

Research article

## Effects of mammalian herbivores on revegetation of disturbed areas in the forest-tundra ecotone in northern Fennoscandia

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### Abstract

Herbivores influence the structure of plant communities in arctic-alpine ecosystems. However, little is known of the effect of herbivores on plant colonisation following disturbance, and on its variability depending on the identity of herbivores and the characteristics of the habitats. To quantify the role of large and small vertebrate herbivores, we established exclosures of two different mesh sizes around disturbed subplots in forest and nearby tundra habitats in four contrasting locations in the forest-tundra ecotone in northernmost Sweden and Norway. The study revealed that herbivores influenced the abundance but not the species composition of regenerating vegetation. Gaps were colonised by the dominant species in the surrounding vegetation. The only exception to this expectation was *Empetrum nigrum*, which failed to colonise gaps even though it dominated undisturbed vegetation. Significant effects of herbivory were only detected when both small and large herbivores were excluded. Herbivores decreased the abundance of three of the most common species *Vaccinium myrtillus*, *Vaccinium vitis idaea*, and *Deschampsia flexuosa*. The effect of herbivory on the abundance of these three species did not differ between habitats and locations. However, the composition of the regenerating vegetation differed between habitats and locations. The disturbance treatment increased the species richness on the scale of plots, habitats, and sites. However, on the scale of whole locations, all species found in disturbed areas were also found in undisturbed areas, suggesting that the natural disturbance regime in arctic landscapes is high enough to sustain colonising species.

### Introduction

During the last decades, numerous studies have shown herbivores to have substantial impacts upon arctic plant communities (Jefferies et al. 1994; Mulder 1999). Herbivores can influence plant community structure directly by reducing the abundance of preferred forage species (Bazely and Jefferies 1986; Virtanen et al. 1997; Bråthen and

Oksanen 2001; Olofsson et al. 2001; Grellmann 2002), and indirectly by modifying competitive interactions between plants (Mulder and Ruess 1998; Olofsson et al. 2002) and/or altering nutrient availability (Bazely and Jefferies 1985, 1989; Olofsson et al. 2001; Olofsson and Oksanen 2002; Olofsson et al. 2004a; Stark and Grellmann 2002). Nevertheless, most plant species in the arctic are long-lived perennials and responses to the direct

and indirect impacts of herbivores are often slow (Jefferies et al. 1994; Mulder 1999; Olofsson et al. 2002).

In temperate systems, disturbance has been found to be essential to maintain high species richness, as many plants only regenerate in gaps within the existing vegetation (Grubb 1977; Harper 1977; Crawley 1997). Disturbance is essential for plant colonisation and seedling regeneration in arctic ecosystems too (Welling and Laine 2002). Arctic plant communities are characterised by a number of disturbance events operating over a wide range of temporal and spatial scales that create gaps in the existing vegetation. The most common disturbance events are abiotic processes such as frost heaving and snow-melt and biotic processes such as trampling, digging, and grazing by herbivores (Tihomirov 1959; Batzli et al. 1980; Walker and Walker 1991; Forbes and Jefferies 1999). When disturbance creates gaps of bare ground within the vegetation, subsequent revegetation often occurs through vegetative ingrowths by clonal plants. Regeneration from seeds is common in some habitats, although such events are often episodic (Freedman et al. 1982; Archibold 1984; Jonasson 1992). However, in contrast to the changes in the relative abundance of established vegetation, the dynamics of plant colonisation following disturbance may respond more rapidly to different grazing regimes (Hulme 1996a; Crawley 1997). The interaction between herbivory and disturbance may significantly shape the dynamics and structure of arctic plant communities. Yet in contrast to our understanding of temperate vegetation dynamics (Crawley 1997) there are no appropriately replicated studies on the impact of herbivory on revegetation following disturbance in the arctic.

The consequences of the interaction between herbivory and disturbance for arctic vegetation will be a function of the herbivores involved, the plant community and whether the prevailing climate facilitates regeneration by seed. Thus, the objectives of the present study are: (1) to quantify the relative role of both large and small mammal herbivores on re-establishment of vegetation; (2) to evaluate whether the interaction between disturbance and herbivory varies between timberline woodlands and open tundra habitats, and (3) to assess the differential responses of areas with oceanic and continental climates.

## Methods

### Study area

The study sites were situated in the mountain birch (*Betula pubescens* spp. *czerepanovii*) forest-tundra ecotone in the Fennoscandian mountain range. The study was conducted at four study locations: Abisko and Våssijávri in northernmost Sweden and Joatka and Seiland in northernmost Norway (Figure 1). The four locations represent different points along an oceanic–continental climate axis as well as different combinations of altitude and latitude (Table 1).

All study locations occur on nutrient poor bedrock, which is typical for northern Fennoscandia as a whole. For more details on study locations see Olofsson et al. (2004b).

### Experimental design

In July 1998, we chose three sites along the forest-tundra ecotone in each of the four locations. The distances between the sites varied between 0.2 and 2 km. Each site comprised an adjacent pair of birch forest and open heathland separated by less than 50 m, selected to minimize the differences between tundra and forest except for the presence of trees. The vegetation consisted of dwarf shrub

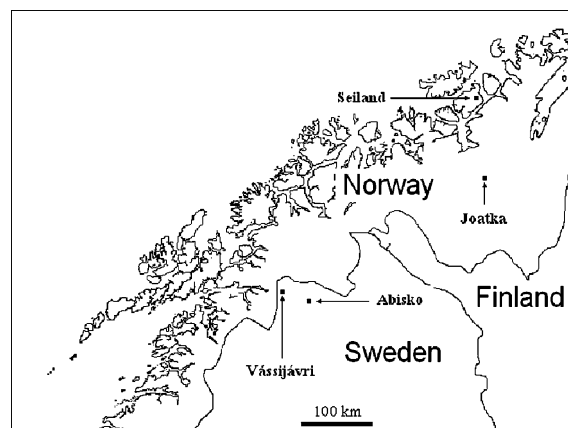


Figure 1. Map of northern Scandinavia showing the positions of the four research locations: (1) Abisko (Sweden), (2) Våssijávri (Sweden), (3) Joatka (Norway) and (4) Seiland (Norway).

Table 1. General description of the four locations used in this study

Location	Position	Altitude (m a.s.l.)	Precipitation (mm/year)	Tree density (trees/hectare), Mean $\pm$ SE
Abisko	68°19'23"N, 18°51'57"E	550–600	304	746 $\pm$ 68
Vassijávri	68°26'26"N, 18°16'29"E	460–500	848	1996 $\pm$ 340
Joatka	69°45'11"N, 24°00'00"E	450	354	399 $\pm$ 79
Seiland	70°30'22"N, 23°31'41"E	100	734	3073 $\pm$ 747

heath in all tundra sites in all locations, and in the forest the field vegetation was dominated by dwarf shrubs, grasses, or forbs depending on local conditions.

Three 8 m  $\times$  8 m experimental plots were established in both the forest and in the tundra at each site, and these plots were randomly chosen to become either the unfenced control plot, an exclosure with a large mesh size or an exclosure with a small mesh size. The exclosures with the smaller mesh size were constructed from galvanised net with a mesh size of 1.2 cm  $\times$  1.2 cm. The net was 1 m high and was dug down into the mineral soil, between 10 and 30 cm deep, to exclude digging animals. These exclosures should exclude all mammalian herbivores, but as a precaution, snap-traps were set in the exclosures throughout the study to catch microtine rodents that might have entered. The exclosures with a large mesh size were constructed from standard sheep fencing. The net was 1.2 m high and was fastened on wooden poles about 10 to 20 cm off the ground. Voles and lemmings could easily enter these exclosures, (so could hares), but large herbivores were excluded. The two small mesh size exclosures in site 3 in Vássiávri were broken in the winter 2000–2001 and are thus excluded from all analyses. Voles and lemmings were found on some occasions to have entered some of the exclosures, especially in the forest in Abisko and Vássiávri. The effect of the small mesh size exclosures might therefore, be underestimated in these locations.

#### *Disturbance treatment*

The disturbance treatment was applied in the spring 1999 to four 0.4 m  $\times$  0.4 m subplots within each exclosure and control. All plants within the

subplots were removed with a spade so that the organic layers or the mineral soil were exposed and the soil thoroughly turned over. The disturbed plots were larger and more homogenous than most of the naturally disturbed plots in the areas. However, the simulated disturbance was comparable to naturally occurring disturbance events, as it removed the dominant plants and exposed the organic and mineral soil.

#### *Vegetation recording*

Plant community composition was recorded in the disturbed subplots within each exclosure and control at all sites in all locations in 2002, 3 years after the disturbance treatment was applied. We quantified the abundance of plant species with a point intercept method (Jonasson 1986). To perform the point intercept analyses, a transparent Perspex board (0.09 m<sup>2</sup>) with 21 randomly placed holes (diameter 4 mm) was fixed over the disturbed plots. A pin (diameter 4 mm) was passed vertically through each hole. All living plant parts touched by the pin were recorded as a hit. The abundance of each species was estimated as number of hits on that species. Plant community composition in undisturbed vegetation was recorded by point intercept analyses at 100 points within adjacent 0.25 m<sup>2</sup> subplots (see Olofsson et al. 2004b for more details). The abundance of plants is presented as % cover [(100  $\times$  hits)/point]. Nomenclature follows Mossberg et al. (1995) for vascular plants, Moberg and Holmåsén (1982) for lichens and Hallingbäck and Holmåsén (1981) for mosses. Microtine rodent densities were studied by snap-trapping in spring and autumn and the abundance of all other vertebrate herbivores was estimated by collecting faeces (see Olofsson et al. 2004b for more details).

### Calculations and statistical analyses

A Detrended Correspondence Analysis (DCA) was performed on plant abundance data to reduce the large number of correlated variables (i.e., abundance of 55 different species). DCA is an appropriate multivariate procedure when gradients are long and some species have unimodal occurrence patterns. The components from axes explaining a large proportion of the variance were then analysed with a univariate ANOVA. By this approach, we avoid Type 1 error problems due to multiple testing. This combination of methods copes better than a MANOVA with the large number of zeros, which is typical of species abundance data and *post-hoc* comparisons of groups are more straightforward (Quinn and Keough 2002). Repeated measure analyses were not undertaken as the data did not fulfil the assumptions of equal variance between years or circularity.

The components from the DCA, the total plant cover, the abundance of the seven most common species, the species richness and Bray–Curtis similarity measure were all analysed as a split-plot experimental design, as the design involves plots of different sizes and hence requires separate error terms for each plot size. The error term in each table is the interaction between blocks and all factors applied at that hierarchical level or higher (Crawley 2002). Appropriate *post-hoc* test was used when needed. Appropriate transformations were used to achieve equal variance on a few individual species before analysing the data.

### Results

The DCA axes identified two major gradients as follows (Figure 2). Along the first axis, species typically growing in wet conditions such as *Sphagnum* spp., *Barbilophozia* spp., and *Cornus suecica* have low or negative scores whereas species growing on dry soil such as *Ptilidium ciliare*, *Empetrum nigrum*, and *Vaccinium vitis-idaea*, have high scores. The second axis reveals a productivity gradient with vascular plants possessing low scores e.g., *Empetrum nigrum*, *Betula nana*, and *Linnea borealis* whereas lichens such as *Cetraria islandica*, *Stereocaulon paschale*, and *Cladonia* spp. have high scores. The mean scores for tundra and forest habitats differed significantly along both axes either

as a main effect (axis 2,  $F_{1,59} = 4.1$ ,  $p = 0.048$ ) or habitat  $\times$  location interaction (axis 1,  $F_{1,59} = 5.0$ ,  $p = 0.029$ ). No effects of the herbivore exclusion were found on the mean score along the first or the second axis from the DCA. We tried to analyse the data with a partial DCA, but residual variation after fitting the effects of habitat and location, was still not influenced by herbivory.

The cover of plants in the disturbed plots did not differ between tundra and forest habitats but did respond to the enclosure treatments ( $F_{1,59} = 17.1$ ,  $p < 0.001$ ). There was a tendency for both small and large mesh size enclosures to increase the cover of plants, but the effect was only significant between the small mesh size enclosures and the controls ( $F_{1,59} = 5.3$ ,  $p = 0.023$ ). On average, excluding both large and small herbivores increased plant abundance by 50% (Figure 3).

Significant effects of excluding herbivores were found for *Deschampsia flexuosa* (Figure 4a,  $F_{2,42} = 19.7$ ,  $p = 0.028$ ), *Vaccinium myrtillus* (Figure 4b,  $F_{2,59} = 11.6$ ,  $p = 0.001$ ), and *V. vitis-idaea* (Figure 4c,  $F_{2,44} = 7.2$ ,  $p = 0.010$ ). In all three cases the trend was similar with only the exclusion of both large and small herbivores significantly increasing plant abundance relative to the controls (by up to 100%).

Herbivores did not influence Bray–Curtis similarity between disturbed and undisturbed vegetation. Over all locations, 9 of the 10 most common species in the disturbed subplots were also among the 10 most common plants in the undisturbed vegetation. However, although similar plant species dominated the disturbed and undisturbed vegetation their relative frequencies differed (Table 2).

Species richness was consistently lower in disturbed than undisturbed subplots at all spatial scales (plots:  $F_{1,213} = 237.4$ ,  $p < 0.001$ , habitat:  $F_{1,69} = 69.2$ ,  $p < 0.001$ , site:  $F_{1,33} = 54.2$ ,  $p < 0.001$ , locations:  $F_{1,9} = 4.2$ ,  $p = 0.051$ ). However, having both disturbed and undisturbed plots in the vegetation increased species richness at the smaller spatial scales of plots and habitats but not at the larger scales of sites and locations (Figure 5).

### Discussion

Herbivory influenced total vegetation cover but not species composition of plants colonising disturbed plots. In addition, species similarity

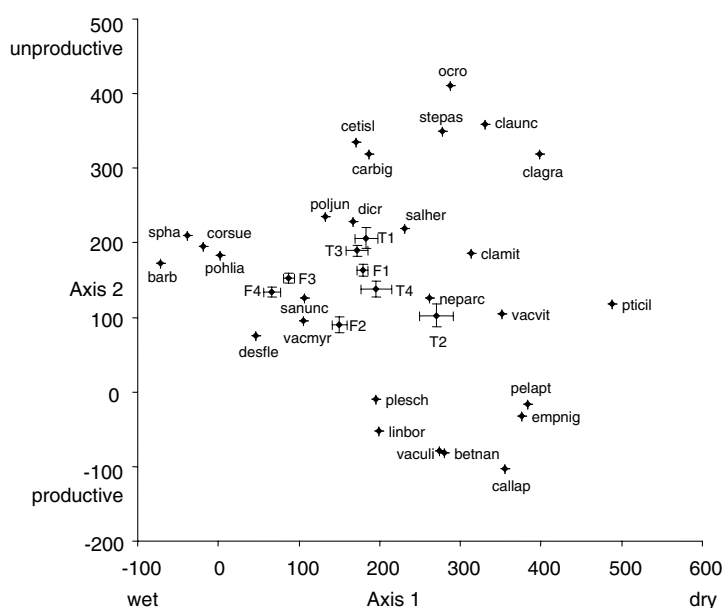


Figure 2. Impact of excluding herbivores on vegetation composition in disturbed subplots in relation to underlying gradients along the first two axes from the Detrended Correspondence Analysis. Mean  $\pm$  1/2 LSD (least significant difference) are displayed and non-overlapping bars indicate that treatments are significantly different. F1 = Forest Joatka, T1 = Tundra Joatka, F2 = Forest Abisko, T2 = Tundra Abisko, F3 = Forest Seiland, T3 = Tundra Seiland, F4 = Forest Vassijaure, T4 = Tundra Vassijaure barb = *barbilophozia* spp., betnan = *Betula nana*, callap = *Calamagrostis lapponica*, carbig = *Carex bigelowii*, cetisl = *Cetraria islandica*, clagra = *Cladonia gracilis*, clamit = *Cladina mitis*, claunc = *Cladonia uncialis*, corsue = *Cornus suecica*, desfle = *Deschampsia flexuosa*, dicr = *Dicranum* spp., empnig = *Empetrum nigrum*, linbor = *Linnea borealis*, neparc = *Nephroma arctica*, ocro = *Ochrolechia* spp., pelapt = *Peltigera aphthosa*, plesch = *Pleurozium schreberi*, pohlia = *Pohlia* spp., poljun = *Polytrichum juniperinum*, pticil = *Ptilidium ciliare*, salher = *Salix herbacea*, sanunc = *Sanionia unciata*, spha = *Sphagnum* spp., stepas = *Stereocaulon paschale*, vacmyr = *Vaccinium myrtillus*, vaculi = *Vaccinium uliginosum*, vacvit = *Vaccinium vitis-idaea*.

between disturbed and undisturbed vegetation was not altered by herbivory. Herbivory had, however, only a marked impact on the cover of three abundant vascular plant species, *Deschampsia flexuosa*, *Vaccinium myrtillus*, and *Vaccinium vitis-idaea*. The two *Vaccinium* species are preferred winter forage for gray-sided voles (*Clethr-*

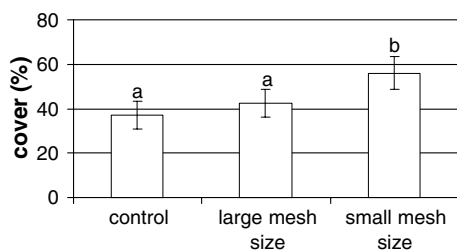


Figure 3. Mean abundance of vegetation in disturbed subplots in the controls, large mesh size exclusions and small mesh size exclusions (Mean  $\pm$  SE). Treatments with the same letter do not differ from each other at  $p = 0.05$ .

*ionomus rufocanus*) (Kalela 1957). Rare species were little affected. This resulted in a large effect on total cover but only a small effect on species composition. Yet, although cover of *Vaccinium* spp. were also reduced by herbivores in the undisturbed subplots, this was not the case for *D. flexuosa* (Olofsson et al. 2004b). The contrasting effect of herbivores on *D. flexuosa* in disturbed and undisturbed vegetation probably indicates that the influence of voles on revegetation is at the seed or seedling stage. This example highlights how the interacting effects of disturbance and herbivory can lead to subtle changes in vegetation dynamics. However, this study indicates that the effect of herbivory was not more pronounced on colonising vegetation than on the established vegetation in the tundra. This is in contrast with temperate systems where herbivory often has been found to be more important on the seed and seedling stage than on the established vegetation (Hulme 1996a, b; Crawley 1997).

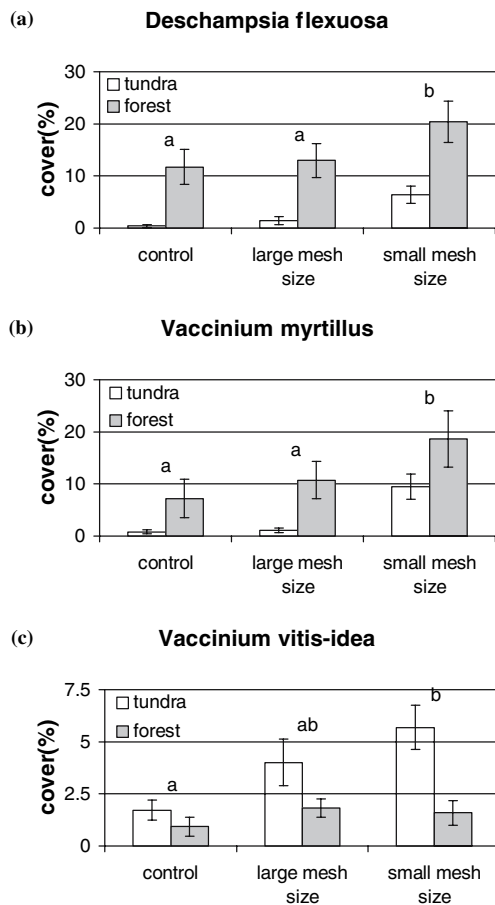


Figure 4. The effect of excluding herbivores with exclosures of different mesh sizes on the abundance of (a) *Deschampsia flexuosa*, (b) *Vaccinium myrtillus*, and (c) *V. vitis-idea* in disturbed subplots in forest and tundra habitats (Mean  $\pm$  SE). Treatments with the same letter do not differ from each other at  $p = 0.05$ .

The densities of herbivores were measured at all study sites, and the data are presented in Olofsson et al. (2004b). In summary, reindeer (*Rangifer tarandus*) was the most abundant large herbivore, while Norwegian lemming (*Lemmus lemmus*) and grey-sided voles were the most common small vertebrate herbivores. All sites experienced a vole peak during the study period, but only the two southern sites experienced high densities of lemmings. Voles were more abundant in the forest than in the tundra, while no differences between habitats were found for the other herbivores.

The influence of herbivores on seedling establishment in arctic tundra forest ecotone does not appear to be as marked as that for temperate ecosystems (Hulme 1994, 1996b; Edwards and Crawley 1999). This undoubtedly reflects that in

Table 2. Relative cover (Mean  $\pm$  SE) across all habitats and location of the most common species in disturbed and undisturbed subplots

	Cover in disturbed (%) subplots	Cover in undisturbed (%) subplots
<i>Vaccinium myrtillus</i>	14.5 $\pm$ 1.2	16.7 $\pm$ 1.9
<i>Dicranum</i> spp. **	14.4 $\pm$ 1.2	5.7 $\pm$ 0.7
<i>Polytrichum</i> spp. *	8.4 $\pm$ 1.0	2.2 $\pm$ 0.3
<i>Vaccinium vitis-idaea</i>	7.1 $\pm$ 0.9	5.4 $\pm$ 0.5
<i>Deschampsia flexuosa</i>	6.2 $\pm$ 0.7	6.8 $\pm$ 1.1
<i>Barbilophozia</i> spp.	5.1 $\pm$ 0.6	2.9 $\pm$ 0.6
<i>Pleurozium schreberi</i>	4.0 $\pm$ 0.7	3.1 $\pm$ 0.6
<i>Cornus suecica</i>	3.9 $\pm$ 0.6	3.0 $\pm$ 0.8
<i>Cladina mitis</i>	3.6 $\pm$ 0.6	4.2 $\pm$ 0.5
<i>Vaccinium uliginosum</i>	3.0 $\pm$ 0.6	3.3 $\pm$ 0.7
<i>Empetrum nigrum</i> ***	1.4 $\pm$ 0.4	23.0 $\pm$ 2.2

\*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

the arctic, many of the plant species found in the disturbed areas were lichens and bryophytes that establish from spores or vegetative fragments, and most vascular species are likely to have established vegetatively rather than from seeds. Even though both mosses and lichens are often strongly influenced by herbivores in the arctic (Moen et al. 1993; Virtanen et al. 1997; Olofsson et al. 2001; Van der Wal et al. 2001), many of the mosses and lichens in the disturbed subplots were, after 4 years, only a few millimeters high and thus be too small to attract herbivores. It is notable that the three species that were affected by herbivory were also

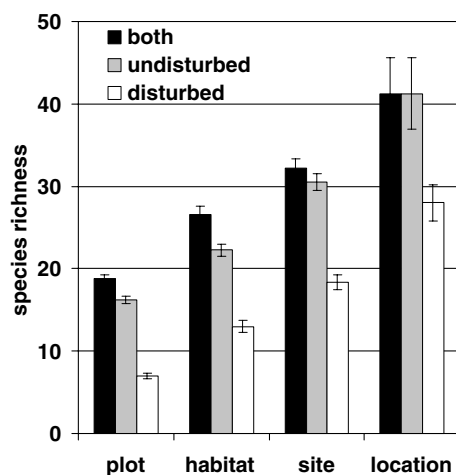


Figure 5. Species richness in disturbed vegetation, undisturbed vegetation and in both undisturbed and disturbed vegetation combined at four different spatial scales: plot (8 m  $\times$  8 m), habitat, site, and location (Mean  $\pm$  SE).

the three tallest species in the disturbed subplots (pers. obs.). Herbivores have been found to influence tundra vegetation not only by consumption and trampling but also indirectly through altering plant competition and nutrient availability (Olofsson et al. 2004a; Van der Wal et al. 2004). However, the effects found in this study are probably all due to direct effects of consumption as the vegetation was still sparse in disturbed plots.

The lack of any interaction between herbivory and either habitat or location on colonisation of disturbed plots mirrors the finding for the undisturbed subplots in the same experiment (Olofsson et al. 2004b). Thus, even in the face of marked variation in plant species composition, herbivore abundance and climate, trends in herbivory were remarkably homogeneous. These contrasts with heterogeneous patterns found in other ecosystems (e.g., McNaughton 1983; Sommer 2000; Adler et al. 2001; Van der Wal et al. 2001; Olofsson et al. 2002) and may enable us to get a better understanding of the role of herbivory for the whole forest-tundra ecotone in northern Fennoscandia.

The dominant species in the disturbed subplots were similar to those found in the undisturbed vegetation. This is consistent with the idea of gaps often being colonised by the dominant species in the surrounding vegetation (Brown and Archer 1988; Collins and Glenn 1991; Williams 1992; Hanski and Gyllenberg 1993; Bullock et al. 1995; Chambers 1995; Kotanen 1997). One exception to this trend is *Empetrum nigrum* ssp. *hermaphroditum*. Although producing fruit in most years, most seed dispersal is within the vicinity of the parent and seeds have low germinability (Hagen 2002), which may explain its failure to exploit gaps. Such slow establishment in disturbed plots by this dominant species might promote the regrowth of other species, as high coverage is associated with low species diversity, greater humus build-up and low tree seedling recruitment (Zackrisson and Nilsson 1992; Wardle et al. 1997). Numerous studies including allelopathic bioassay and field experiments have suggested that *E. nigrum* ssp. *hermaphroditum* has allelopathic properties against seed germination and growth of associated species (Zackrisson and Nilsson 1992; Nilsson and Zackrisson 1992; Nilsson 1994). Breaking the dominance of *E. nigrum* ssp. *hermaphroditum* might thus be the most important way in which disturbance promotes seedling establishment in

tundra heathlands. In the absence of reindeer, thick lichen mats might dominate the vegetation and prevent other plants from establishing. However, this study is too short to reveal such indirect effects of herbivory.

The effect of disturbance on species richness is highly dependent upon the spatial scale considered. At the scale of subplots, disturbance decreased species richness whilst at the largest spatial scales disturbance has no marked effect. Thus although fewer species were found in disturbed plots, at intermediate scales the increased heterogeneity following disturbances also increases species richness. This suggests that the natural disturbance regime in tundra areas is high enough to create gaps for colonizing species at the landscape scale, even though gaps are rare at the scale of local plant communities.

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