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Recruitment of Scots pine *Pinus sylvestris* L. beyond the edge of its current distribution range in the forest-tundra ecotone of northern Norway

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Master's degree in Ecology

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Preface

This MSc thesis in Ecology was completed at The University of Life Sciences (NMBU), under The Faculty of Environmental Sciences and Natural Resource Management on the 15th of May 2022. It focused on the recruitment of Scots pine on its northern distribution range in northern Norway, with the use of dendro-ecological methods. Fieldwork was conducted in Finnmark during the first weeks of August 2022, followed by processing of dendro-ecological samples at the lab facilities of The Norwegian Institute for Nature Research in Tromsø, and at NMBU.

The present study was designed as part of the activities of the tundra-forest ecotone module of The Climate-Ecological Observatory for Arctic Tundra (COAT) in collaboration with The County Governor of Troms and Finnmark and The Norwegian Forest Seed Center. Permission for invasive sampling was granted by the Finnmark Estate.

Much of the work lying behind the result of this thesis was shared with my fellow student at NMBU, Giacomo Favero, who has finalized his own thesis under the same project.

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Mikael, I am grateful for your additional support and suggestions, particularly during the writing phase. Your broad expertise in the field of forest ecology is inspiring.

I thank my fellow master student at NMBU, Giacomo Favero. Our close collaboration throughout the project has been a pleasure, and I am grateful for our many discussions and shared experiences on this journey. An additional appreciation goes out to Mirella Karppinen and Florent Déry for assisting in fieldwork, persisting through long and tough days.

I further extend my appreciation to COAT for their financial support of this project, including its associated institutions, The Norwegian Institute for Nature Research in Tromsø, which made an intensive lab effort possible, and The Arctic University of Tromsø (UiT) for providing the necessary vehicles for fieldwork.

I finally thank the Leader of COAT, Rolf Anker Ims; Helge Molvig at The County Governor of Troms and Finnmark; and Øyvind Meland Edvardsen at The Norwegian Forest Seed Center, which have provided insight and knowledge along the way.

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Lars Mikkjel Hus Kråkenes

Abstract

The forest-tundra ecotone in Northern Fennoscandia has experienced significant abiotic and biotic changes in recent decades which may ultimately affect the distribution of tree species. In this study, I investigate the factors influencing the density and distribution of Scots pine at the northern distribution range to assess the potential for spread northwards. The study area covered three selected regions in northern Norway (west, south and east), each represented by two survey sites: one placed well within the current distribution of pine ('core' sites) and one placed at the leading edge of the current distribution ('edge' sites). In all sites combined, data on a total of 146 seed trees and 1642 recruits were collected. Three GLM models were fitted, looking at the regional differences in recruit density, the underlying local conditions that contribute to this variation, and the factors that influence effective dispersal distance from the seed tree.

The main results showed that; **1.** There was generally lower recruitment at the leading edge of the distribution range, although this was not the case for the south region. **2.** Recruit density decreased rapidly with the distance from the seed tree, even at the relatively short sampling distance. **3.** Of the seed tree attributes, crown diameter was the only significant predictor, and positively influenced recruit density. **4.** The proxy for graminoid abundance was the single significant predictor among the vegetation and soil variables and had a negative effect on recruit density. **5.** Reindeer presence, as indicated by pellet density, negatively influenced recruit density, while moose presence showed a tendency for the opposite effect. **6.** Birch density and stem diameter negatively influenced recruit density.

In conclusion, warming can be expected to facilitate the recruitment and expansion of Scots pine, possibly aided by reduced competition with birch due to moth outbreaks. However, the rate of expansion may be limited by short dispersal distances from the seed tree, and extreme weather events related to climate change. The large amount of unexplained variation in the models signifies the complex influences on tree recruitment. Future studies should consider the influences of microclimate, biotic interactions, and microsites, to make robust forecasts of climate change effects on tree recruitment.

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Introduction

The spatial distribution of plants is limited by a combination of historical factors that influence colonization and current environmental conditions that determine their ability to grow and reproduce (Woodward and Woodward 1987). Globally, the distribution and fitness of many plant species are being affected by climate change, acting through changes in the factors that regulate phenological events, such as time of blooming, as well as changes in growth and how species interact with each other (Parmesan 2006, Pörtner et al. 2022). These changes are often most obvious at species range edges, where changes to the conditions that previously limited the species distribution can lead to range shifts (Holtmeier and Broll 2005, Körner 2021).

In Northern Fennoscandia, the forest-tundra ecotone has experienced significant abiotic and biotic changes in recent decades. This is partly due to climate change which has caused an increase in both summer and winter temperatures (Pedersen 2021, met.no 2022). Temperatures at northern latitudes have increased disproportionately to the global average, frequently referred to as arctic or polar amplification (Kivinen et al. 2017). Compared to the climate normal period 1961-1990, the transition zone towards the low-arctic tundra in NW Norway currently experiences mean annual temperatures which are approximately 2°C higher and a snow free season which is 3-4 weeks longer.

The resident birch (*Betula pubescens* var. *pumila*) is currently the main forest-forming tree species within northern Fennoscandia. Over time, however, reduced climatic constraints could affect growing conditions and eventually the distribution of other tree species, such as the resident Scots pine (*Pinus sylvestris* L.). While a future decline of Scots pine is predicted in southern latitudes, populations in the north, which grow far from their climate optimum, is assumed to increase their reproduction and growth (Rehfeldt et al. 2002, Matías and Jump 2012, Kausrud et al. 2022). In past geological times, the northern distribution limits of Scots pine fluctuated significantly in response to climate-variability driven by ocean currents, sometimes extending further north than the current range (Huntley et al. 2013). Some evidence also suggests that Scots pine has progressed higher in elevation compared to birch during the period of recent warming in Fennoscandia (Kullman and Öberg 2009), indicating that rising temperatures may favor evergreen coniferous species at the expense of broadleaved species (MacDonald et al. 2008) in northern regions. While Scots pine is currently sparse within the forest-tundra ecotone, it is reasonable to ask whether this conifer tree species has the potential to spread further north causing a greater degree of intermixture with birch. Answers to this

question would provide a better understanding of how northern ecosystems may respond and adapt to climate change. It is therefore of considerable interest to investigate the potential for Scots pine to spread beyond its current distribution range.

The expansion of many tree species is limited by the recruitment of seedlings, which is highly sensitive to environmental conditions such as substrate characteristics, climate, facilitative or competitive interactions with other plant species, and herbivory (Eriksson and Ehrlén 2008). Recruitment potential is dependent on the *availability of seeds* and the seed's ability to *establish, survive and grow*. The former is controlled largely by the density and quality of local seed trees, as well as the frequency of years that are climatically favorable for seed set and maturation (Henttonen et al. 1986, Almqvist et al. 1998, Parfenova et al. 2021). The latter can be influenced by multiple and complex factors, including microclimate, substrate, ground vegetation composition and trophic interactions (Kuuluvainen and Pukkala 1989, Bergström and Bergqvist 1997, Bognounou et al. 2018). The presence of the seed tree itself can also affect the growth potential of seedlings in the immediate neighborhood in a predictable manner due to its effect on nutrients, water and solar radiation (Kuuluvainen and Pukkala 1989).

Coinciding with a warming climate, species of forest pest insects have expanded their range in northern Fennoscandia, inflicting substantial damage and mortality to the birch forest (Jepsen et al. 2008, Jepsen et al. 2011). This includes the geometrid moth species *Operophtera brumata* Bkh. (Winter moth), *Epirrita autumnata* L. (Autumnal moth) and the more recent *Agriopis aurantiaria* Hb. (Scarce umber moth). Populations of these moths fluctuate in a cyclic fashion with outbreaks happening approximately every decade, and oftentimes synchronized across large geographical regions (Vindstad et al. 2019a). During moth outbreaks, the ground vegetation layer can be affected by defoliation and from a fertilization effect given by a high number of larvae and their feces decomposing on the forest floor. Crowberry *Empetrum nigrum* (*ssp. hermaphroditum*) L. which can form dense mats within northern ecosystems can prevent the establishment of other plant species due to allelopathic compounds, affecting soil conditions through reduced nutrient availability (Nilsson 1994, Tybirk et al. 2000). Typically following outbreaks, there is a shift in understory communities where crowberry is replaced by the graminoid pioneer species, *Avenella flexuosa* (Karlsen et al. 2013). One can speculate, whether outbreak-induced disturbance to the birch forest and the ground vegetation layer, may benefit the recruitment of Scots pine through reduced competition and enhanced conditions for seedlings.

Ungulates and rodents are other functionally important herbivores in Northern Fennoscandia (Bergström and Bergqvist 1997, Bognounou et al. 2018). In this region, semi-

domesticated reindeers (*Rangifer tarandus tarandus* L.) are prevalent through husbandry and can negatively affect recruitment via browsing, trampling or breaking branches when rubbing antlers up against the stem of the tree (Suominen and Olofsson 2000, Horstkotte et al. 2017). Indirectly, reindeer reduce lichen cover, which can promote growth of higher growing vegetation, inhibiting pine seedling success (Väre et al. 1996, Den Herder et al. 2003). Rodent herbivores, such as voles and lemmings, can have a similar but positive effect on recruitment by limiting the growth of vegetation competing with pine (Olofsson et al. 2009). However, seedlings of pine are also grazed by rodents, demonstrating a potentially direct negative effect, especially during rodent population peak years (Bognounou et al. 2018). Furthermore, seed predation by rodents have been found to inhibit conifer regeneration (Ellingsen et al. 2017).

Determining the individual factors that influence recruitment ability is apparently complex and therefore difficult to predict. For this reason, a common approach when comparing the potential of spread between species and/or geographical regions, is to make use of inverse modelling on seedling distribution (Ribbens et al. 1994, LePage et al. 2000, Uriarte et al. 2005, Debain et al. 2007) to estimate “effective dispersal”. Effective dispersal explains the proportion of dispersed seeds which successfully result in new plants (i.e. dispersal of seedlings), providing an actual measure of the recruitment that allows a species to colonize new areas and adapt to changing environmental conditions. These models can be developed using dendro-ecological samples (e.g. tree cores or cut cross sections of the stem), which provides age counts and annual growth of seedlings (Gärtner et al. 2015). That is also the approach taken in this research. The study aims to quantify the density and effective dispersal in naturally occurring Scots pine at the northern edge of the current distribution of the species in northern Norway to assess the potential for spread beyond the current range. Three regions (west, south, and east) on the northern distribution limit in northern Norway were selected, each represented by two survey sites: one placed well within the current distribution (core sites) and one placed at the leading edge of the current distribution (edge sites). Inverse modeling was used to understand the mechanisms behind the effective dispersal of Scots pine and how it might affect the density and distribution of recruits. With the projected progression towards a warmer climate, one can expect Scots pine to eventually establish itself as a more prominent tree species in the region of today’s birch-dominated forest-tundra ecotone.

Research questions:

1. How do density and distribution of recruits vary between sites (core and edge) and between regions (west, south and east), and what is determining this variation?
2. What do the density and distribution of recruits indicate for the potential of Scots pine to spread beyond its current distribution range in northern Norway?

Materials and methods

Study area and design

The study was conducted in the county of Finnmark (48,618 km²) in northern Norway. Finnmark is a vast and diverse county with large mountainous, coastal and plateau areas. Coastal areas are milder and more humid, while inland areas have relatively dry and cold climate. Average annual precipitation ranges from around 1000 mm in the west to under 400 mm in inner fjords and the highland plateaus (Norsk klimaservicesenter 2022). While birch is the dominating tree species in the region, there are considerable areas of Scots pine and occasional occurrences of rowan *Sorbus aucuparia* L. aspen *Populus tremula* L and willows *Salix spp.* L. The field vegetation is largely comprised of dwarf shrubs such as bilberry *Vaccinium myrtillus* L. and crowberry, with lichen heaths frequent on drier soils.

Based on the known current distribution of pine, three regions spanning the northern distribution limit of pine were selected (69°25′ to 70°20′N; 24° to 30°E, Figure 1). This was done with the assumption that northward expansion of pine beyond its current range will happen from three main regions across the northern distribution belt (west, south, and east). Each region was represented by two survey sites; one placed well within the current distribution of pine (termed ‘core sites’) and one placed at the leading edge of the current distribution (termed ‘edge sites’) (Figure 1). The edge sites were placed as far as possible towards the north (i.e. east of the western region, north of the southern region and west of the eastern region). No systematic mapping exists which can support the choice of edge sites. The choice of both core and edge sites was supported by existing ortho photos (www.norgebilder.no), and Google Maps. In addition, an aerial survey using a small airplane was conducted over the lesser-known sites in the south and west on May 18th, 2022. During the aerial survey, occurrences of pine stands (or individual trees) were approximately mapped using a GPS supported by overview photographs.

The aerial survey served to confirm i) whether preliminary sites identified from ortho photos were suitable (e.g. contained a sufficient number of larger trees, no stands which appeared to be planted, no major obstacles for access), and ii) to explore whether edge sites could be pushed even further north than anticipated based on ortho photos. The eastern core and edge sites were sufficiently well known from previous field campaigns conducted by The Climate-Ecological Observatory for Arctic Tundra (COAT; <https://coat.no/tundra-forest-ecotone>), to allow suitable stands within both the core and edge sites to be located in the field without a prior aerial survey. A brief description of the individual sites is given below (see ‘Site description’).

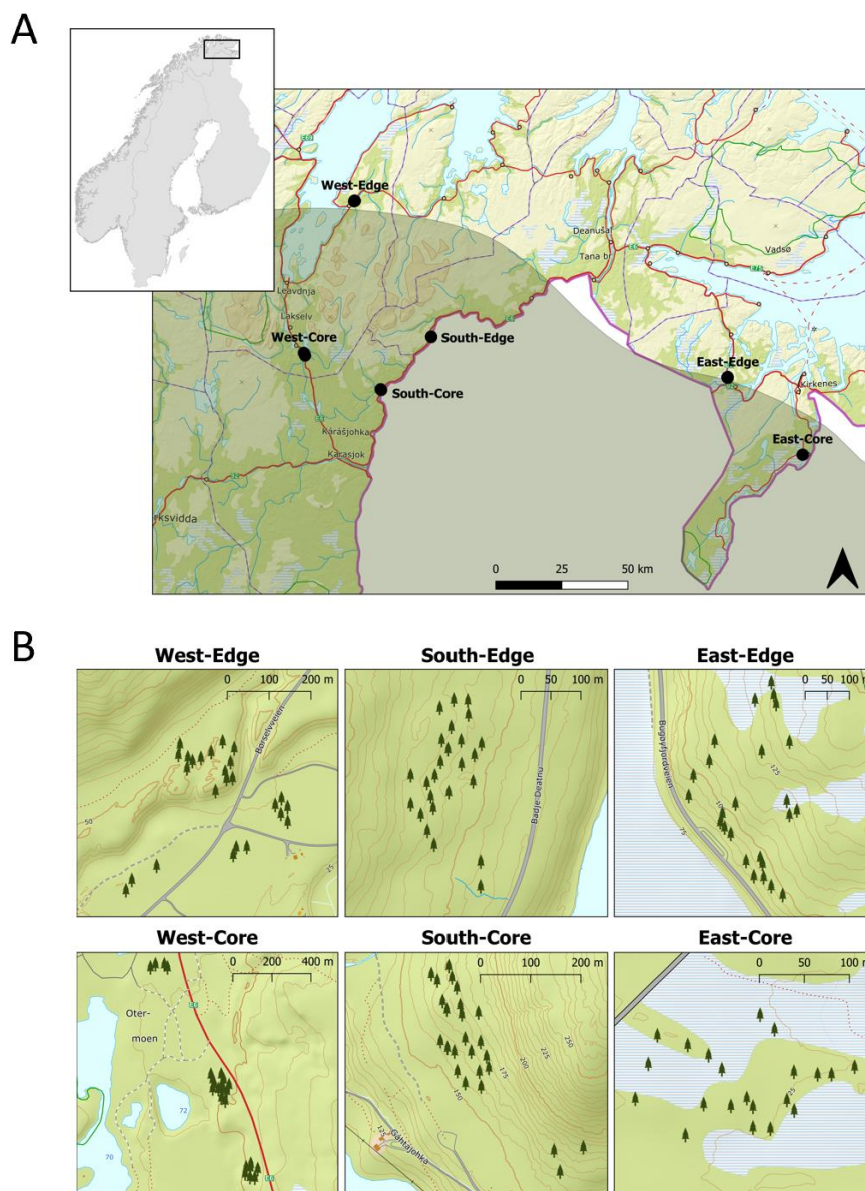


Figure 1. **A.** Overview map showing the general location of the study in northern Norway and the six selected sites. Dark shade represents the approximate northern distribution limit of Scots pine, according to Caudullo et al. (2017). **B.** Boxes show the distribution of seed trees (based on GPS coordinates recorded in the field) within each site.

Site description

A summary of the average temperatures (July and January), annual mean precipitation and the elevation range of the seed trees can be found in Table 1.

In the *east region*, the edge represented localized stands to the east of Færdesmyra, a wetland area of Sør-Varanger municipality. The core represented dense stands located north of the Pasvik Nature Reserve near Svanvik. The core site contained some relatively wet ground conditions (mires), indicated by hatched, grey sections of the map (Figure 1 B: East-Core). In the *south region*, the edge represented localized stands about 3 km south of Levajok (Image 1). Here, seed trees were positioned on a slight east-facing slope. The core site represented stands located just northeast of where Valjoki river runs into Tana River to the east. Seed trees were positioned on a southeast-facing slope. In the *west region*, the edge was represented by localized stands near Børselv, with high proximity to the ocean, while the core site represented dense stands ~ 3 km south of Skoganvarre (Image 2). The more southern seed trees of west core were located on a slight west-facing slope.

Table 1. Mean temperature, precipitation and elevation ranges of seed trees within the six study sites.

| Site | July mean (°C) | January mean (°C) | Precipitation mean (mm) | Elevation range (m.a.s.l.) |
|-------------------|----------------|-------------------|-------------------------|----------------------------|
| East Edge | 12.6 | -11.6 | 589 | 90-145 m |
| East Core | 12.0 | -12.1 | 541 | 25-45 m |
| South Edge | 12.8 | -14.3 | 529 | 115-180 m |
| South Core | 12.3 | -14.0 | 503 | 155-195 m |
| West Edge | 11.9 | -8.5 | 669 | 10-55 m |
| West Core | 12.8 | -12.1 | 493 | 80-195 m |



Image 1. Edge site with low-density pine trees, interspersed with birch. Here from south edge during fieldwork in August 2022. Drone photo by Giacomo Favero.



Image 2. A higher-density core site. Here from west core during fieldwork in August 2022. Photo by Lars Mikkjel Hus Kråkenes

Study species

Scots pine *Pinus sylvestris* L. is a coniferous tree species in the pine family *Pinaceae*, native to Europe and Asia with a wide natural distribution range in the northern hemisphere. Scots pine can be found across a broad range of ecological and climatic conditions, including very dry sites, acidic soil and wet peatland conditions (Giertych and Mátyás 2017). Morphological traits vary greatly according to growing conditions, but it is often characterized by a tall, straight trunk and conical shape. Scots pine can grow up to 30 m tall and typically live up to around 200-300 years, although individual trees near the age of 800 have been recorded in northern Fennoscandia (Wallenius et al. 2010). The bark is thick and scaly, with a reddish-brown color. It has long, needle-like leaves that grow in clusters of two to five. Scots pine produces both male and female cones on the same tree (monoecious). In northern latitudes, seed set typically occurs in late spring or early summer when the trees produce their cones. The male cones produce pollen, which is released and carried by the wind to the female cones. The female cones, which are larger and develop on the upper branches of the tree, are fertilized by the pollen, and begin to develop seeds. The seeds mature during the growing season and into the fall of the second year. At this point, the cones begin to dry and open, releasing the seeds. The timing of cone opening can vary depending on factors such as temperature, humidity, and moisture content. Mast years (i.e. years of high seed production) can be relatively frequent but less so at range limits where seed maturation is hindered due to a shorter growing season (Giertych and Mátyás 2017). During mast years, Scots pine trees can produce an abundance of cones, resulting in a higher than usual seedling recruitment and subsequent population growth. Due to its ability to grow in a variety of conditions, Scots pine is considered an important tree for reforestation and afforestation projects (Vacek et al. 2021). With a good strength to weight ratio, Scots pine holds high economic value, especially in Nordic countries where its timber is used for building and construction, as well as for furniture and paper. In the US among other countries it is widely used as Christmas trees, and its resin was tapped by the former USSR and eastern Europe (Durrant et al. 2016).

Field sampling and seed tree selection

Within each site, three types of pine trees, designated as either ‘seed trees’, ‘neighbors’ or ‘recruits’, were defined. The sampling unit in the field was a seed tree with a 9 m radius (~250 m², Figure 2). Seed trees (source trees) were older, sexually mature, pine trees (>10-15 years old), forming the center of the 9 m radius (referred to as ‘plot’). Neighbors were defined as all

other potential seed trees within the plot with a height > 4 m, allowing for their potential influence on recruit density to be considered in the statistical models. Recruits were defined as all pines, excluding the seed trees, found within the plot with a height < 4 m. Variables recorded in the field are listed in Table 2.

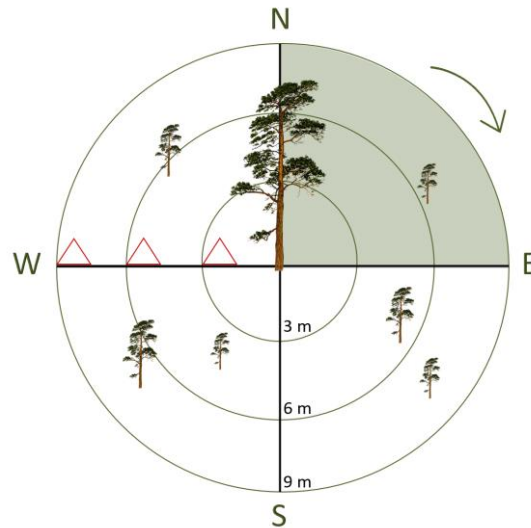


Figure 2. Illustration of the sampling unit (seed tree with a 9 m radius) as part of the study design. Each of the 4 sectors are named according to the cardinal direction they span (NE, SE, SW, NW). All pines within the radius with a height < 4 m are recorded as recruits. Red triangles: ground layer vegetation design, measured at 3 points in each cardinal direction.

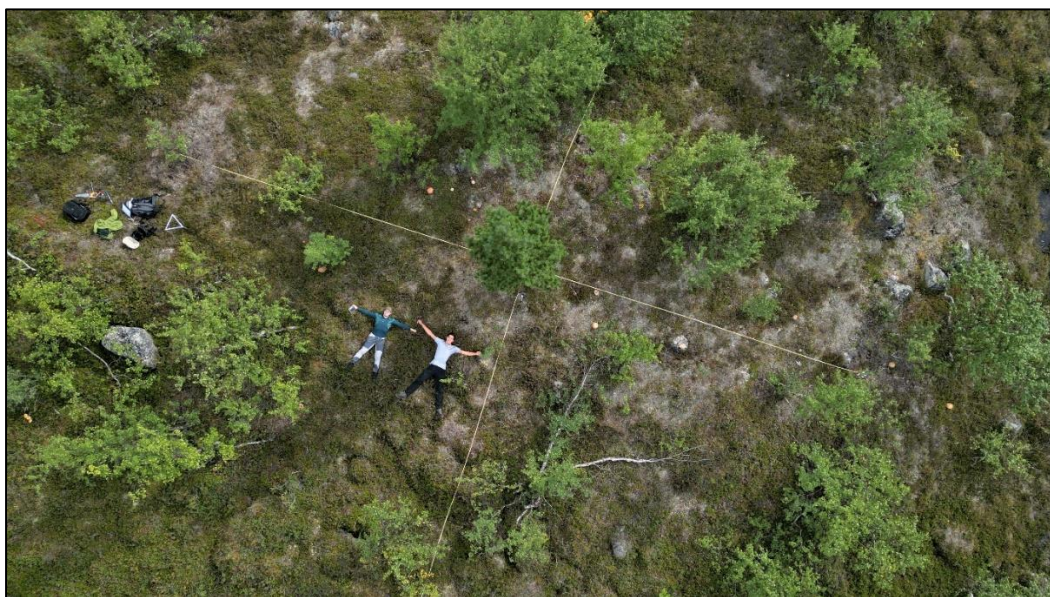


Image 3. Real depiction of the sampling area for each plot. Measuring tapes are laid out 9 m from the seed tree in the N-S and E-W direction. Drone photo by Giacomo Favero.

Table 2. Variables collected in the field, their units, and abbreviations.

* Representing more than one variable (e.g. measured for each species of vegetation/pellet group)

| | Variable | Unit | Abbreviation |
|-----------------|--------------------|-----------------|---------------------|
| Seed tree level | Waypoint | degree, minutes | coord |
| | Height | m | tree_height |
| | Diameter | cm | tree_dbh |
| | Age | years | tree_age |
| | Dendro height | cm | tree_dheight |
| | Crown diameter | m | crown_diam |
| Recruit level | Height | cm | recruit_height |
| | Diameter | cm/mm | recruit_diam |
| | Sector | NE/SE/SW/NW | sector |
| | Distance | m | distance |
| | Dendro | binary (yes/no) | dendro |
| | Dendro height | cm | recruit_dheight |
| | Age | years | recruit_age |
| | Cones | binary (yes/no) | cones |
| Plot level | Neighbors | trees per plot | neighbors |
| | Birch density | % | birch_dens |
| | Birch state | % | birch_state |
| | Birch diam at BH | cm | birch_dbh |
| | Vegetation hits* | hits | x_hits |
| | Vegetation height* | cm | x_height |
| | Organic layer | cm | org_layer |
| | Ungulate pellets* | n. of pellets | x_pellets |

When arriving at a site, individual seed trees were located and selected in the field. Age was approximated in the field based on a combination of the number of branch whorls, height and diameter. Scots pine is usually monoecious (male and female organs on the same tree), but in Finnmark dioecious (male only or female only trees) do occur (Ø. M. Edvardsen, personal communication) The presence of cones either in the canopy or on the ground below the canopy, was therefore a requirement for selection. When selecting seed trees, trees with obvious damage (e.g. extensive crown loss, breakage of main stems, split tree etc.) were avoided. Once a seed tree had been selected, all other potential seed trees with overlapping neighborhoods were excluded as sample trees (Figure 3 A). Two measuring tapes were then laid out in the cardinal directions (N-S and E-W) with the seed tree forming the center with a radius of 9 m in each direction out from the tree.

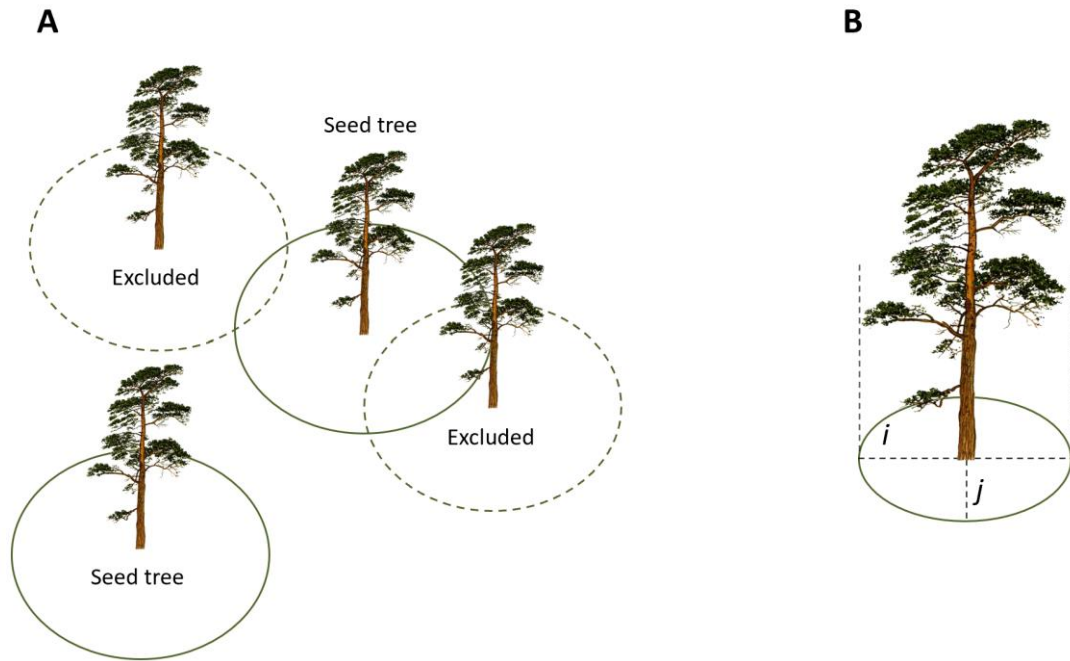


Figure 3. *A. Illustration of seed tree selection where potential seed trees that overlap are excluded. B. Measurement of crown diameter in two directions: i and j .*

Variables on the seed tree level

Waypoint coordinates of seed trees were recorded with a handheld GPS (in WGS84, UTM35N). Variables on the seed tree included height (m), recorded with a Suunto height meter (PM-5/1520) and diameter, measured at breast height using a measuring rod. Crown diameter was obtained visually by projecting the edges of the crown to ground level and measuring the distance (m) between outer edges in two directions: N-S and E-W (Figure 3 B).

Variables on the recruit level

The target sample size was 30 recruits per plot. The minimum number of recruits was counted within the seed tree neighborhood starting at the north-east sector working clockwise. Sampling within a sector was completed even if this meant that the final sample size was exceeding the target (Figure 4). This was to ensure that the total area sampled was known (either 1, 2, 3 or 4 full sectors), permitting calculation of recruit density per sector (recruits per m^2 surveyed).

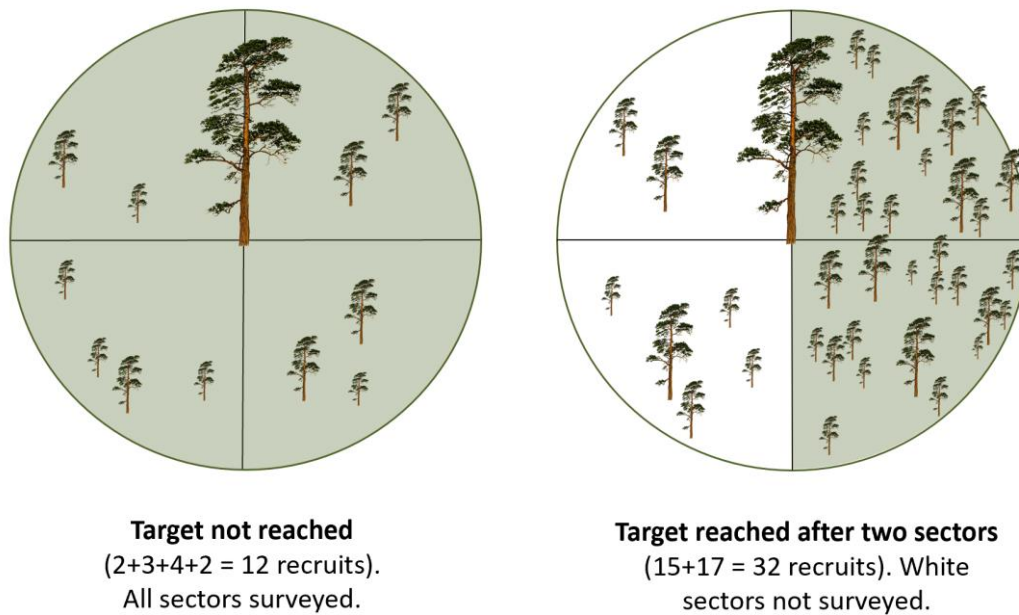


Figure 4. Examples of how the target sampling rule of a minimum of 30 recruits played out in practice.

Recruits were marked using small, numbered pins and then measured. The numbered pins were used for randomly selecting recruits for dendro-sampling (see section: ‘*Dendro-ecological field sampling*’). The distance to the seed tree was measured to the nearest half-meter or dm (for recruits close to the seed tree (< 3 m)). Height was measured using a measuring rod to the nearest cm for small recruits or to the nearest half-meter for larger recruits. Diameter was measured using a caliper to the nearest mm for small recruits or a ruler to the nearest cm for larger recruits. The diameter was measured at ground level, as close to the root crown as possible. The presence of cones on recruit were also recorded.

Variables on the plot level

The state and density of birch found within the seed tree neighborhood was recorded to give a rough estimate of whether the plot was located in an area which has been affected by moth outbreaks in the past and the degree of intermixture with birch. The % of dead birch stems within the 9 m neighborhood was estimated on a scale from 0 – 100%, to the nearest 10%. Birch stem density was the approximate number of birch stems within the 9 m neighborhood, estimated to 4 classes: < 5 stems, 5-10 stems, 10 – 25 stems, >25 stems. Additionally, the stem diameter (cm) was measured of the 5 thickest birch stems at breast height, as a rough estimate meant to tell us whether the plot was located in large statured or small statured/shrubby birch forest.

Variables of the ground vegetation focused on a few species/species groups which are likely to directly influence germination conditions for Scots pine, and which also contain information about the local site condition (richness). The species recorded were crowberry and the species groups graminoids and herbs. While crowberry is allelopathic, and commonly found growing in nutrient poor soils, graminoids and herbs typically grow in more nutrient rich soils. These three species/species groups were recorded every 3 m along the measuring tape in every cardinal direction (3 m, 6 m and 9 m), totaling 12 plots per tree (Figure 2). Recordings of the abundance and height of each species were done using the point intercept method, in a 30 cm triangle with one pin in each corner. As a variable quantifying the depth of the organic layer, four soil cores were taken at a the 3m distance from the seed tree in all four directions (N, S, E, W).

As a proxy for ungulate presence, variables of the total minimum number of pellet groups of moose and reindeer/sheep were recorded by searching along a 2-meter corridor centered on each measuring tape (1 m out on each side of the N-S, E-W measuring tapes) within the plot. Pellets found in clumps/aggregations were counted as one group. If pellets were found where the two corridors overlapped, they were only counted once in either the N-S or E-W direction.

Dendro-ecological field sampling

Dendro-ecological samples were taken from the seed tree, and from a subset of recruits within each seed tree neighborhood. Each seed tree was cored with a 5 mm Haglöf increment borer (<https://haglofsweden.com/project/increment-borers/>) at breast height (1.3 m above ground). The core was taken horizontally and included the pith of the tree. Within each seed tree neighborhood, a maximum of 15 recruits were selected for dendro-ecological sampling. If more than 15 recruits were present, a ‘random number generator’ app was used to make random selection based on the numbered flags. Recruits were sampled as close to the ground as possible to estimate the minimum age. Recruits large enough to be cored (> ~3 cm in diameter) were sampled as close to the ground as the corer permits (usually 10-20 cm). When a quality core was obtained, it was transferred into a plastic storage plate and labeled using a permanent marker. Cores were inserted with the same end in (either pith or bark), to avoid confusion in cases where the bark loosens from the core. The ends of the channel were closed using paper tape, and a small hole in the tape was made at both ends for ventilation. In the evenings after field work, the plates were inspected, replacing any wet tape, and kept in a ventilated place.

Smaller recruits inadequate for dendro-ecological sampling, were pulled up with the root and cut below the root collar, and a cross-sectional piece of 6-8 cm of the lowest part of the stem was tagged with an ID and sampled in plastic bags. After each field day samples were transferred into paper bags and stored in cardboard boxes to dry.

Lab-processing of dendro-ecological samples

Processing of the dry dendro-ecological samples of seed trees and recruits were split respectively between lab facilities at The Norwegian University of Life Sciences (NMBU) and The Norwegian Institute for Nature Research (NINA) in Tromsø. At NMBU samples of the seed trees were processed by fixing seed tree cores in a clamp and sanding them with sandpaper to form a flat and smooth surface (Image 4). A zinc salve was applied to the wood using a toothbrush to enhance interpretation of the annual tree rings. Sanded samples were laid face down and scanned at 1200dpi using an ordinary printer (HP Deskjet 2723e), creating a digital PNG file.



Image 4. A Seed tree dendro-core (here from east edge) have been sanded with sandpaper and scanned with a conventional printer creating a digital image (PNG) for reading of annual rings (brown bark on the left end of the sample, and tree-pith towards the right end).

Samples of smaller recruits demanded a finer and more intensive approach, facilitated by lab equipment at NINA. Here, thin slices/micro sections of the wood samples were cut using a WSL lab microtome (<https://wsl.ch/en/services-and-products/research-instruments/microtomes>, Image 5). The sliced wood sections were placed on glass slides and double-stained using an astra blue and safranin solution, which stains the lignin and the non-lignin parts of the wood respectively to enhance reading of the tree rings (Gärtner et al. 2015). Excess stain was rinsed off using alcohol and xylene prior to being mounted to slides (Image 6) using Canada Balsam (resin obtained from balsam fir trees). Slides were dried overnight at 60 °C, cleaned, and could

then be scanned at 46383dpi resolution into PNG files through a microscope (Zeiss AXIO) connected to the manualWSI software (<https://microvisioneer.com/manualwsi>, Image 6).

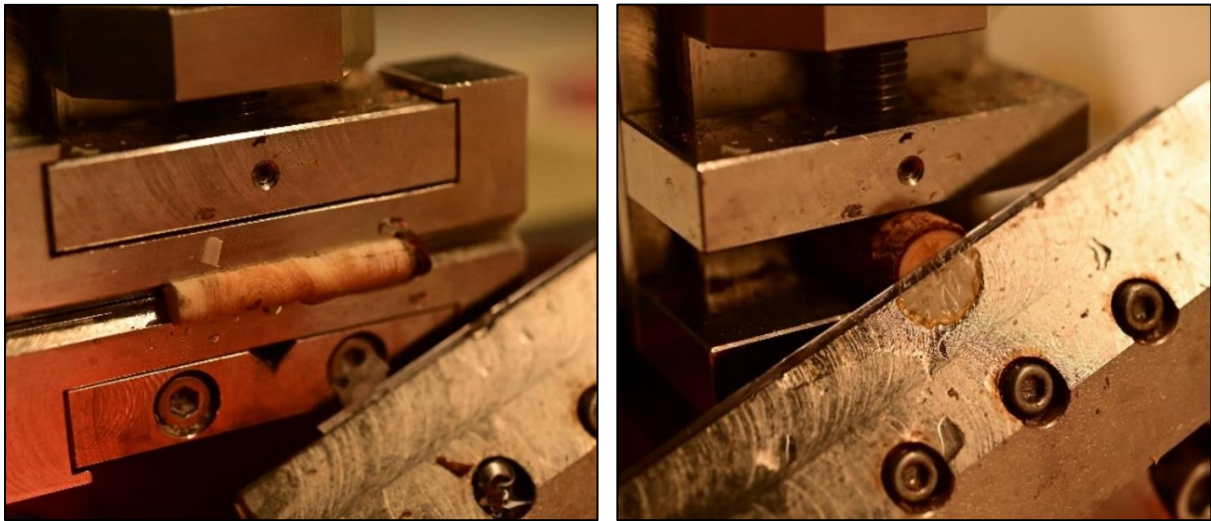


Image 5. Cutting thin slices of cores (left) and cross-sections (right) using a WSL lab microtome. Photo by Giacomo Favero.



Image 6. Canada Balsam (resin) is applied to make permanent slides, after samples have been stained using an astra blue and safranin solution to visualize annual rings. Photo by Giacomo Favero.

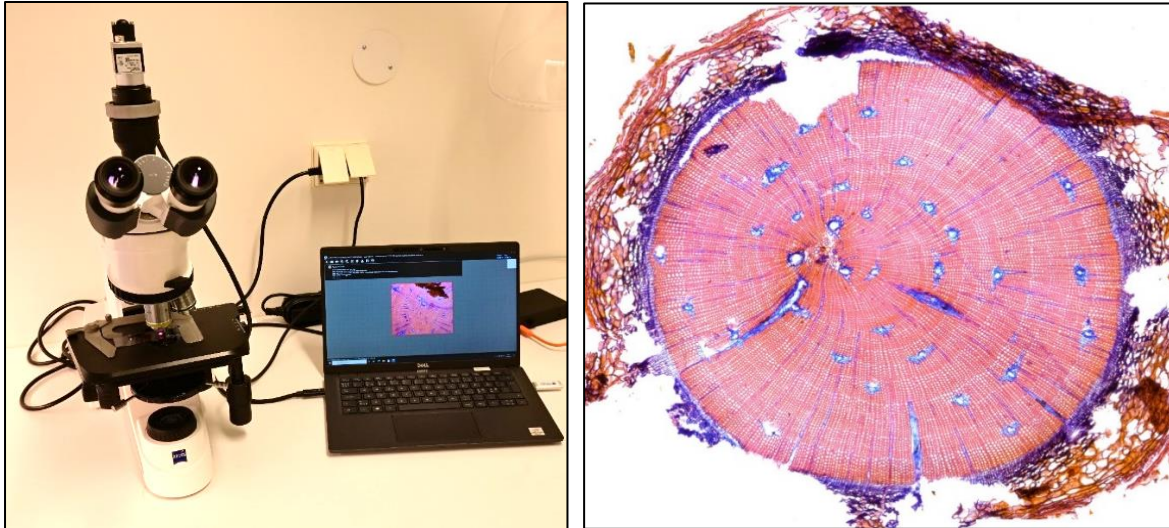


Image 7. Creating digital images of prepared slides using the manualWSI software connected to the microscope.

Reading annual rings of the dendro-ecological samples

Digital PNG image files of scanned samples were loaded into the tree-ring reading software Coorecorder 9.8.1 (<http://cybis.se/forfun/dendro>) allowing the recording of age and ring-width. Starting from the outer edge of the tree (year of sampling), the program lets you click on each annual ring towards the pith, and automatically measure the distance (growth) in mm between years creating a growth time series stored as a coordinate file (.pos). In some cases, samples did not include the pith making dating of the first/oldest tree year difficult. A built-in tool (*DTP: distance to pith*) within Coorecorder was then used to estimate missing years and distance from the pith based on ring curvature. Coordinate files were loaded into the partnering software Cdendro, which allows simple data overview and storage through the commonly used format for dendro-ecological data, Tucson (rwl.). The Tucson format contains columns representing each tree/recruit and rows of growth increments per year.

Many of our samples showed asymmetrical growth (displaced pith), where growth was unequally distributed across the stem due to the formation of *reaction wood*; an adaptive strategy that allows trees to orient themselves and stay upright, commonly produced by a gravitational stimulus such as growing at an inclination or due to wind or mechanical stressors (Groover 2016). Because of this asymmetry, as a rule, annual rings were counted on the longest side of the asymmetrical cross-sections.

Statistical analysis

Climate data

Variables on climate were used to consider the general climatic conditions affecting differences in recruit density across sites. Due to the broad study area and a scarcity of weather stations which are sufficiently local to capture site differences, gridded climatic data with a 1 x 1 km resolution for Finnmark county was obtained from The Norwegian Meteorological Institute ('seNorge', 2023). Three variables of interest, namely the average temperature for the months July and January, and the annual mean precipitation for the available time range 1961-2019. The data was imported using the *rast* function of the *terra* package in R and extracted for the core and edge sites of the three regions. This was done by grouping the seed tree coordinates of each site and applying a 500m buffer around this area, allowing a sufficient overlap of grids to attain representative climate data for each site.

Aim of analysis

The main aim of the statistical analysis was to evaluate the density of pine recruits for each of the six sites, and whether local variables collected in the field could explain any variation in recruit density. Predictors of interest included the seed tree age (years) and their crown diameter (mean of the N-S and E-W directions). The expectation was that older seed trees have produced higher recruit density due to having had more time for recruitment events, while a larger crown diameter was expected to reduce light conditions, negatively influencing recruit density. Neighbors were included with the expectation that a higher number of potential seed sources would positively influence recruit density. The organic layer (mean per plot) was included with the expectation that a thicker organic layer provides better access to nutrients, positively influencing germination and seedling conditions. Graminoid hits and crowberry hits, both aggregated per plot, were expected to have a negative effect on recruits, due to resource competition and allelopathy (crowberry). Vegetation height (max height of all species/groups per plot) could indicate a tall growth understory which may compete with recruits for light and nutrients. Birch variables of interest included birch density (as factor) and birch state (as factor). The interaction between birch density and birch diameter at BH (mean per plot) was to check whether the effect of birch density would depend on the stem diameter.

Before fitting the models, I checked for collinearity between predictor variables. Collinearity occurs when predictor variables have a similar sloped relationship with the response, thus hiding the effect that each predictor has on the response. Collinearity between

the model predictors was tested via linear regressions and the corresponding coefficient estimates. None of the predictors were highly correlated (Correlation coefficients < 0.6). For both models potential influential outliers were explored visually through boxplots/scatterplots and through the measure of Cooks distance, commonly used in regression analysis to identify data points that may have a disproportionate impact on the model results (Fox 2019). Cooks distance is often stated as the cutoff threshold of $4/N$ where N represents the number of observations. The models measured influential outliers by Cooks' distance (threshold above 0.1) but were not rejected in further analysis. This decision was reasoned by the fact that the conclusions of the models would not change when the outliers were excluded, and that the outliers were not wrongfully recorded and represented part of the natural variation recorded in field. All statistical analysis was carried out in R 4.2.3 (<https://cloud.r-project.org/>).

Regional (sites and regions) effects on recruit density

A generalized linear model (GLM) was used to evaluate the overall regional differences of site and region on recruit density. The model was fitted with a negative binomial error distribution (*glm.nb* function within the MASS R package) which is appropriate for highly aggregated count data and accounting for overdispersion (Zuur et al. 2013). The number of recruits was used as response variable, including an offset describing the “rate” of recruits observed per m^2 surveyed. The offset represents the log of the area surveyed, accounting for the likelihood of observing a higher number of recruits when more sectors are surveyed (Parry 2020). The predictor variables ‘region’ and ‘site’ were included with an interaction term (region*site) to check for spatial differences between the sites (core and edge) in recruit density, and whether this effect varied between regions (west, south and east). Predicted values were generated on the response scale with *2 standard error (SE) included as an approximate confidence interval to provide a measure of uncertainty. Predicted values and their 95% confidence intervals (CI) were plotted over the observed data points using the *ggplot* function (*ggplot2* package) to facilitate visual interpretation of differences in recruit density between sites.

Local (environmental) effects on recruit density

To analyze the effect of local environmental conditions on recruit density, a GLM with the same general setup as above (negative binomial using the same response variable and offset) was employed with a range of predictor variables. Due to the relatively small sample size ($N=146$), leaving all predictors in the model was considered to diminish model power. Diminished model

power can lead to difficulties detecting significant effects of the predictors on the response, as the model must estimate more parameters, reducing the effective sample size and increasing the variance of the estimates. This issue was addressed through ‘backward selection’ (also termed ‘backward stepwise regression’), a procedure in which one begins with a full model including all potential predictors and subsequently works backwards eliminating the least significant predictors from the model in a stepwise manner until a certain threshold is met (in the case of this study: when only the significant/near significant predictors were left in the model). The adequacy of the model was partly evaluated by obtaining fitted values via the *predict* function in R, which produces predictions of recruit density for each data point. These predictions were then plotted against field observations for each site. To understand the marginal effect of single predictors on the response, partial dependence plots were used to visualize the individual relationships between recruit density and selected predictors. These were created by predicting for the individual predictors in the GLM while holding all other predictors at a constant (mean for continuous predictors and the most common category for categorical predictors.).

Influences on recruit distance from the seed tree

A GLM with the same general setup as for the density analysis described above (negative binomial accounting for overdispersion) was used to examine whether the predictors (same as used for the local model) effect on recruit density depends on the distance from the seed tree (0-9 m). To test this, a factor variable (‘circle’) was created with three levels representing three concentric circles out from the seed tree (0-3 m, 3-6 m and 6-9 m). I used ‘circle count’ (number of recruits within each concentric circle) as the response variable. Distances were allocated inward, meaning that a recruit measured at the 6 m distance was assigned to level 2 (3-6 m) and a 3 m recruit was assigned to level 1 (0-3 m). The model contained an offset accounting for the area of each circle, divided by the number of sectors surveyed. For example, if two sectors were surveyed, the area of the circle was divided by two. The predictors were included in interaction with circle. Any significant interaction between the circle variable and other predictors would indicate that the effect of the any predictor depends on the circle within the plot (i.e. the distance from the seed tree).

It was difficult to formulate strong a-priori expectations for which interactions would be important, thus a full model with all the predictor variables was used and variables were gradually removed via backward selection (as explained for the local model).

Results

In all sites combined, data on a total of 146 seed trees was collected (WC=25, WE=25, SC=25, SE=25, and EC=21, EE=25), with 1642 recruits recorded within the 9 m radius. The recruits recorded represent minimum estimates as young/small recruits could have been missed in the field. All sectors of the neighborhood were surveyed for most plots, except for 10 plots (WC=4, EC=3, EE=2, SC=1).

Variation in recruit density across sites and regions

The density of recruits (recruits per m^2) showed high overall variation between sites and regions (Mean=0.058, SD=0.100, Figure 5). There was a tendency for higher densities in core sites compared to edge sites. The mean recruit density per site was highest in west core (0.109 ± 0.176 recruits/ m^2) and east core (0.099 ± 0.131 recruits/ m^2), while the lowest density was observed in south edge (0.034 ± 0.029 recruits/ m^2) and west edge (0.027 ± 0.036 recruits/ m^2). The south core had a mean density of 0.036 ± 0.036 recruits/ m^2 , which was slightly lower than the east edge (0.054 ± 0.067 recruits/ m^2).

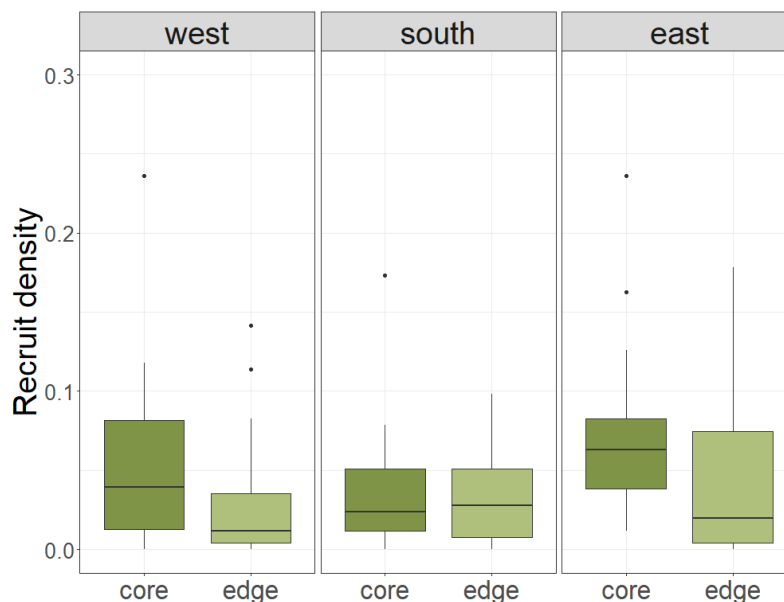


Figure 5. The density of recruits per m^2 for each site. The limit on the y-axis is set to 0.3 to better visualize differences between sites; four outliers above 0.3 (WC=0.79, 0.47, 0.31, EC=0.63) are included in the estimate, but not visualized in the plot.

The results of the regional GLM model (Table 3) showed that in the west region there were clearly fewer recruits in edge (-1.373, SE = 0.326, $p < 0.001$) compared to core. In the east region there were also fewer recruits in edge than core, but not as much of a difference between the sites as found for the west region. In the south region there was no difference in recruit density between edge and core, resulting in a highly significant interaction term for edge site*south region. This seems to be caused mainly by fewer recruits at core sites, compared to the east and west regions. Predicted values of recruit density is found in Figure 6.

Table 3. GLM results of the regional model showing the spatial differences in the effect of site (core and edge) and region (west, south, and east) on recruit density per m^2 . West core is used as reference level in the model.

| Variables | Estimate | Std. Error | Z value | P-value |
|------------------------|----------|------------|---------|------------|
| (Intercept) | -2.256 | 0.226 | -9.986 | <0.001 *** |
| edge sites | -1.373 | 0.326 | -4.215 | <0.001 *** |
| south region | -1.077 | 0.323 | -3.331 | <0.001 *** |
| east region | -0.088 | 0.334 | -0.262 | 0.793 |
| edge site*south region | 1.318 | 0.462 | 2.854 | 0.004 ** |
| edge site*east region | 0.777 | 0.468 | 1.660 | 0.097 |

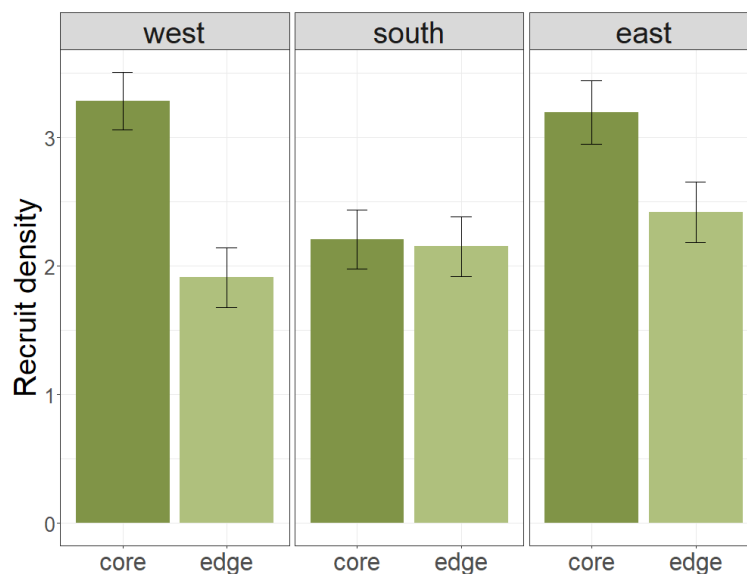


Figure 6. Predicted values of recruits per m^2 in each site based on the regional model using the interaction site*region as predictors.

GLM results of the local model

The results of the local model left a set of predictors which had a significant effect on the density of recruits (Table 4), while some were non-significant and consequently removed from the model (seedtree_age, neighbors, empetrum_hits, max_height_vegetation and org_mean). The interaction between birch density*birch stem was also rejected and these variables were therefore reduced to strictly additive effects. Overall, the model provided a noticeably poor fit, due to much unexplained variation. This was also shown by the predicted vs observed recruit density (see Appendix A).

Table 4. GLM results of the local model showing the effects of local site characteristics on recruit density.

| Variables | Estimate | Std.Error | Z value | P-value |
|-----------------------------|----------|-----------|---------|----------|
| (Intercept) | -2.600 | 0.408 | -6.375 | <0.001 |
| crown_mean | 0.140 | 0.063 | 2.232 | 0.026 * |
| graminoid hits | -0.025 | 0.011 | -2.232 | 0.026 * |
| moose pellets | 0.087 | 0.050 | 1.741 | 0.082 |
| reindeer/sheep pellets | -0.116 | 0.059 | -1.965 | 0.049 * |
| birch_mean_dbh | -0.009 | 0.004 | -2.022 | 0.043 * |
| birch_density (5-10 stems) | 0.074 | 0.301 | 0.245 | 0.807 |
| birch_density (10-25 stems) | -0.826 | 0.307 | -2.687 | 0.007 ** |
| birch_density (>25 stems) | -1.017 | 0.315 | -3.231 | 0.001 ** |

Seed tree and neighbor effects on recruit density

The age of seed trees did not have a significant effect on recruit density, but varied greatly between sites, where the seed trees were clearly older in core sites. Both core and edge sites of the south region had the oldest seed trees with the oldest belonging to core. The number of neighbors did not have a significant influence on recruit density. The core sites in all regions had a higher number of neighbors, indicating that core sites are denser and contain a higher number of potential seed sources. The number of neighbors were clearly higher in west and east core compared to south core which had a relatively low number of neighbors.

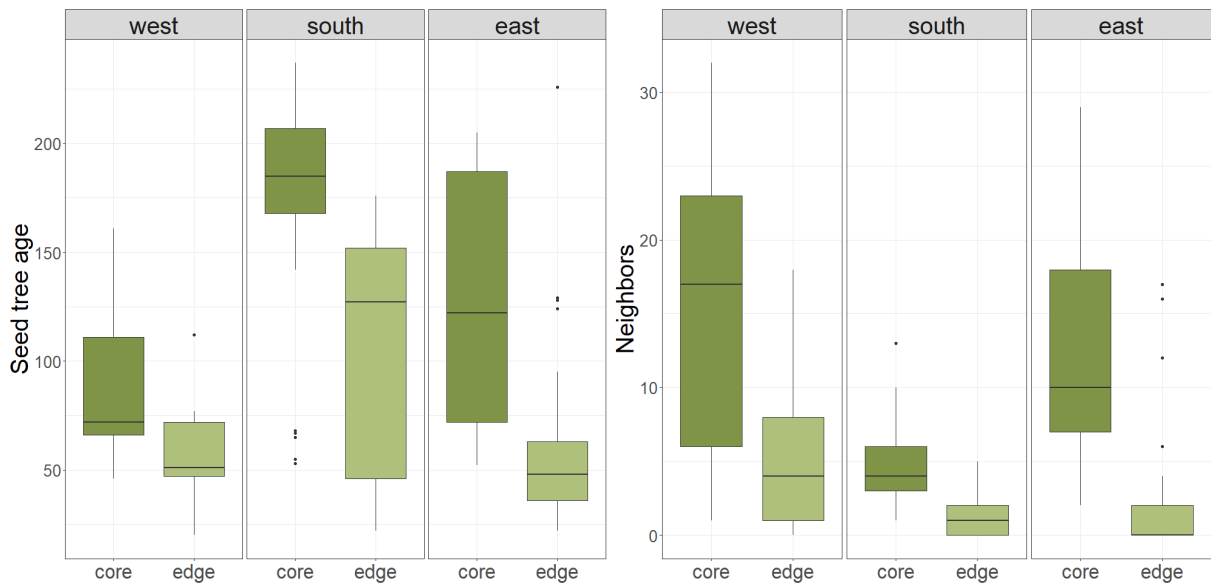


Figure 7. Age of seed trees in years (left), and the number of neighbors per plot (right) in each of the six sites

Crown diameter of the seed trees had a positive effect on recruit density (0.140, SE = 0.063, $p = 0.026$), suggesting that seed trees with wider tree crowns have higher recruit densities. Crown diameter showed a tendency to be larger in core sites compared to edge, with the exception of the west region, and was the largest among seed trees in south core (Figure 8). The predicted recruit density showed high uncertainty, indicated by wide confidence intervals, for the largest crowns.

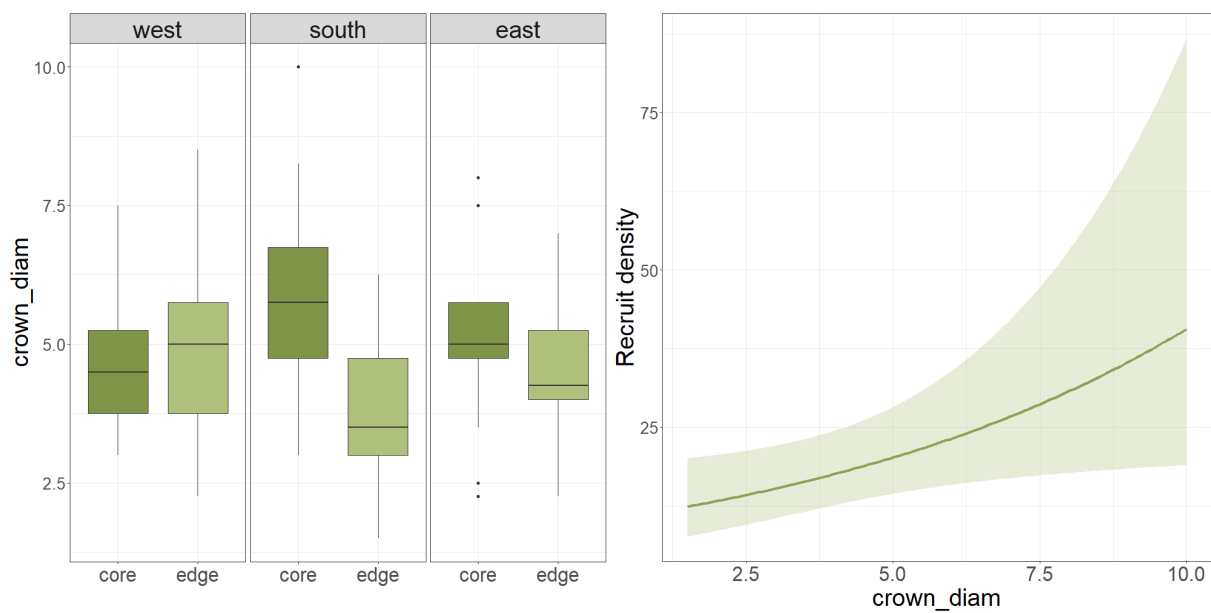


Figure 8. Crown diameter of seed trees within the six sites (left) and partial dependence plot showing the predicted values of recruit density according to crown diameter (right).

Ground vegetation and soil organic layer

Graminoid hits had a significant negative effect on recruit density (-0.025 , $SE = 0.011$, $p = 0.026$), indicating that areas with higher graminoid abundance have lower recruit densities of pine. However, partial dependence plots of the effect show large confidence intervals (Figure 11). Graminoid hits were near similar showing a generally low abundance of the species across the sites, apart from west edge which had nearly twice the abundance compared to the other sites (Figure 9). Strawberry hits and max vegetation height did not show significant effects on recruit density and was thus dropped from the final model. Strawberry hits tended to be higher in edge sites with plots at east edge generally having the highest abundance and also a relatively high amount of variation between plots. The pattern for organic layer showed somewhat of a similar pattern as that for strawberry, indicating that strawberry may proliferate on thicker organic soil layers.

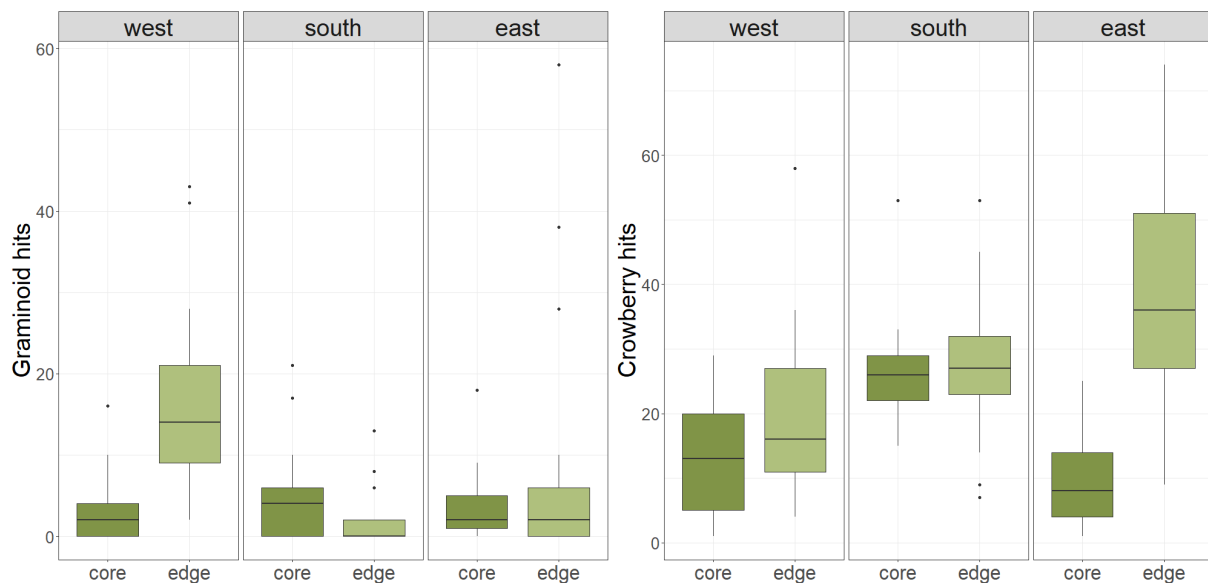


Figure 9. Hits of graminoids (left) and strawberry (right) recorded within the plots of each site.

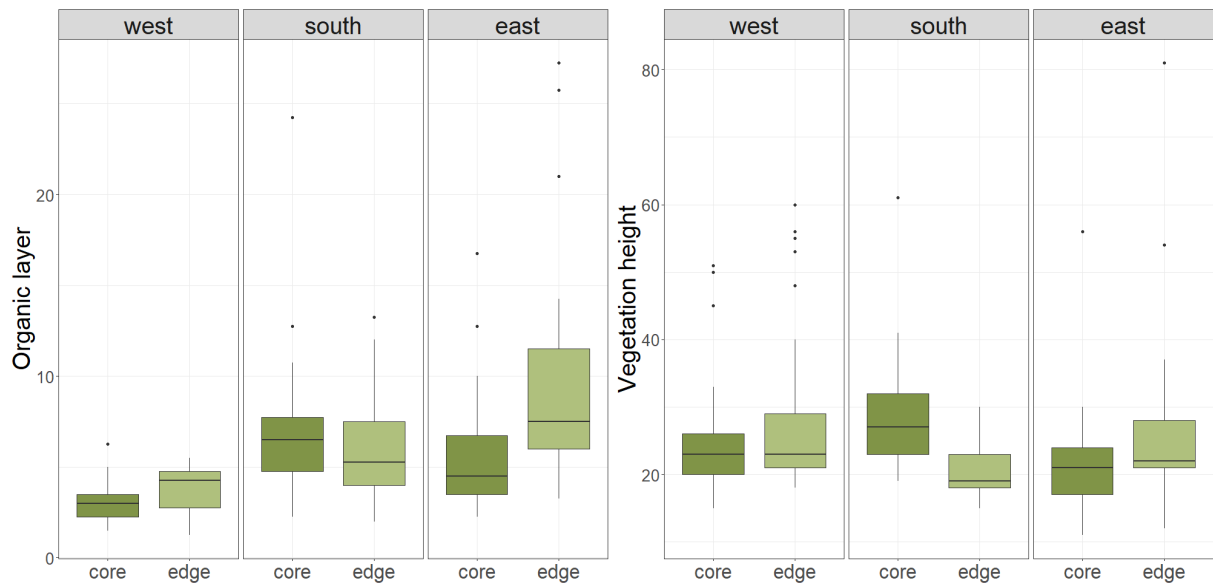


Figure 10. Organic layer (left) and max height vegetation (right) recorded within the plots of each site.

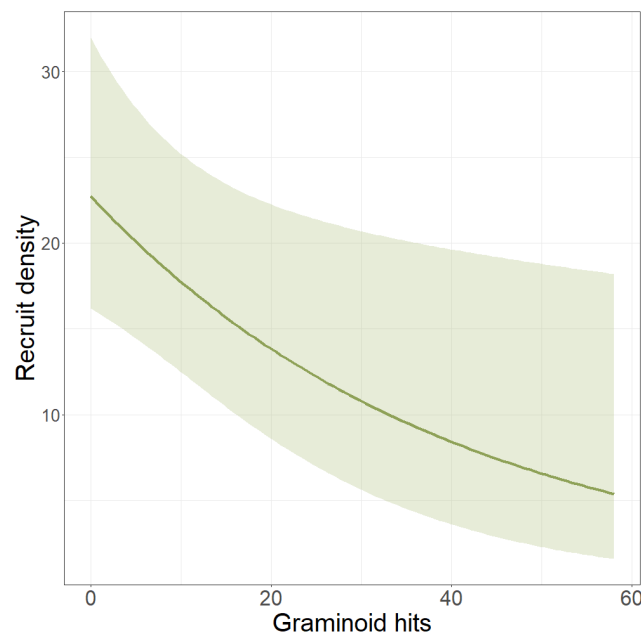


Figure 11. Partial dependence plot showing the effect of graminoid hits (as proxy for abundance) on recruit density per m^2 .

Effect of ungulate presence on recruit density.

Of the two pellet variables included in the model, reindeer/sheep pellets had a negative estimate (-0.116, SE = 0.059, $p = 0.049$), suggesting that areas with more reindeer/sheep presence have lower recruit densities. Moose pellets however, had a tendency for a positive

effect (0.087, SE = 0.050, p = 0.082), although this effect was not significant at the 0.05 level. Partial dependence plots of the two pellet groups contain large uncertainty indicated by the wide confidence intervals (Figure 12).

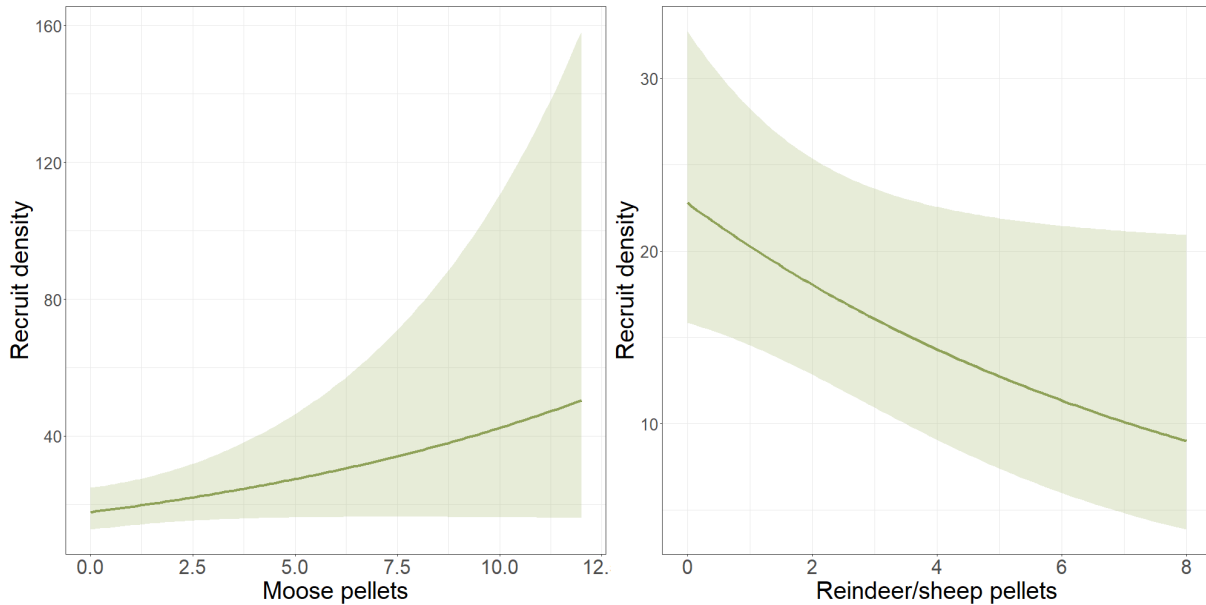


Figure 12. Predicted values of moose (left) and reindeer/sheep (right) pellets based on the local model.

There seemed to be a relatively higher presence of ungulates in the south region suggested by the higher pellet counts, particularly in the edge site (Figure 13). A relatively high number of reindeer/sheep pellets were also observed in the core site of the east region.

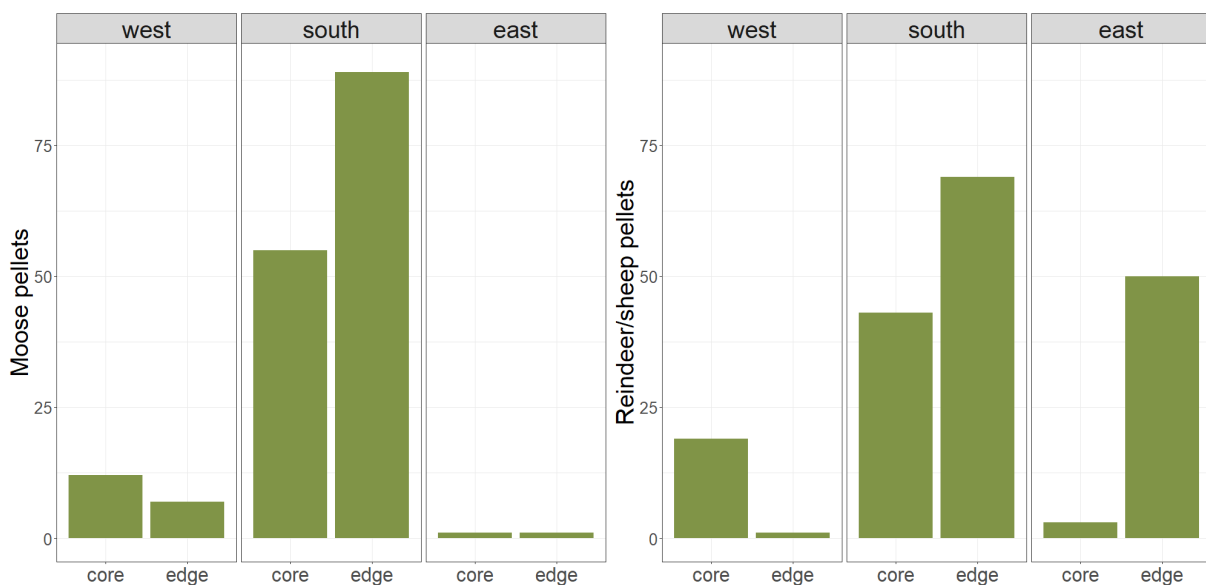


Figure 13: The total number of pellet groups from moose and reindeer/sheep recorded for each site.

Effect of birch on recruit density

The effect of birch density was significantly negative for the two highest levels of birch density, 10-25 stems (-0.826, SE = 0.307, $p = 0.007$), and > 25 stems (-1.017, SE = 0.315, $p = 0.001$), suggesting that plots with high birch density have lower recruit density. Birch stem diameter (measured at breast height) also had a negative estimate (-0.009, SE = 0.004, $p = 0.043$), indicating that areas with larger birch trees result in lower recruit densities. The interaction effect between these two predictors (birch density*birch_dbh) were dropped from the final model as it was non-significant.

There was considerable variation in birch density within each site (Figure 14). In particular, the south region had many plots found within the highest birch density category (>25) in the core, with the edge site tending to the same pattern. In the west region, the edge had a high proportion of sites in the third category (10-25), while the core had relatively few plots with high birch density, with most in the second category (5-10) and no plots belonging to the highest category. In the east region, plots were relatively evenly distributed among the categories, however, there was a higher number of plots in the second and third category for the core and edge site respectively. Figure 15 shows that the predicted values of recruit density for the two highest classes of birch density are roughly half of the two lower classes. However, the standard error of the two lower classes was large.

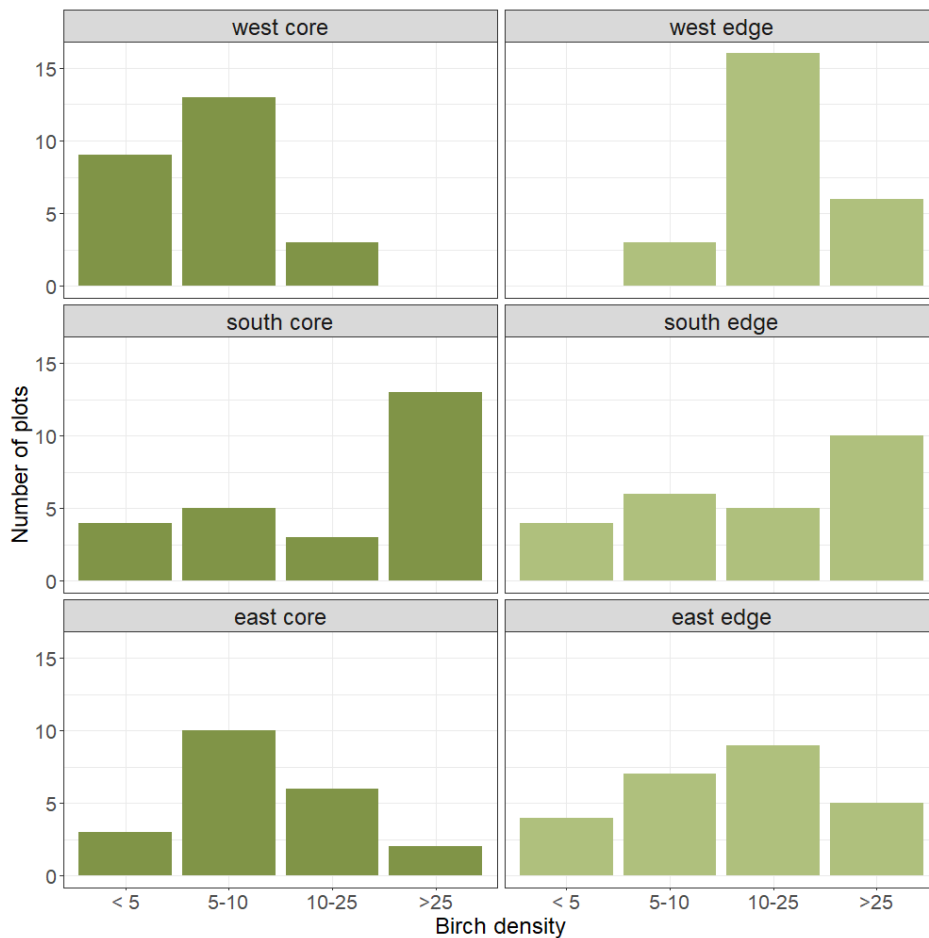


Figure 14. The number of plots per site found within each category of birch density (number of stems).

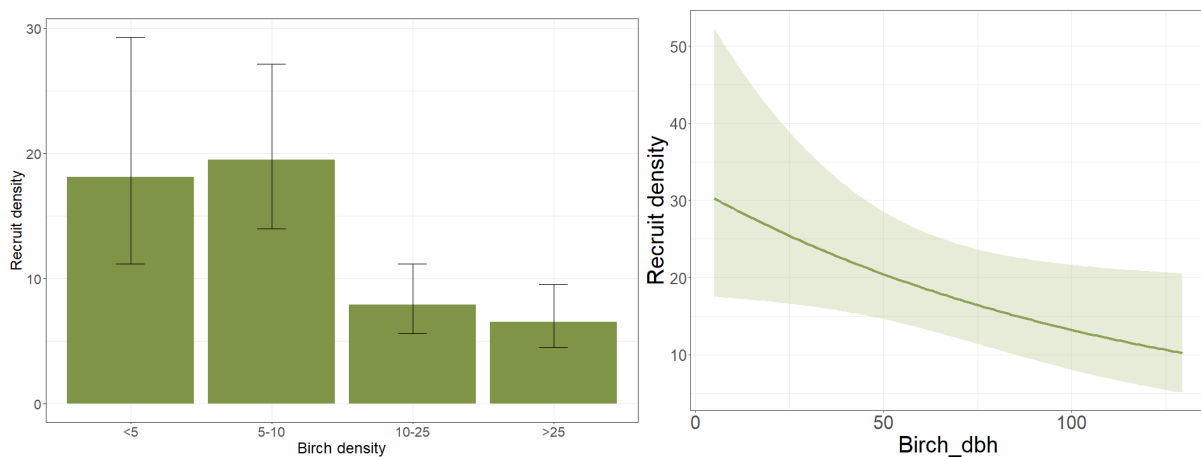


Figure 15. Predicted values of recruit density per m^2 for each category of birch density (left), and partial dependence plot of the effect of birch stem diameter (measured at BH) on recruit density.

Birch state, which contained categorical measures of birch mortality (with 10% intervals) was not included in the model, due to sites of high mortality not being represented in the data (see

table for each category of birch density and birch state in Appendix B). The mortality span of the birch was no more the 0-40% with relatively few plots (12) representing 40% mortality.

Distribution of recruits from the seed tree

Judging from the plotted density of recruits per distance (Figure 16), the truncated distance from the seed trees (9 m) appears to capture the distance of the highest recruit density; the density increases as you get further away from the seed tree, reaches a maximum density and is on a downward slope after 6-8 m distance.

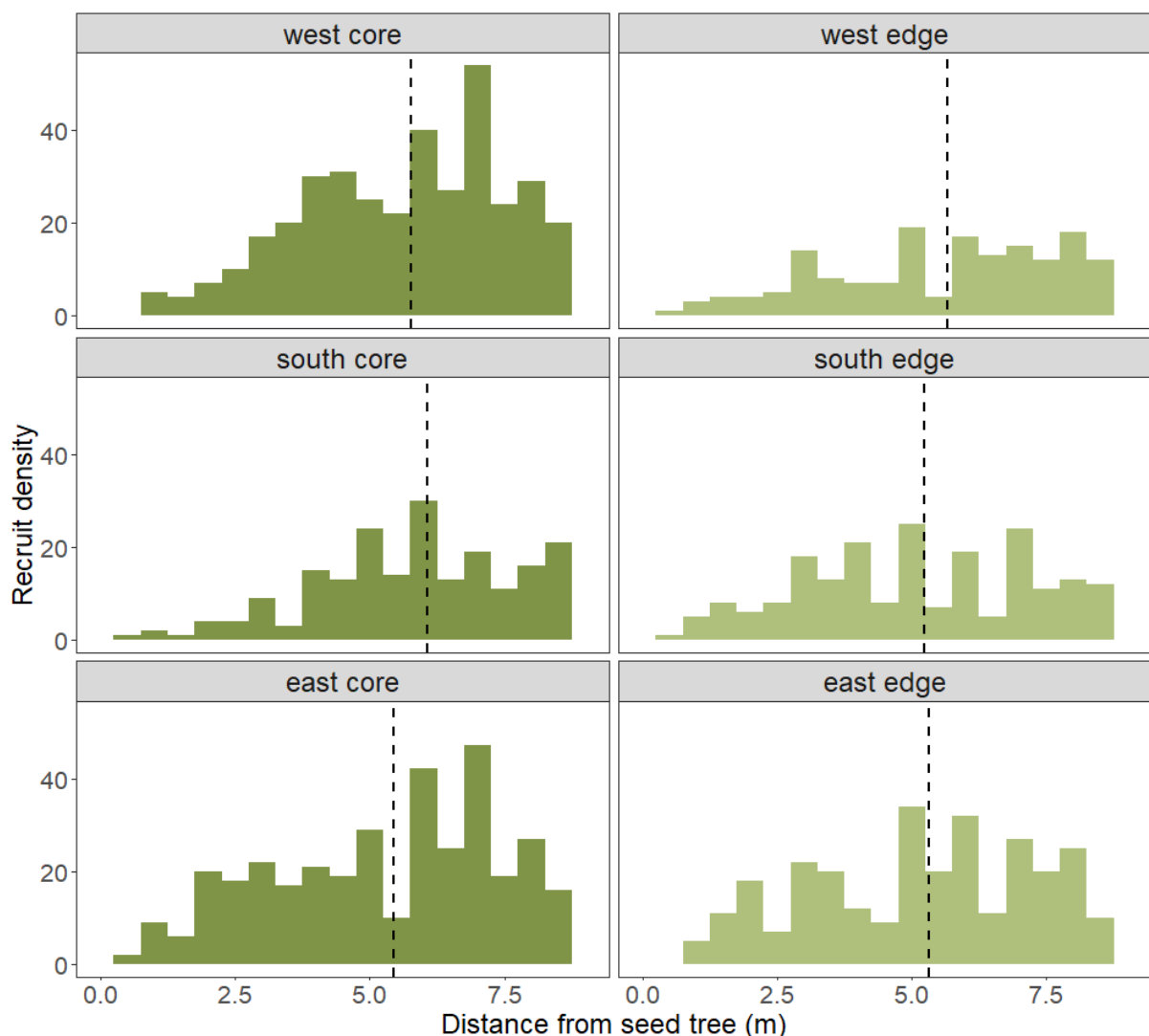


Figure 16. The distribution of recruits with distances from the seed tree (cutoff at 9 m). Dashed lines show the mean effective dispersal distance of recruits for each region and site: EC (mean=5.4m, SD=2.2), EE (mean=5.3, SD=2.1), SC (mean=6.1, SD=2.0), SE (mean=5.2, SD=2.2), WC (mean=5.8, SD=1.9), WE (mean=5.7, SD=2.2).

The backward stepwise regression on the distance model showed that none of the predictors had significant interaction with the factor variable circle. Ultimately all predictors were eliminated from the model leaving only the effect of the circle variable. Recruit density was lower for the two outer circles and significantly so for the outer circle (6-9 m, -0.680, SE = 0.158, $p < 0.001$), compared to the innermost circle (0-3 m) which was the reference level in the model. Thus, there was a clear distance-relationship even at the considerable short sampling distance of 9m considered in this study. This distance-relationship is visualized in Figure 17, showing the predicted values of recruit density for each concentric circle.

Table 5. GLM results of the distance model showing the single effect of distance (circle) on recruit density. The factor variable circle is defined as three concentric circles out from the seed tree, representing the intervals 0-3m (model reference), 3-6m and 6-9m.

| Variables | Estimate | Std. Error | Z value | P-value |
|-----------------|----------|------------|---------|------------|
| (Intercept) | -2.312 | 0.116 | -19.933 | <0.001 |
| Circle 2 (3-6m) | -0.150 | 0.158 | -0.953 | 0.341 |
| Circle 3 (6-9m) | -0.680 | 0.158 | -4.311 | <0.001 *** |

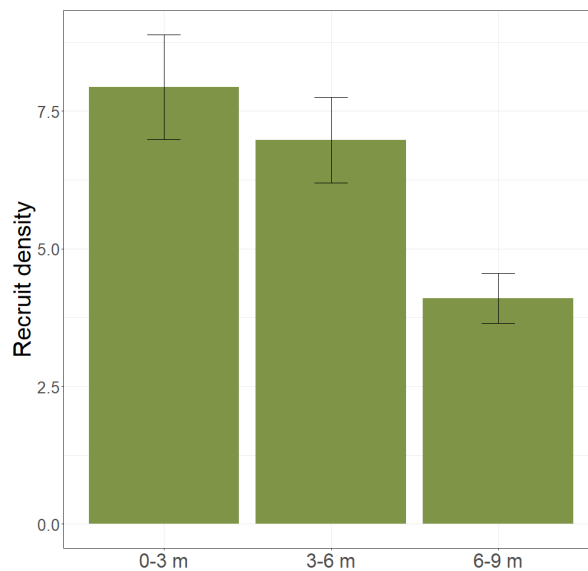


Figure 17. Predicted values of recruit density per m² for each concentric circle out from the seed tree.

Discussion

The purpose of this study was to analyze the factors which determine the density and distribution of Scots pine recruits across the northern distribution range in northern Norway.

The main results were the following: **1.** There was generally lower recruitment at the leading edge of the distribution range, although this was not the case for the south region. **2.** Recruit density was found to decrease rapidly with the distance from the seed tree, even at the relatively short sampling distance. **3.** Of the seed tree attributes, crown diameter was the only significant predictor, and positively influenced recruit density. **4.** The proxy for graminoid abundance was the single significant predictor among the vegetation and soil variables and had a negative effect on recruit density. **5.** Reindeer presence, as indicated by pellet density, negatively influenced recruit density, while moose presence showed a tendency for the opposite effect. **6.** Birch density and stem diameter negatively influenced recruit density. In the following sections, I discuss the ecological implications of these results and the potential mechanisms underlying the observed recruitment patterns between sites and regions.

Abiotic factors limiting recruitment of Scots pine

Climate change is generally believed to reduce the constraints of tree lines growing at their latitudinal and elevational margins, promoting the growth and recruitment of new trees (Körner 2021). This is owed to the fact that temperature and precipitation are critical drivers of plant distributions and drive the timing of important phenological events such as the initiation and breaking of seed dormancy and germination (Walck et al. 2011).

The edge of the west region clearly had fewer recruits compared to the core. In the east region there was also fewer recruits in edge than core, but this difference was not as apparent as found for the west region. Edge sites selected in this study were pushed northwards as far as possible in the three regions, while simultaneously allowing stands or individual trees to be located within a generally small area. Evidently, the edge sites not only represent pines growing at slightly higher latitudes, but also in relatively more open, low-density pine stands compared to the denser core sites. Both these factors may influence climatic conditions that affect growth and ultimately the recruitment of new trees.

The difference in recruit density between the edge and core of the south region did not display the same pattern as for the west and east regions. In the south region, recruit density

was nearly identical in the edge and core, mainly explained by fewer recruits in the core site, compared to regions east and west. Although the location of the south region lies within a lower latitude, the more continental location of this region provides a colder climate relative to the other two regions. The sites of the south region show similar mean temperatures in the month of January, that are generally 2 °C colder than sites in the east and west (and ~ 4 °C colder compared to west edge). A greater contrast between sites is evident in the west region, which displays a gradient of a milder oceanic climate in the edge site, and a colder continental climate in the core. While cold periods are necessary for development of seeds and serves to break dormancy which enables growth in the spring, extreme cold, such as severe frost and prolonged cold periods can delay the timing of important phenological events such as bud burst and maturation of seeds (Kramer 2012). Extended cold periods also result in soil taking longer to thaw which may limit the trees' ability to take up water and nutrients, ultimately impacting recruitment.

Tough climatic conditions can be further accentuated in low-density stands with greater gaps between trees (Rose et al. 2020). Trees that grow in dense stands with a more closed canopy provide a gentler microclimate with more stable temperatures, sheltering against wind and snow accumulation (Renaud et al. 2011). Such reduced climatic stress may support seedling recruitment and be especially important for trees growing beyond their optimum. Although the number of neighbors is not a definitive measure of stand density, fewer neighbors may suggest lower density stands with greater gaps between trees. The number of neighbors was relatively low for both sites in the south region, suggesting that a contrast in stand density may be less pronounced in this region. Contrary, the west and east region showed noticeably higher number of neighbors in the core sites compared to edge. The more severe climatic stressors that are found outside denser stands, can be demonstrated by the abrupt boundaries of tree lines, where few individual trees are able to exist beyond the edge of the boundary (Harsch and Bader 2011). For some tree species, these discontinuous spatial patterns of tree lines have been linked to seed limitation (Cuevas 2000, Sirois 2000), suggesting a lower production of seeds outside a closed canopy. It is difficult, however, to determine whether low recruitment outside denser stands is due to a low seed supply or due to the harsher abiotic factors limiting germination and establishment in these areas. Neighbors were not a significant predictor in this study; hence, a higher number of potential seed sources may not necessarily produce higher recruitment. In fact, the concept of density-dependent mortality proposes that dense pine stands compete more intensely for resources (water, nutrients), which can lead to lower growth and survival among individuals, especially in young forests (Szmyt and Tarasiuk 2018).

Differences in recruit density among sites and regions could be further explained by differences in seed tree elevations, which also affect climatic conditions. Higher elevations can insinuate tougher microclimatic conditions, such as cooler temperatures, stronger winds, or potential changes in precipitation patterns. These conditions may contribute to lower recruitment, unfavorable for young trees to grow and establish. The elevations of seed trees were similar in the core and edge of the south region, which were both located at higher elevations compared to seed trees in the east and west regions. In the east, seed trees in the edge site were generally located at higher elevations compared to the core, demonstrating a possible negative effect of elevation on recruit density between the sites. Still, the west region shows the opposite pattern with a higher elevation edge site compared to the core.

The role of biotic interactions on recruitment

While abiotic factors is suggested to be the controlling determinant of range limits under harsh conditions, recruitment potential also depend on biotic interactions (Neuschulz et al. 2018). In northern Norway, reindeer and moose are two common herbivores which can influence recruitment of Scots pine directly through physical contact or consumption of pine (Heikkilä and Härkönen 1996), or indirectly by modifying soil biota and plant dominance hierarchies in the environment (Stark et al. 2000, Bråthen and Oksanen 2001). Reindeer in northern Norway is semi-domesticated through husbandry, while moose is free-ranging and has over the recent last decades become more common across Finnmark county. The clearly higher pellet counts of both moose and reindeer in the south region and in the east edge, indicate a high presence of these species, compared to the other sites and regions. Pellet counts should not be taken as a direct measure of interference with pine, as the number of pellets observed in the field could depend on the vegetation composition, height of the understory and the forest structure. In addition, ground conditions, patterns in precipitation, and sun exposure influence pellet decomposition rates and the potential for accumulated pellets over an uncertain time-period, making it difficult to interpret the results solely based on pellet counts. However, the striking difference in pellets counts between regions is likely to indicate differences in ungulate habitat use. The models revealed that reindeer presence had a negative influence on recruit density. Previous studies conducted in northern Fennoscandia support a negative effect of reindeer on pine regeneration, perhaps most importantly through mechanical damage in young seedlings in the form of branch breakage. Additionally, a reduction in lichen by reindeer can invite competition from other plants (Den Herder et al. 2003). Moose presence showed a tendency

for a positive effect on recruit density. This contradicts a general consensus of moose as limiting, commonly feeding on pine during winter, including the shoots, needles, and bark, as well as young cones (Bergström and Hjeljord 1987). Yet, the effect of moose was not significant and showed high uncertainty.

Insect outbreaks are another key disturbance agent in the northern boreal ecosystem which could influence recruitment of Scots pine. During population outbreaks, geometrid moth species inflict extensive damage to the birch forest which can be synchronized across large geographical regions (Jepsen et al. 2008, Vindstad et al. 2019b). Between 2002-2008, there were significant outbreaks of the *O. brumata* and the *E. autumnata* in northern Norway (Vindstad et al. 2019a). This resulted in severe defoliation affecting roughly one third of the birch forest in northern Fennoscandia for one or more years (Jepsen et al. 2009). Outbreak records suggest that *O. brumata* has expanded its range further north and east, while *E. autumnata* has moved into colder, more continental regions (Jepsen et al. 2008). These range expansions coincide with higher winter temperatures and a greater phenological match between budburst in birch and the egg hatching, which may intensify the negative impact on the birch (Jepsen et al. 2011). In this study, both high density and a thicker stem diameters of birch negatively influenced recruit density of pine. This points to birch as a meaningful competitor and implies that outbreaks targeting the birch forest, which may support the recruitment and subsequent range expansion of Scots pine. While sites with high moth-induced birch mortality were not represented in the data, it is reasonable to believe that outbreak-induced damage and mortality sustained by birch, may lower its density and ability to compete with Scots pine. A study which focuses on pine recruitment under varying degrees of birch mortality may provide additional evidence for this claim. Both the core and edge of the south region have similar distribution of birch density, with most plots within the highest density class. Yet, the other two regions show a tendency for higher birch density in edge sites compared to core. This further supports the relatively low recruitment found for the south region, and the contrast between core and edge in the east and west region.

The effects of moth outbreaks extend beyond the impacts it has on birch, making predictions on the effect on Scots pine recruitment more difficult. Evidence of shifts in understory composition in outbreak-affected regions is one such effect, where dominance of crowberry is surpassed by the graminoid *A. flexuosa* (Jepsen et al. 2013). The vegetation cover and composition is an important limitation to the growth and survival of tree seedlings (Picon-Cochard et al. 2006, Wagner and Robinson 2006). An experimental study conducted on former agricultural lands in southern Finland found that percent vegetation cover negatively affects the

mortality, basal diameter, height and volume of Scots pine (Jylhä and Hytönen 2006). Although crowberry is known for its inhibitory effects on germination, growth and establishment of neighboring plants (Odén et al. 1992, Tybirk et al. 2000), only graminoids significantly affected recruit density in this study. Graminoids are fast growing species which compete against pine for the same resources. An intact cover of graminoids have been found to severely reduce radiation and water supply necessary for pine seedlings to emerge (Picon-Cochard et al. 2006). Linked to the increase in *A. flexuosa*, numerical responses in rodents has also been reported in moth-affected habitats (Jepsen et al. 2013). A higher abundance of rodents in response to graminoid abundance could lead to higher seed predation on pine (Ellingsen et al. 2017). However, the increase in rodents may simultaneously help to reduce graminoids and other vegetation competing with Scots pine (Moorhead et al. 2017) The effects of moth-outbreaks demonstrates that while a competitive advantage may be gained by Scots pine from a weakened birch forest, there may be less obvious and cascading impacts affecting ecosystem functioning in this region.

In the current study, there was large amounts of unexplained variation in the data, which points to the complex and intricate factors that explain recruitment success of Scots pine. This was despite a comprehensive sampling design which tried to provide representative measures of the local environment within a relatively small plot (~250 m²). Several studies, have highlighted the importance of microsites on recruitment success (McCarthy and Facelli 1990, Ohlson and Zackrisson 1992, Hörnberg et al. 1997). Microsites are fine-scale (< 0.1 m²) structures which display distinct variation in topography, soil properties, vegetation cover, snow accumulation patterns or wind conditions. Small-scale perturbations such as fallen trees, rodent runways, trampling by animals are factors which, individually and combined, make up unique microsites which may be more or less suitable for seedlings (Kuuluvainen 1994). Including these fine-scaled heterogeneities, preferably in interaction with the microclimate, may help to sort out the factors which determine recruitment patterns among sites.

Recruit distribution in relation to the seed tree

While animals can move across geographical regions to find better suited habitats, range expansion in plants generally takes longer due to being immobile (Corlett and Westcott 2013). This is particularly true for trees which have an extended life cycle, where several years are necessary in order to reach maturity and produce seeds. Seed dispersal by plants is typically described as a distribution where the abundance of established seeds decreases rapidly with the

distance to the seed source (Lambert et al. 2005). Recruitment that is limited to short dispersal distances from the seed tree indicates a limited potential for range expansion. When seedlings are primarily dispersed near the seed tree, it suggests a clustered distribution pattern and fewer opportunities for establishing populations in distant regions. Here, it is demonstrated that despite a truncated sampling within a relatively short 9 m distance from the seed tree (the assumed source), the distance was still sufficient to find evidence of higher recruitment closer to the source. This may suggest a recruitment pattern with a localized distribution of seedlings in close proximity to existing trees and further indicate a profound influence of the seed tree on recruit distribution.

Kuuluvainen and Pukkala (1989) describe how the presence of the seed tree can affect nutrients, water and solar radiation within its proximity through their roots, crown and stem spatial influences. In this study, larger crowns were found to have a positive effect on recruit density. The crown of a tree can block light and water and thus alter soil temperatures, but at the same time add nutrients to the ground below via litter and decrease soil evaporation due to shading (Kuuluvainen and Pukkala 1989). These effects on resources can influence seedlings directly, or indirectly by shaping the ground composition. However, the model on recruit distance revealed no significant interactions between the concentric circle and vegetation and soil variables.

This study does not address long distance dispersal, which are more rare and random, but nevertheless an important part of a species genetic structure and rate of expansion which cannot be explained by short distance dispersal alone (Cain et al. 2000). Range expansion relies on seeds being dispersed over greater distances, allowing seedlings to colonize new areas and move beyond its distribution range. Studies of long-distance dispersal are often underrepresented due to being difficult to measure. Still, some reports have been made on the potential evolutionary significance of long-distance wind dispersal in Scots pine (Lindgren et al. 1995, Robledo-Arnuncio 2011). Most notably, a study conducted on the pollen transfer in Finnish Scots pine, reported wind-dispersal of several hundred kilometers (Varis et al. 2009). Incorporating both short and long-distance dispersal could provide a more complete understanding of the mechanism behind range expansion and the expected rate during climate change.

Recruitment potential under climate change

Most studies predict that populations in the north will increase their reproduction and growth in response to increased temperatures (Rehfeldt et al. 2002, Matías and Jump 2012, Kausrud et al. 2022). Future climate scenarios project the highest warming to occur in the interior parts of northern Norway, and includes an increase in annual precipitation and rainfall intensity (Hanssen-Bauer et al. 2017). The most pronounced temperature increase is projected during winter, resulting in delayed snow accumulation and earlier snowmelt (Vikhamar-Schuler et al. 2010), effectively giving shorter periods of snow. In recent years, permafrost has thawed and disappeared in some parts of Norway, and model projections under the A1B emission scenario predict that most areas with permafrost on the Finnmarksvidda plateau will have thawed within 2050 (Hanssen-Bauer et al. 2017). This could potentially enable more ground suitable for seedling establishment and aid a northward expansion of Scots pine into the tundra-ecotone. It is worth noting, however, that the west edge considered in this study, is characterized by milder winter temperatures and higher precipitation compared to other sites. This climate pattern aligns with the relatively warmer and wetter conditions often associated with climate change. Surprisingly, despite these assumingly more favorable conditions, the west edge had the lowest mean recruitment density among the sites.

Impact assessment of climate change on recruitment require a focus not only on changes in average conditions, but also the associated increase in variation and occurrence of extreme events (Kivinen et al. 2017). Soluble sugars which accumulate in conifers during late summer and autumn as a defense against the cold temperatures. An increase in ‘rain-on-snow’ events and warm spells during winter can lead to frequent thaw–freeze cycles, and compacted snow which can damage and deplete the defenses against cold in young pines especially (Ögren et al. 1997). An increase in these climatic extremes may be extra critical at the leading edge of the distribution, which are more open and provide limited shelter from these conditions. There is therefore the potential for hostile conditions to counteract the otherwise positive effects of warming on tree recruitment (Domisch et al. 2018).

Conclusion

In conclusion, warming can be expected to facilitate the recruitment and expansion of Scots pine, possibly aided by reduced competition with birch due to moth outbreaks. However, the rate of expansion may be limited by short dispersal distances from the seed tree, and extreme

weather events related to climate change. The large amount of unexplained variation in the models signifies the complex influences on tree recruitment. Future studies should consider the influences of microclimate, biotic interactions, and microsites, to make robust forecasts of climate change effects on tree recruitment.

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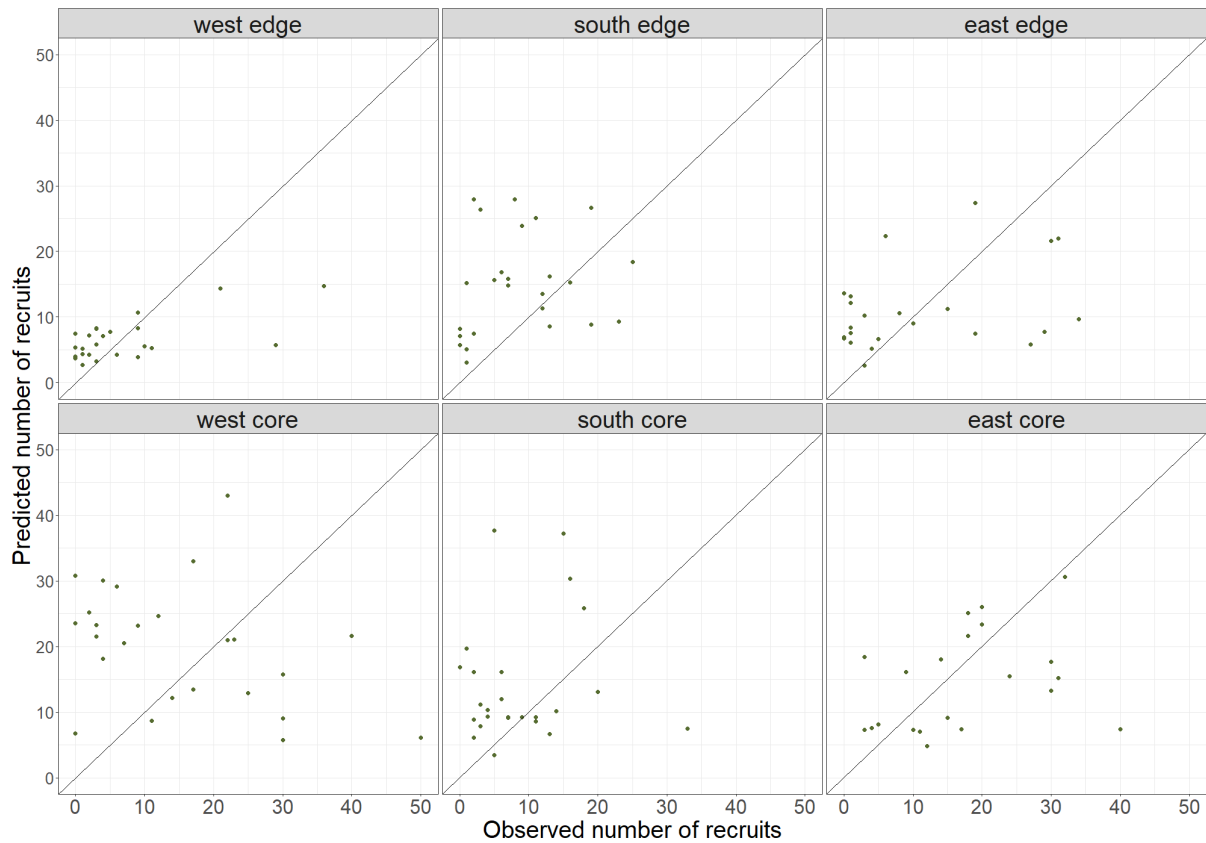
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Appendices

Appendix A:

Predicted vs observed values of the number of recruits for each site. Based on the local (environmental) GLM model:



Appendix B:

Table showing the number of represented sites under each category of birch density and birch state.

| | 0 % | 10 % | 20 % | 30 % | 40 % |
|-------------|-----|------|------|------|------|
| < 5 stems | 4 | 3 | 4 | 6 | 7 |
| 5-10 stems | 3 | 17 | 10 | 10 | 4 |
| 10-25 stems | 2 | 18 | 10 | 11 | 1 |
| > 25 stems | 11 | 23 | 2 | 0 | 0 |



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