



Arctic, Antarctic, and Alpine Research

An Interdisciplinary Journal

ISSN: 1523-0430 (Print) 1938-4246 (Online) Journal homepage: <http://www.tandfonline.com/loi/uaar20>

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To cite this article: Anna-Liisa Ylisirniö & Anna Allén (2016) Plant Communities of Fennoscandian Subarctic Mountain Ecosystems 60 Years After Human Disturbance, Arctic, Antarctic, and Alpine Research, 48:3, 469-483, DOI: [10.1657/AAAR0015-068](https://doi.org/10.1657/AAAR0015-068)

To link to this article: <https://doi.org/10.1657/AAAR0015-068>



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Published online: 05 Jan 2018.



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Plant communities of Fennoscandian subarctic mountain ecosystems 60 years after human disturbance

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A B S T R A C T

We studied the vegetation cover of 60-year-old military sites in the subarctic mountain area in northwestern Finnish Lapland, comparing the vegetation of observation posts in the barren mountain and camps in the mountain birch zone to the undisturbed control sites. These kinds of old disturbance areas give us valuable information about resilience and recovery of vegetation in a fragile subarctic environment and allow us to follow up and predict changes under changing climate.

Vegetation of the disturbed sites had not recovered to the initial condition in 60 years; the recovery was slower in the mountain birch zone where the intensity of disturbance had been higher. The coverage of dwarf shrubs, especially *Empetrum hermafroditum* and *Vaccinium myrtillus*, was lower at the military sites as compared to the controls; instead, increased coverage of some graminoids was observed in the observation posts and the transition zones of camps. At the most disturbed patches, cryptogams were still prevailing. The results confirm the observations of earlier studies that rather than ecological recovery, the long-term development of vegetation in disturbance areas in high latitudes shows a shift to functionally different plant communities.

INTRODUCTION

Disturbance of subarctic vegetation has increased during past decades due to increased human activities in the high latitudes (Forbes, 2005). Trampling, camping, industrial activities, and use of all-terrain vehicles cause vegetation damages, having substantial ecological effects on plant communities, soil composition, and microclimate of the sites (e.g., Marion and Cole, 1996; Forbes et al., 2005). Vegetation and topsoil disturbance change species richness, floristic composition, and biomass of plants, increase soil erosion and compaction, and reduce water holding capacity of soil (e.g., Tolvanen et al., 2001; Forbes et al., 2005; Tolvanen and Kangas, 2016). High-latitude regions are characterized by short growing season, low temperatures, low availability of nutrients and thin

humus layers (e.g., Bliss, 1962; Billings, 1987), restricting plant growth and recovery after disturbance. Besides environmental factors, plants' tolerance to disturbance and regeneration after damage are much determined by the specific characteristics of an individual plant species. In general, graminoids and deciduous dwarf shrubs have better tolerance to trampling and higher regeneration rate after disturbance than cushion plants and evergreen dwarf shrubs, due to their high photosynthesis rate and belowground storages of nutrients (Chapin, 1980; Bryant et al., 1983; Karlsson, 1985; Cole, 1995a, 1995b; Tolvanen et al., 2001).

Despite relatively large-scale research on the effects of trampling and soil removal on vegetation (e.g., Cole, 1995a, 1995b; Gellatly et al., 1986; Marion and Cole, 1996; Hautala et al., 2001; Törn et al., 2006), relatively little is known on the long-

term recovery of vegetation in the high latitudes. Most of the studies conducted have examined recovery in the short term, the average time after disturbance being 1–5 years, and there are only a few studies covering a time frame of several decades. Even though some of the short-term studies show relatively rapid recovery of vegetation after damage (e.g., Emanuelsson, 1984; Tolvanen et al., 2001), the few existing long-term studies indicate that the recovery can be incomplete (Wielgolaski, 1998; Jorgenson et al., 2010) or temporary (Willard et al., 2007), or that the plant communities have not recovered to initial communities but have changed toward different stable-state communities (Forbes, 1996; Becker and Pollard, 2016). The long-term studies to date have been conducted in barren mountain regions, and our knowledge on the long-term natural regeneration of vegetation is limited, especially concerning the subarctic mountain birch (*Betula pubescens* ssp. *czerepanowii*) zone, which is typical for Fennoscandian mountain areas between barren mountain belt and coniferous forest located at lower altitudes. The upper limit of the mountain birch zone in the southeastern Norwegian mountains is at about 1300 m a.s.l., whereas in the northernmost Fennoscandia (at 71°N) it is almost at the sea level (Aas and Faarlund, 2001).

The aim of this study was to investigate the plant communities at the 64-year-old military sites in Malla Strict Nature Reserve, NW Finnish Lapland. We compared the vegetation of the observation posts in the barren mountain zone and the camps located in the mountain birch zone to the control sites on each zone. Our expectation was that the vegetation cover would be more disturbed in the barren mountain than in the mountain birch zone, because earlier studies indicated that mountain biotopes are more vulnerable to trampling than forested biotopes (Hoogesteger, 1984; Kangas et al., 2007). We also wanted to investigate if there were differences in regeneration in the spots with different disturbance intensity on the camps, where the bases of former huts had inevitably been subjected to more disturbance than their surroundings. These kinds of studies are important in order to understand the resilience and recovery of vegetation in a fragile subarctic environment, and also to follow up and predict changes under changing climate conditions, which may alter substantially environmental circumstances in the high latitudes.

MATERIALS AND METHODS

Study Area

The Malla Strict Nature Reserve (69°04'N, 20°40'E) is located in the Kilpisjärvi area in western Lapland, representing the most northeastern part of the Scandes mountain range (Fig. 1). The reserve area (30.5 km²), is characterized by subarctic mountains ranging in the altitudes between 472 and 951 m a.s.l. The region is composed of caledonian bedrock with limestone, and it is known for its rare vegetation. The lower parts of the mountains are covered by mountain birch with the tree line limit at ~600 m a.s.l. (Kauhanen and Mattsson, 2005). The area is among the coldest regions in Finland with an annual mean temperature of -1.9 °C and growing season of approximately 109 days (Finnish Meteorological Institute, 1998–2002).

The reserve has been mainly out of human use since 1916, when the area was protected, except for one hiking route that traverses the reserve and is open to the public. Nowadays, the route attracts about 10,000 hikers yearly (Ohenoja, 2009). Before protection, the area was used by Sámi reindeer herders as a summer pasture. After establishment of the reserve, grazing was forbidden, and reindeer have been mainly out of the area except for some years during past decades, when reindeer have occasionally escaped into the reserve and grazed there during the summer months (Jokinen and Heikkinen, 2005; Heikkinen et al., 2005). The main human activity in the reserve was, however, at the end of World War II, when the German army established military sites in Malla and the other nearby mountains before retreating to Norway. About 1000 men spent seven months in the reserve area in 1944–1945 between mid-September and the end of April. The occupied sites were documented on a map made by the Finnish army in May 1945 (Anonymous, 1945), and they comprised both observation posts in the barren mountain zone and camps where the soldiers lived, located lower, in the mountain birch zone. The observation posts, built of stones and metal, were occupied by 4–5 men at a time. The camps consisted of plywood huts, each of which housed 16–18 men (Urho Wiik, personal communication, 22 June 2009). The vegetation damage caused by

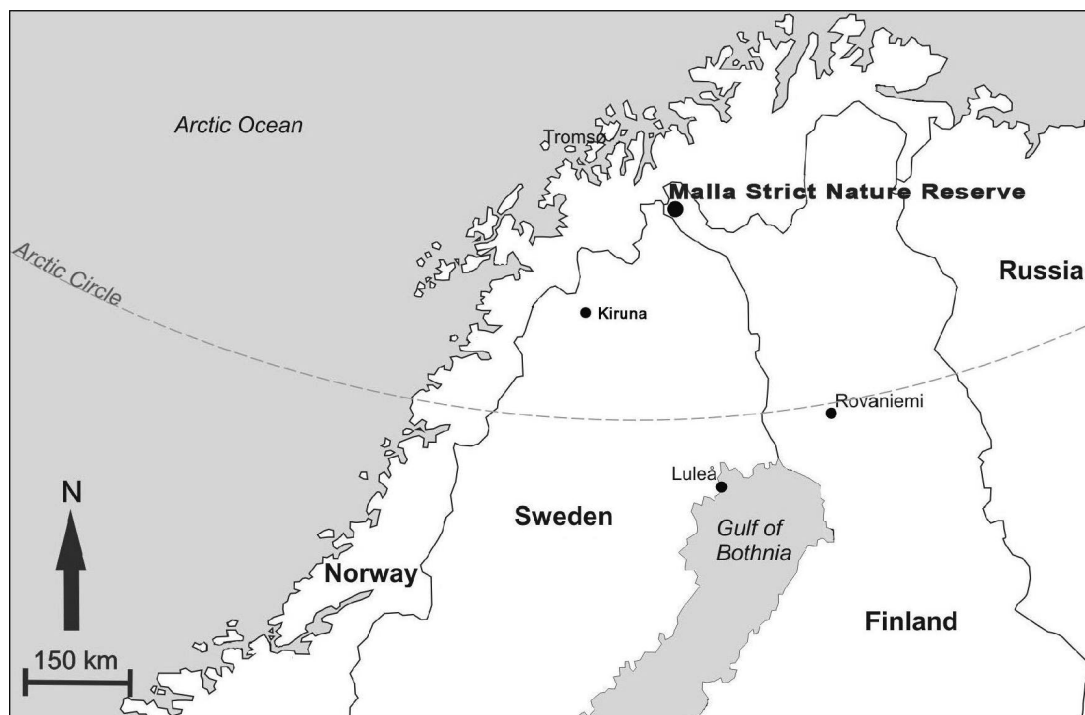


FIGURE 1. Location of the study area.

the soldiers gives us an opportunity to study natural succession of vegetation in a timeframe of over 60 years. Apart from the collection of wood and metal from the camps immediately after the war and one operation to clean up metal waste in the 1980s, the sites have remained untouched without human interference. We expect that the possible influence of other environmental factors, such as variation in climate and occasional short-term grazing by reindeer have affected equally both the military sites and their controls.

Study Sites

We made a field survey using the map made by the Finnish army in May 1945 (Anonymous, 1945) to detect sites that could be reliably recognized as old military sites. Among those, we selected five observation posts in the barren mountain and five camps in mountain birch zone, choosing sites that were visually as similar as possible to each other by their vegetation type and topography on both zones. A control site was set up 100–200 m apart from each military site, totaling 20 study sites. We assumed that the control sites were not

considerably disturbed during the military activity because their vegetation was similar to overall vegetation of each vegetation site type and had no visible signs of disturbance. The sites in the barren mountain zone were located 602–687 m a.s.l. and represented suboceanic heath vegetation with *Empetrum hermaphroditum*, *Betula nana*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Cassiope hypnoides*, and *Salix herbacea* as dominating plants; exceptions were one site and its control, which represented oligotrophic heath with lower coverage of vascular plants and higher coverage of lichens in the group *Cladonia cornuta* coll. and mosses of *Polytrichum* family. The sites in the mountain birch zone were located 501–560 m a.s.l. and were characterized by 3–4 m tall birch trees (*B. pubescens* ssp. *czerepanovii*) at the control sites, the dominant higher plants being *E. hermaphroditum*, *V. myrtillus*, *Vaccinium uliginosum*, and *Deschampsia flexuosa*.

At each site we established 10 study plots of 1 m². In the barren mountain zone, the plots were located at 5 m intervals along a 50 m line starting from the observation post. On the camps in the mountain birch zone, the plots were located at 5 m intervals along two or three parallel lines

reaching across the former camp, with a distance between the lines of 3 m. At the control sites, the study plots were located along one 50-m-long line with 5 m intervals. The percentage coverage of bottom layer (mosses and lichens) and field layer (vascular plants <50 cm) were studied at each 1 m² plot, using visual estimation. In addition, trees or bushes >50 cm were estimated separately. We also recorded the altitude and exposition of the site by global positioning system (GPS), and measured the thickness of the humus layer by exposing the soil layers by knife in the four corners of each plot, but outside the 1 m² area, and measured the thickness of humus layer by a measure with an accuracy of one millimeter. In addition, we estimated visually the percentage coverage of exposed soil, stones, litter, and metal waste. To avoid bias in estimation, all the investigations were conducted by the same person. On the camps, we also used the same study plots to examine three damage intensity categories in relation to the location of former huts: (1) the area under the bases of the huts (22 plots), (2) the transition zone (the strip of land between the huts and the visibly less disturbed vegetation cover between the huts, 11 plots), and (3) the area between the huts (with visibly less disturbed vegetation, 17 plots). All the measurements were made in July–August 2009.

Data Analysis

We used nonparametric multi-response permutation procedures (MRPPs) to examine the differences in the plant coverage between military camps and controls within both zones, using Bray–Curtis matrix calculated from plant species percentage cover. The distance matrix was rank transformed to make the analysis more sensitive (McCune et al., 2000; McCune and Grace, 2002). The test-value T shows the difference between groups: the greater the difference is, the more negative the T value. The p -value shows the probability that the T -value was obtained by chance. The test value A expresses the chance-corrected within-group agreement; $A = 1 - (\text{observed } \Delta / \text{expected } \Delta)$, where Δ is the overall weighted mean of within-group means of the pairwise dissimilarities among sampling units.

$A_{\text{max}} = 1$ when all items are identical within groups ($\Delta = 0$)

$A = 0$ when heterogeneity within groups equals expectation by chance

$A < 0$ with more heterogeneity within groups than expected by chance

Indicator species analysis (IndVal; Dufrene and Legendre, 1997) was used to detect the indicator value of a plant species or functional group in each study category. The value indicates how often a species occurs in the specific group, and how faithful it is to the group. The Monte Carlo method was then used to test the reliability of the indicator value. In this method, random groups are created from the original data and tested to ascertain whether these give indicator values as high as those in the real data. The procedure is repeated 5000 times, and the resulting p -value expresses the probability of obtaining an equal or greater indicator value from the randomized data (Dufrene and Legendre, 1997).

Nonmetric multidimensional scaling (NMS, McCune and Grace, 2002) was used to detect similarities in the species composition. The NMS analysis was conducted with seven functional groups of plants: (1) bushes and trees, (2) dwarf shrubs, (3) herbs, (4) graminoids (including grasses and grass-like plants such as sedges and *Luzula* species), (5) mosses, (6) liverworts and (7) lichens. Differences between environmental variables (thickness of humus layer, coverage of exposed soil, stones, litter, metal waste, and altitude and exposition of the site) and between the vegetation coverage of bottom and field layers were examined using the Mann–Whitney nonparametric test, because all the variables were not normally distributed. The environmental variables were also used as explanatory variables in the ordination analysis. Differences in the vegetation cover among the three damage intensity categories of the camps were studied using both MRPP and indicator species analyses. All the analyses were performed with PC-ORD (McCune and Grace, 2002) except for the Mann–Whitney pairwise tests, which were run using SPSS 16.0 for Windows (SPSS incorporated). The number of vegetation plots was equal ($5 \times 10 \text{ plots} = 50$) in all other analyses except in the analysis of damage intensity categories, where the number of plots was 22 under the huts, 11 in the transition zone, and 17 between the huts.



FIGURE 2. Camp site in the mountain birch zone, showing a distinct boundary between the dwarf shrub vegetation of an undisturbed area and the camp site covered mainly by lichens of the *Cetraria* and *Cladonia* genera, mosses of the *Polytrichum* genus, and graminoids such as *Deschampsia flexuosa*.

RESULTS

Vegetation Coverage at the Military Sites and Their Controls

In the mountain birch zone, the camps were clearly visible in the terrain as circles several meters in diameter (Fig. 2). A great deal of mineral soil was exposed at the bases of camps (difference to the controls $p = 0.032$, Table 1), and metal rubbish was found commonly (Table 1). The mean thickness of

the humus layer was more than double at the control sites compared with the camps (Table 1), however, the difference was not statistically significant due to large variation among the control sites. The MRPP analysis showed significant differences in the species composition between the camp sites and their controls ($T = -2.406$, $A = 0.149$, $p = 0.017$). The coverage of dwarf shrubs was lower at the camps than at the controls ($IV = 64.1$, $p = 0.009$); especially *V. myrtillus* ($IV = 69.8$, $p = 0.007$) and *E. hermafroditum* ($IV = 66.0$, $p = 0.040$) showed lower coverage (Table 2).

TABLE 1

The mean values (\pm S.D.) of site variables measured at camp sites and their controls (Control CS) in the mountain birch zone, and at the observation posts and their controls (Control OP) in the barren mountain zone. All values except for humus (cm) are percentages of the maximum coverage (100%). The p -values of the Mann-Whitney (M-W) pairwise comparison between the disturbed sites and their controls are given with the significance limit $p = 0.05$. Significant differences are in bold.

	Mineral soil	Stones	Litter	Pieces of wood >0.5 cm	Metal rubbish	Humus
Camp sites	2.6 \pm 3.5	1.3 \pm 1.0	39.8 \pm 12.3	0.8 \pm 0.7	3.7 \pm 4.4	17.6 \pm 10.9
Control CS	0.2 \pm 0.7	0.3 \pm 0.3	52.0 \pm 5.9	0.6 \pm 0.6	0.0	37.7 \pm 25.6
M-W U	2.00	3.50	20.50	11.00	2.50	18.00
M-W p -value	0.032	0.056	0.095	0.841	0.032	0.310
Observation posts	2.9 \pm 3.7	7.8 \pm 4.8	21.0 \pm 4.6	0.1 \pm 0.3	2.1 \pm 4.6	22.5 \pm 10.1
Control OP	1.2 \pm 1.0	3.2 \pm 2.9	32.6 \pm 17.4	0.2 \pm 0.5	0.0	42.3 \pm 11.9
M-W U	11.00	6.00	34.00	13.00	7.5	25.00
M-W p -value	0.841	0.222	0.222	1.00	0.310	0.008

TABLE 2

Results of indicator analysis of functional plant groups and some individual species and genera comparing the camp sites and their controls in the mountain birch zone. IV = indicator value. The p -value shows the probability of obtaining an equal or greater indicator value by chance. Significant differences are in bold.

	Highest coverage	IV	p
Functional group			
Dwarf shrubs	Control	64.1	0.009
Mosses	Control	54.5	0.393
Herbs	Control	54.1	0.655
Graminoids	Control	35.4	0.673
Liverworts	Camp site	65.1	0.183
Lichens	Camp site	58.7	0.517
Bushes/trees	Camp site	52.1	0.878
Genera			
<i>Cetraria</i>	Camp site	75.3	0.350
<i>Peltigera</i>	Camp site	69.3	0.236
<i>Stereocaulon</i>	Camp site	58.5	0.452
<i>Polytrichum</i>	Camp site	57.3	0.563
<i>Nephroma</i>	Control	66.5	0.386
<i>Dicranum</i>	Control	62.8	0.262
<i>Pleurozium</i>	Control	42.7	0.881
Species			
<i>Vaccinium myrtillus</i>	Control	69.8	0.007
<i>Empetrum hermaphroditum</i>	Control	66.0	0.040
<i>Vaccinium uliginosum</i>	Control	56.2	0.312
<i>Deschampsia flexuosa</i>	Camp site	52.9	0.711
<i>Epilobium angustifolium</i>	Camp site	60.0	0.156

The vegetation in the barren mountain zone was generally sparse and open (Fig. 3). The humus layer at the observation posts was significantly thinner as compared with the control sites (22.5 mm vs. 42.3 mm, $p = 0.008$, Table 1). No significant differences were detected in the vegetation coverage of observation posts and their controls in the MRPP analysis ($T = 0.117$, $A = -0.007$, $p = 0.454$); however, the indicator analysis showed that the coverage of *E. hermaphroditum* was lower at the observation posts than at the controls, the difference being nearly significant ($IV = 68.9$, $p = 0.090$, Table 3). Furthermore, the data indicated increased coverage of graminoids *Carex bigelowii*, *Juncus trifidus*, and *Deschampsia flexuosa* at the observation posts (Table 4), and the species had high

indicator values (Table 3), even though the differences were not statistically significant. Similarly, *Salix herbacea* showed higher and *Cassiope hypnoides* lower coverage at the disturbed sites compared with the control sites (Table 4).

Ordination Analysis

The two main axes explained a total of 79% of the variation in the data in the ordination analysis. The highest explanatory value (58%) was shown by axis one (vertical axis), which correlated positively with altitude and negatively with litter and woody material on the ground (Fig. 4). It divided the sites of the barren mountain zone from those in the birch zone, having a positive



FIGURE 3. Two collapsed observation posts in the barren mountain zone. The undisturbed vegetation on the steep slope in the foreground consists of dwarf shrubs and lichens mainly of the genera *Cladonia* and *Stereocaulon*, whereas the disturbed area in front of and between the remains of the two observation posts consists mainly of graminoids.

correlation with lichen coverage (Pearson $r = 0.875$) and a negative correlation with liverworts ($r = -0.808$) and bushes and trees ($r = -0.732$). The second (horizontal) axis (explanatory value 21%) distinguished disturbed areas from their controls, correlating positively with the coverage of stones and metal waste and negatively with the thickness of the humus layer (Fig. 4) and the coverage of dwarf shrubs ($r = -0.695$) and mosses ($r = -0.648$). In general, the disturbed and undisturbed sites were more clearly separated from each other in the mountain birch zone, whereas both the observation posts and their controls of the barren mountain zone resembled more each other in their vegetation communities.

Damage Intensity Categories at the Camp Sites

The MRPP analysis revealed distinct variation in vegetation cover among the three damage intensity categories of the camp locations (1 = the area under the huts, 2 = the transition zone, 3 = the area between the huts), the greatest difference being in the vegetation under the huts and between the huts ($T = -3.48$, $A = 0.25$, $p = 0.005$). The indicator analysis revealed that *E. hermafroditum* had the highest coverage in the area between the huts ($IV = 57.6$, $p = 0.010$), whereas the moss *Polytrichum* thrived under the huts ($IV = 58.3$, p

$= 0.003$, Table 5). The difference in the coverage of mountain birch seedlings and sprouts between the damage intensity categories was nearly significant ($IV = 70.2$, $p = 0.072$, Table 5). In general, mountain birch seedlings and sprouts were found equally on the camps (the average coverage 3.8%) and their controls (4.2%), but at the camp sites they were clearly more abundant between the huts (the average coverage 9.3%) compared with their coverage under the huts (0.5%) or in the transition zone (0.8%). The transition zone showed increased coverage of graminoids (Fig. 5), especially *Deschampsia flexuosa* (Table 5).

DISCUSSION

The results show that the subarctic mountain vegetation that was disturbed at the military sites during World War II had not recovered in 64 years. The MRPP analysis showed distinct differences in the species composition between the disturbed sites and their controls in the mountain birch zone, with reduction of dwarf shrubs *Vaccinium myrtillus* and *Empetrum hermafroditum*. Contrary to expectations and the results of some earlier studies (e.g., Hoogesteger, 1984; Kangas et al., 2007), differences in the vegetation as compared to the controls were greater on the camps in the mountain birch zone than at the observation posts above the tree line.

TABLE 3

Results of indicator analysis of functional plant groups and some individual species and genera comparing the observation posts and their controls in the barren mountain zone. IV = indicator value. The *p*-value shows the probability of obtaining an equal or greater indicator value by chance. Significant differences are in bold.

	Highest coverage	IV	<i>p</i>
Functional group			
Lichens	Control	57.7	0.180
Dwarf shrubs	Control	55.7	0.279
Bushes	Control	53.8	0.507
Mosses	Control	52.4	0.759
Graminoids	Observation post	72.7	0.168
Herbs	Observation post	58.0	0.673
Liverworts	Observation post	50.8	0.923
Genera			
<i>Stereocaulon</i>	Control	71.6	0.288
<i>Cladonia cornuta</i> coll.	Control	58.7	0.236
<i>Ochrolechia</i>	Control	57.4	0.360
<i>Cetraria</i>	Observation post	60.5	0.282
Species			
<i>Empetrum hermaphroditum</i>	Control	68.9	0.090
<i>Hierochloë alpina</i>	Control	58.8	0.176
<i>Cassiope hypnoides</i>	Control	53.0	0.638
<i>Juncus trifidus</i>	Observation post	76.1	0.185
<i>Carex bigelowii</i>	Observation post	68.2	0.224
<i>Salix herbacea</i>	Observation post	67.0	0.209
<i>Solidago virgaurea</i>	Observation post	63.6	0.277
<i>Deschampsia flexuosa</i>	Observation post	60.3	0.477
<i>Agrostis mertensii</i>	Observation post	53.8	0.282

This can be attributed to several factors—for example, differences in the intensity of trampling and the physical factors affecting the vegetation coverage of these two habitats. Vegetation in the barren mountains of the area is naturally sparse and open due to frost and harsh climate conditions, containing bare soil and unestablished plant communities even in undisturbed areas (Kauhanen and Mattsson, 2005). The trampling intensity has evidently been lower at the observation posts, which were occupied by 4–5 men at a time, compared to the camp sites, where 16–18 men occupied one hut continuously and several huts were grouped together. Trampling experiments in northern Fennoscandia show a relatively low threshold in the trampling

tolerance of mountain heath vegetation: 150–200 tramples caused 30%–40% loss in vegetation (Gellatly et al., 1986; Törn et al., 2006), and even 25 trampling passes caused visible signs in vegetation (Tolvanen et al., 2001). Our study lacks information on the initial coverage of vegetation before the sites were established, but the differences in vegetation around the observation posts and camp sites compared to the present controls indicate that the damage had exceeded the threshold limit and altered the plant communities at the disturbed sites. Furthermore, the thinner humus layer at the military sites in both zones as compared to the control sites indicates long-term effects of disturbance on plant biomass accumulation and decomposition.

TABLE 4

The mean coverage of vascular plants and genera of lichens and liverworts per site at the observation posts and their controls (Control OP) in the barren mountain zone, and the camp sites and their controls (Control CS) in the mountain birch zone.

	Observation post	Control OP	Camp site	Control CS
<i>Agrostis capillaris</i>	0.01	0.02	0.0	0.0
<i>Agrostis mertensii</i>	0.4	0.1	0.0	0.0
<i>Andromeda polifolia</i>	0.0	0.0	0.0	0.2
<i>Anthoxanthum odoratum</i> ssp. <i>alpinum</i>	0.01	0.0	0.0	0.0
<i>Arctostaphylos alpina</i>	0.1	0.1	0.1	0.0
<i>Arctostaphylos uva-ursi</i>	0.1	0.4	0.4	0.1
<i>Bartsia alpina</i>	0.0	0.0	0.0	0.0
<i>Betula nana</i> L.	11.1	10.1	4.1	3.2
<i>Betula pubescens</i> ssp. <i>czerepanovii</i>	0.0	0.0	3.8	4.2
<i>Bistorta vivipara</i>	0.2	0.2	0.0	0.0
<i>Calamagrostis neglecta</i>	0.8	0.6	0.0	0.0
<i>Campanula rotundifolia</i>	0.0	0.0	0.02	0.0
<i>Cardamine bellidifolia</i>	0.01	0.0	0.0	0.0
<i>Carex bigelowii</i>	1.4	0.7	0.0	0.2
<i>Carex canescens</i>	0.0	0.01	0.0	0.0
<i>Carex vaginata</i>	0.01	0.0	0.0	0.0
<i>Carex norvegica</i>	0.01	0.0	0.0	0.0
<i>Cassiope hypnoides</i>	0.3	2.2	0.0	0.0
<i>Cassiope tetragona</i>	0.0	0.01	0.0	0.0
<i>Cornus suecica</i>	0.0	0.0	1.2	2.5
<i>Deschampsia flexuosa</i>	3.0	2.0	6.6	5.8
<i>Diapensia lapponica</i>	0.1	0.0	0.0	0.0
<i>Diphasiastrum alpinum</i>	1.7	0.8	0.1	0.0
<i>Empetrum hermafroditum</i>	8.7	19.2	8.6	16.7
<i>Epilobium angustifolium</i>	0.0	0.0	0.1	0.0
<i>Festuca ovina</i>	0.1	0.1	0.2	0.0
<i>Gnaphalium norvegicum</i>	0.4	0.0	0.0	0.0
<i>Gnaphalium supinum</i>	0.1	0.1	0.0	0.0
<i>Hieracium alpina</i>	0.2	0.1	0.0	0.0
<i>Hierochloë alpina</i>	0.0	0.3	0.0	0.0
<i>Huperzia selago</i> ssp. <i>arctica</i>	0.04	0.0	0.0	0.0
<i>Juncus trifidus</i>	2.7	0.9	0.1	0.0
<i>Juniperus communis</i>	0.0	0.3	0.8	0.8
<i>Linnaea borealis</i>	0.0	0.0	0.2	0.3
<i>Loiseleuria procumbens</i>	0.5	0.6	0.1	0.0
<i>Luzula multiflora</i> ssp. <i>frigida</i>	0.1	0.0	0.0	0.0
<i>Luzula spicata</i>	0.0	0.02	0.0	0.0
<i>Lycopodium annotinum</i> ssp. <i>alpestre</i>	0.0	0.1	0.0	0.0
<i>Oxyria digyna</i>	0.02	0.0	0.0	0.0
<i>Phyllodoce caerulea</i>	1.1	1.0	2.4	1.7
<i>Pedicularis lapponica</i>	0.2	0.1	0.1	0.1
<i>Pyrola rotundifolia</i> ssp. <i>norvegica</i>	0.02	0.02	0.03	0.0

TABLE 4
Continued

	Observation post	Control OP	Camp site	Control CS
<i>Rubus chamaemorus</i>	0.0	0.03	0.0	0.0
<i>Salix galuca</i>	0.1	0.0	0.1	0.0
<i>Salix hastata</i> ssp. <i>hastata</i>	0.0	0.0	0.1	0.0
<i>Salix herbacea</i>	5.5	2.7	0.1	0.6
<i>Salix polaris</i>	0.0	0.01	0.0	0.0
<i>Salix reticulata</i>	0.0	0.1	0.0	0.0
<i>Saussurea alpina</i>	0.0	0.1	0.0	0.0
<i>Selaginella selaginoides</i>	0.01	0.01	0.0	0.0
<i>Sibbaldia procumbens</i>	0.1	0.2	0.0	0.0
<i>Solidago virgaurea</i>	0.8	0.5	1.3	0.9
<i>Tofieldia pusilla</i>	0.0	0.04	0.0	0.0
<i>Trientalis europaea</i>	0.1	0.0	0.2	0.0
<i>Trisetum spicatum</i>	0.01	0.0	0.0	0.0
<i>Trollius europaeus</i>	0.0	0.04	0.0	0.0
<i>Vaccinium myrtillus</i>	3.3	4.6	5.7	13.1
<i>Vaccinium vitis-idaea</i>	4.0	3.4	4.0	5.0
<i>Vaccinium uliginosum</i>	0.3	0.9	0.3	5.1
<i>Vahlodea atropurpurea</i>	0.2	0.0	0.0	0.0
<i>Viola biflora</i>	0.2	0.3	0.0	0.0
<i>Alectoria</i> sp.	0.1	0.0	0.0	0.0
<i>Cetraria</i> sp.	1.8	1.2	0.5	0.1
CLADCORN coll.	10.5	14.9	8.0	5.0
CLADRANG coll.	3.5	4.1	1.2	1.8
<i>Flavocetraria</i> sp.	0.7	0.2	0.0	0.0
<i>Icmadophila</i> sp.	0.0	0.0	0.0	0.0
<i>Nephroma</i> sp.	1.5	1.6	1.1	2.2
<i>Ochrolechia</i> sp.	0.7	0.9	0.0	0.0
<i>Peltigera</i> sp.	0.7	0.5	1.3	0.2
<i>Solorina</i> sp.	0.1	0.1	0.4	0.0
<i>Sphaerophorus</i> sp.	0.2	0.1	0.0	0.0
<i>Stereocaulon</i> sp.	3.2	8.1	1.7	1.2
<i>Thamnia</i> sp.	0.02	0.0	0.0	0.0
<i>Dicranum</i> sp.	13.8	15.1	6.9	11.7
<i>Hylocomium</i> sp.	0.1	0.4	0.7	0.4
<i>Pleurozium</i> sp.	0.0	1.2	3.2	3.7
<i>Racomitrium</i> sp.	0.02	0.0	0.0	0.0
<i>Pohlia</i> sp.	0.3	0.0	0.0	0.0
<i>Polytrichum</i> sp.	5.3	4.5	6.7	5.0
<i>Ptilidium</i> sp.	1.3	0.8	0.1	0.0
<i>Sphagnum</i> sp.	0.0	1.0	0.0	0.3
Marchantiidae	3.3	3.2	13.8	7.4

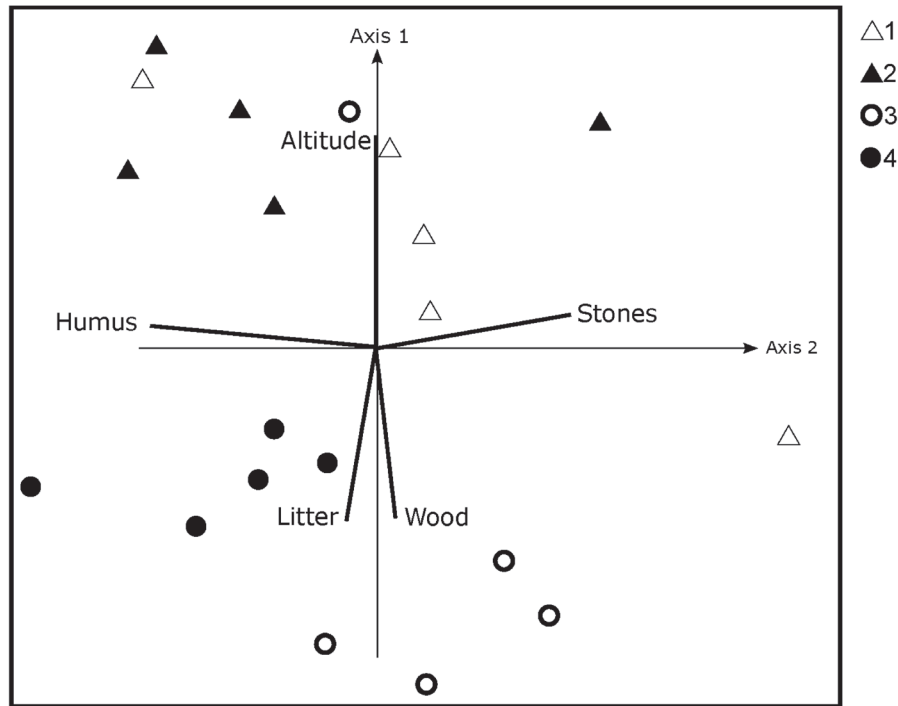


FIGURE 4. Nonmetric multidimensional scaling (NMS) ordination of the study sites, based on the environmental variables and functional groups of plants (bushes and trees, dwarf shrubs, herbs, graminoids, mosses, liverworts and lichens). Symbols: 1 = observation post, barren mountain, 2 = control, barren mountain, 3 = camp, mountain birch zone, 4 = control, mountain birch zone.

In general, the vegetation at the camp sites in the mountain birch zone differed significantly from the thick dwarf shrub coverage found at the control sites. Site characteristics such as slope steepness, exposition, and soil texture affect the vulnerability of vegetation to damage (e.g., Törn et al., 2006). Compacted soil, exposed mineral soil, and destruction of the humus layer decrease absorption of water and increase erosion (Marion and Cole, 1996) and also intensify frost and variation in microclimate (Mäkipää, 1999). Even though these physical and chemical factors influence the extent of damage and the recovery rate of vegetation, earlier studies indicate that morphological characteristics of plants may contribute even more to explaining the variation in response to trampling (Cole, 1995a, 1995b). At our study sites, *E. hermafroditum* and *V. myrtillus* were the vascular plants most affected in terms of coverage in both vegetation zones, and *C. hypnoides* showed reduced coverage at the disturbed sites in the barren mountain zone, all these being chamaephytes with their perenniating buds above

the ground surface. This life form has been found to be more vulnerable to trampling than hemicryptophytes and geophytes (Cole, 1995b). *E. hermafroditum* is known to be very sensitive to mechanical disturbance, whereas *V. myrtillus* and *V. vitis-idaea* are intermediate in their trampling tolerance (Hoogesteger, 1984; Tybirk et al., 2000; Tolvanen et al., 2001). *Vaccinium* species are able to grow from belowground stems, which can assist in recovery provided that they have been saved from the damage (Hautala et al., 2001), which may explain their better tolerance to trampling compared with *E. hermafroditum*. However, in 60- to 70-year-old disturbance areas in Disko Bay, Greenland, *Empetrum* had reentered the disturbed areas after 60 years, whereas recovery was slower in the *Vaccinium* and *Cassiope* dominated dwarf shrub heaths (Tybirk et al., 2000). Our study did not show substantial differences between these species in recovery at the observation posts, but at the camp sites, *E. hermafroditum* and *Juniperus communis* had the highest coverage between the huts, indicating some recovery of shrubs and

TABLE 5

Results of indicator analysis of functional plant groups and some individual species and genera in the three damage intensity categories of the camps: under the huts (Under), in the transition zone between the huts and the vegetation cover between them (Transition), and on visibly less disturbed vegetation between the huts (Between). IV = indicator value. The *p*-value shows the probability of obtaining an equal or greater indicator value by chance. Significant differences are in bold.

	Highest coverage	IV	<i>p</i>
Functional group			
Bushes and trees	Between	83.1	0.007
Dwarf shrubs	Between	54.3	0.008
Mosses	Between	39.2	0.562
Herbs	Between	35.9	0.715
Graminoids	Transition	49.8	0.124
Lichens	Under	45.6	0.370
Liverworts	Under	31.9	0.990
Genera			
<i>Cetraria</i>	Under	67.4	0.065
<i>Polytrichum</i>	Under	58.3	0.003
Species			
<i>Betula pubescens</i> ssp. <i>czerepanovii</i>	Between	70.2	0.072
<i>Empetrum hermaphroditum</i>	Between	57.6	0.010
<i>Pleurozium schreberi</i>	Between	57.2	0.162
<i>Juniperus communis</i>	Between	50.3	0.176
<i>Deschampsia flexuosa</i>	Transition	51.4	0.100
<i>Hierochloë alpina</i>	Under	58.8	0.176

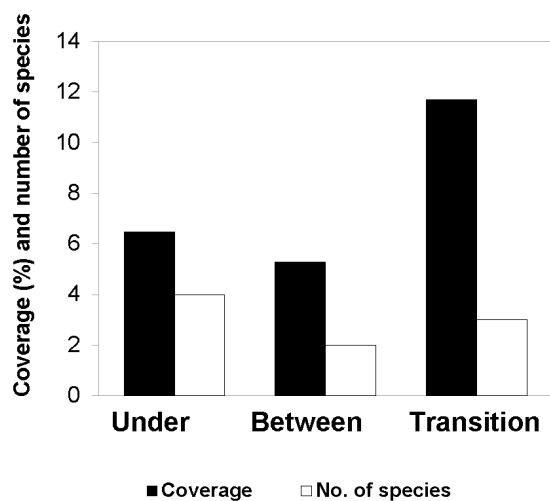


FIGURE 5. The percent coverage and number of species of graminoids in the three damage categories of the camp sites: under the huts, between the huts, and in the transition zone.

dwarf shrubs at the least disturbed patches of the sites. Unlike other dwarf shrubs, *S. herbacea* seemed to be favored by the open space created in the barren mountain zone.

Studies monitoring long-term vegetation recovery in Arctic-alpine regions are few; all those that have been done indicate slow recovery or nonrecovery of original vegetation after disturbance (Forbes, 1996; Wielgolaski, 1998; Willard et al., 2007; Jorgenson et al., 2010; Becker and Polard 2016; see also review by Tolvanen and Kangas, 2016). Instead, these studies show resistance of, or recovery by, different graminoids such as *Deschampsia*, *Alopecurus*, *Poa*, and *Juncus* species. In our study, *C. bigelowii*, *J. trifidus*, and *D. flexuosa* were the dominant graminoids at the observation posts, and the latter dominated also at the transition zones of the camp sites in the mountain birch

zone. Caespitose, or matted, graminoids are the most resistant of the vascular plants to trampling (Cole, 1995b). Many graminoids (e.g., *C. bigelowii*) have a high regeneration rate due to a high photosynthetic capacity and belowground rhizomes, which serve as energy stores and produce daughter tillers after damage, aiding their establishment at exposed sites (Chapin, 1980; Bryant et al., 1983; Tolvanen et al., 2001). They can also benefit from the possible short-time addition of nitrogen in the surroundings of campsites, unlike dwarf shrubs, which have limited capacity to utilize added nutrients (Chapin et al., 1986; Mäkipää, 1999). *J. trifidus*, which is a pioneer species in open areas of barren mountain, also has a high seed production capacity and high seed germination percentage, which contribute to its establishment in barren soils (Marchand and Roach, 1980).

The bottom layer of our study sites in the mountain birch zone comprised lichens in the genera *Cetvaria*, *Peltigera*, and *Stereocaulon*, and mosses in the genera *Polytrichum* and *Dicranum*, showing similar species composition to that in the harvesting holes in Wielgolaski's study (1998). These cryptogams are resistant to trampling and it is assumed that they assist in the stabilization of the soil after disturbance (Hoogesteger, 1984; Wielgolaski, 1998). Lichens, as well as several mosses, are able to grow vegetatively from pieces of their thallus (Studlar, 1980; Törn et al., 2006). Of the mosses, especially *Polytrichum* species thrived under the huts in the mountain birch zone. *Polytrichum commune* has been found to invade exposed and disturbed areas, and its shoots have shown almost finite life expectancy, the species being also successful in sexual reproduction and having a proliferating underground system that can compensate for the damages to the aboveground shoots (Callaghan et al., 1978). The comparison of damage intensity categories at the camp sites demonstrated the above-mentioned recovery strategies and potentials of different plant growth forms: dwarf shrubs and mountain birch seedlings were growing between the huts at the least disturbed plots, whereas graminoids prevailed in the transition zone where they could take advantage from the open space. However, they had not been able to invade the most disturbed plots under the huts, where only cryptogams prevailed.

Many studies looking at the short term suggest that vegetation recovers relatively rapidly after trampling in mountain heaths (Emanuelsson, 1984; Tolvanen et al., 2001). Nevertheless, such recovery can be temporary. Willard et al. (2007) studied the recovery after trampling damage over a period of 42 years in the Rocky Mountains, U.S.A., and noticed that the regrowth that took place during the first 10 years stopped and even declined during the later decades of the study due to unfavorable climate conditions. Our results show very little ecological recovery (cf. Hylgaard, 1980) of the sites to their original state in the 64 years. Rather, the results suggest stagnation or slight functional recovery; that is, the new vegetation at the sites has started to develop as a functioning plant community with a different species composition than the original (cf. Walker et al., 1987). Similarly, Becker and Pollard (2016) found in a 60-year study on the recovery of vegetation in Canadian High Arctic that the disturbed landscape had not recovered to initial conditions but changed toward a different stable-state community. In a longer time frame, Forbes (1996) found indications of permanent vegetation shift in 800-year-old Inuit settlements on the Canadian Arctic islands; the study shows that the grass vegetation that took over the old settlement areas had persisted for several hundred years. The weak ecological recovery of the sites in our study may be related to the fact that the stress-tolerant, slow-growing dwarf shrubs and cryptogams, which are typical for the low-productive communities in the study region, have been found to respond weakly to the changes in resource levels or changing environmental conditions (Virtanen et al., 2010). At the moment, there are contradictory predictions on the effects of changing climate on the dwarf shrub communities in subarctic ecosystems (see, e.g., Bokhorst et al., 2009; Virtanen et al., 2010). Nevertheless, many recent studies indicate that the development of future climatic and edaphic conditions may shift the vegetation cover of Arctic and subarctic heaths toward increased coverage of deciduous shrubs (e.g. Walker et al., 2006; Elmendorf et al., 2012; Myers-Smith et al., 2011), which may increase gross ecosystem production (see Tolvanen and Kangas, 2016). Different scenarios stress the importance of further monitoring of vegetation changes in old disturbance areas.

ACKNOWLEDGMENTS

We are grateful to Kari Viertola for his help with the figures, and to the associate editor and two anonymous reviewers for their valuable comments. The research has been supported financially by the European Regional Development Fund Northern Finland, operational programme project CCI 2007 FI 162 PO 002.

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MS submitted 13 October 2015

MS accepted 15 June 2016