



Rodent population dynamics affect seedling recruitment in alpine habitats

Kristin O. Nystuen, Marianne Evju, Graciela M. Rusch, Bente J. Graae & Nina E. Eide

Keywords

Disturbance; Gap; Grazing; Lemming; Microsite; Mountain; Norway; Regeneration; Sexual reproduction; Sheltered heath; Snowbed; Vole

Nomenclature

Lid & Lid (2005)

Received 10 October 2013

Accepted 2 January 2014

Co-ordinating Editor: Beverly Collins

Nystuen, K.O. (corresponding author, kristin.o.nystuen@hint.no),

Rusch, G.M. (graciela.rusch@nina.no) &

Eide, N.E. (nina.eide@nina.no): Norwegian Institute for Nature Research, P.O. Box 5685 Sluppen, NO-7485, Trondheim, Norway

Nystuen, K.O. & Graae, B.J.

(bente.graae@bio.ntnu.no): Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, NO-7491, Trondheim, Norway

Evju, M. (marianne.evju@nina.no): Norwegian Institute for Nature Research, Gaustadalleen 21, NO-0349, Oslo, Norway

Nystuen, K.O.: Current address:

Nord-Trøndelag University College, P.O. Box 2501, NO-7729, Steinkjer, Norway

Abstract

Questions: How do rodents with cyclic population dynamics affect seedling recruitment in alpine habitats? Does disturbance from rodents have larger implications on seedling recruitment in some plant communities than in others?

Location: Snowbeds and sheltered heaths in the low-alpine zone in areas of Børgefjell and Dovrefjell, Norway.

Methods: We recorded seedling emergence, rodent activity and cover of mosses, lichens, litter and bare ground in 270 plots in snowbeds and sheltered heaths in a rodent population peak year and in the following low-density year.

Results: Seedling recruitment was positively correlated with disturbances from lemmings and voles in both years. More seedlings emerged in the low-density year than in the year of the population peak. Snowbeds had higher seedling recruitment than the sheltered heaths, but both habitats were equally affected by disturbances from rodents.

Conclusions: Rodent activity created gaps and increased seedling emergence in these alpine plant communities, particularly in the year after the rodent peak, both in snowbeds and sheltered heath habitats. Our study therefore suggests that regeneration patterns in alpine vegetation are tightly linked to the population cycles of lemmings and voles, which peak in density at 3- to 5-yr intervals.

Introduction

Disturbances, i.e. the mechanisms that limit plant biomass by causing its partial or total destruction (*sensu* Grime 2001), are important in shaping plant communities (Pickett et al. 1999; Walker 2012). In arctic-alpine communities, both abiotic and biotic disturbances are important. Disturbances from herbivores can even counteract climate-driven vegetation change (Post & Pedersen 2008; Olofsson et al. 2009). It is therefore of interest to reveal both the direct (through grazing) and indirect (e.g. creation of microsites for seedling recruitment through trampling) impacts of herbivore disturbances on plant communities to more fully understand the dynamics of tundra communities and to better predict the responses to climate change.

Small rodents strongly affect plant community structure, diversity and ecosystem functioning (Hulme 1994;

Olofsson et al. 2005; Rebollo et al. 2013). For instance, North American pocket gophers (*Thomomys bottae*) and plateau zokors (*Myospalax fontanierii*) act as ecosystem engineers by generating distinct patterns of soil heterogeneity (Reichman & Seabloom 2002; Zhang et al. 2003). In Scandinavia, the cyclic fluctuation in small-rodent population densities observed in the Norwegian lemming (*Lemmus lemmus*) and the voles *Microtus agrestis*, *Myodes rufocanus* and *Microtus oeconomus*, create a cyclic disturbance regime that regularly has high impacts on the vegetation cover in arctic-alpine habitats (Stenseth 1999; Ims & Fuglei 2005), which are even visible on satellite images (Olofsson et al. 2012). Their effect on tundra plant communities has been shown to be stronger than that of large herbivores (Olofsson et al. 2004). In addition to the plant biomass they consume, these arctic-alpine rodents also impact their habitats through activities such as trampling, cutting,

burrowing (Hambäck et al. 1998; Turchin & Batzli 2001) and through deposition of urine and faeces, which increases the overall nitrogen availability (McKendrick et al. 1980; Jonasson 1992).

Bare soil offers space for colonization (Rusch & Fernández-Palacios 1995), and rodent disturbances are expected to increase the availability of vegetation gaps, thus creating suitable microsites for seedling emergence (Eskelinen & Virtanen 2005; Mayer & Erschbamer 2011), even though successful recruitment can take decades (Forbis et al. 2004). Austrheim et al. (2007) found that the amount of exposed soil was positively related to rodent grazing in alpine habitats. On the other hand, high frequencies and intensities of disturbance could also cause high seedling mortality due to herbivory and trampling (Weltzin et al. 1997; Munier et al. 2010).

Abiotic factors such as temperature, light, moisture, wind and the availability of nutrients are crucial for seedling emergence (Grubb 1977; Chambers 1995). Seedling density varies in tundra vegetation, with high germination in moist and productive habitats, declining with increasing levels of environmental stress (Bell & Bliss 1980; Milbau et al. 2013). Vegetation composition in alpine habitats also affects recruitment dynamics, with the number of emerging seedlings being closely related to the regenerative strategy of the species in the mature vegetation (Welling & Laine 2000). Fewer seedlings emerge in heath vegetation, which is dominated by perennial clonal species compared to meadows and snowbeds with high forb richness (Gough 2006; Graae et al. 2011).

Lemmings and vole species use tundra habitats differently, depending on the availability of preferred food plants and the distribution of snow (Batzli 1975; Sætnan et al. 2009). Snowbeds and heaths are habitats frequently used by both lemmings and voles (Moen et al. 1993). Disturbances could be expected to have a higher impact on recruitment in habitats with favourable germination conditions as in snowbeds, whereas abiotic factors may be more limiting in heath vegetation. The role of rodent disturbances on seedling recruitment in snowbeds has been studied (Eskelinen & Virtanen 2005), but the relative importance of disturbance for the recruitment of plants in snowbeds vs. heaths has not yet been explored.

In addition to the presence of bare ground caused by disturbance, the cover of mosses, lichens and litter can contribute to spatial variation in seedling numbers (Rusch & Fernández-Palacios 1995). Cover of mosses and lichens is often found to be inhibitory for germination and seedling survival, depending on the plant species (Hobbs 1985; Zamfir 2000; Eckstein et al. 2011; Soudzilovskaia et al. 2011). Lemming grazing can decrease the cover and abundance of mosses (Virtanen et al. 1997; Austrheim et al. 2007). On the other hand, lichens are non-preferred forage

and likely unaffected by rodent herbivory (Virtanen 2000; Soininen et al. 2013), but could be affected by trampling. Depending on habitat productivity (Suding & Goldberg 1999) and litter amount (Loydi et al. 2013), litter can inhibit (Dalling & Hubbell 2002) or have no influence (Welling & Laine 2000; Forbis 2009) on seedling emergence. Some studies suggest that grazing and other rodent activities prevent the accumulation of plant litter (Sirotnak & Huntly 2000; Virtanen 2000), while Moen et al. (1993) found that winter lemming grazing in snowbeds increases the amount of litter. Lemmings and voles could therefore also indirectly have an impact on alpine plant recruitment through potential interactions with the bottom layer, which – to the best of our knowledge – are not well explored in the literature.

In this study, we investigated the impacts of lemmings and voles on the recruitment of new plant individuals in alpine habitats. We collected data on seedling emergence and rodent activity in two alpine habitats; snowbeds and sheltered heaths, in the low-alpine zone in two mountain regions in Norway in a rodent peak population year and in the following low-density year. We expected that: (1) disturbances from lemmings and voles would enhance seedling emergence, as their activity would affect the ground cover and create vegetation gaps that provide microsites suitable for recruitment; (2) this effect would be stronger the year after a rodent population peak when little direct disturbances such as trampling and grazing were exerted; (3) the number of seedlings emerging would differ between habitats according to differences in the degree of use by rodents; and (4) at equal levels of rodent disturbance, seedling recruitment would be higher in snowbeds than in sheltered heaths, since snowbeds have more favourable conditions for seedling recruitment.

Methods

Study sites

The study was carried out in two mountain regions: Dovrefjell (62°29' N, 9°40' E) in central Norway and Børgefjell (65°27' N, 14°10' E), ca. 350 km further north (Appendix S1). Both regions are characterized by having large ranges in altitude and precipitation, and in each region, three study sites were established in the low-alpine zone. At Dovrefjell, the Forollhogna site is located within the Forollhogna National Park, whereas the Hjerkins and Grødalen sites are located within the Dovrefjell-Sunndalsfjella National Park. At Børgefjell, all three sites (Kjukkelen, Tiplingan and Ranseren) are located within the Børgefjell National Park. The characteristics of the study sites are shown in Table 1.

Lemmings and voles are present in both study regions. Over the past 20 yr, rodents in Børgefjell have had regular

population peaks, while in Dovrefjell the peaks have been rather irregular, with comparatively low densities until recently (Fig. 1). Both regions experienced a peak in 2010–2011, followed by a low-density year in 2012. Note that the numbers in Fig. 1 are from the trapping of rodents during autumn (September), whereas records of rodent activity in this study are from June to August. The peak in Dovrefjell started to build up earlier, and also appears to have crashed earlier compared to Børgefjell, which resulted in the low catch seen for Dovrefjell in autumn 2011 (Framstad 2013). Børgefjell is an important area for reindeer husbandry (Evju et al. 2010), while Dovrefjell has wild populations of reindeer and muskoxen, as well as a long history of extensive grazing by sheep (Hagen et al. 2006).

Sampling and field design

At each site, we subjectively located a total of nine transects of 50 m each in habitats without tall shrubs at three altitudinal levels in the low-alpine zone (Fig. 2). We observed the vegetation at each meter along the transect and classified it as either ridge, exposed heath, sheltered heath or snowbed habitat, with this study focusing on snowbeds and sheltered heaths. The snowbed habitat occurs in depressions and has a short growing season due to long-lasting snow cover. The vegetation is dominated by herbs, graminoids and mosses, and by *Salix herbacea* L. in late-melting areas. The sheltered heath habitat is located in sites with comparatively more exposed topography with earlier snow melt, and is dominated by the dwarf shrubs *Empetrum nigrum* subsp. *hermaphroditum* (Lange ex Hagerup) Böcher and *Vaccinium myrtillus* L.

For this study, we randomly selected plots of snowbed and sheltered heath habitat along the transects. In most cases, each transect had five plots, but sometimes up to ten or only one plot were selected, depending on the occurrence of the habitat type. Vegetation and rodent

activity were recorded within each plot (a 0.5 m × 0.5 m quadrat divided into 16 subplots). In 2011 vegetation records included the total number of seedlings present without recording the species identity, but including adult individuals of annual plants (primarily *Euphrasia* spp.) in four pre-selected subplots. We recorded the number of subplots per plot with grazing marks, tunnels and faeces (each with a range of 0–16). The percentage cover of bottom layers (mosses, litter and bare soil) was visually estimated for the entire plot. The records were repeated in 2012; however, the bottom layer cover was recorded in the four seedling subplots only, and we also included the cover of lichens. Since the plots were not permanently marked in the first summer, exact relocation was not possible in 2012. The total number of plots was 270 in 2011 and 272 in 2012, which is roughly balanced between sites and habitats (Appendix S2).

The fieldwork in 2011 was conducted in late June and in August in Dovrefjell, and in July in Børgefjell. In 2012, the fieldwork was carried out in July in Dovrefjell, where late snowmelt resulted in many waterlogged plots with newly exposed vegetation in two of the sites, and in the first half of August in Børgefjell (see Appendix S3 for more details on sample timing).

Statistical analyses

We used two indices as a measure of rodent activity in the plots. The first was based on records of rodent faeces only, and calculated as the number of subplots with faeces (range 0–16). The second index was based on independent records of faeces, grazing marks and tunnels present in the 16 subplots (range 0–48). All analyses were conducted with both measures of rodent activity.

To assess possible differences in the level of rodent activity between habitats and years, we used a zero-inflated generalized linear mixed model (ZIGLMM) fitted with the

Table 1. Characteristics of the study sites in: (a) Dovrefjell and (b) Børgefjell with latitude and longitude, altitudinal range, mean annual temperature, mean July and January temperature, annual precipitation and bedrock composition. Temperature and precipitation data are from the period between 1961–1990, interpolated to the centre of each site based on data from surrounding weather stations; see Tveito et al. (2005) for details.

Site	Lat. and Long.	Altitude (m a.s.l.)	Mean Annual Temp. (°C)	Mean July Temp. (°C)	Mean Jan Temp. (°C)	Annual Precip. (mm)	Bedrock
(a) Dovrefjell							
Grødalen	62°53' N, 8°93' E	1052–1236	−0.4	5.7	−5.5	864	Amphibolite and mica schists
Hjerkinn	62°29' N, 9°40' E	1188–1326	−2.6	6.7	−11.8	787	Precambrian metamorphosed rock, patches of gneiss and grit
Forollhogna	62°72' N, 11°09' E	923–1044	−0.9	7.4	−9.0	1010	Micaceous gneiss
(b) Børgefjell							
Kjukkelen	65°17' N, 13°81' E	704–914	−2.2	7.7	−11.5	1237	Micaceous gneiss and mica schists
Tiplingan	65°27' N, 14°10' E	751–905	−2.2	7.9	−11.8	1033	Gneiss and granite
Ranseren	65°19' N, 14°26' E	841–968	−2.5	7.6	−12.0	961	Quartz-diorite

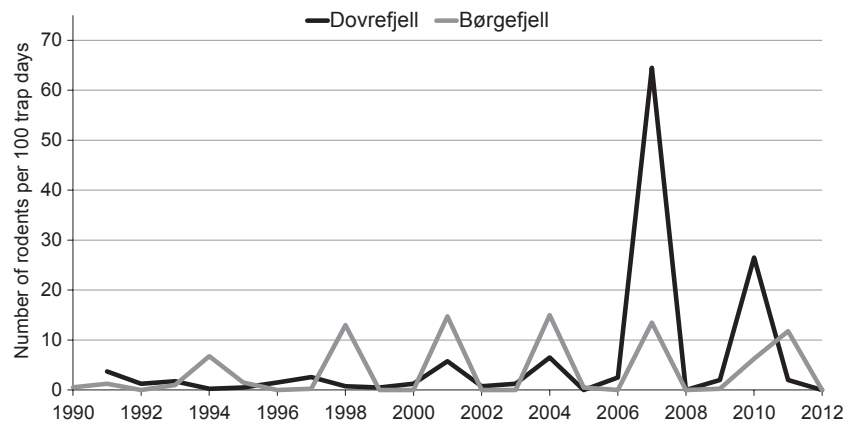


Fig. 1. Rodent abundance in Børgefjell (light grey line) and Dovrefjell (black line) based on the number of lemmings and voles caught during 100 trap days in September each year from 1990/1991 until 2012. The rodent populations peaked in both regions in 2010–2011, but crashed earlier in Dovrefjell (low catch in autumn 2011). The oscillations are historically stable in Børgefjell, while they have been almost absent in Dovrefjell until recent years; source: Framstad (2013).

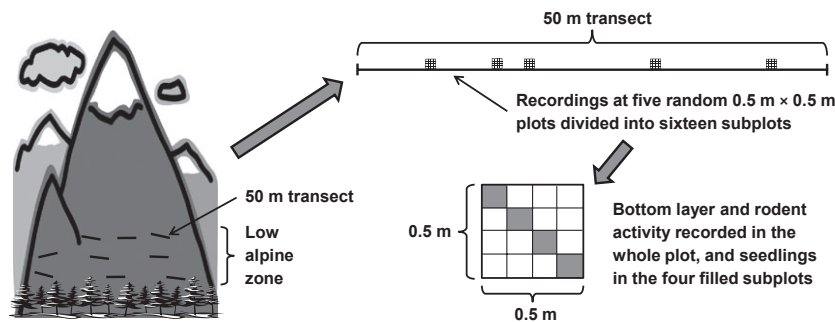


Fig. 2. Schematic representation of the sampling design. To the left is a study site with nine 50-m transects in the low-alpine zone. At the top right is a zoom-in of one transect with five randomly chosen plots. On bottom right, a plot (0.5 m × 0.5 m) divided into 16 subplots where bottom layer and rodent activity records were obtained. On the four subplots on the plot diagonal (filled squares), the number of seedlings and adult individuals of annual species was counted.

‘glmmadmb’ function in the ‘glmmADMB’ package (Fournier et al. 2012) with a Poisson error structure; consequently, all estimates are on a log scale. We used a generalized linear mixed model to account for the spatial dependency between plots within the same transect and a zero-inflated model because the rodent activity records had many plots with no signs from rodents (108 out of 544). The minimally adequate model was found by model simplification based on a comparison of AIC values and Wald tests.

We tested whether seedling emergence was related to rodent activity and whether the correspondence differed between habitats and years. We used seedling counts as the response variable and rodent activity (Hypotheses 1 and 2), study region and habitat (Hypothesis 3) as explanatory variables, including two-way interactions (testing Hypothesis 4). The cover of bottom layers was included as covariates (lichen, litter, moss and bare ground), and

separate models for 2011 and 2012 were constructed. The seedling counts were zero-inflated (many plots with no seedlings; Appendix S4), over-dispersed for the non-zero data, and non-independent (spatial dependency between plots within the same transect), thus ZIGLMMs with a negative binomial error structure ‘NB1’ were used, with transect as a random effect. The minimally adequate model for each year was found by successively including explanatory variables and two-way interactions. Comparison of AIC values and Wald tests were used for model selection.

Two outliers, a heath plot at Hjerkin in 2011 with 90 seedlings, and a snowbed plot at Kjukkelen in 2012 with 70 seedlings, were excluded from the analyses because they had a large influence on the outcome of the analyses.

All statistical analyses were done using the software R, version 2.15.1 (R Foundation for Statistical Computing, Vienna, AT, USA).

Results

Regional and between-year differences in rodent activity

The two indices of rodent activity produced similar results in the analyses, although only the results from analyses performed with records of rodent faeces are presented here.

Rodent activity was higher in 2012 than in 2011 ($\beta \pm \text{SE}$: 0.158 ± 0.052 ; Table 2), and the difference in rodent activity between 2011 and 2012 was smaller in Dovrefjell than in Børgefjell (significant study region \times year interaction; Table 2). In the low-density year 2012, tunnels, holes, faeces and litter caused by lemmings and voles were still visible in the vegetation (Fig. 3a, b), despite the fact that the rodent populations had crashed (Fig. 1).

Impact of rodent activity on seedling emergence

In 2011, a total of 665 seedlings were recorded in 99 plots, and no seedlings were found in the remaining 171 plots (Appendix S5), but there were more seedlings in Dovrefjell than in Børgefjell ($\beta \pm \text{SE}$: 1.520 ± 0.484 ; Table 3a), 415 and 250, respectively. Furthermore, rodent activity significantly explained the number of seedlings found in both regions ($\beta \pm \text{SE}$: 0.086 ± 0.038 ; Table 3a).

In 2012, a total of 1232 seedlings were observed in 152 plots, of which 543 were in Børgefjell and 689 in Dovrefjell, and in 120 plots no seedlings were found (Appendix S5). In contrast to 2011, there was no difference between regions in the number of seedlings emerged ($\beta \pm \text{SE}$: 0.319 ± 0.298 , $P = 0.285$), but in 2012, seedling emergence was also positively related to rodent activity ($\beta \pm \text{SE}$: 0.086 ± 0.023 ; Table 3b). In general, the number of seedlings recorded in the rodent low-density year was higher in plots which had

Table 2. Zero-inflated generalized linear mixed model (ZIGLMM with Poisson distribution) of rodent activity (records of faeces) as a function of habitat, study region, year and an interaction between study region and year ($n = 544$). The reference level (intercept) is the study region of Børgefjell and the habitat sheltered heath. The transect is the model's random factor with $n = 57$. The parameter estimates of random effects are not shown.

Fixed Effects	Estimate	SE	Z-Value	P-Value
Intercept	1.703	0.113	15.07	<0.001***
Habitat (Snowbed vs. Heath)	0.181	0.059	3.08	0.002**
Study Region (Dovrefjell vs. Børgefjell)	-0.301	0.160	-1.89	0.059'
Year (2012 vs. 2011)	0.158	0.052	3.07	0.002**
Study Region \times Year 2012	-0.584	0.089	-6.60	<0.001***

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ' $P < 0.1$.

experienced a high level of rodent activity before the populations crashed.

Interaction of ground cover and rodent activity on seedling recruitment

In 2011, the amount of bare ground was positively associated with seedling emergence ($\beta \pm \text{SE}$: 0.110 ± 0.032 ; Table 3a). There was a small positive main effect of litter cover on seedling emergence ($\beta \pm \text{SE}$: 0.023 ± 0.011 ; Table 3a), although with a negative interaction between rodent activity and litter cover, thereby suggesting that seedling emergence was highest in plots with a high rodent activity when litter cover was low. No effects on seedling numbers of moss cover were detected.

In contrast to 2011, there were no effects of bare ground and cover of litter on seedling emergence found in 2012, but the seedling number was negatively related to the cover of lichens ($\beta \pm \text{SE}$: -0.031 ± 0.015 ; Table 3b). A small negative interaction between rodent activity and moss cover suggested that fewer seedlings emerged in plots with high rodent activity when the moss cover was high.

Interaction of rodent activity and habitat on seedling recruitment

Rodent activity was higher in snowbeds than in sheltered heaths ($\beta \pm \text{SE}$: 0.181 ± 0.059 ; Table 2, Fig. 3a,b). In 2011, the seedling number was higher in snowbeds than in sheltered heaths ($\beta \pm \text{SE}$: 1.933 ± 0.474 ; Table 3a, Fig. 3c,d), although the difference between habitats was smaller in Dovrefjell than in Børgefjell (significant region \times habitat interaction; Table 3a). As in 2011, significantly more seedlings were found in 2012 in snowbeds compared to sheltered heath habitats ($\beta \pm \text{SE}$: 0.637 ± 0.222 ; Table 3b, Fig. 3c,d), but in this case the differences between habitats were similar in both regions (no significant region \times habitat interaction; Table 3b).

We did not find any differences in either year between habitats on the effect of rodent activity on seedling emergence (no significant rodent activity \times habitat interaction; Table 3a,b).

Discussion

This study reveals that small rodent population dynamics are an important driver of seedling recruitment patterns in alpine plant communities and that the disturbance from rodents is equally important for recruitment in snowbeds and sheltered heaths, even though seedling emergence in general is higher in snowbeds. Rodent activity interacts with bottom layers, including the cover of litter and

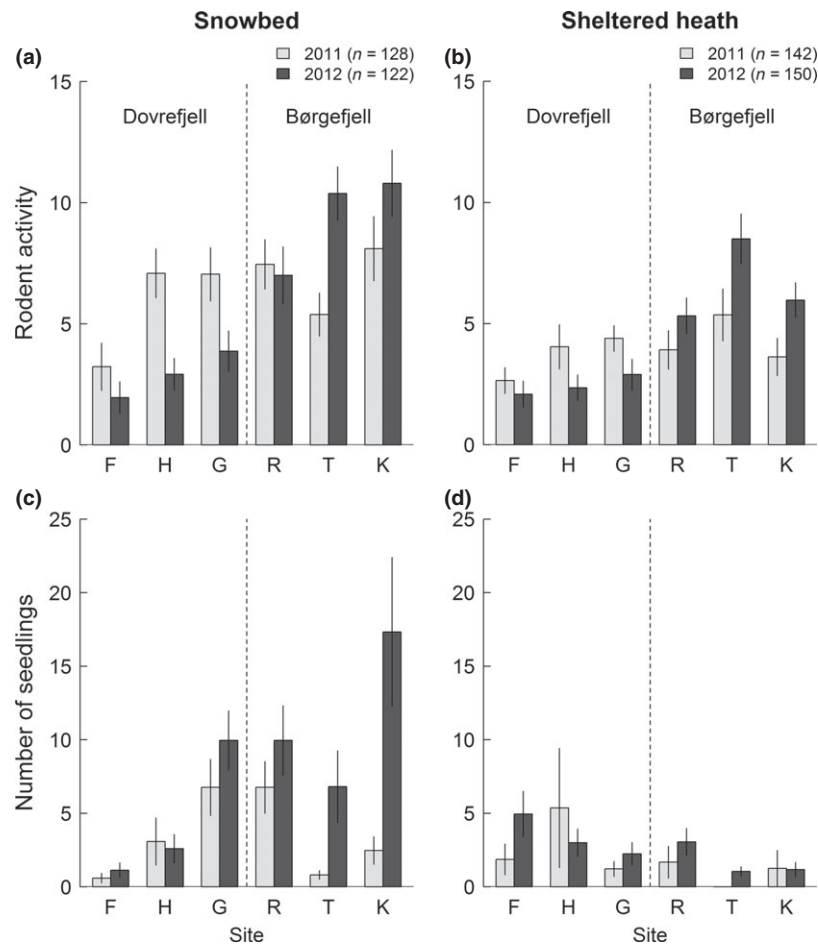


Fig. 3. Mean observed rodent activity based on records of faeces (range 0–16) (a, b) and number of seedlings (c, d) in snowbed and sheltered heath habitat in the six study sites (in Dovrefjell: F, Forollhogna; H, Hjerkin; and G, Grødalen and in Børgefjell: R, Ranseren; T, Tiplingan; and K, Kjukkelen) in 2011 (light grey bars) and 2012 (dark grey bars). Vertical lines show ± 1 SE from the mean.

mosses, thereby also indirectly influencing seedling recruitment.

Seedling emergence and rodent disturbance

We revealed the positive effects of rodent activity on the number of seedlings in both the population peak and the low-density year, as found by Eskelinen & Virtanen (2005). The availability of open space is one of the main limitations for seed regeneration in many plant communities (Grubb 1977), including arctic-alpine communities (Welling & Laine 2002; Graae et al. 2011). Our results indicate that disturbances from rodents in peak densities (e.g. herbivory, grubbing for rhizomes, trampling in tunnels, digging holes, cutting of vegetation) create gaps in the vegetation where seedlings can emerge. Much of the influence of herbivores on plant communities is assumed to be indirectly caused through the alteration of abiotic factors (Mulder 1999). For example, disturbed plots

experience more temperature fluctuations than closed vegetation (Graae et al. 2011), which is important for breaking seed dormancy for many species (Fenner & Thompson 2005). A higher light availability due to biomass removal is also beneficial for germination, particularly for small-seeded species (Grime et al. 1981), and several species also respond to light quality, germinating only in gaps and not when light is filtered through the canopy (Silvertown 1980; Smith 1985). Furthermore, the substantial amounts of faeces deposited in peak years could have a positive fertilization effect on seedling survival and growth (Chambers et al. 1990).

The impact of rodent disturbances on seedling recruitment appears to be a function of the ground cover. In accordance with Suding & Goldberg (1999), we found a small, positive effect of litter cover on seed recruitment in the peak year, but there was also a small, negative interaction between rodent activity and litter, indicating that fewer seedlings emerged in plots with high rodent activity

Table 3. Zero-inflated generalized linear mixed models (ZIGLMMs with negative binomial 'NB1' distribution) of seedling counts as a function of region, habitat and bottom layer covers in: (a) the peak year 2011 and (b) in the low-density year 2012. The reference level (intercept) is the study region of Børgefjell and the habitat sheltered heath. The transect is the models' random factor with $n = 54$ in 2011 and $n = 55$ in 2012. The parameter estimates of random effects are not shown.

Fixed Effects	Estimate	SE	Z-Value	P-Value
(a) 2011 (Peak Year)				
Intercept	-1.511	0.490	-3.08	0.002**
Rodent Activity	0.086	0.038	2.28	0.023*
Habitat (Snowbed vs. Heath)	1.933	0.474	4.08	<0.001***
Study Region (Dovrefjell vs. Børgefjell)	1.520	0.484	3.14	0.002**
Study Region × Habitat	-1.315	0.554	-2.37	0.018*
Bare Ground	0.110	0.032	3.48	<0.001***
Litter	0.023	0.011	1.99	0.047*
Rodent Activity × Litter	-0.004	0.001	-2.52	0.012*
(b) 2012 (Low-Density Year)				
Intercept	0.472	0.274	1.72	0.085'
Rodent Activity	0.086	0.023	3.78	<0.001***
Habitat (Snowbed vs. Heath)	0.637	0.222	2.87	0.004**
Lichen	-0.031	0.015	-2.11	0.035*
Moss	0.006	0.005	1.11	0.268
Rodent Activity × Moss	-0.002	0.001	-2.74	0.006**

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ' $P < 0.1$.

when the amount of litter was high. To some extent, these results are contradictory, indicating that both litter and rodent activity facilitate seedling emergence, although to a lesser extent when both litter cover and rodent activity are high. Lemming disturbance can result in a three-fold increase in litter due to the cutting of graminoids and mosses (Moen et al. 1993). Thus, litter accumulation due to high rodent activity may counteract the positive effects of disturbance on seedling emergence, as high litter amounts may inhibit seedling recruitment (Loydi et al. 2013).

A negative effect of lichen cover on seedling emergence was found in the low-density year (lichen cover was not recorded in the peak year), and several factors related to the presence of lichens could contribute to the observed pattern: lichens prevail in dry environments, where the gap quality could be expected to be comparably low, a dense lichen cover reduces light availability and several lichen species have allelopathic effects (Hobbs 1985; Lawrey 1986; Zamfir 2000). Mosses usually suppress seedling emergence (Eckstein et al. 2011; Soudzilovskaia et al. 2011), but in this study no main effect of moss cover on seedling emergence was found. Both herbivory and other

activities by rodents could potentially suppress the negative effect of mosses by reducing the thickness of the moss carpet (Moen et al. 1993; Virtanen 2000).

Rodent population dynamics and consequences for plant recruitment

As predicted, we found higher seedling recruitment rates in the low-density year compared to the peak year. Small rodents often have a substantial impact on seed populations through seed predation (Hulme 1994; Fox 2011). Seeds are indeed common in the diet of field voles, but not for lemmings (Sætman et al. 2009), and it is possible that seed predation during the peak year may have contributed to lower seedling recruitment rates. Although seedling herbivory by lemmings and voles is considered to be negligible (Olofsson et al. 2005; Shaw et al. 2010), it is probable that high rodent activity resulted in both seedling herbivory and damage to seedlings in the peak year, hence contributing to the lower number of seedlings compared to the low-density year. Moreover, many seedlings were observed in tunnels that were still visible among the vegetation during the low-density year (K.O. Nystuen, pers. obs.). Vegetative growth in alpine areas is a slow process (Evju et al. 2012), and gaps created during the peak year could therefore be expected to still be available in the subsequent growing season, thus providing opportunities for successful seedling emergence when the disturbance intensity is lower. Between-year differences in recruitment could also be a result of differences in the availability of seeds in the seed bank or of other abiotic factors not measured, such as rainfall or temperature.

The cyclic population dynamics of lemmings and voles constitutes a disturbance regime with extensive disturbance and gap formation taking place at peaks typically occurring every third to fifth year (Angerbjörn et al. 2001). Consequently, seedling recruitment patterns in arctic-alpine habitats should be reflected by the rodent population cycles, with an especially high recruitment in the year following a peak (Ericson et al. 1992). Recurrent disturbances resulting in opportunities to reproduce by seeds every third to fifth year, followed by years with a much lower disturbance level, could be important to maintain species richness in arctic-alpine habitats by providing frequent opportunities for recruitment (Warner & Chesson 1985; Chesson 1986) and by preventing competitive exclusion (Chesson 1986; Chambers 1993). The rodent population cycles have been fading out in many places in Scandinavia and in the rest of Europe over the past two decades (Ims et al. 2008; Kausrud et al. 2008; Cornulier et al. 2013), and the absence of the regular disturbance regime could be hypothesized to influence plant recruitment patterns in these sites. In our southern study region

of Dovrefjell, major rodent population peaks have been absent between 1989 (Gjershaug 1996) and 2006 (Fig. 1). If the absence of predictable rodent cycles had resulted in a loss of – or reduced – population sizes of plant species dependent on the regular creation of open space for recruitment, lower seedling numbers could have been expected in Dovrefjell than in Børgefjell. However, our results suggest no such effect. The lack of differences in seedling emergence between the two regions could be due to few species and small populations relying on frequent disturbances in these arctic-alpine habitats, therefore comprising only a minor portion of the bulk of seedlings emerging in gaps. Another reason could be the importance of other sources of disturbance in arctic-alpine habitats, such as frost heave, snowmelt and grazing, as well as trampling from large herbivores, which may contribute to creating microsites for seedling emergence independently of small rodents. The additional positive effect of bare soil on seedling numbers in the peak year supports this, and is in line with the results from Shaw et al. (2010).

Seedling emergence and habitat type

In accordance with our predictions, we found more seedlings in snowbeds than in sheltered heaths. In addition, we expected that a certain disturbance level would result in more seedlings emerging in snowbeds than in sheltered heaths, as the seed rain is higher and germination conditions comparatively better in snowbeds than in sheltered heaths (Graae et al. 2011) where seedling emergence may be hindered by environmental constraints such as drought (Welling & Laine 2002). We also found that rodent activity was higher in snowbeds compared to sheltered heaths, but in contrast to our expectations, no interaction between rodent activity and habitat was found. Our results are in concordance with Olofsson et al. (2005), who found no difference in the impact of experimental disturbance on recolonization in low (heath) and high (birch forest) productive mountain habitats, but in contrast to Evju et al. (2012), who found a larger increase in seedling numbers in sheltered heaths than in snowbeds after severe experimental disturbance.

The lack of a significant rodent activity–habitat interaction could be due to within-habitat differences of snowbeds in our study. The snowbeds in the study ranged from productive, dominated by graminoids and forbs with a high seedling emergence, to late-melting and less productive snowbeds dominated by mosses and *Salix herbacea*, where fewer seedlings are expected to emerge (Welling & Laine 2000). The latter is a preferred winter habitat for lemmings, and is thus expected to have high rodent activity (Moen et al. 1993). The small, though significant, negative interaction between rodent activity and moss cover in

the low-density year points to lower seedling numbers in plots with a high moss cover and high rodent activity, compared to plots with a low moss cover and high rodent activity. This further indicates that variable seedling numbers in snowbeds, due to within-habitat differences, could contribute to explaining the absence of rodent activity–habitat interactions. Additionally, the 2012 records in Dovrefjell (especially in two of the sites) were carried out shortly after snowmelt (Appendix S3), and several snowbed plots were waterlogged; thus, seedling emergence in snowbed plots may be somewhat underestimated.

Even though the overall rodent activity was higher in snowbeds compared to sheltered heaths, the relatively high rodent activity recorded in both habitats (Fig. 3a,b) suggests that additional factors contribute to limit seedling emergence. Relevant factors are seed availability and gap quality (Grubb 1977; Dullinger & Hülber 2011). The total number of seedlings varied largely among the study plots, also within habitats (Appendices S4 and S5), and in some plots no seedlings were present at all despite high rodent activity. Such a large spatial variation in seedling abundance is a common feature in arctic-alpine (Forbis 2003) as well as in other systems (Aguir et al. 1992). The spatial structure of seeds, including both the seed rain and the seed bank, is highly clumped and heterogeneously distributed in space (Rusch & Fernández-Palacios 1995; Molau & Larsson 2000). Shelter effects of microrelief or neighbour plants, resulting in a highly variable microclimate within short distances, might also contribute to the clumping of seedlings (Diemer 1992; Graae et al. 2012).

This study shows that rodent dynamics are an important structuring factor of the vegetation through recruitment. Studies, including data on the species identity of seedlings and the mature vegetation, would further help to understand the effect of rodent disturbances and of the loss of rodent population peaks (Ims et al. 2008; Kausrud et al. 2008) on species assemblage processes, species richness patterns and the invasibility of alpine plant communities. Knowledge about these processes is also important in order to understand the effects of drivers such as climate change, which may enhance the rate of change in alpine vegetation.

Acknowledgements

The study was funded by the Research Council of Norway through the projects 208418/F40, Direct and indirect climate forcing of ecological processes: Integrated scenarios across freshwater and terrestrial ecosystems (grant 208418/F40) and EcoDriver (grant 172529), and by the Norwegian Environment Agency. We are grateful to Jesamine Bartlett, Lise Tingstad and the rest of the team assisting in the fieldwork, to Bård Pedersen for the statistical

advice and to two anonymous referees for valuable comments on an earlier version of this manuscript.

References

- Aguiar, M.R., Soriano, A., & Sala, O.E. 1992. Competition and facilitation in the recruitment of seedlings in Patagonian steppe. *Functional Ecology* 6: 66–70.
- Angerbjörn, A., Tannerfeldt, M., & Lundberg, H. 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. *Ecography* 24: 298–308.
- Austrheim, G., Myrsetrud, A., Hassel, K., Evju, M., & Økland, R.H. 2007. Interactions between sheep, rodents, graminoids, and bryophytes in an oceanic alpine ecosystem of low productivity. *Ecoscience* 14: 178–187.
- Batzli, G. 1975. The role of small mammals in arctic ecosystems. In: Golley, F.B., Petruszewicz, K. & Ryszkowski, L. (eds.) *Small mammals: their productivity and population dynamics*, pp. 243–268. Cambridge University Press, Cambridge, UK.
- Bell, K.L. & Bliss, L.C. 1980. Plant reproduction in a high Arctic environment. *Arctic and Alpine Research* 12: 1–10.
- Chambers, J.C. 1993. Seed and vegetation dynamics in an alpine herb field – effects of disturbance type. *Canadian Journal of Botany* 71: 471–485.
- Chambers, J.C. 1995. Disturbance, life-history strategies, and seed fates in alpine herbfield communities. *American Journal of Botany* 82: 421–433.
- Chambers, J.C., MacMahon, J.A., & Brown, R.W. 1990. Alpine seedling establishment: the influence of disturbance type. *Ecology* 71: 1323–1341.
- Chesson, P.L. 1986. Environmental variation and the coexistence of species. In: Case, T.J. & Diamond, J. (eds.) *Community ecology*, pp. 240–256. Harper & Row, New York, NY, USA.
- Cornulier, T., Yoccoz, N.G., Bretagnolle, V., Brommer, J.E., Butet, A., Ecker, F., Elston, D.A., Framstad, E., Henttonen, H., & Hörmfeldt, B. 2013. Europe-wide dampening of population cycles in keystone herbivores. *Science* 340: 63–66.
- Dalling, J.W. & Hubbell, S.P. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology* 90: 557–568.
- Diemer, M.W. 1992. Population dynamics and spatial arrangement of *Ranunculus glacialis* L., an alpine perennial herb, in permanent plots. *Vegetatio* 103: 159–166.
- Dullinger, S. & Hülber, K. 2011. Experimental evaluation of seed limitation in alpine snowbed plants. *PLoS One* 6: article e21537.
- Eckstein, R.L., Pereira, J.S., Milbau, A., & Graae, B.J. 2011. Predicted changes in vegetation structure affect the susceptibility to invasion in bryophyte-dominated subarctic heath. *Annals of Botany* 108: 177–183.
- Ericson, L., Elmqvist, T., Jakobsson, K., Danell, K., & Salomonson, A. 1992. Age structure of boreal willows and fluctuations in herbivore populations. *Proceedings of the Royal Society of Edinburgh Section B-Biological Sciences* 98: 75–89.
- Eskelinen, A. & Virtanen, R. 2005. Local and regional processes in low-productive mountain plant communities: the roles of seed and microsite limitation in relation to grazing. *Oikos* 110: 360–368.
- Evju, M., Hagen, D., Blumentrath, S., & Eide, N.E. 2010. *Value- and vulnerability assessment in Borgefjell national park*. Norwegian Institute for Nature Research [report no. 583], Trondheim, NO. [In Norwegian].
- Evju, M., Hagen, D., & Hofgaard, A. 2012. Effects of disturbance on plant regrowth along snow pack gradients in alpine habitats. *Plant Ecology* 213: 1345–1355.
- Fenner, M. & Thompson, K. 2005. *The ecology of seeds*. Cambridge University Press, Cambridge, UK.
- Forbis, T.A. 2003. Seedling demography in an alpine ecosystem. *American Journal of Botany* 90: 1197–1206.
- Forbis, T.A. 2009. Negative associations between seedlings and adult plants in two alpine plant communities. *Arctic, Antarctic and Alpine Research* 41: 301–308.
- Forbis, T.A., Larmore, J., & Addis, E. 2004. Temporal patterns in seedling establishment on pocket gopher disturbances. *Oecologia* 138: 112–121.
- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A., & Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27: 233–249.
- Fox, B.J. 2011. Review of small mammal trophic structure in drylands: resource availability, use, and disturbance. *Journal of Mammalogy* 92: 1179–1192.
- Framstad, E. 2013. *Terrestrial ecosystem monitoring in 2012: Ground vegetation, epiphytes, small mammals and birds*. Summary of results. Norwegian Institute for Nature Research [report no. 952], Oslo, NO. [In Norwegian].
- Gjershaug, J.O. 1996. Breeding success and productivity of Golden Eagle *Aquila chrysaetos* in Central Norway, 1970–1990. In: Meyburg, B.-U. & Chancellor, R.D. (eds.) *Eagle studies*, pp. 475–482. World Wildlife Fund, Berlin, DE.
- Gough, L. 2006. Neighbor effects on germination, survival, and growth in two arctic tundra plant communities. *Ecography* 29: 44–56.
- Graae, B.J., Ejrnæs, R., Lang, S.I., Meineri, E., Ibarra, P.T., & Bruun, H.H. 2011. Strong microsite control of seedling recruitment in tundra. *Oecologia* 166: 565–576.
- Graae, B.J., De Frenne, P., Kolb, A., Chabrerie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., & Milbau, A. 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* 121: 3–19.
- Grime, J.P. 2001. *Plant strategies, vegetation processes and ecosystem properties*. Wiley, Chichester, UK.
- Grime, J.P., Mason, G., Curtis, A., Rodman, J., & Band, S. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* 69: 1017–1059.

- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52: 107–145.
- Hagen, D., Gaare, E., Erikstad, L., & Hoem, S.A. 2006. Grazing resources in Snøhetta area – mapping pasture for wild reindeer, musk and sheep using satellite images and visual point estimates. Norwegian Institute for Nature Research [report no. 135], Trondheim, NO. [In Norwegian]
- Hambäck, P.A., Schneider, M., & Oksanen, T. 1998. Winter herbivory by voles during a population peak: the relative importance of local factors and landscape pattern. *Journal of Animal Ecology* 67: 544–553.
- Hobbs, R.J. 1985. The persistence of *Cladonia* patches in closed heathland stands. *The Lichenologist* 17: 103–109.
- Hulme, P.E. 1994. Postdispersal seed predation in grassland – its magnitude and sources of variation. *Journal of Ecology* 82: 645–652.
- Ims, R.A. & Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *BioScience* 55: 311–322.
- Ims, R.A., Henden, J.A., & Killengreen, S.T. 2008. Collapsing population cycles. *Trends in Ecology & Evolution* 23: 79–86.
- Jonasson, S. 1992. Plant-responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos* 63: 420–429.
- Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M., Mysterud, I., Solhøy, T., & Stenseth, N.C. 2008. Linking climate change to lemming cycles. *Nature* 456: 93–98.
- Lawrey, J.D. 1986. Biological role of lichen substances. *Bryologist* 89: 111–122.
- Lid, J. & Lid, D. T. 2005. Norsk flora. Det Norske Samlaget, Oslo, NO. [In Norwegian]
- Loydi, A., Eckstein, R.L., Otte, A., & Donath, T.W. 2013. Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. *Journal of Ecology* 101: 454–464.
- Mayer, R. & Erschbamer, B. 2011. Seedling recruitment and seed/microsite limitation in traditionally grazed plant communities of the alpine zone. *Basic and Applied Ecology* 12: 10–20.
- McKendrick, J.D., Batzli, G.O., Everett, K.R., & Swanson, J.C. 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arctic and Alpine Research* 12: 565–578.
- Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B.J. 2013. Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist* 197: 1002–1011.
- Moen, J., Lundberg, P.A., & Oksanen, L. 1993. Lemming grazing on snowbed vegetation during a population peak, Northern Norway. *Arctic and Alpine Research* 25: 130–135.
- Molau, U. & Larsson, E.L. 2000. Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany* 78: 728–747.
- Mulder, C.P.H. 1999. Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics* 2: 29–55.
- Munier, A., Hermanutz, L., Jacobs, J.D., & Lewis, K. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for tree-line advance with climate warming. *Plant Ecology* 210: 19–30.
- Olofsson, J., Hulme, P.E., Oksanen, L., & Suominen, O. 2004. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* 106: 324–334.
- Olofsson, J., Hulme, P.E., Oksanen, L., & Suominen, O. 2005. Effects of mammalian herbivores on revegetation of disturbed areas in the forest-tundra ecotone in northern Fennoscandia. *Landscape Ecology* 20: 351–359.
- Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T., & Suominen, O. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15: 2681–2693.
- Olofsson, J., Tømmervik, H., & Callaghan, T.V. 2012. Vole and lemming activity observed from space. *Nature Climate Change* 2: 880–883.
- Pickett, S.T.A., Wu, J., & Cadenasso, M.L. 1999. Patch dynamics and the ecology of disturbed ground: a framework for synthesis. In: Walker, L.R. (ed.) *Ecosystems of disturbed ground*, pp. 707–722. Elsevier, Amsterdam, NL.
- Post, E. & Pedersen, C. 2008. Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 105: 12353–12358.
- Rebollo, S., Milchunas, D.G., Stapp, P., Augustine, D.J., & Derner, J.D. 2013. Disproportionate effects of non-colonial small herbivores on structure and diversity of grassland dominated by large herbivores. *Oikos* 122: 1757–1767.
- Reichman, O.J. & Seabloom, E.W. 2002. The role of pocket gophers as subterranean ecosystem engineers. *Trends in Ecology & Evolution* 17: 44–49.
- Rusch, G. & Fernández-Palacios, J.M. 1995. The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. *Journal of Vegetation Science* 6: 417–426.
- Sætnan, E.R., Gjershaug, J.O., & Batzli, G.O. 2009. Habitat use and diet composition of Norwegian lemmings and field voles in Central Norway. *Journal of Mammalogy* 90: 183–188.
- Shaw, R.F., Iason, G.R., Pakeman, R.J., & Young, M.R. 2010. Regeneration of *Salix arbuscula* and *Salix lapponum* within a large mammal enclosure: the impacts of microsite and herbivory. *Restoration Ecology* 18: 1–9.
- Silvertown, J.W. 1980. Leaf-canopy-induced seed dormancy in a grassland flora. *New Phytologist* 85: 109–118.
- Sirotnak, J.M. & Huntly, N.J. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* 81: 78–87.

- Smith, H. 1985. Light quality, photoreception, and plant strategy. *Annual Review of Plant Physiology* 33: 481–518.
- Soininen, E., Zinger, L., Gielly, L., Bellemain, E., Bråthen, K., Brochmann, C., Epp, L., Gussarova, G., Hassel, K., (...) & Ims, R. 2013. Shedding new light on the diet of Norwegian lemmings: DNA metabarcoding of stomach content. *Polar Biology* 36: 1069–1076.
- Soudzilovskaia, N.A., Graae, B.J., Douma, J.C., Grau, O., Milbau, A., Shevtsova, A., Wolters, L., & Cornelissen, J.H.C. 2011. How do bryophytes govern generative recruitment of vascular plants? *New Phytologist* 190: 1019–1031.
- Stenseth, N.C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87: 427–461.
- Suding, K.N. & Goldberg, D.E. 1999. Variation in the effects of vegetation and litter on recruitment across productivity gradients. *Journal of Ecology* 87: 436–449.
- Turchin, P. & Batzli, G.O. 2001. Availability of food and the population dynamics of arvicoline rodents. *Ecology* 82: 1521–1534.
- Tveito, O.E., Bjørndal, I., Skjelvåg, A.E., & Aune, B. 2005. A GIS-based agro-ecological decision system based on gridded climatology. *Meteorological Applications* 12: 57–68.
- Virtanen, R. 2000. Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland. *Oikos* 90: 295–300.
- Virtanen, R., Henttonen, H., & Laine, K. 1997. Lemming grazing and structure of a snowbed plant community – A long-term experiment at Kilpisjärvi, Finnish Lapland. *Oikos* 79: 155–166.
- Walker, L.R. 2012. *The biology of disturbed habitats*. Oxford University Press, Oxford, UK.
- Warner, R.R. & Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist* 125: 769–787.
- Welling, P. & Laine, K. 2000. Characteristics of the seedling flora in alpine vegetation, subarctic Finland, I. Seedling densities in 15 plant communities. *Annales Botanici Fennici* 37: 69–76.
- Welling, P. & Laine, K. 2002. Regeneration by seeds in alpine meadow and heath vegetation in sub-arctic Finland. *Journal of Vegetation Science* 13: 217–226.
- Weltzin, J.F., Archer, S., & Heitschmidt, R.K. 1997. Small-mammal regulation of vegetation structure in a temperate Savanna. *Ecology* 78: 751–763.
- Zamfir, M. 2000. Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. *Oikos* 88: 603–611.
- Zhang, Y.M., Zhang, Z.B., & Liu, J.K. 2003. Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. *Mammal Review* 33: 284–294.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Map of the study sites and the study regions' location in Norway.

Appendix S2. Table showing the distribution of plots among study sites, habitats and year.

Appendix S3. Table with detailed information on data sampling time.

Appendix S4. Histograms with frequency distribution of seedlings in the recorded plots.

Appendix S5. Table with details on seedling occurrences (mean \pm SE, total number, number of plots with no seedlings) for all combinations of habitat, study region and year.