lived, the lack of fire manifests itself gradually, but
472 eventually leads to changes in structure and composition in forests previously shaped by
473 fires. For example, pine regeneration may be impeded while fire-sensitive spruce may gain
474 dominance especially on more moist and fertile sites capable of supporting spruce (Linder et

475 al. 1997; Sutinen et al., 2005). The absence of fire is also reducing the occurrence of early
476 successional deciduous forest in the landscape and the regeneration possibilities for rare
477 biodiversity-maintaining pioneer tree species, such as *Salix caprea*. A climate-induced
478 broadening of the distribution of defoliating insects, such as *Epirrita autumnata*, may
479 potentially hasten this development through reduction of deciduous mixture in conifer-
480 dominated mountain forests (Jepsen et al., 2008).

481 However, predicting the future development of complex ecological systems and their
482 disturbance dynamics is difficult (Messier et al., 2014). In particular, we lack knowledge of
483 possible ecological thresholds of different kinds of mountain forest ecosystems to changing
484 environmental factors, stressors and disturbances. An important question is the interaction
485 of different disturbance factors in a warming climate. We can qualitatively predict, for
486 example, that increased tree mortality due to abiotic factors such as wind or droughts can
487 increase biotic damages (e.g., due to bark beetles) (Kuuluvainen et al., 2014). However,
488 quantitative prediction is difficult because of the unknown ecosystem thresholds and
489 stochastic nature of climate-driven disturbance phenomena, increasing the possibility of
490 unexpected events and surprises (Scheffer et al. 2014). These uncertainties, and the notion
491 that climate change will manifest itself earlier in ecosystems at climatic margins, calls for
492 increasing monitoring of the mountain forest ecosystems.

493 The North Fennoscandian mountain forests are of paramount importance as
494 biodiversity hotspots, for monitoring of environmental change, and as a reference for forest
495 restoration and ecosystem based management (Kuuluvainen and Aakala, 2011; Halme et al.,
496 2013). They also have a rich cultural heritage. Northern mountain forests are important for
497 the indigenous Sápmi people and their reindeer herding culture. However, there is a history
498 of conflicts between reindeer herding and logging activities especially in Finland (Helle and

499 Jaakkola, 2008) and Sweden (Berg et al., 2008), and there will possibly be increasing pressure
500 for timber harvesting in the so far unprotected mountain forests. New economically
501 important and rapidly increasing land uses affecting mountain forests are nature-based
502 tourism and mining. This complex development and potential conflicts between different
503 competing land uses, highlight the need for conservation and ecologically sustainable
504 management based on adequate understanding and prediction of future trajectories of
505 mountain forest ecosystems.

506 Then what could be the main lessons learned from ecological research in North
507 Fennoscandian mountain forests concerning conservation and ecosystem-based
508 management? A major conclusion to be drawn from the ecological research literature is that
509 fine scale processes of disturbance and regeneration, and long-term continuity of structural
510 characteristics are essential features of mountain forests and their dynamics. These are also
511 the ecosystem characteristics and their historical range or variability, which need to be
512 respected if biomass harvesting is considered. However, it could be argued that the main
513 value of the remote and slow-growing Fennoscandian mountain forests is not as a biomass
514 resource. Instead they harbor significant values related to cultural heritage, tourism and
515 recreation, biodiversity, and serving as reference monitor of the effects of climate change in
516 marginal forest ecosystems.

517

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524

525 **References**

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816 **Figure legends**

817

818 Fig. 1. The geographic region (dashed area) indication the mountain forests that are in focus
819 in this paper. Grey shows the distribution of forest.

820

821 Fig. 2 Pine forest in different site types and developmental stages. (a) Old pine forest with
822 standing and fallen Kelo trees (Maltio Strict Nature Reserve, Finnish Lapland). (b) Paludified
823 pine forest on mountain slope (central Norway). (c) Burned pine forest with deciduous
824 regeneration (Murmansk region, Russia). (d) Abundant pine regeneration after forest fire
825 (Murmansk region, Russia). Photos: Timo Kuuluvainen.

826

827 Fig. 3 Forest dynamics stages in mostly spruce dominated moist forests. (a) Old spruce
828 dominated forest with thick raw humus layer (Värriö Strict Nature Reserve, eastern Finnish
829 Lapland). (b) Burned spruce forest with abundant deciduous regeneration (Murmansk region,
830 Russia). (c) Canopy gap in old spruce forest with deciduous regeneration (Murmansk region,
831 Russia). (d) young deciduous forest regenerated after fire in a spruce forest (Pallas-Ylläs
832 National Park, Finnish Lapland. Photos: Timo Kuuluvainen.

833

834 Fig. 4. Mountain birch forest is characterizing large parts of the North Fennoscandian
835 mountain region. (a) Birch trees and forest in autumn color (Abisko, northwestern Sweden).
836 (b) Grass-dominated (*Descampsia flexuosa*) forest floor one year after tree canopy
837 defoliation by autumnal moth (*Epirrita autumnata*) and subsequent nutrient release (Abisko,
838 northwestern Sweden). (c) Slush avalanche track in birch forest, (Tärna Mountains, Sweden).
839 (d) Former mountain birch forest turned into tundra after autumnal moth outbreaks in the
840 1960s (Kevo area, northern Finland). Photos: Annika Hofgaard (a)-(c) and Timo Kuuluvainen
841 (d).

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Figure

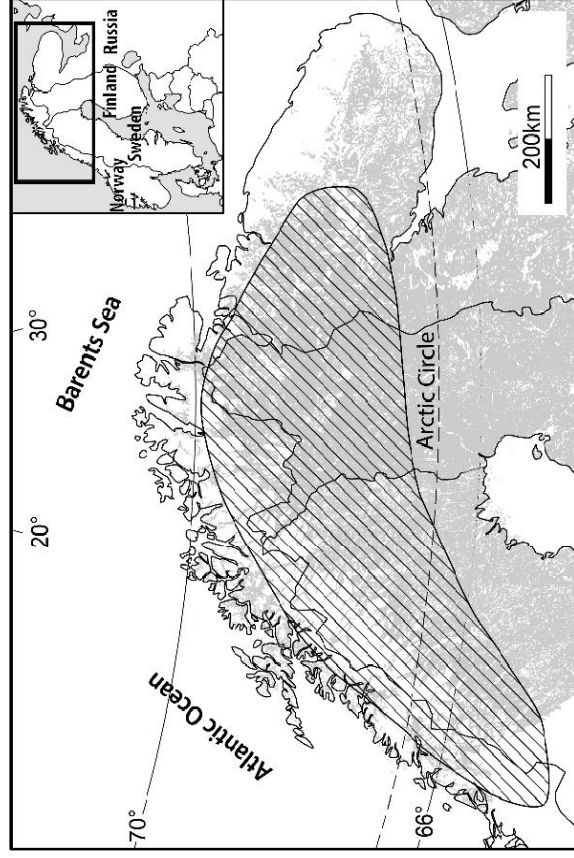


Fig. 1

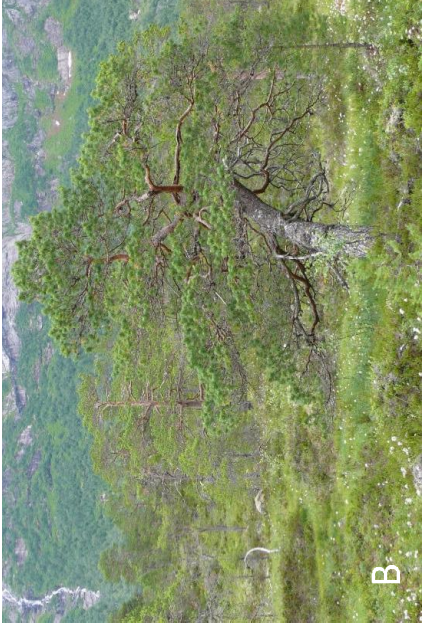


Fig. 2



Fig. 3



Fig. 4

