

Title

Comparison of methods for revegetation of vehicle tracks in High Arctic tundra on Svalbard

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Abstract

Natural regeneration after anthropogenic disturbance is slow in the tundra biome, but assisted regeneration can help speed up the process. A tracked off-road vehicle damaged a High Arctic dwarf shrub heath in Svalbard in May 2009, drastically reducing vegetation cover, soil seed bank and incoming seed rain. We assisted regeneration the following year using six different revegetation treatments, and monitored their effects one month, and one and eight years after their application. By 2018, all treatments still had a lower vegetation cover and limited species composition than the undamaged reference vegetation. The fertiliser treatment was the most effective in restoring vegetation cover (71 % vegetation cover, of which 62 % were bryophytes and 38 % vascular plant species). Compared to the reference plots (98 % vegetation cover, of which 32 % were bryophytes and 66 % were vascular plant

species), the composition of the disturbed vegetation was still far from regenerated to its original state nine years after the tracks were made. The slow regrowth demonstrated in this study underlines the importance of avoiding disturbance of fragile tundra, and of implementing and upholding regulations restricting or banning such disturbance.

Introduction

Natural regeneration in cold-dominated ecosystems is slow (Babb and Bliss 1974; Forbes and Jefferies 1999; Forbes et al. 2001), rendering the landscape less resilient to anthropogenic disturbance (Rickard and Brown 1974; Komarkova 1983; Walker and Walker 1991; Urbanska and Chambers 2002; Krautzer et al. 2012). For instance, it took up to 75 years to re-establish complete vegetation cover after removing mesic above-ground vegetation, roots and soil in northern Alaska (Forbes et al. 2001). However, it might take several hundred years or more for a disturbed area to return to its original vegetation composition after disturbance, if at all, and plant diversity might still be lower than in undisturbed areas (Komarkova 1983; Forbes and Jefferies 1999).

Off-road tracked vehicles are commonly and extensively used in various industries and by military, management personnel and scientists throughout the Arctic. Since the 1950s, regulations have severely restricted their use with general rules and establishing protected areas where they are banned. For instance, more than 60% of the land on Svalbard is currently protected, and the use of vehicles is strictly regulated. However, a long history of coal mining and drilling (Theisen and Brude 1998) has left many historic vehicle tracks and other surface disturbances leading to linear or patchy scars on the tundra that may facilitate erosion, drainage and further expansion of the vegetation damage.

58 In addition to these long-term historical impacts, humans are increasingly disturbing the
59 fragile Arctic vegetation and landscapes (Walker and Walker 1991; Forbes et al. 2001). After a
60 change from coal mining as the main economic activity on Svalbard, tundra disturbance today
61 is mainly linked to a growing human population (e.g., roads, drainage, residences, and related
62 installations), as well as research and tourism. Large double-tracked vehicles are used to
63 transport heavy materials (for moving ready-constructed cabins, mining machinery etc.),
64 while smaller vehicles (snowmobiles) are commonly and increasingly used for recreational
65 purposes. Although driving on snow-covered frozen ground has little-to-no effect on soils and
66 vegetation, the use of vehicles on unfrozen and non-snow covered tundra directly or indirectly
67 leads to vegetation removal, soil erosion, increased permafrost thaw depth, water run-off,
68 nutrient leaching and more (Rickard and Brown 1974; Abele et al. 1984; Felix and Reynolds
69 1989; Slaughter et al. 1990; Racine and Ahlstrand 1991; Forbes 1992; Emers et al. 1995; Kevan
70 et al. 1995; Forbes et al. 2001; Li et al. 2007). Disturbance caused by vehicle tracks may be
71 visible in the tundra for many decades (Forbes et al. 2001). Thus, damage prevention
72 measures should be given the highest priority within management. In order to counterbalance
73 such anthropogenic vegetation disturbances, an understanding of practical revegetation
74 techniques on Svalbard is much needed but is currently lacking.

75 Assisted regeneration may speed up natural regrowth and reduce or even reverse damage to
76 the original vegetation (MEA 2005; Suding 2011). Many experiments have aimed to pinpoint
77 the best techniques and methods to assist revegetation in the tundra biome in general (Babb
78 and Bliss 1974; Firlotte and Staniforth 1995; Forbes and McKendrick 2002; Mehlhoop et al.
79 2018). During the last decades, a refinement of the desired outcomes of such assisted
80 regeneration activities has also been developed. For instance, while the rehabilitation of the
81 original plant species composition may be the goal in some areas and under certain contexts,

the reestablishment of vegetation cover irrespective of its composition may suffice in other areas or contexts. Facilitating the return of the original plant species composition requires more sophisticated methods. It is typically slower than primarily aiming for non-species-specific plant cover (Forbes et al. 2001) and requires a better understanding of the habitat's species' ecology (Deshaies et al. 2009). Thus, the optimal practice is very context-specific, and the most appropriate treatments may vary depending on the communities or ecosystems in question.

Every restoration method studied during the last few decades yields different results and have their own shortcomings (Firlotte and Staniforth 1995; Forbes and McKendrick 2002). In cold, nutrient-poor environments, for instance, fertiliser addition has been shown to cause relief from nutrient limitation and increase plant growth (Onipchenko et al. 2012; Gu and Grogan 2020). Furthermore, placing fibre cloths over disturbed areas increases the temperature and moisture and has been shown to create safe sites for propagule germination and plant species establishment (Stetson 1996). Another study has shown that tilling of devegetated areas activates the natural seed bank and generally increases soil aeration (Wilson and Gerry 1995), especially in cases where the disturbance resulted in soil compression. Additionally, sowing of seeds, cuttings and other propagules have been applied to create a fast replacement of removed vegetation (Chapin and Chapin 1980; Barak et al. 2017; Vloon et al. 2021). And finally, an early revegetation study near Longyearbyen (close to the field site we are reporting on her) was carried out in 1980 by the local authority, focusing on the sowing of introduced grass species (Låg 1986).

All the methods outlined here accelerate the re-appearance of any vegetation irrespective of species composition (Chapin and Chapin 1980; Densmore 1992; Forbes et al. 2001). However, undesired effects have also been reported, such as creating atypical species assemblages or

106 composition after fertiliser addition (Klokk and Rønning 1987), or naturalized stands of
107 introduced species after sowing non-native seeds (Densmore 1992; Hagen et al. 2014). Such
108 side-effects are commonly accepted as an unavoidable trade-off in assisted regeneration in
109 the tundra for users causing the disturbances (e.g. industry, military), as the main aim is
110 usually to bring back just enough vegetation cover – preferably using local species – to prevent
111 erosion and expansion of disturbed patches in the most cost-effective manner possible (cf.
112 Forbes et al., 2001, Forbes and McKendrick 2002). Just how undesirable these artefacts are,
113 depends on the specific case and on the practitioners' and stakeholders' goals, expectations
114 and time frames, making the choice of method complex. A thorough evaluation of each
115 method's effects, side effects and best practice will be necessary for choosing the optimal
116 strategy for each site.

117 Despite numerous ecological restoration and rehabilitation studies, the relatively few
118 observations from specific ecosystems still limit meaningful comparisons. Thus, even simple
119 experiments represent valuable contributions to the literature towards more rigorous
120 estimations of revegetation time and/or success. Similarly, a general lack of long-term post-
121 treatment and/or systematic monitoring, challenges the interpretation and applicability of
122 results for adaptive management (Bash and Ryan 2002; Miller and Hobbs 2007; Hagen and
123 Evju 2013), but see circumpolar review comparing post-treatment conditions using many
124 common assisted revegetation techniques in Forbes and McKendrick (2002).

125 Here, we test which of the outlined, commonly used assisted regeneration techniques may be
126 suitable to regenerate damaged vegetation, specifically in High Arctic Svalbard. We describe
127 their potential side effects in terms of vegetation composition, an essential factor, not only
128 for the wellbeing of the ecosystem, but also for the eco-conscious community visiting and
129 living near our field site. We applied these methods to devegetated tracks in the tundra, which

were accidentally created by a large double-tracked off-road vehicle driving unduly late in the spring, i.e., when snowmelt and soil thawing were very advanced and the tundra vulnerable to disturbance. We report the revegetation of the tracks 1, 2 and 9 years after the disturbance, (i.e., one month, and one and eight years after their treatments were applied). Our findings are relevant for stakeholders interested or in need of assisted regeneration of damage to tundra in Svalbard after severe disturbance.

Methods

Study area

The study site was a *Cassiope* heath, classified as *Cassiope tetragona* L.D. Don. tundra (Elvebakk 2005), which corresponds to the *Cassiope tetragona* – *Dryadetum octopetalae* phytosociological association (Hadač 1946; Hadač 1989). The most abundant vascular plant species in the study area were *Cassiope tetragona* L.D. Don., *Bistorta vivipara* (L.) Delarbre, *Dryas octopetala* L. and *Salix polaris* Wahlenb. The site is situated in bioclimatic zone C - the middle Arctic tundra zone (Walker et al. 2005), near Longyearbyen, Svalbard, High Arctic Norway. The annual average temperature and precipitation during 1976-2020 were -4.7°C and 196 mm respectively, with most of the precipitation falling during winter (MET Norway 2021). The bedrock consists of flat-lying sediments of sandstone, silt and shale and large fluvial deposits with active alluvial plains and fans nearby. The growing season is about 70 days (Rozema et al. 2009), with average summer air temperature (1 June - 31 August 1976-2020) of 5.1°C (MET Norway 2021).

The study site is located on the south side of Adventdalen (78°10'N, 16°02'E), 25 m a.s.l. and was selected because a double-tracked off-road vehicle left scars in the landscape in May 2009. The two parallel tracks were each approximately 47 m long, 0.5 m wide, and were 2 m

154 apart. Vegetation cover was greatly reduced in the tracks compared to the undisturbed
155 vegetation in the surrounding area (see Fig. 1). Within the tracks, seed density in the soil seed
156 bank was lower and seed influx reduced compared to the surrounding intact vegetation (Fig.
157 2 and Appendix I-II). Soil density was somewhat lower in the tracks than in the intact
158 vegetation, so it seems that the vehicle may have removed soil with attached vegetation
159 rather than compressed it (Appendix III).

160
161 Field measurements

162 In June 2010, we installed 80 permanent 35 x 35 cm quadratic plots distributed within the
163 vehicle tracks (see Fig. S1). The size of the plots was determined by the width of the vehicle
164 tracks, and 35 x 35 cm squares fitted well without being too close to the tracks' edges. The
165 criteria for selecting the plots were made opportunistically and adjusted according to the soil,
166 and topographic conditions inside the tracks, which were sometimes unsuitable (i.e., parts
167 which were more rocky or depressed, leading to waterlogging, than the bulk of the tracks
168 were excluded). The plots were placed along the suitable, zonal parts. The selected plots were
169 about 10-200 cm apart and permanently marked with labelled plastic sticks in two corners so
170 that we could place a quadrat/ frame on the same location in the future. Ten of the initially
171 selected plots were excluded due to unforeseen waterlogging after the first rain, resulting in
172 a total of 70 permanent plots.

173 To document the disturbance to the vegetation caused by the vehicle tracks prior to
174 experimental treatment application, we recorded vegetation composition within- (disturbed
175 vegetation) and outside (intact, reference vegetation) the vehicle tracks (Table S1) with the
176 point-frame method during 23-30 June 2010. Outside the tracks (reference vegetation), we
177 used 11 approximately equally spaced plots about 2m away from the tracks. These plots were

178 evenly distributed along the entire length of the tracks, with five plots being on one side and
179 six plots being on the other side of the tracks. Inside the tracks (disturbed vegetation), we
180 used the 70 experimental plots already described (prior to treatment addition). We used
181 point-frame quadrats of size 35x35cm with strings spun across the frames every five cm,
182 resulting in a total of 25 string crossings per frame. At each string crossing, a wooden pin was
183 carefully stuck vertically through the vegetation. Each plant touching the pin (i.e., each 'hit')
184 was noted for each vascular species or species group until we reached the ground layer
185 (bryophyte, fungi, bare ground, or droppings), which we also recorded. This resulted in up to
186 three 'hits' per pin in the reference and up to two 'hits' per pin in the disturbed vegetation.
187 For hits without any vegetation cover, we also noted whether they were on bare ground, fungi
188 or animal droppings.

189 In July 2010, six different treatments were applied to the 70 plots, with ten replicates per
190 treatment plus an unmodified control (Fig. S1). The six treatments were only applied once at
191 the beginning of the experiment in July 2010 and not repeated thereafter. The allocation of
192 treatment type to each plot was random.

193 To avoid edge effects from treatments, we monitored the vegetation only in the centre 20 x
194 20 cm of the plots. We did this regularly during the growing seasons in 2010 and 2011 (see
195 Fig. S2, Fig. 3 temporal development) and at peak season in 2018 (20 July 2018) in the
196 following way. Each plot inside the tracks was divided into nine equally sized subplots with the
197 help of a portable square dissected with equally spaced strings (Fig. S3). In each subplot, the
198 per cent cover of plant species was documented as visual estimates on a 1 % scale, looking
199 from above, with the maximum cover being 100 % per subplot and species, resulting in
200 possibly more than 100 % cover when summing up the cover across all species.

Young graminoids as well as bryophytes were not identified to species level and are henceforth treated as two groups. However, the most common bryophytes in the area are *Sanionia uncinata*, *Tomentypnum nitens*, *Hylocomium splendens*, *Dicranum* and *Distichium* spp., *Polytrichum* spp., and *Aulacomnium* spp. (Mörsdorf and Cooper 2021) and we assume the species in the experimental plots were the same. *Sanionia* is a bryophyte that doubled in abundance after shrub death due to increased snow in a nearby field experiment and is likely to play an important role in this revegetation experiment. Similarly, the unidentified young graminoids most likely were of the same species we could identify as mature plant species, namely *Luzula arcuata* subsp. *confusa* and *Alopecurus magellanicus*, but we cannot exclude that they were also one of the other species present in the study site, e.g., *L. nivalis*, *Poa* spp.

Experimental regeneration treatments

The following six treatments were applied randomly to defined plots inside the vehicle tracks once only in July 2010. Each treatment was applied to ten plots, resulting in 60 experimental plots plus ten unmanipulated control plots. The treatments were chosen to be realistic and could be applied at a large scale in the tundra, if necessary.

The fertilisation treatment (F) consisted of diluted commercial plant fertiliser. The fertiliser (Substral Pflanzenæring from The Scotts Company Nordic AS, 0214 Oslo, Norway) contained 6 % nitrogen, 1.3 % phosphorus and 5 % potassium. Arctic tundra communities have a natural nitrogen uptake of 0.752 - 1 g per m² per year (Chapin et al. 1988; Baddeley et al. 1994). The fertiliser treatment (17.5 ml) was sprayed evenly onto 0.25 m² covering the plots manually with a spray bottle once at the beginning of the first growing season, similar to previous fertilisation experiments in the Arctic (Bigger and Oechel 1982; Baddeley et al. 1994; Robinson et al. 1998). We used mild amounts of fertilisation as too much in nutrient-poor soils might

lead to a decrease in the number of plant individuals and percent cover (Forbes and Jefferies 1999; Gordon et al. 2001).

Treatment G was the addition of a fibre cloth/ garden fabric (Gardener's Supply Company, Vermont, USA) spread out over the plot area, exceeding it by 15 cm on each side and pinned down using nails. The cloths were intended to slightly increase the soil temperature and moisture (<https://www.gardeners.com/how-to/row-covers/5111.html>), similar to a greenhouse (Gu and Grogan 2020). Temperature and moisture probes (HOBO-loggers, HOBO®, Massachusetts, USA) were placed 2 cm below the surface during July - September 2011 and showed that the fibre cloths increased temperature on average by 0.3 °C (the mean temperature in the controls was 6 °C during this period). Relative humidity was measured by the same loggers, in the same time period and were 0.1 % lower in plots with cloths (based on measures from two plots only covered with cloths) compared to the plots without cloths (based on measures from four plots not covered with cloths). The cloths of treatment G were left throughout the year and replaced when the snow melted in the second season. Some cloths were also replaced during the summer if we noticed damage (e.g., caused by reindeer), nevertheless, one blew away unnoticed, thus leaving treatment G with nine instead of ten replicates. We also applied a treatment using fibre cloths in combination with fertilizer (treatment FG).

Treatment S was the addition of seeds and bulbils to the plots. We sowed an evenly spread-out mixture of 50 seeds from *Silene acaulis* (L.) Jacq. and 50 seeds from *Saxifraga oppositifolia* (L.), as well as 50 bulbils from *B. vivipara* that were all opportunistically gathered from the local area for this and other ongoing projects. These species are locally common. The propagules are easy to gather and relatively easy to germinate in the field (Cooper et al. 2004; Müller et al. 2011), as opposed to seeds of *C. tetragona* that are less available because their

seeds are tiny and their flowers face downwards (thus releasing their seeds quickly), and they are known to not readily germinate in experimental settings (Alsos et al. 2013).

For treatment P, the addition of plant cuttings, we composed a mixture of cut pieces of *S. polaris* and the prostrate form of *S. oppositifolia* from the surroundings. The two species can propagate easily through cuttings (Hagen 2002; Hartmann et al. 2002; Hagen 2003; Cooper 2006) and were therefore suitable choices for this revegetation study. Approximately 1.15 litre of vegetation mixture was necessary to cover each plot. The material was sprinkled on the plot but was not held in place by any netting or cloth.

The tilling treatment (T) was performed to aerate compacted soil, using a dinner fork with two of its prongs bent downwards at a 90° angle in a spinning movement through the soil layer with a maximum depth of 3 cm. An equal amount of time was spent tilling each treatment plot (approx. 1 min).

Statistical analyses

Disturbance in vehicle tracks

To illustrate the disturbance caused by the vehicle tracks and the homogeneity of the floral composition inside the vehicle tracks, we used constrained correspondence analysis (CCA) using the vegan package (Oksanen et al. 2012) on the point-frame data from June 2010 (i.e. 1 year following disturbance, but before treatments were added). Constraining variables were treatment and reference vegetation, i.e., whether the plots were outside of the vehicle tracks. We tested the significance of the constraining variables by applying a permutation test with 999 permutations.

Total vegetation cover

273 To compare the inter-annual (i.e. across the years 2010-2011-2018) development of the
274 disturbed plots without confounding it with seasonal developmental growth, phenology or
275 die-back (see Fig. S2 and Fig. S4 for within-year temporal development), we here concentrate
276 on the vegetation in the experimental plots during peak season on 21 July 2010, 17 July 2011
277 and 20 July 2018. Effects of the different revegetation assistance methods (treatments) were
278 modelled as total vegetation cover, defined as the sum of cover estimates per sub-plot for all
279 identified vascular plant species, unidentified (young) graminoid species, and unidentified
280 bryophyte species. For this analysis, we removed (unidentified) fungi species and droppings,
281 as fungi only appeared in one plot, and droppings do not contribute to the revegetation
282 success (Fig. 3). In 2018, it was not possible to relocate all plots, thus the control and treatment
283 plots for 2018 consists of the following replicates C (n=7), F (n=8), FG (n=9), G (n=9), S (n=10),
284 P (n=10), T (n=10).

285 The total vegetation cover data can be considered as counts since only non-negative, integer
286 numbers were recorded as percentage cover, and the maximum total vegetation cover could
287 be higher than 100 %. Hence, we used generalised mixed-effects models with Poisson
288 distribution and log-link through the glmer function from the lme4 package in R (Bates et al.
289 2015; R Core Team 2021). The full model included the treatment by year interaction as fixed
290 effects, and random intercepts for plots (to account for pseudoreplication (Hurlbert 1984)).
291 Residual variance of each model was visually checked for normality and heterogeneity across
292 all predictor variables, which were both fulfilled. Backward model selection was performed
293 via likelihood ratio tests and AIC comparison between the full model and an additive model
294 excluding the treatment by year interaction, with the result that the full model was selected
295 for further interpretation of the data. Finally, we calculated simultaneous, Tukey-corrected
296 pairwise 95% confidence intervals (CIs) with the glht function from the multcomp package

(Hothorn et al. 2008) and interpreted contrasts as significant if the CIs excluded zero. Back-transformed estimated marginal means of the final model with 95% CIs were created with the emmeans function of the multcomp package (Hothorn et al. 2008) to illustrate total vegetation cover in Fig. 4.

Results

Disturbance in vehicle tracks

Concerning species composition prior to treatment application (i.e., point-frame data June 2010), the permutation test of the constraining term treatment/reference in the CCA analysis is highly significant when the reference vegetation is included in the analysis ($p < 0.001$), i.e. at least one of the factors in treatment/reference had a significantly different species composition than the others (Fig. S5). When removing the reference vegetation term from the analysis (Fig. S6), the treatment term is not significant anymore ($p = 0.992$), i.e., the species composition does not differ across the treatments within the vehicle tracks (disturbed vegetation). These results indicate that the disturbed vegetation was clearly different from the reference vegetation. This difference was mainly caused by the absence of *D. octopetala*, *C. tetragona* and bryophytes, and the predominance of bare ground in the disturbed vegetation (Fig. 3, Fig. S5, Fig. S6, Table S1). These results further indicate that the plots that the treatments were later assigned to have no initial floral composition difference influencing the plots' trajectories (Fig. S6).

Total vegetation cover

In the peak-season total vegetation cover analysis, the treatment by year interaction was significant, i.e., the treatment effects differed across years (likelihood ratio test p -value <

0.0001). Indeed, the strongest effects were due to years alone (Table S2, Fig. 4), i.e., vegetation cover increased with time independently of treatment, albeit at different rates across treatments. In 2010, the summer of treatment application, there was no significant effect of the treatments except for treatment G (garden cloth), which had 1.05-1.97 (95% CI) times higher cover than controls.

In 2011, one year after the application of the treatments, treatments F (fertilizer), FG (fertilizer plus garden cloth), and G had significantly higher vegetation cover than controls, while the remaining treatments were not significantly different from controls (Fig. 4, Table S2). Within the named three treatments, FG had significantly higher vegetation cover than G, but not than F.

In 2018, eight years after the application of the treatments, F, FG and G had significantly higher vegetation cover than controls, with each of the three treatments' effect sizes being about the same and not significantly different from each other (Fig. 4, Table S2). While F, FG and G had significantly higher vegetation cover than the controls in 2018, the remaining treatments P (plant cuttings), S (seeds) and T (tilling) tended to have higher cover, although not significantly so. Similarly, P, S and T had qualitatively but not significantly lower cover than F, FG and G.

Discussion

We systematically assisted the regeneration of landscape scars created by off-road driving in High Arctic Svalbard tundra. Nine years after the disturbance, the vehicle's tracks were still clearly visible in the landscape. Inside the tracks, vegetation composition was significantly different to the surrounding reference vegetation. During the eight-year study period, the tracks did not regain their original vegetation composition. Vegetation cover increased with

time independently of treatment, with the strongest effects due to years alone; however, the six regeneration treatments differed in their effects.

We found that adding fertiliser was the most effective treatment to increase total vegetation cover, corroborating with previous studies in cold environments (Baddeley et al. 1994; Robinson et al. 1998). Low soil nutrient availability is common in these harsh environments due to slow nutrient cycles (Callaghan et al. 2004; Walker and del Moral 2009), thus removing this nutrient limitation was expected to be a valuable method to help regenerate the vegetation in the tracks (Krautzer et al. 2012). During the initial study year, our model found no effect between treatments at peak season, likely because there was not enough time for the slowly growing vegetation to respond. However, detailed weekly monitoring showed an increase in vegetation cover already during late summer in the two fertiliser treatments in 2010 (Fig. S4), which was mainly caused by an increase in cover of *Poa pratensis*. This was further enhanced during the second and ninth year after disturbance, where treatments F, G and FG had significantly higher vegetation cover than controls. Since the total vegetation cover of G alone has far more bare ground in our raw data (Fig. 3, Table S1) than F and FG, we interpret the effect of FG as being foremost because of fertilisation. Nevertheless, using garden cloth, mesh netting or similar cover or erosion matting as in our treatment G has proved valuable in studies in other habitats (Lewis 1995; Lavendel 2002) and in cold habitats (Whitall 1995). The FG treatment showed stronger effects in 2018 than in 2011, indicating a possible increase in the effect of the treatments. It would be interesting to examine the effect of climatic differences during these seasons, but this is beyond the remit of this study.

Large parts of the effects of the fertiliser treatments were due to bryophyte growth (Fig. 3). Although this study does not allow us to test this in detail due to incomplete bryophyte identification in the field, their species composition was shown to differ between original

369 vegetation and disturbed vehicle tracks even when vascular vegetation did not differ. We aim
370 to test this by future monitoring of the experiment. Our findings are in line with other studies
371 from nutrient-limited ecosystems, which have shown that the addition of fertilizer increases
372 the growth of taxonomic groups demanding or making use of high nutrient levels, such as
373 grasses and bryophytes (Densmore 1992; Sjögersten et al. 2010; Moulton and Gough 2011).
374 In any case, even though we cannot name the individual species here, to supplement the
375 incomplete bryophyte identification and help the reader to interpret our results, the
376 bryophytes species present in the surroundings were identified by another study close to our
377 field site in 2017 and were, in descending order of abundance: *Sanionia uncinata*,
378 *Tomentypnum nitens*, *Hylocomium splendens*, *Dicranum* and *Distichium* spp., *Polytrichum*
379 spp., and *Aulacomnium* spp., (Mörsdorf and Cooper 2021). Bryophyte sods have been used
380 with considerable success in assisted revegetation of tundra wetlands affected by vehicle
381 tracks in the Canadian High Arctic (Forbes 1993). This shows that we need a better
382 understanding of the highly significant bryophyte component when conducting future studies
383 on regeneration of High Arctic disturbances (Lett *et al.* 2021; Mörsdorf and Cooper 2021).
384 Independently of fertilisation, we also found other ruderal species establishing after the
385 vehicle disturbance. For instance, *Poa pratensis* is not in the reference vegetation but occurred
386 in all treatments (Fig. 3, Table S1). Such establishment is an important step towards plant
387 succession and further regeneration (both natural and assisted) in disturbed tundra
388 vegetation (Fig. 3, Forbes, 1994, Forbes et al., 2001, Forbes & McKendrick, 2002, Hagen &
389 Evju, 2013). However, this may be interpreted as a change in vegetation composition, and the
390 disturbance of vegetation in the area of our field site in western Svalbard may be a gateway
391 for non-native or invasive species to naturalize here due to the lack of competition in these
392 disturbed areas.

393 The vehicle tracks may have removed, rather than compressed, the soil's topmost layer,
394 leaving a severely reduced seed bank (Appendix I). Without vegetation cover, the microhabitat
395 is also less susceptible to trapping dispersing seeds (Chapin et al., 1994, Appendix II) in an
396 already poor recruitment habitat (Bliss 1958; Havström et al. 1993; Müller et al. 2011).
397 Although introduced seeds and bulbils in a depleted soil bank are expected to have a
398 competitive advantage, we found only a little effect of this on vegetation cover, in contrast to
399 other studies (Grant et al. 2011; Hagen and Evju 2013). Seeded species in revegetation
400 experiments are typically fast-growing grasses that provide erosion protection and vegetation
401 cover quickly. Though such treatments are found to both facilitate and reduce the
402 establishment of original species (Olofsson et al. 1999; Gretarsdottir et al. 2004; Hagen et al.
403 2014), thus risking lower species richness than without seeding (Densmore 1992; Rydgren et
404 al. 2016). To account for this, we collected seeds/bulbils/cuttings from the local surroundings,
405 expecting them to be better adapted to local conditions (Grant et al. 2011), and to avoid
406 persistent introduced species (Rydgren et al. 2016). However, there is also a risk of poor
407 seedling survival (Ebersole 2002; Müller et al. 2011), and our seeding method might also have
408 been less than optimal in such a barren, wind-exposed and easily eroded microhabitat. When
409 revisiting the site shortly after adding the treatments it seemed many of the cuttings in
410 treatment P had been removed by the wind. For future studies, this may be avoided by
411 combining seeding/addition of cuttings with a net or garden cloth (treatment G); soil addition;
412 water; or to transplant turfs instead (Bay and Ebersole 2006; Mehlhoop et al. 2018). Notably,
413 it was only in treatment S in 2011 and 2018 that we found *S. acaulis* (also found in treatment
414 P in 2010) and *S. oppositifolia*. We did not test to what extent seeding of non-native species
415 may have increased vegetation cover. We suggest that in combination with fertilizer (Evans
416 and Kershaw 1989), seeding local species might lead to a more diverse vegetation type instead

of the predominance of bryophytes in the fertiliser treatments, albeit in our case, it would not match the vegetation type in the reference as the three added species are not/almost not present in the reference vegetation. Based on this study, we cannot interpret any specific effects from tilling in treatment T except fungus appearance in one plot, possibly due to exposure of mycorrhiza or spores finding fertile soil.

Despite trialling the various assisted regeneration methods, the strongest effects on total vegetation cover were due to time alone (i.e., years), meaning that vegetation cover increased with time independently of treatment. Our findings confirm the results of alpine large-scale restoration projects (Hagen et al. 2019) where disturbing areas follow succession and are revegetated even without the application of assisted restoration methods (Walker and Walker 1991; Chapin et al. 1994). Vegetation cover itself can be advantageous, especially in Arctic–alpine environments (Krautzer et al. 2012), to prevent further loss of topsoil due to soil erosion, which may even surpass the initial disturbances (Vasil'Evskaya et al. 2006). Such a cover may also aid the area with increased moisture, nutrients and microsites for germination (Urbanska and Chambers 2002).

This study demonstrates that tundra vegetation, and *Cassiope* heath in particular, is very vulnerable to off-road tracked vehicles driving on unfrozen ground. Short growing seasons, low temperatures, strong winds and often low nutrient availability slow down germination and establishment processes, and hence the vegetation needs longer to recover (Kevan et al. 1995; Urbanska and Chambers 2002; Bay and Ebersole 2006). Also, *Cassiope* heath is one of the less frequent of the common vegetation types in the study area. This is a well-established vegetation type, not typical "pioneer" vegetation, and slow to regenerate after disturbance (Speed et al. 2010). This may be partly due to *Cassiope* and *Dryas* being species with low rates of seed germination (Müller et al. 2011) and establishment (Cooper et al. 2004), and generally

441 very slow growth (Mallik et al. 2011). Within regeneration treatments, none were successful
442 in advocating the growth of the dwarf shrubs *Dryas* and *Cassiope*. The lack of revegetation of
443 these two locally common species exemplifies the experiment's conclusion that the slow-
444 growing Arctic vegetation, with important species possibly having low germination efficiency,
445 need a time window much longer than the nine years used in this study until they can recreate
446 a *Cassiope* heath.

447 Even after nearly a decade following disturbance, and despite various active regeneration
448 treatments, our study clearly shows that these tracks will take many decades to become
449 completely revegetated (Fig. S7). Time stands out as the most important factor for the
450 regeneration of slow-growing plant communities in cold biomes, and this should be
451 communicated to policy makers, environmental protection officers, tracked vehicle drivers,
452 project owners and to the public and tourists to ensure realistic expectations of recovery time.
453 The literature rarely reports the development after long time frames, as long-term monitoring
454 studies are rare (Evju et al. 2020). Our study is short-term considering the successional
455 timescale of tundra vegetation with its slow growth rates (Forbes et al. 2001) and confirms
456 previous findings of extremely slow revegetation in the Arctic.

457 We do show a clear reestablishment of vegetation cover after nine years, which can be
458 considered a success given that recovery to any state of vegetation is the goal of most
459 regeneration schemes' mandates. However, in terms of species composition, we show that
460 that the community of plant species that grow in the tracks do not have the same species
461 composition as in the surroundings. Due to low germination, establishment and slow growth
462 of the shrub species *Cassiope* and *Dryas* in particular, it may take many decades for the tracks
463 to reach a species composition similar to the original vegetation, if it occurs at all (Forbes et
464 al. 2001).

Our results may be an incentive to adjust rules for the use of tracked vehicles at the end of the snow season. It may call for stricter local regulations, especially concerning less common vegetation types or those which take a very long time to establish, for example, *Cassiope* heath. The best way to avoid severe vegetation damage is to prevent it from happening. Regulations against driving on unfrozen or snow-free ground already exist in Svalbard as in other countries and ecosystems, but the rules may not be sufficiently enforced with consequences for rule-breakers. As tundra scientists are often in the field, International Tundra Experiment (ITEX) members and other field workers should also try to limit their own disturbance of the vegetation and raise awareness locally and internationally. Unfortunately, anthropogenic disturbances have been increasing globally since the 1960s (Kevan et al. 1995), but we hope that the current UN Decade on Ecosystem Restoration (<https://www.decadeonrestoration.org>) will inspire a change in local authority administrators' attitudes and management actions and increase public awareness of the issue. The increasing amount of disturbance in the Arctic and alpine tundra, together with low regeneration rates, should warn us to be pre-emptive and adopt policies and practices that minimize such disturbance.

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Competing interests

The authors declare that there is no conflict of interest.

Contributors' statement

MN: formal analysis, investigation, methodology, validation, visualisation, writing – original draft, writing – review & editing. **PS:** formal analysis (lead), investigation, methodology, resources, validation, visualisation, writing – review & editing. **EN:** conceptualisation, formal analysis, investigation (lead), methodology, project administration, resources, validation, visualisation, writing – review & editing. **EJC:** conceptualisation (lead), funding acquisition (lead), methodology (lead), project administration, resources, supervision, validation, visualisation, writing – review & editing.

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Data availability statement

Data available upon request.

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Figure 1 showing the vehicle tracks in June 2010 in Adventdalen, Svalbard. Vegetation cover was clearly reduced in the tracks compared to the surrounding vegetation. Here, showing the multiple pairs of plastic sticks, before the sticks were cut, marking each plot. Marker sticks were cut at ground level and left in place for the 8 year duration of the study, and remain in place for future monitoring. The photo was taken soon after snow had melted. Photo credit: Erica Neby.

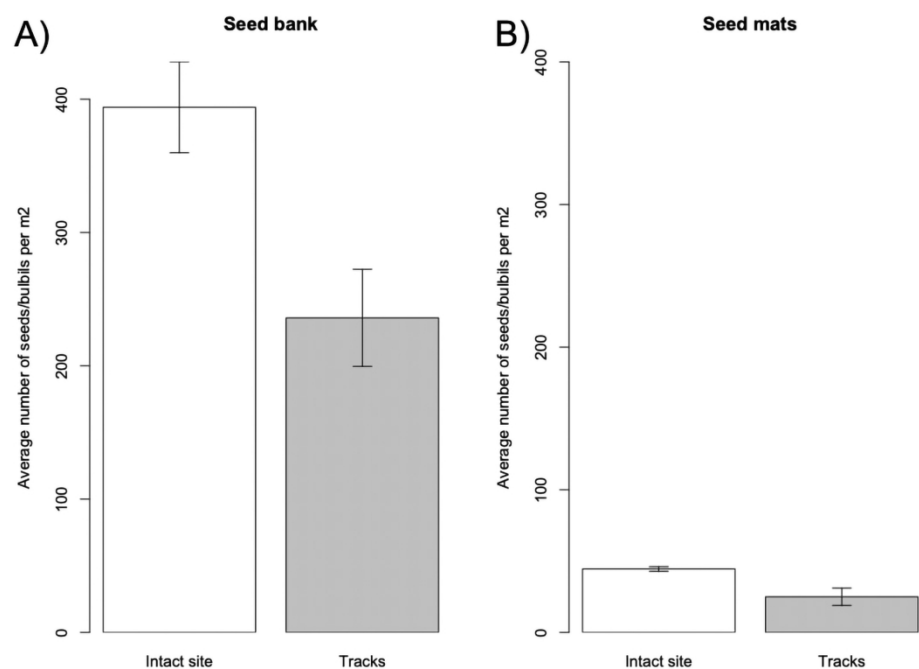


Figure 2. Density of seedlings/propagules germinated from A) soil from under intact reference vegetation and from within the tracks, B) seeds and propagules (seed rain) collected in mats placed within intact reference vegetation and within the tracks. The top layer of soil containing the seed bank was probably removed from the vegetation by the vehicle. This natural seed bank is very important as a source of local seeds for revegetation. See Appendix I-II for details on methods and results.

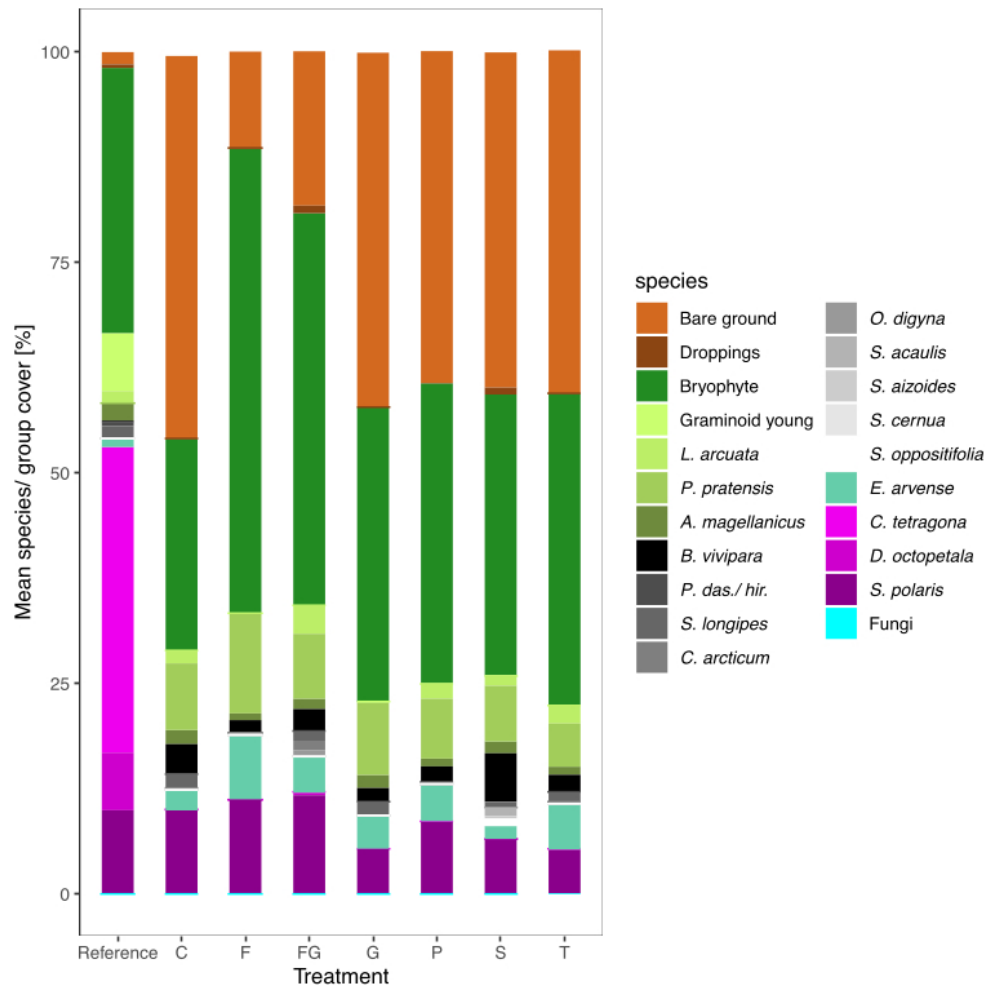


Figure 3. Cover of each species/group (including bare ground and animal droppings, i.e. unvegetated portions) observed in the reference vegetation in 2010 and the treatment plots in the tracks in 2018. Treatment codes: C = control, F = fertilizer, FG = fertilizer x garden cloth, G = garden cloth, S = seed/ bulbil addition, P = plant cutting addition, T = tilling. Please note that the reference vegetation composition was recorded in another year (2010) and with another methodology (point framing) than the composition in the treatment plots (2018, visual cover estimates) and may, hence, only be compared qualitatively together here and with Table S1, i.e. to illustrate the obvious differences in composition between the groups. Both *Pedicularis dasyantha* and *P. hirsuta* are present but not abundant in the surrounding vegetation, but note that *P. dasyantha* is only found here in the reference vegetation and *P. hirsuta* only in plots of treatment 'S'. Graminoids that were too immature to be identified (mainly in 2010) were grouped into 'Graminoid young' group. Bryophytes were not identified in the field in this study, but species present in the surroundings in 2017 were, in descending order of abundance: *Sanionia uncinata*, *Tomentypnum nitens*, *Hylocomium splendens*, *Dicranum* and *Distichium* spp., *Polytrichum* spp., and *Aulacomnium* spp., (Mörsdorf and Cooper, 2021).

19685x19685mm (1 x 1 DPI)

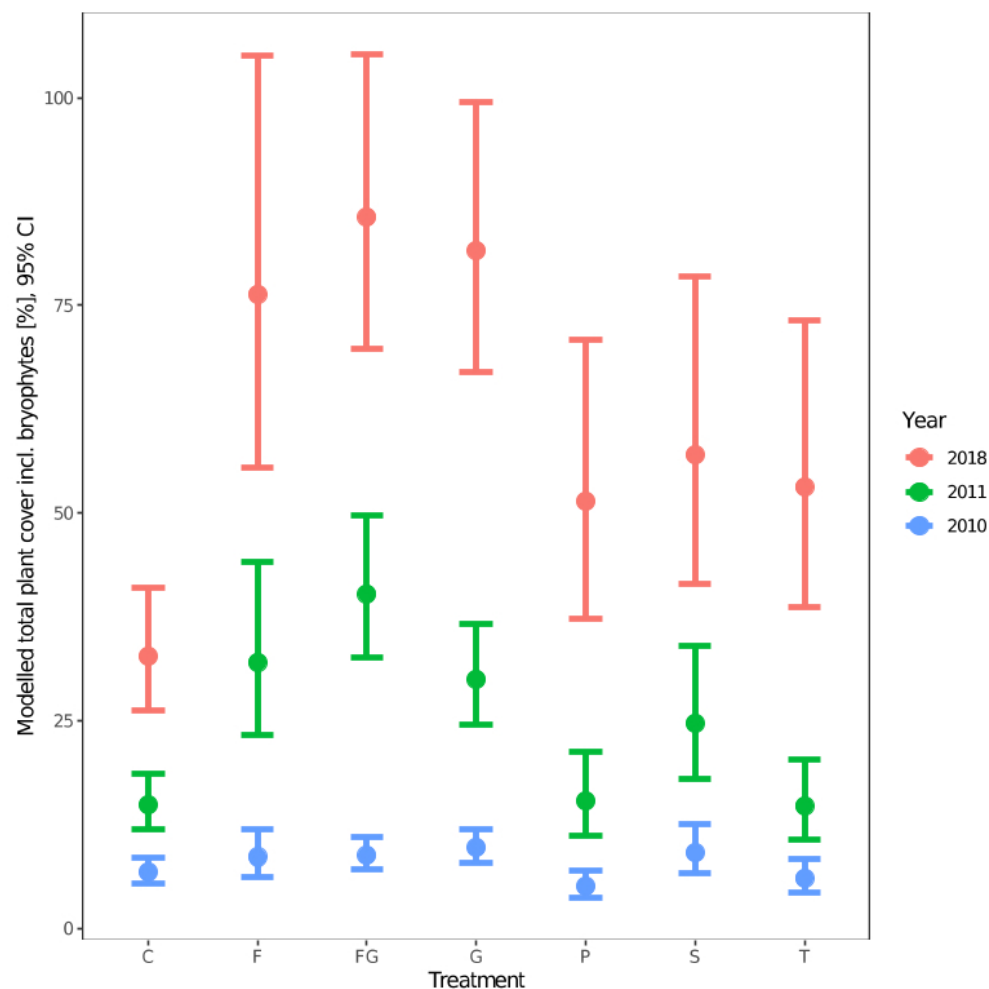


Figure 4. Modelled percentage of plot covered by vegetation (both vascular plants and bryophytes) in peak growing-season late July 2010, 2011 and 2018. Displayed are back-transformed estimates with 95% confidence intervals from a generalized linear mixed effects model (see methods for details). C = control, F = fertilizer, FG = fertilizer x garden cloth, G = garden cloth, S = seed/ bulbil addition, P = plant cutting addition, T = tilling.

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Appendix I. Disturbance effect on natural seed bank

Methods

To evaluate the seed bank in the disturbed tracks and reference vegetation, we sampled soil in two rows on each side of the tracks and two rows within each track in 2010. We used a 3.5 cm wide corer to a depth of 2 cm (ca 30 cores per row, but some spots in the tracks contained too many stones to make the coring possible, in total $n=243$ (2338 cm²). The soil cores in reference vegetation were evenly distributed between *Cassiope*-rich and *Cassiope*-poorer vegetation to cover the complete spectrum of the site. The soil cores were collected in July and August 2010, then put on filter paper into Petri dishes with lids and kept at -5 °C without light for another seven weeks to stratify the seeds/bulbils. Then the soil was acclimatised in +0.5 °C for four days and in +5 °C for four days. The Petri dishes were moved into a phytotron and kept at +18 °C for 12 weeks with 24 hours of light (150 μ mol) to simulate the germination period in Svalbard (Cooper et al., 2004). The soil was moistened every third day, and the registration of seedlings and seedling survival were made once a week. Germinating seedlings were replanted into small pots and remarked to distinguish between different species easily and to determine whether they were grown from seeds, bulbils or cuttings. In this study we used the data from the germinating seeds and bulbils but did not include vegetative growth from cuttings. We hereafter use the terminology “seedlings” for all the germinating seeds and bulbils.

The number of observed seedlings emerging from each soil core was treated as counts, and a zero-inflated Poisson model was needed due to an excessive amount of zeroes (i.e. about 50% of all collected soil cores had no observed seedling emergence). The model we used was a mixture model modelling the likelihood of a count being zero for each of the two groups (inside and outside of the tracks, i.e. soil cores collected from under disturbed and undisturbed vegetation) independently from the counts observed in non-zero cases. The likelihood of a count being zero was drawn from a Bernoulli distribution for each group separately, and the regression parameter for the non-zero cases drawn from a Poisson distribution with a log-link. We used a Bayesian approach with JAGS (Plummer, 2003) and the runjags package (Denwood, 2016) in R v. 3.4.1 (R Core Team, 2021).

As we had no prior knowledge or expectations of the potential effect of belt wagon disturbance on seed bank density, we used marginally informative reference prior distributions and initial values. We used 2 MCMC chains with 10000 samples each. After running the sampler, we observed that the two chains converged (visually and Gelman-Rubin statistics < 1.05) and that the effective sample size > 1000 . In cases when the effective sample size < 1000 , we added a further 10000 samples to each chain until it was, which was the case for only one more time. All further calculations were done on the MCMC chains produced by JAGS and Highest Posterior Density (HPD) intervals and means extracted from those chains.

To calculate the absolute modelled counts per group, we took the inverse logit of the modelled non-zero counts and multiplied it with the estimated proportion of it being non-zero (i.e. the non-zero probability).

Due to the soil core sampling pattern along transects within or parallel to the vehicle tracks, we included the variable “distance from west to east” in metres as a continuous, additive term in the model. As that term was insignificant (i.e. very small and including zero), we dropped it from the analysis.

Results and discussion

The proportion of non-zero counts was significantly higher in undisturbed (HPD 0.59-0.8) than in disturbed vegetation (HPD 0.22-0.45). The number of emerging seedlings in undisturbed vegetation (non-zero counts) was significantly higher than in disturbed vegetation (inverse logit effect size HPD 1.03-2.19). On average, per sample 0.47 seedlings germinated in disturbed (HPD 0.32-0.65), and 1.49 in undisturbed vegetation (HPD 1.21-1.75). These lower values in the disturbed area was probably due to the removal of the uppermost soil layer containing a high seed density by the tracked vehicle's belt (Kinugasa and Oda, 2014).

The dominant germinating species were *Bistorta vivipara* and *Luzula arctica* (Table A1 below). Two of the most common plants in the reference vegetation, are the shrubs *Dryas* sp and *Cassiope* sp. (Figures 3-4 in main text), that did not germinate in our soil seedbank

trials, which may be due to the thermophilic or transient nature of seed of these species (Fox, 1983, McGraw and Antonovics, 1983, Molau and Larsson, 2000, Cooper, 2004).

Seed banks are important as seed reservoirs for vegetation recovery after disturbance in the Arctic (Cargill and Chapin, 1987, Gartner et al., 1983, Ebersole, 1989). Our data shows that removal of the top layer of soil by the tracked vehicle negatively affected the density of the germinable soil seedbank. The species that germinated from the soil seedbank were herbs and graminoids – functional types that tend to germinate easily but were not dominant in the reference vegetation. The dominant species in undisturbed vegetation were shrubs and tend to have lower germination rates. This mis-match indicates that any revegetation from seedling germination from the soil seedbank would be at lower densities and of different taxons in the disturbed tracks than within reference vegetation. Vegetative growth of plants into the tracks from the reference vegetation is therefore crucial for recovery.

Table A1. Soil seed bank germination of seeds and bulbils per m². Species composition of germinating seedlings and propagules from seeds and bulbils collected with soil cores in 2011 in reference vegetation (outside the tracks, n=119 soil cores) and disturbed vegetation (inside the tracks, n= 124 soil cores).

Functional Type	Species	Reference	Disturbed
		Seedlings & propagules / m ² Total (n=124)	Seedlings & propagules / m ² (n=119)
Graminoids	<i>Alopecurus magellanicus</i>	9	0
	<i>Deschampsia alpina</i>	8	9
	<i>Deschampsia sukatschewii</i>	25	0
	<i>ssp. borealis</i>		
	<i>Luzula confusa</i>	84	61
	<i>Luzula arctica</i>	8	17
	<i>Poa pratensis</i>	9	9
	Total graminoids	142	96
Herbs	<i>Bistorta vivipara</i>	186	122
	<i>Cardamine bellidifolia</i>	0	9
	<i>Cerastium arcticum</i>	8	0
	<i>Equisetum arvense</i> ssp. <i>alpestre</i>	9	0
	<i>Oxyria digyna</i>	16	0
	<i>Papaver dahlianum</i>	9	0
	Total herbs	228	131
	Unidentified to species	42	9
	Sum	411	236
No. of germinating graminoid species		6	4
No. of germinating herb species		5	2

Appendix II. Seed influx in the reference versus disturbed tracks

To assess the seed and propagule influx of the reference and the disturbed sites, we used doormats following the ITEX manual (Molau, 1996) in July 2011 to trap dispersing diaspores. The doormats were placed ca 1 meter from the tracks, in rows, on both sides of the tracks and similarly inside each track, making a total of 4 rows of mats. They were fastened with long nails along the edges. Each row consisted of 16 seed mats, two meters apart, each of 44 x 24 cm (1056 cm²). Thus, 32 mats were sampled covering an area of 33,792 cm² inside the tracks, and an equal area outside the tracks. In late September 2011 the doormats were collected, rinsed with water to release their contents, filtered through a 150 µm sieve, dried at +30 °C for 24 hours, before germinating the seeds and propagules +20 °C for six weeks on individual Petri dishes. Seedlings of monocotyledons or dicotyledons were counted and recorded for each petri dish.

The germinating seed and propagule influx densities revealed that the reference vegetation had 43.6 ± 4.0 seeds and propagules /m², while the tracks had 24.6 ± 5.9 seeds and propagules /m², 44 per cent less than in the reference vegetation. The majority of species trapped by the seed mats (>95 %) were dicotyledons and their densities were in the lower range of those found in a high alpine heath (Molau and Larsson, 2000) in Swedish Lapland. The difference between values suggest that within the tracks the seed rain is limited by fewer surrounding dispersers (Speed et al., 2010), indicating that dispersal is extremely local, since the tracks were only 50 cm wide.

Appendix III. Measures of soil density in the study area

To evaluate the soil compaction from driving on unfrozen ground, soil density was measured in late August 2011 with soil corers. A corer with the diameter of 3 cm (18.8 cm^3) was pushed 6 cm into the soil layer at 30 randomly selected locations; 10 inside the tilled plots, 10 inside the untreated parts of the track and 10 in the surrounding reference vegetation. The soil samples were dried at $+50^\circ\text{C}$ for 24 hours and weighed to the nearest gram. One-way ANOVA was used to test for soil density differences between the reference vegetation, the disturbed vegetation and the tilled plots.

The average soil mass in the reference site was $11.9 \text{ g} \pm 1 \text{ (SE)}$ per core, while the average soil mass in the tracks was $8.8 \text{ g} \pm 1.3 \text{ (SE)}$ per core. The soil density measurement of the tilled plots, where the soil had been aerated in July the previous year, had the average mass of $9.1 \text{ g} \pm 1.2$. However, no significant differences were found between the three sites (One-Way ANOVA, $F(2, 27) = 2.10$, $p = 0.141$). This data indicates that the vehicle did not compact the soil. However, by pulling off vegetation and its roots attached to the top layer of soil, damage to the soil and vegetation structure was done in other ways.

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