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Master's Thesis 2020   60 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Seed rain and seedling emergence along hiking trails on elevation gradients in Dovre, central Norway

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Acknowledgments

Oslo, 15 May 2020

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Abstract

Seed dispersal and seedling emergence represent critical events in the life history of plants and are fundamental agents in the formation of plant communities in time and space. Insight into the effects of human movement on these processes has traditionally focussed on roads, however it is assumed that hiking trails also have the ability to function as dispersal corridors. Improving our knowledge of the role of hiking trails on dispersal and community dynamics is particularly relevant as warming global temperatures promote the upslope migration of species and nature-based tourism increases in popularity. I sampled seed rain and recorded seedling occurrence along four mountain hiking trails in Dovre, a popular hiking region in central Norway, and analyzed the data with generalized linear mixed models. I found that seed rain decreased with elevation and, minimally, with distance from the trail. Seedling density decreased away from the trail at lower elevations, but remained level at higher elevations, in concordance with the stress-gradient hypothesis. Standing vegetation coverage was more important than seed rain in mediating seedling emergence, suggesting that seedling emergence is limited by competition for resources rather than seed availability. Seed rain correlated with standing adult vegetation, suggesting localized seed dispersal. My findings suggest that hiking trails in the study area do not represent an ecologically significant dispersal corridor at the scale studied. The topic merits further study as applying the same methodology at a finer scale may reveal meaningful cumulative spatial trends mediated by localized dispersal and microsite characteristics not discovered here.

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1. Introduction

Seed dispersal and seedling recruitment are critical events in the life history of plants. Dispersal has several functions, providing access to alternative sites conductive to germination and establishment (Fenner & Thompson, 2005). On broader temporal and spatial scales, it shapes local populations and communities as well as the large-scale distribution of species (Morgan & Venn, 2017). Patterns of dispersal also have a direct influence on the demographic and genetic structure of populations, can affect inter- and conspecific competition, and determine migration patterns (Gurevitch et al., 2006). Seed dispersal is thus a fundamental agent in the formation of plant communities in time and space (Bruun & Ejrnæs, 2006). Its current relevance is made even more apparent as many recent studies have documented an upward shift in alpine plant species' optimum elevation as the global climate has warmed throughout the 20th century (Lenoir et al., 2008; Pauli et al., 2012; Steinbauer et al., 2018).

Multiple studies have documented the role roads can play as corridors for seed dispersal and the subsequent redistribution of plant communities (Alexander et al., 2016; Lembrechts et al., 2017). For example, species richness generally decreases with distance away from roads (Harper et al., 2005). In their study of a sub-arctic mountain ecosystem, Lembrechts et al. (2014) found that roadside edges contained more competitive and ruderal species than natural communities, a result they posited was a product of higher propagule pressure and more favourable abiotic growing conditions such as higher temperatures and more light. They also proposed that the observed species richness along roads was a result of successional setback due to reduced vegetation cover and greater amounts of bare ground, enhancing germination (Lembrechts et al., 2014).

Hiking trails affect vegetation through direct mechanical disturbance and can promote the spread of species that thrive in disturbed areas, a trait typical of non-native species (Wolf & Croft, 2014). These disturbances include soil compaction, erosion, run-off (Jägerbrand & Alatalo, 2015), as well as increased decomposition, mineralization and reduced root penetration (Forbes, 1993). Considering the similar roles roads and hiking trails play for human movement, it is assumed that hiking trails can also act as dispersal corridors by means of epizoochory - adhesive

dispersal - on hikers' clothing, shoes or equipment (Ware et al., 2012). Large herbivores which also occasionally travel on trails, such as sheep (*Ovis aries*)*,* cattle (*Bos Taurus*) and reindeer (*Rangifer tarandus*) may also function as efficient dispersal vectors as propagules become entangled in fur (Couvreur et al., 2004). Indeed, epizoochory is capable of transporting seeds further than many other dispersal mechanisms (Fenner & Thompson, 2005), including long distances (Pickering et al., 2011). Several studies have also highlighted the importance of endozoochory in facilitating long distance propagule dispersal as seeds are ingested and later excreted, particularly by frugivorous mammals (Clark et al., 1998; Graae et al., 2004; Liebe, 2019). Both of these dispersal mechanisms have potentially meaningful implications for the redistribution of plant communities and species dynamics in popular outdoor recreation areas as seed rain is channelled along open hiking trails.

Dispersal dynamics have little long-term biotic relevance unless deposited propagules germinate to become seedlings. Seedling recruitment has major implications for population dynamics, community turnover and species range dynamics (Meineri et al., 2020), and is controlled primarily by disturbance in alpine tundra (Graae et al., 2011) and biotic characteristics such as vegetation density and biomass in alpine grasslands (Meineri et al., 2020). It is thus reasonable to assume that seedling recruitment varies along elevational gradients and at various distances from a physical disturbance such as a hiking trail. The stress-gradient hypothesis postulates that competition is the dominant form of plant-plant interaction in productive (i.e., lowland) sites (Bertness & Callaway, 1994). Here, community invasibility and seedling recruitment may be increased by small-scale disturbances such as trampling by humans or herbivores which create gaps in vegetation, leading to competitive release by increasing access to light and space and the removal of competitor species (Klanderud et al., 2017; Milbau et al., 2013). In environments where abiotic stress is more pronounced, such as in higher elevation alpine zones, facilitation is generally believed to be the more common form of community interaction. Trampling here is more likely to inhibit seedling recruitment as facilitation is weakened through the removal of surrounding vegetation (Klanderud et al., 2017).

Alpine plant populations are particularly vulnerable to spatial redistribution from changes in land use because their limited competitive traits increase vulnerability to ecosystem change such as a

shift in community composition towards competitive species (Gottfried et al., 2012; Mondoni et al., 2010). Sustained seasonal hiking along designated trails is considered to be such a change in land use here. Trampling affects plant species in a number of ways, but generally occurs at the expense of sensitive fern, shrub and forb species with broad leaves, vertical or woody stems, and reproductive structures high on the plant (Hill & Pickering, 2009), which subsequently decline following a loss of diversity, cover and biomass (Pickering et al., 2011). Conversely, hiking often promotes the diversity and cover of graminoid species which are more able to withstand trampling and which, as along roads, may exploit patches of bare soil along trail edges to germinate (Forbes, 1993; Pickering et al., 2011). By channelling human and animal movement along elevation gradients, hiking trails could theoretically promote the upslope migration of more competitive lowland species at the expense of alpine species in a two-step process: 1) the creation of denuded ground, and 2) propagule establishment following hiker/animal assisted dispersal or increased dispersal distances as the suppression of standing vegetation eliminates a physical barrier to dispersal. This two-step process could have meaningful implications for local extinctions as alpine species are outcompeted by their lowland counterparts (Gottfried et al., 2012; Lesica & McCune, 2004; Wehn et al., 2014). Despite this risk, there is currently a lack of knowledge around how hiking trails act as conduits of persistent vegetation change across the seed and seedling life-stages.

There are two contemporary contexts which make this knowledge gap particularly relevant. Firstly, tourism is a massive global industry, and nature-based tourism is a rapidly expanding sector in northern Europe and beyond (Bell et al., 2009). On a worldwide basis, national parks alone attract eight billion visits annually (Balmford et al., 2015). In Norway, hiking remains one of the most popular land uses in the sphere of outdoor recreation and national parks are a major part of the tourism landscape. Mitigating the increasing ecological effects of recreational activity is thus a persistent challenge for managers, particularly in mountain areas (Khodadadi, 2016).

Secondly, hiking trails as seed dispersal and seedling emergence corridors could in fact play duelling roles in the context of global warming. Evidence relating the upward shift of alpine plants to recent climate warming exists from the Alps and the Scandes and the effects of these upslope range shifts could result in local extinctions though competitive exclusion (Pauli et al.,

2007). On the other hand, hiking trails could play an important role in the survival of some plant species by facilitating the upslope migration of species heretofore optimized for lowland climatic conditions to safe sites at higher elevations. Knowledge of how hikers may influence these diverging factors associated with dispersal and changes in community composition are thus increasingly important for conservation planning and management in popular hiking areas.

In this study I aim to shed light on the role of hiking trails as dispersal corridors and plant community reorganizers by examining the relationship between seed rain, seedling recruitment, and adult standing vegetation along four hiking trails and elevation gradients in the Dovre region of central Norway. Studying the role of hiking trails as conduits for change not only provides insight into the potential role people and animals play as dispersal vectors. It also allows for the study of human/animal movement corridors in areas above the typical elevation range of roads, allowing for a broader understanding of plant species movement and community dynamics in alpine ecosystems.

I ask:

1. **How does seed rain differ with elevation and at different distances from trails?**
2. **How does seedling density differ with elevation and at different distances from trails?**
3. **Do hiking trails act as conduits for the upslope migration of lowland species?**
4. **To what extent is seedling density mediated by local seed rain and adult vegetation cover?**

I predict that 1) because of adhesive dispersal on hikers and large herbivores, hiking trails act as conduits for seed dispersal and therefore that seed rain decreases with distance from the trail. Because above ground net primary productivity is typically higher at lower elevations (Hansen et al., 2000), and because of the importance of seedless reproduction in alpine plants common at higher elevations, I also predict that seed rain decreases with elevation (Molau & Larsson, 2000). Based on the stress gradient hypothesis, I predict that 2) at lower elevations, seedling density is higher closer to the trail due to competitive release following trampling. At higher elevations,

facilitation from surrounding vegetation should limit the positive effect of trampling on seedling emergence, resulting in a more uniform seedling density across all distances from the trail. I also predict that 3) hiking trails act as conduits for the upslope migration of lowland species, and so that species present as adults at a given elevation should be present as seeds in the next upslope sampled elevation, even though no adult specimens are present there, and 4) that overall seedling density increases with decreased vegetation cover and the number of seeds recorded.

2. Materials and methods

2.1 Study region

The study area is located in the vicinity of Hjerkinn, Norway (62°13′N 9°33′E). The region is characterized by mountainous terrain ranging from 900-1000 m a.s.l. in valley bottoms to 1500-1700 m a.s.l. at the highest mountain peaks. Much of the local terrain belongs to Dovre and Dovre-Sunndalsfjella national parks and their numerous hiking trails. The regional treeline is formed by mountain birch (*Betula pubescens*) at approximately 1050-1100 m a.s.l. (Paus et al., 2011). Data for 1990-2019 in the lowlands of the region at Fokstugu (62°06′N 9°17′E) indicate a continental climate characterized by a mean annual temperature of 0.8°C and an average precipitation of 438 mm (Norsk Klimaservicesenter, 2020). The bedrock is predominantly porous and calcareous, which has contributed to a rich alpine plant biodiversity, particularly east of the E6 roadway (Rondane-Dovre Nasjonalparkstyret, 2013; Stiftelsen iNasjonalparker, 2013). Common species above the treeline include shrubs (e.g. *Vaccinium* spp., *Salix* spp., *Betula nana*), numerous forbs (eg. *Viola* spp., *Silene acaulis*), grasses (e.g. *Poa alpina, Festuca* spp.), sedges (*Carex bigelowii*) and rushes (*Juncus trifidus*), forming an open alpine landscape. The high species richness, particularly among forbs, has given the area its reputation as northern Europe's most diverse region for alpine plants (Stiftelsen iNasjonalparker, 2013).

2.2 Trail selection

Four trails were selected after confirming sustained levels of usage, as determined by Strava heat maps. Trails A and B (Figure 1) are popular day-hike trails (A in particular is used for tourists who wish to see muskox). C, with its trailhead being approximately two kilometers from the nearest publicly accessible road, is less used. D is the northern end of a popular hiking route leading to Rondane national park. All four trails begin in close proximity to major transportation

corridors (Figure 2), facilitating access for hikers, and span an elevational range from approximately 900 m a.s.l to 1400 m a.s.l, allowing for the observation of seed rain and seedling emergence trends along elevation gradients.

Figure 1. Alpine landscape in the Dovre region, central Norway. Taken from the upper section of trail B. Photo: Ilias Janssens.
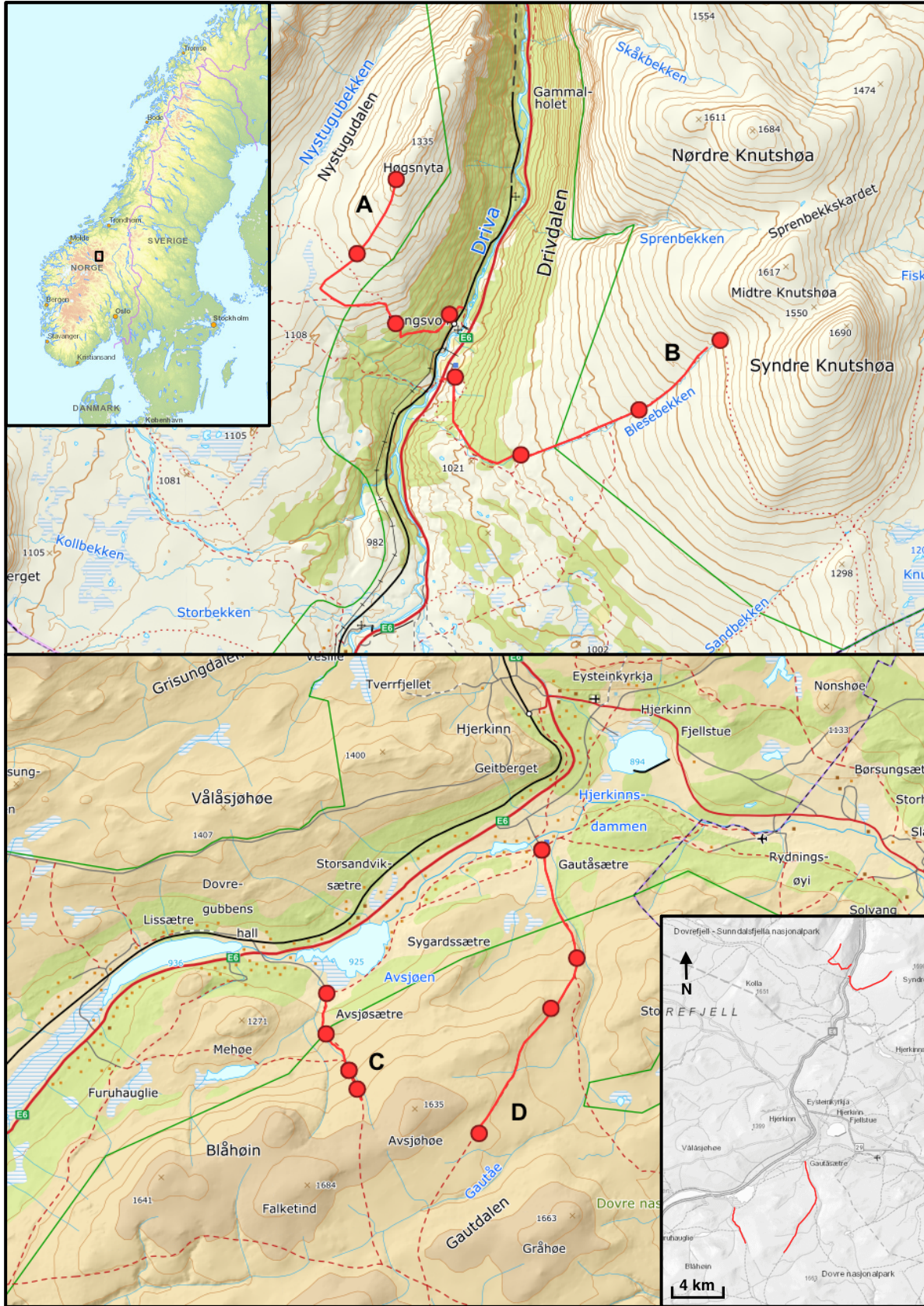
Figure 2. Location of the study area in central Norway. Red lines designate sampled trails, green lines boundaries of Dovrefjell-Sundalsfjella (upper) and Dovre (lower) national parks. Red dots designate transect locations.

2.3 Transect design and placement

Sixteen T-shaped transects were used to record seed rain, seedling density and vegetation cover along trails. Transect placement was determined by registering elevation data with a handheld GPS at the trail head and at the highest point at which the trail was still clearly visible. With low and high elevation extremes registered, the elevational range of each trail was divided by ten and transects were placed at fixed intervals corresponding to 1) the trail head elevation, 2) 40% up the trail, 3) 70% up the trail, and 4) where the trail becomes indistinguishable from surrounding terrain. Thus, four transects were used per trail.

Transects consisted of three plots of 2×10 metres (Figure 3). This transect design is traditionally used in roadside vegetation studies and is adapted from Seipel et al. (2012). The first plot was placed lengthwise parallel to the trail side. The two remaining plots were placed at a 90-degree angle to the trail from the middle of the trailside plot, covering a distance of 2 to 12 and 12 to 22 metres from the trail, respectively. Four seed traps were placed 0.5 metres from the trail in the first plot. Here, the two innermost and two outer traps were placed one and three metres from the centre of the plot, respectively. Four more traps were placed in the second plot, seven metres from the trail edge, 0.5 metres and one metre from the centre of the plot. This configuration was repeated in the third plot, 17 metres from the trail (Figure 3). If rocks or tall, dense shrubbery inhibited the placement of traps, the nearest available spot closer to the trail was chosen. Quadrats for seedling surveys were placed in the middle of each plot at the same distance from the trail as seed traps (Figure 3). All distances from the trail within transects were measured with a measuring tape. A coin toss determined which side of the trail the transect was placed on, unless scree, rocky outcrops, streams or cliffs made only one side feasible for study.
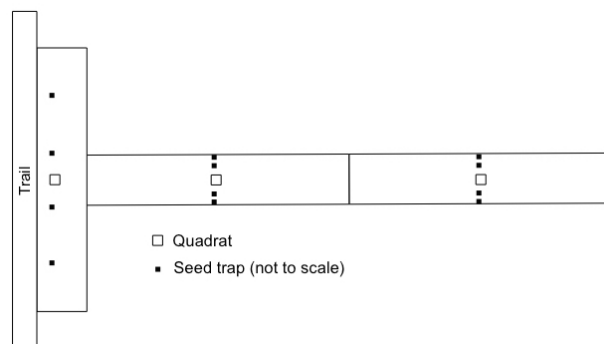

Figure 3. Schematic representation of the T-transect design.

2.4 Seed rain sampling

A total of 192 15×15 centimetre Astroturf® doormat-style seed traps were placed along the sampled trails from the 6th to 12th of July 2019. These simulate vegetation cover, trapping seeds from surrounding vegetation, and have proven useful in similar studies (Molau & Larsson, 2000). All traps were fastened to the ground with two or three nails and, if necessary, leveled with rocks to minimize seed loss from runoff during rainfall. All traps were then left in the field until collection from the 9th to the 11th of September 2019, when they were placed in resealable plastic bags and transported to the NMBU campus for processing. Traps that did not end up being used in the analysis, either because they were found displaced or because they were not found at all, were registered as NA during processing.

Traps were emptied into a basin by knocking on the base of each trap. Remaining material was extracted with a scalpel and seeds were subsequently picked out by naked eye or with a microscope or stereomicroscope at various magnifications. Seeds were identified as precisely as possible (i.e. down to species level), however in some cases identification was limited to genus, or was not possible at all. Identification was conducted through comparison with reference papers, online databases, a reference collection at the Norwegian University of Science and Technology, and help from academics with seed knowledge. All seeds were counted following identification. The term seed as used in this thesis includes *Bistorta vivipara* bulbils.

Because I suspected that seed rain would be greater below the treeline, the average treeline elevation across all four sampled trails was calculated by obtaining treeline elevations from Google Earth using satellite imagery from 2020.

2.5 Seedling surveys

Seedlings were recorded from one 50×50 centimetre quadrat per plot in each transect in mid-August 2019. If no seedlings were found after searching a quadrat, it was moved so that its new placement was adjacent to the previous location. This process was repeated up to three times, or until at least one seedling was found. For the purposes of this thesis, a seedling is defined as a sporophyte with up to two cotyledons and up to two leaves. As with seeds, some seedlings were identifiable only at genus level, or classified as an unknown forb or graminoid seedling.

Identification was carried out in the field with reference photos and the assistance of a seedling expert.

2.6 Vegetation and pellet count surveys

Vascular vegetation coverage and pellet counts were determined by conducting surveys of all 2×10 metre plots from July to August 2019. This work was carried out by other members of the research team. Coverage was assessed visually, and each species present was given a percentage value representative of its relative coverage in a plot. Numerous sheep and cattle were observed on and adjacent to trails, and the Dovre region is also home to wild reindeer, potentially affecting dispersal dynamics and vegetative cover through grazing and trampling. Pellet count surveys were thus conducted in each plot to estimate large herbivore abundance. This was done by walking lengthwise back and forth and counting each pellet individually, by species.

2.7 Upslope migration and factors influencing seedling emergence

Seed rain, seedling emergence and adult coverage data were combined to analyze seed and seedling recruitment along the elevational gradient. Quantifying the variation in lowland and alpine species' occurrence in the plots gives an indication of how susceptible upland transects are to long distance seed dispersal originating from downslope transects, as well as how successful lowland species are in reaching seedling establishment at higher elevations. To achieve this, the entire bioclimatic elevational range as defined in Lid and Lid (1994) was first divided into lowland (zones 1-4) and alpine (zones 5-8) categories. I then assigned species to a category by calculating the median of its bioclimatic range, again as determined by Lid and Lid (1994), which I considered to be its optimum elevation, as performed in Grindrud (2019).

For cases in which seeds or seedlings were identified only to genus, but in which adult plants were identified at species level, I assumed that the seed/seedling belonged to the same species as the adult specimen in the same plot. If an adult specimen of a seed/seedling genus was not present in the same plot I assigned identity to the adult specimen observed in the same transect, if present. If adult specimens were not found at either plot or transect level, I examined coverage data for the entire trail and assigned identity if an adult specimen was found. For cases in which adult specimens of two different known species of the same genus as a seed/seedling were

observed, I categorized the observation as lowland/alpine by averaging the bioclimatic values of both adult species (e.g. *Luzula* sp. seeds were assigned the average of *L. spicata* and *L. arcuata* when the latter two species were observed as adults in the same plot/transect). Unknown specimens were not assigned a lowland/alpine category and marked as NA.

2.8 Statistical analysis

Statistical analyses were carried out in R version 3.6.2 (2019, R Foundation for Statistical Computing).

2.8.1 Seed rain and seedling emergence

Negative binomial generalized linear mixed models (GLMM) were performed to examine how seed rain and seedling emergence vary with elevation and distance from trail. Both full models included elevation, distance from trail, and an elevation × distance from trail interaction as fixed predictor variables. Large herbivore pellet count was included as a covariate. Trail ID and transect ID were included as nested random predictor variables. Since extant vegetation plays an important role in regulating seedling emergence (Klanderud et al., 2017), I included habitat type as a categorical covariate in the full seedling model. This, however, was shown to be collinear with elevation and was thus removed. Number of seeds per trap and number of seedlings per quadrat were the response variables. In order to include the interaction between elevation and distance from trail in the seedling model, both of these variables had to be rescaled. Both models were run with the glmmTMB package to account for over-dispersion and null-inflation in the seed count data, and null-inflation in the seedling data. The most parsimonious model was selected through backwards elimination from the full model and comparison of AIC values.

2.8.2 Upslope migration and factors influencing seedling emergence

Negative binomial generalized linear mixed models (GLMM) were performed to analyze factors influencing seed rain and seedling recruitment along the elevational gradients. To investigate if the sample hiking trails act as conduits for upslope seed dispersal, a full model including the fixed predictor variables elevation, distance from trail, and the interaction thereof, was run. This model also included adult coverage values and a categorical variable separating each observed species into lowland or alpine native elevation ranges as covariates. A fixed Boolean covariate

indicating whether a species was *absent* in a given transect (as adult) but *present* in the transect below (as adult), was also included. Trail ID and transect ID were included as nested random predictor variables. Number of seeds per trap was the response variable. To investigate the extent to which seedling density is mediated by seed rain and adult coverage, a full model with factors and covariates identical to the model described above, with the addition of number of seeds per trap as a fixed effect, was run. Number of seedlings per quadrat was the response variable.

3. Results

3.1 Seed rain

In total, 1995 seeds belonging to at least 16 families and 24 genera were collected from the seed traps (Figure 4). 17 species were identified to species level. Eight genera were not identified to species level (*Luzula*, *Festuca*, *Poa*, *Carex*, *Galium*, *Papaver*, *Veronica*, *Cerastium*). 70 seeds belonging to nine different species were classified as unknown forbs or graminoids. Of the seeds identified to genus or species level, the most represented family was Poacea with at least seven species. Overall, 759 seeds belonged to graminoid species, 146 to shrubs, and 209 to forbs. 881 (44%) seeds belonged to *Betula pubescens* (Figure 5). Of the 192 seed traps that were set in the field, 27 were either displaced upon retrieval, or not found at all. The final amount of analyzed seed traps was thus 165. No scat was found in the seed traps.

Figure 4. A selection of propagules caught in traps. From left to right: Bistorta vivipara, Anthoxanthum nipponicum, Betula pubescens, Empetrum nigrum, Phleum alpinum.
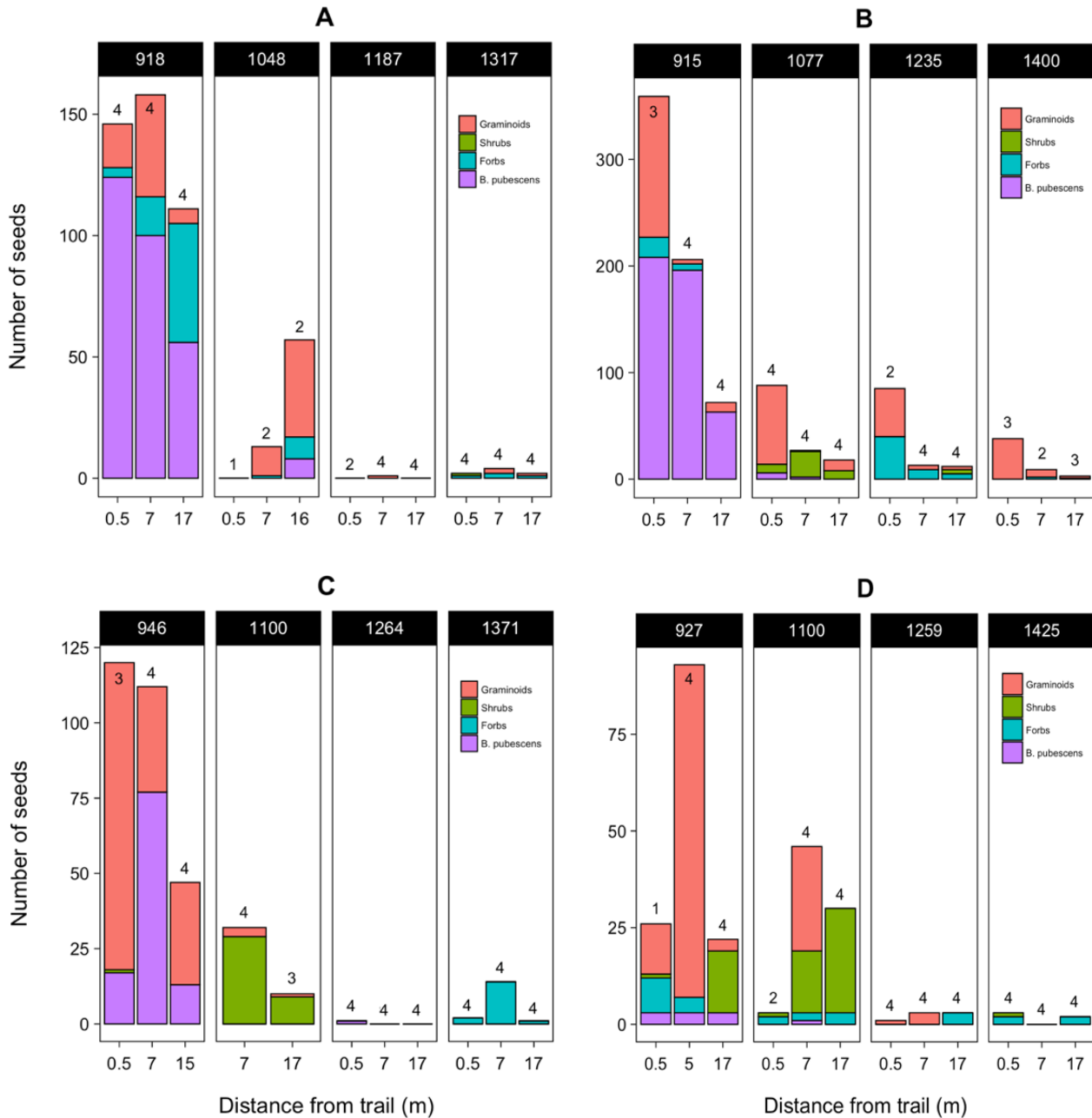
Figure 5. Raw number of seeds collected in seed traps. Note that not all seed traps were recovered/usable: data for each distance at each elevation is sourced from 1-4 traps (numbers in/above histogram bars). Numbers at top of sections denote transect elevations in metres. Letters in bold denote trail IDs.

Seed rain decreased with elevation and distance from trail (Figure 6). The most parsimonious GLMM consisted of elevation (m) and distance from trail (m) as fixed predictor variables and transect ID as a random predictor variable. Elevation and distance from trail showed a statistically significant effect on seed rain (Table 1).

Table 1. The relationship of elevation (m) and distance from trail (m) with seed rain in the Dovre region, central Norway.

	Estimate β	SE	z	P-value
Intercept	11.420	2.085	5.476	< **0.001**
Elevation	-0.008	0.001	-4.567	< **0.001**
Distance from trail	-0.069	0.015	-4.415	< **0.001**
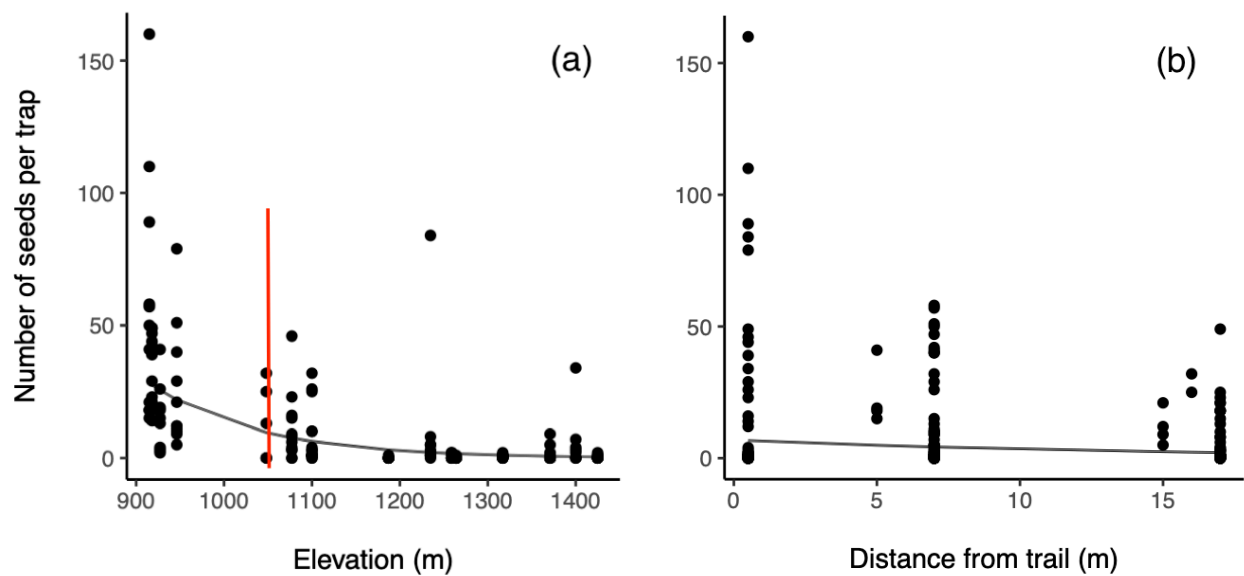
Figure 6. The relationship (GLMM) between seed rain and (a) elevation (m), and (b) distance from trail (m). Each dot represents one seed trap. The red line in Figure (a) represents the average treeline elevation calculated from the sampled trails.

3.2 Seedling emergence

In total, 185 seedlings belonging to at least 14 families and 20 genera were recorded. Of these, 154 belonged to forb species, 12 to shrubs, and 19 to graminoids (Figure 7). 18 species were identified to species level. Some but not all seedlings from six genera were not identified to species level (*Alchemilla*, *Euphrasia*, *Gnaphalium*, *Luzula*, *Taraxacum*, *Vaccinium*). 16 and 18 seedlings were classified as unknown graminoid and forb seedlings, respectively. Of the seedlings identified to genus or species level, the most represented families were Rosacea (3-4 species) and Asteraceae (3 species).
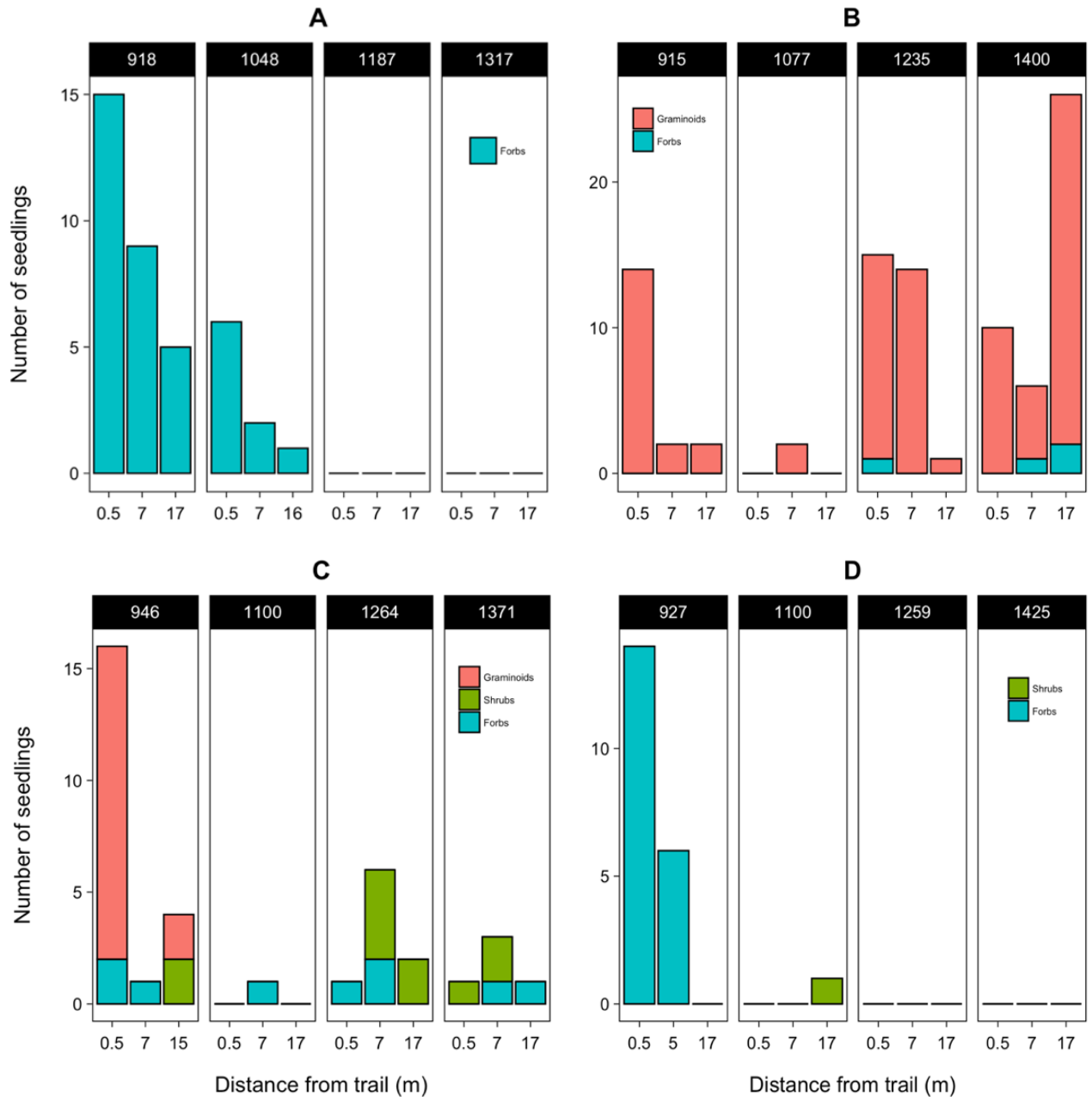
Figure 7. Raw number of seedlings recorded in quadrats. Numbers at top of columns denote transect elevations. Letters in bold denote trail IDs.

Seedling density decreased with distance from trail and the interaction between elevation and distance from trail showed a decrease in seedling density with distance from trail at lower elevations, and an overall more uniform seedling density distribution at higher elevations (Table 2, Figure 8). The most parsimonious GLMM consisted of the fixed variables elevation (m), distance from trail (m), and their interaction. The covariate large herbivore pellet count was also

included. Transect ID was included as a random predictor variable. Distance from trail and the elevation × distance from trail interaction were statistically significant (Table 2, but see discussion below).

Table 2. The relationship between seedling density and elevation (m), distance from trail (m), large herbivore pellet count, and the elevation × distance from trail interaction in the Dovre region, central Norway.

	Estimate β	SE	z	P-value
Intercept	0.407	0.494	0.850	0.395
Elevation	-0.489	0.467	-1.046	0.295
Distance from trail	-0.322	0.143	-2.249	**0.024**
Large herbivore pellet count	-0.019	0.013	-1.389	0.164
Elevation × distance from trail	0.323	0.127	2.548	**0.010**

Figure 8. The relationship (GLMM) between distance from trail (m) and seedling density, sorted by transect elevation. Dots represent one survey quadrat. Grey areas represent 95% confidence intervals. A "jitter" is added to visualize all the data points.

3.3 Upslope migration and factors influencing seedling emergence

Seed rain increased with adult plant coverage in the most parsimonious seed rain GLMM (Table 3). This model consisted of elevation (m) and distance from trail (m) as fixed variables a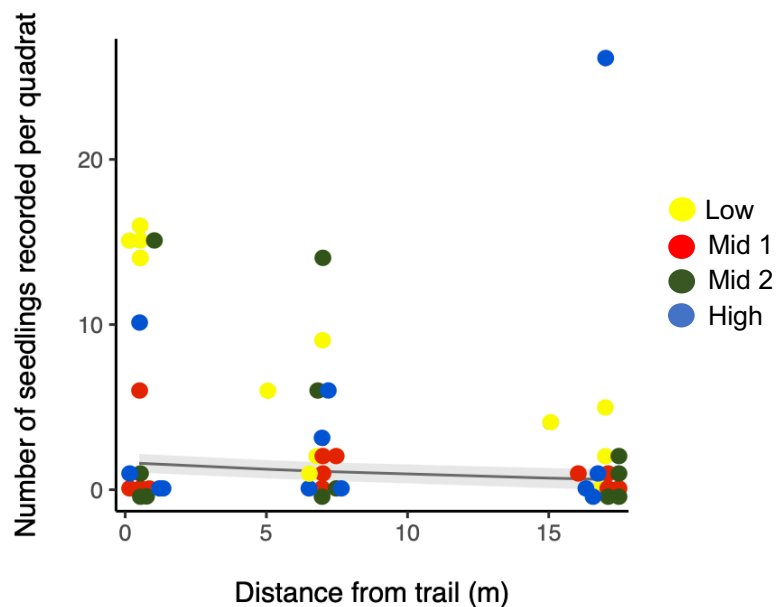nd the categorical lowland/alpine species classification, adult coverage and absence/presence of species as adults as covariates.

Table 3. The relationship between seed rain and elevation (m), distance from trail (m), lowland/alpine species, adult coverage and absence of adult specimens in a given transect in combination with its presence in the transect below.

	Estimate β	SE	z	P-value
Intercept	4.265	5.471	0.780	0.435
Elevation	-0.003	0.003	-0.981	0.326
Distance from trail	-0.070	0.048	-1.457	0.145
Lowland/Alpine	0.087	0.491	0.178	0.858
Adult coverage	0.057	0.025	2.251	**0.024**
Absence/presence	0.983	1.475	0.666	0.505

The most parsimonious seedling recruitment GLMM consisted of the fixed variables elevation (m) and distance from trail (m), and the categorical lowland/alpine species classification, adult coverage and absence/presence of species as adults as covariates. Adult coverage was the closest to statistical significance, with results showing a decrease in seedling density with adult plant coverage (Table 4).

Table 4. The relationship between seedling density and elevation (m), distance from trail (m), lowland/alpine species, adult coverage and the absence of adult specimens in a given transect in combination with its presence as adult in the transect below.

	Estimate β	SE	z	P-value
Intercept	-5.137	4.578	-1.122	0.262
Elevation	0.002	0.003	0.550	0.583
Distance from trail	0.019	0.036	0.544	0.587
Lowland/Alpine	-0.471	0.511	-0.922	0.357
Adult coverage	-0.133	0.086	-1.549	0.121
Absence/presence	0.688	1.473	0.467	0.641

4. Discussion

4.1 Main findings

I found that seed rain decreased with elevation and, minimally, with distance from trail. In addition, seed rain appeared to originate from nearby standing vegetation at the plot or transect level. Seedling emergence relative to the trails appeared to follow a pattern consistent with the stress gradient hypothesis, with a decrease in seedling density away from the trails at lower elevations, and an overall more consistent distribution in higher areas, although this pattern was affected by one outlier in the data. I also found that seed rain did not appear to be a strong mediator of seedling emergence.

4.2 Seed rain

Seed rain decreased with elevation and distance from trail, as expected. Average rates of decrease of seed rain with elevation and distance from trail (-0.008 and -0.069 seeds per metre, respectively), however, suggest that hiking trails in Dovre play a negligible role in facilitating seed dispersal. Seed rain displayed a distinctly non-linear decrease with elevation, falling off at a rate of approximately 8 seeds per 100 metres before stabilizing above the treeline. This pattern could be explained by the nature of the dominant standing vegetation below the treeline, which is characterized by a high abundance of *Betula pubescens*, which gradually decreases in density from the valley bottoms towards the treeline. One explanation for the levelling off of seed rain above the treeline could be that, whilst many alpine species reproduce sexually, the alpine tundra is dominated by long-lived, clonally reproducing species (Graae et al., 2011). The finding that seed rain decreases with elevation is also in line with studies which have examined the role of hiking trails as conduits for the upslope migration of invasive species. Indeed, Liedtke et al. (2019) found that the presence of hiking trails in Chile explained only 4-8% of the variation in number and cover of invasive species along elevation gradients, suggesting that hikers play a limited role as dispersal vectors there. To my knowledge, this thesis is the first project to demonstrate similar results for seed rain along hiking trails in the Scandes.

The limited role of hiking trails as conduits for seed dispersal, especially when compared to roads, could be due to two main factors: hikers transport less seeds than vehicle traffic and trails are simply less frequently used than roads (Liedtke et al., 2019). The implications of these results for the preservation of current species pools in the alpine plant communities of Dovre can be interpreted in different ways. If trails play a limited role as conduits for seed dispersal, then there is little risk of trails resulting in increased competition for cold-adapted, competitively weak upland species (Klanderud & Totland, 2007). On the other hand, global climate change is occurring at such a high magnitude and fast rate that many plant species may not be able to rely on adaptation and tolerance in order to survive (Engler et al., 2009), yet evidence from recent decades points towards time lags in plant establishment upslope mountainsides relative to climate change (Lamprecht et al., 2018; Molau & Larsson, 2000). In other words, some alpine species appear unable to migrate upslope fast enough to colonize new areas with favourable climatic conditions. Previous studies have also found that even when reproducing sexually, alpine plants have limited capacity for long-distance dispersal, with most seeds landing less than 10 metres away from the parent plant (Morgan & Venn, 2017). My results suggest that hiking trails in Dovre do not alleviate these limitations. However, other research indicates that local climate variation at scales of hundreds or even tens of metres keeps dispersal distances required for immigration and establishment rather short as species take advantage of site-specific traits (Lenoir et al., 2013). Replicating the methodology used here at a finer scale along the same trails may thus reveal meaningful trends not detected in this thesis.

Raw seed rain data for trail B showed a consistent pattern of decreasing seed rain with distance from trail at all elevations. This trail, however, had a high proportion of graminoid cover along the entire elevation gradient. Graminoids are generally considered to be more resistant to trampling than other functional plant types (Forbes, 1993; Jägerbrand & Alatalo, 2015). Marchand and Roach (1980) also noted that graminoids appeared to be well adapted to early colonization of disturbed sites through sexual reproduction, producing large numbers of seeds. The trend in decreasing seed rain with distance from the trail observed along trail B may thus be the result of high fecundity among persistent and/or opportunistic graminoids along patchy, disturbed trail sides, rather than seed dispersal by hikers or large herbivores.

Seed rain results should be approached with a degree of caution, particularly with respect to generalization in time and space. Indeed, results depend on the species considered and the study area (Engler et al., 2009). In addition, seed rain abundance in the Scandinavian alpine tundra is known to vary significantly from year to year as a result of climatic constraints (Molau & Larsson, 2000) – results from the 2019 growing season are thus not necessarily representative of a consistent regional interannual pattern. Finally, retrieval of the seed traps under the cover of snow would have proven problematic. The timing of the collection of the seed traps was thus determined out of an abundance of caution with respect to first snowfall, which is not uncommon in mid-September in Dovre. The sampled seed rain is thus not necessarily representative of the entire seed dispersal season.

4.3 Seedling emergence

Seedling density decreased with distance from trail. However, the interaction between elevation and distance from trail showed that seedling density decreased away from the trail at lower elevations, but showed a neutral relationship at higher elevations. This appears to confirm my hypothesis that seedling density at lower elevations should be higher closer to the trail due to competitive release following trampling, but that facilitation from surrounding vegetation should limit the positive effect of trampling on seedling emergence at higher elevations, resulting in a more uniform seedling density across all distances from the trail here. Thus, my results point to a gradual shift from competition to facilitation as the dominant from of plant interaction along the elevational gradient, in accordance with the stress-gradient hypothesis. Neighbouring vegetation is thought to facilitate plant growth and survival by maintaining warmer temperatures and insulating the substrate from growth-stunting abiotic environmental variables such as frost, soil heave from needle ice, and wind, which the alpine tundra is consistently exposed to (Choler et al., 2001; Venn, 2007). Looking at the raw data however, the number of plots with no seedlings in the upper transects along trails A and D suggests that facilitation played a limited role in these locations. This finding appears to be in line with previous studies which have found that competition outweighed facilitation as the dominant biotic interaction, even at high elevations (Graae et al., 2011; Klanderud et al., 2017; Milbau et al., 2013). One explanation for this may simply be that plant physiological response to environmental stress is not necessarily linear along

a gradient such as elevation (Holmgren & Scheffer, 2010; Maestre et al., 2009). Another explanation may be that ground level microclimatic and topographic variation is strong even along elevation gradients such as those studied here, and as such does not necessarily reflect the climatic gradient along sampled trails (Graae et al., 2012; Scherrer & Körner, 2011). In other words, the higher elevations sampled along trails A and D, in combination with other local factors unidentified here, may inhibit seedling establishment, leaving resident species to rely on vegetative reproduction.

Though none were found in the upper two transects of trails A and D, multiple seedlings were documented at similar elevations along trails B and C. This discrepancy may point to the importance of site-specific limitations to seedling emergence. This would be in line findings of previous empirical studies which have demonstrated the importance of microsites and local biotic and abiotic contexts for seedling emergence (Daleo & Iribarne, 2009; Graae et al., 2011; Venn & Morgan, 2009). Minor deviations from optimal conditions within transects may be sufficient to impose an amount of stress large enough to inhibit seedling emergence (Holmgren & Scheffer, 2010). However, seedling recruitment among clonally reproducing plants may be encouraged by the exploitation of spatial and temporal windows of opportunity (Eriksson & Fröborg, 1996). Since the number of seedlings sampled for this study is relatively low (n=185), it is difficult to draw any definitive conclusions from either raw data or statistical models. However, both in combination suggest a study area characterized by a mixture of small (transect-level properties) and large scale (the effects of elevation) limitations on seedling recruitment. Any interpretation of my results should also keep in mind the effect of one outlier in the seedling data. Indeed, 26 seedlings were recorded in one plot of the upper transect of trail B. Removing these observations from the data set and running the same GLMM yielded no statistically significant interaction between elevation and distance from trail.

Although not statistically significant, large herbivore pellet count also correlated negatively with seedling density, albeit to a limited extent. This suggests that trampling and gap creation from large herbivores play a minor role in seedling emergence, either through competitive release or suppression from trampling. This is in contrast to previous studies which have found that the creation of gaps similar to those made by grazing herbivores, as well as rodent activity,

correlated positively with seedling emergence (Klanderud et al., 2017), including in Dovre (Nystuen et al., 2014). In Dovre, it appears that the effect of trampling from large herbivores functions more as a limiting disturbance rather than a facilitative one. The discrepancy in results for distance from trail and large herbivore pellet count compared to previous studies may also be a result of the amount and severity of the disturbances – since hiking trails channel foot traffic into one limited area over sustained periods of time, their disturbing effect on vegetation could be seen as more severe than sporadic large herbivore foraging.

4.4 Upslope migration and factors influencing seedling emergence

Adult coverage, that is, the relative coverage of species in each plot, was the strongest predictor of seed rain, suggesting that seed dispersal occurs on a local plot or transect scale. This is in keeping with Molau and Larsson's (2000) analysis which found that seed rain in Swedish Lapland largely reflected local flora within a ten-metre radius of seed traps. My results show that seed rain was not mediated by whether a species was native to lowland or alpine environments; the presence of a given species as an adult in a transect whilst also being present only as a seed in the next upslope transect was also not shown to be meaningful. This in turn suggests that hiking trails do not function as conduits for the upslope dispersal of lowland species. This is in line with the findings of Haugum (2016), who found no evidence of hiking on the elevational range shift of vascular plant species in the Scandes, albeit via a different methodology (using estimates of the average number of hikers visiting mountain summits during a growth season). However, it may well be that uphill migration occurs on a finer scale than that studied here, abetted by microsite hospitality. Over longer time periods this more localized dispersal could theoretically result in cumulative, landscape-level species range shifts.

Adult standing vegetation in the plots displayed a negative relationship with seedling density. This may reflect the importance of standing vegetation in limiting the emergence of seedlings by way of resource limitation, for example by limiting light penetration. The fact that no correlation was found between seed rain and seedling emergence also suggests that the latter is not governed by seed rain. This finding may once again reflect the importance of microsite availability in the plots. In other words, seedling emergence may be governed by extremely small-scale biotic and

abiotic variations which may enable or inhibit seed germination and seedling emergence on a fine scale.

5. Conclusion

Seed rain decreased with elevation, most likely a reflection of the amount of seed-bearing standing vegetation (notably *Betula pubescens*) below the treeline, as well as the importance of vegetative reproduction among alpine species at higher elevations. Whist the results of this study indicate that hiking trails do function as corridors for seed dispersal, they appear to do so only in a limited capacity. Within a global change context, it appears that hiking trails in Dovre cannot be relied on to assist in the dispersal of alpine plant species to safe sites with more appropriate conditions for establishment, survival and seed set. In addition, seed rain appeared to originate from nearby standing vegetation at the plot or transect level. Seedling emergence data reflected that of previous studies and was in line with the stress-gradient hypothesis, as the effect of trails appeared to only play a role at lower elevations where trail traffic presumably eliminates competing vegetation in productive environments. Theoretically, an increase in seed rain could result in an increase in seedling emergence as seeds are deposited in safe sites to germinate. However, seed rain appeared to have a limited effect on seedling emergence, suggesting that micro-site characteristics are more important than seed limitations in determining seedling emergence. The results of this thesis thus suggest that future studies of the ecological effects of hiking trails on alpine vegetation should focus on the effects of sustained usage on the creation of exposed ground, which may require managers to adopt different conservation strategies at different elevations. Though limited to the scope of a master's thesis, this study revealed some interesting ecological patterns that warrant confirmation via further study. Indeed, replicating the methodology used here at a finer scale and over a longer period may reveal a cumulatively meaningful spatial effect of localised dispersal and microsite characteristics along hiking trails on elevation gradients.

6. References

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Appendix

Table A1: Total individual abundance of all species recorded in the seed rain and as seedlings, sorted by transect level. Species names follow Lid and Lid (1994).

Species	Growth form	Seed rain				Seedlings			
		Transect level				Transect level			
		Low	Mid 1	Mid 2	High	Low	Mid 1	Mid 2	High
Alchemilla alpina	Forb	-	-	-	-	1	-	-	-
Alchemilla sp.	Forb	-	-	-	-	-	-	-	2
Anthoxanthum nipponicum	Graminoid	45	44	5	11	-	-	-	2
Avenella flexuosa	Graminoid	17	-	-	-	-	-	-	-
Betula nana	Shrub	17	13	-	-	-	-	-	-
Betula pubescens	Tree	863	17	1	-	-	-	-	-
Bistorta vivipara	Forb	2	-	1	4	23	-	7	20
Calamagrostis neglecta	Graminoid	4	-	-	-	-	-	-	-
Campanula rotundifolia	Forb	-	-	-	-	6	2	2	-
Carex sp.	Graminoid	-	-	1	-	-	-	-	-
Cerastium sp.	Forb	1	-	-	-	-	-	-	-
Cerastium alpinum	Forb	-	-	-	-	2	-	2	6
Deschampsia cespitosa	Graminoid	261	29	1	31	-	-	-	-
Empetrum nigrum	Shrub	1	109	4	2	-	-	-	-
Euphrasia frigida	Forb	-	-	29	-	-	-	-	-
Euphrasia sp.	Forb	-	-	-	-	-	-	-	5

Festuca sp.	Graminoid	87	79	48	3	-	-	-	-
Gallium sp.	Forb	-	-	1	1	-	-	-	-
Geranium sylvaticum	Forb	12	2	-	-	-	-	-	-
Gnaphalium sp.	Forb	-	-	-	-	-	-	1	-
Luzula sp.	Graminoid	-	1	-	18	-	-	-	1
Melampyrum sylvaticum	Forb	2	2	-	-	-	-	-	-
Myosotis decumbens	Forb	1	-	-	-	4	-	-	-
Phleum alpinum	Graminoid	15	-	-	-	-	-	-	-
Papaver sp.	Forb	-	1	-	-	-	-	-	-
Poa sp.	Graminoid	8	6	-	4	-	-	-	-
Ranunculus acris	Forb	30	4	-	-	18	1	12	-
Rumex acetosa	Forb	12	-	-	-	-	2	-	-
Salix herbacea	Shrub	-	-	-	-	-	-	4	2
Sibbaldia procumbens	Forb	-	-	1	-	-	-	4	1
Silene acaulis	Forb	-	-	-	-	-	-	-	1
Solidago virgaurea	Forb	-	-	-	-	1	2	2	-
Taraxacum sp.	Forb	-	-	-	-	-	-	-	1
Thalictrum alpinum	Forb	-	-	-	-	-	-	1	1
Trientalis europaea	Forb	-	-	-	-	2	1	-	-
Vaccinium vitus-idea	Shrub	-	-	-	-	1	-	2	1
Vaccinium myrtillus	Shrub	-	-	-	-	1	-	-	-
Vaccinium sp.	Shrub	-	-	-	-	-	1	-	-
Veronica sp.	Forb	1	1	-	-	-	-	-	-

Viola biflora	Forb	45	2	23	2	1	1	-	-
Viola canina	Forb	-	-	-	-	1	-	-	-
Unknown 1	-	-	3	2	-	-	-	-	-
Unknown 2	-	-	-	-	1	-	-	-	-
Unknown 3	-	-	-	-	1	-	-	-	-
Unknown 4	-	-	-	-	1	-	-	-	-
Unknown 5	-	1	-	-	-	-	-	-	-
Unknown 6	-	1	-	-	-	-	-	-	-
Unknown 7	-	1	-	-	-	-	-	-	-
Unknown 8	-	-	-	1	-	-	-	-	-
Unknown graminoid	Graminoid	47	10	-	1	14	-	1	1
Unknown forb	Forb	-	-	-	-	11	3	1	3