Norwegian University
of Life Sciences

Distribution, age and growth dynamics of Scots pine recruits on its northern distributional limit in Norway

Giacomo Favero

Master in Ecology

Preface and acknowledgements

Abstract

Growth and age structures of Scots pine (*Pinus sylvestris* L.) at its northern distribution are influenced by both regional climate and microsite conditions. While large-scale trends for stand regeneration and annual growth are known to be tightly related to summer temperatures and precipitation, these may not always reflect the local responses. Scots pine recruits were sampled in three locations along the northern distributional limit in Nort-East Norway in August 2022. The locations represent the three approximate positions of East, South and West of the distribution limit. I then compared the age structures and growth between a Core site in forest stands and an Edge site at the distributional limit of each location. Ages where significantly different between the different locations and the Core and Edge site for each. Four sites had a multimodal age structure typical of a periodical recruitment success, while two had a unimodal distribution. A GLMM revealed how the ring width in the first 10 years after establishment did not differ significantly between recruits from different locations or within the East and South sites. It however resulted significantly higher for the Edge site within the East location. Vertical growth was surprisingly higher in all Edge sites. With both radial and vertical growth showing higher values in the Edge sites, the results suggest that variations at microscale might be more important than regional climate on the regeneration and growth rates.

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Introduction

The global average temperature has increased of 1.09 °C in comparison to the reference period 1850-1900 (IPCC, 2022). Even under the most conservative scenario concerning greenhouse emissions, the global mean is expected to surpass the 1.5 °C threshold in the near future (by 2040). The abiotic effects of warming in the Northern hemisphere are widespread and can be seen as a reduction in snow cover extent, a sea ice decrease in both extent and seasonal duration, and changes in the soil temperature and nutrient cycling (Post et al., 2009; Screen & Simmonds, 2010). Researchers already confirm the effects of global warming on the northern ecosystem composition and functioning, predicting changes in the future as well (Post et al., 2009; Shiyatov et al., 2007). Furthermore, changes in the northernmost areas occur approximately two to four times as fast than the rest of the globe, adding pressure to the arctic and subarctic ecosystems (Rantanen et al., 2022). One of the most notable effects of a warming climate is distributional range shifts of several species, with expansion to higher altitudes and latitudes (Chen et al., 2011). These shifts seems to be mainly the result of changes in biotic interactions as consequences of abiotic condition modification such as increased summer temperatures (Freeman et al., 2018).

The area of Fennoscandia is experiencing milder winters (IPCC, 2022), with reduced snow cover and shortened snow-cover period. The increase of degrees days, the growing degree day sum in the growing season and increasing precipitation are affecting the plant community (Førland et al., 2004). This is driving a termophilisation of the tundra flora, with warm adapted species replacing cold adapted species, resulting in increased proportion and cover of boreal and woody species (Elmendorf et al., 2015; Gottfried et al., 2012). At the same time, the higher occurrence of winter melts (Vikhamar-Schuler et al., 2016) and the decrease of extreme cold events could cause freeze damage and modified herbivory patterns (Ammunét et al., 2012) which may counteract the climate-driven woody biomass increase. An example of this is the dynamics of geometrid moth outbreaks, which can severely damage deciduous/shrubby forest through defoliation (Jepsen et al., 2008; Karlsen et al., 2013; Vindstad et al., 2018) The predictions for the future are hence not clear about the overall response of the plant community.

The temperature increase and the changes in the phenology are expected to have consequences on tree recruit establishment and stand regeneration (Körner, 2007). And while on a macroclimatic scale temperature are increasing, the opposite may also be true locally. The impact of microclimatic scale, with possible stable or decreasing trends and specific topoclimatic conditions, complicates modelling of global responses (Körner, 2007). Despite temperature increase can explain some of the variation of

stand densification, other factors can have direct or indirect effects. The overall response can modified by precipitation (Bekker, 2005), cold-induced photoinhibition (Danby & Hik, 2007), disturbance (Cullen et al., 2001), plant-plant interactions (Wang et al., 2006) and plant-herbivore interactions (Bråten et al., 2017).

The Scandinavian peninsula is mainly occupied by the boreal forest, with strong presence of pine (*Pinus sylvestris*), birch (*Betula pubescens*), and spruce (*Picea abies*). Holtmeier (2011), revealed how the expansion of Scots pine in northern Finland seemed to be result of either establishment during a particularly favourable climatic period or microsite facilitation. The establishment of pine in the region is the result of the balance between viable seed production and transportation and the climatic/microsite conditions.

 The long-range expansion of pine stands is hindered by the physical properties of seeds. Heavier seeds are directly correlated with positive establishment success, but are less likely to be transported over long distances by wind (Sveinbjörnsson et al., 1996). As a result, a high number of successful recruits will be situated in the proximity of the tree which released the seed. Pine stand regeneration is directly dependent on local viable seed production, which can be positively linked with summer temperature increase (Kullman, 2007). In combination, the low dispersion of viable seeds and the higher production during warm years, leads to higher density pine recruitment. This calls into play other variables regarding the growth potentials of recruits, which will be affected by the seed tree as for nutrient and water availability, and solar radiation. Scots pine recruits can affect the ground layer vegetation, by hindering species not adapted to poorer soils (annual grasses and herbs), allowing instead the thriving of lower nutrient-requiring vegetation (mosses). The opposite effect is also true, as growth can be severely affected by nutrient requiring annual grasses and herbs (Kuuluvainen & Pukkala, 1989). This is also the case for interactions beyond pure resource competition. For example, the common low-growing shrub *Empetrum nigrum* can heavily hinder seed germination and growth through allelopathy (Nilsson & Zackrisson, 1992). The study by Hörnberg et al. (1997) shows how different ground layers can affect the recruitment of Norway spruce, where different bryophyte species could hinder settlement success, mainly by recruit smothering. Overall soil richness, surrounding ground species and microsite relief seem to be determining factors in recruit recruitment and growth (Holtmeier, 2011; Kuuluvainen & Pukkala, 1989).

In the norther limit of pine distribution, the growth of a recruit can be heavily affected by precipitation regimes and temperatures. Scots pine recruits showed particular predilection for high temperatures and

moisture but high sensibility to desiccation (Gunnarsson & Rydin, 1998). Vertical growth can be mainly influenced by air temperature, as trees benefit from reduced vertical growth and increased radial development in lower air temperatures. These adaptations allow for more favourable ground temperature and protection from atmospheric damage (Körner, 2012). Precipitation and summer temperatures are the most sensitive variables related to tree ring width responses. Summer temperature variation can be the most relevant factor, positively affecting the ring growth at high latitude sites (>65 ˚ N). Tree ring widths resulted instead more sensitive to precipitation with the decrease in latitude, so that the main effect on growth shifts to moisture levels at lower latitudes. This is especially true in Scandinavia, where due to relatively mild winters compared to other parts of the boreal forest at similar latitudes, the effect of winter temperatures seems rather low (Hellmann et al., 2016).

The large-scale influence of climate on the growth and age distribution of Scots pine is acknowledged, with warmer temperatures and increased precipitation inducing northbound expansion of the distributional range and densification of established stand. But the high heterogeneity of response to climate makes it necessary to research on a fine scale. This allows the observation to account for regional differences and site-specific conditions. With the aim of better understanding how pine recruits respond to climate at the distributional limit, I address the contrast between recruits in established stands and recruits in the leading edge of distributional range by analysing the age distribution and growth patterns in the light of local climatic and ground vegetation conditions. This contrast can be explored in the North-East part of Norway, which coincides with the northernmost edge of the European boreal forest distribution (Matías & Jump, 2012) , and borders with the subarctic deciduous forest and tundra. For the scope, three locations were selected in the Troms and Finnmark County (Norway), namely East, South and West, indicating the approximate directions of the current distribution. Two sites were then investigated within each region: a site well within the distributional range of Scots pine, and one site at its distributional edge, at the limit with the birch-dominated forest-tundra ecotone. Seed trees were selected as plot units, within which Scots pine recruits were measured and harvested for age and growth determination. The possible expansion of Scots pine in the region could indicate a possible advantage of conifer species in the light of the recent warming, with repercussions on the broadleaf community typical of the area and cause important modifications to the local landscape. This would have profound effects on various factors such as wind and snow patterns, soil parameters and nutrient cycling (Bekker, 2005).

Research questions

The study focuses on the following questions:

1. What is the age distribution of the Scots pine recruits in the east, south and west locations? Is there any contrast between the Core and Edge site withing each location?
2. Is there any period where the recruit establishment was most or least successful, and if yes, can it be correlated with climatic conditions?
3. Is there any contrast in the growth pattern of the recruits in the different regions and their Core and Edge sites? And can these differences, if any, be related to the local vegetation and characteristics?

What I expect from the data is to show a younger population in Edge sites rather than in the Core sites, where we expect an older and more dense community. There is the possibility that the settlement year in edge zones might be more hindered by less warm periods, while a lower effect is expected in Core areas. The same is valid for growth patterns: tree ring analysis should show slower growth in the Edges. This meaning that overall, the expectation is for a more visible difference in both recruitment spurs and radial growth between more and less favourable climatic periods. Finally, I anticipate a possibly minor effect of the dwarf shrub *Empetrum nigrum* on the number of recruit and on their growth.

Methods

Study area

The study was carried out in the Troms and Finnmark County, in northern Norway. The region has an average temperature of 11°C in July and -12 °C in January and average precipitation of 730mm/year (Norwegian Meteorological Institute, average for the period 1961-2019). The inland area of Finnmark has broader seasonal temperature oscillations and a lower precipitation level. This makes it more suitable for more continental biomes, marking the northern limit for the boreal forest which leaves the place to a low-arctic tundra typical vegetation. The region chosen for the study is crossed the by the edge of the northern natural distribution of the Scots pine and is characterized by a strong presence of mountain birch (*Betula pubescens* var. *pumila*) which represent the majority of the canopy cover, with markedly lower incidence of rowan (*Sorbus aucuparia* L.) and aspen (*Populus tremula L.*). The area has, in recent years, suffered from heavy defoliation from range expanding geometrid moths (Jepsen et al., 2008). The area is rich in grazers such as moose (*Alces alces*) and semi domestic reindeer (*Rangifer tarandus*) which can hinder the settlement and growth of Scots pine recruits by browsing. As a result of the rugged landscape and deep indentation of sea stretches which mitigate the otherwise adverse climatic conditions of similar latitudes, the acidic and organic rich soil in the region is not subjected to continuous frost. The absence of permafrost allows for the northbound spread of boreal species. (Bandekar et al., 2020; Centre et al., 2010; Harris et al., 2009).

Study design

The study area was located in NE Norway at the northern edge of the current distribution of Scots pine. The area was then divided into 3 regions representing the approximate direction of the sites, namely East, South and West (hereafter "locations"). The locations were in turn divided into 2 sites each: a Core site and an Edge site (hereafter "sites"). The Core sites were located well within the distribution of the Scots pine, while the Edge sites were located on the edge of the northern distribution. These six locations (Figure 1) were firstly determined in an approximate way using data on the current registered individuals of Scots pine (artsdatabanken, 2022), Google street view and Google Earth. An aerial survey with a fixed wing small aircraft was conducted in the spring of 2022 to assess the presence of a sufficiently large number of pines in the West and South locations. Prior knowledge of the East location by the supervisors was deemed sufficient to assure a sufficient pool of pine trees. The timing of the aerial survey was planned to take advantage of the snow cover and lack of leaves in birch so to easily

identify pine individuals. All the final decisions regarding the study areas were done in the field after inspection of the area, with attention on the avoidance of clear signs of logging activity and keeping good distance from roads and tracks.

Figure 1 Map of the study area, showing the location of the 6 study sites in the Finnmark area. The grey shade represents the approximate northern distribution of Scots pine according to Caudullo et al. (2017)

Figure 2 Map showing the detailed location of the single seed trees sampled in each study site.
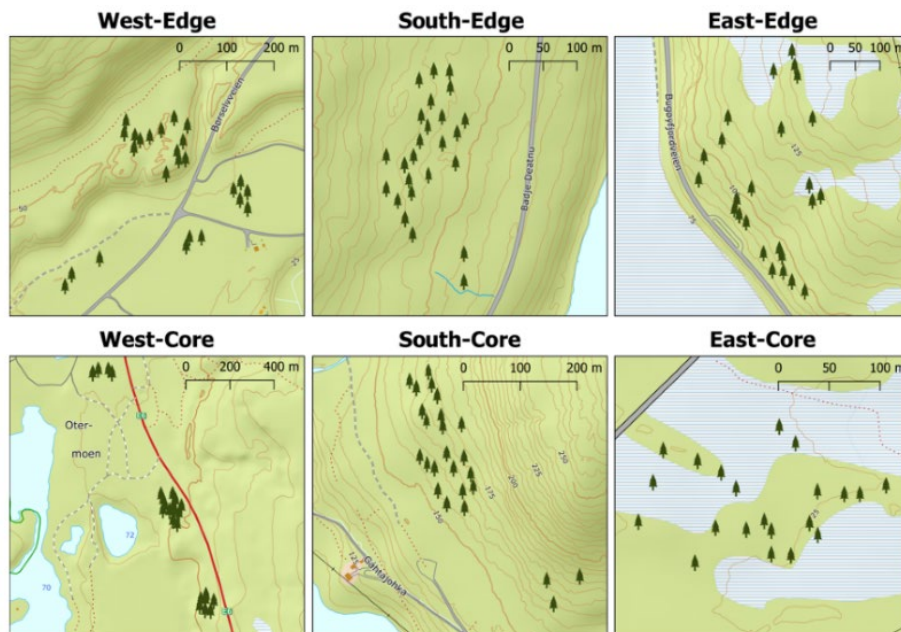
Field work

In preview of the detailed sampling methods, the measured variables are summarized in Table 1.

Table 1 Table summarizing the measured variables at the different levels, comprehensive of measurement units and abbreviation used in the analysis.

	Variables	Units	Abbreviation
Plot level	Waypoints	degree minutes	coord
	E. nigrum hits	hits	en_hits
	E. nigrum height	cm	en_height
Recruit level	Height	cm	recruit_height
	Diameter	cm/mm	recruit_diam
	Dendro sampling	binary (yes/no)	dendro
	Cones	binary (yes/no)	cones
	Age	years	recruit_age

Plot level

Data collection was carried out in the period 1st to 17th of August 2022. In each site, adult pine trees (hereafter seed trees) were selected as sample unit (= a plot). The selection criteria for a seed tree were the following: over four meters height, minimum distance from main roads of 20 meters, no clear signs of forest management, presence of pinecones on the canopy as confirmation of the adult life stage and no evident extensive damage (part of the crown missing or splits in the trunk). In the case of two close candidates, the visually oldest and tallest was selected. Once the seed tree was selected, the study plot of 9 m radius was established using two measurement tapes laid out in the cardinal directions. A GPS waypoint was obtained on a handheld GPS device (Garmin Etrex 32x) in WGS84, UTM35N.

The field layer vegetation recordings were taken using the point intercept method with a 30 cm triangle, with a pin in each corner. The presence and height of the dwarf shrub *Empetrum nigrum* was recorded every 3 meters (at 3, 6 and 9 meters) from the seed tree in every cardinal direction, for a total of 12 measurements.

Once all needed measurement were complete, a new plot was chosen. The new seed tree was selected as the first tree respecting the parameters mentioned above, and which was found at least 2 times the radius of the plot (18 meters) to avoid overlapping. This was repeated until the goal of 20-25 adult trees per region was complete (Figure 2).

Recruit level

 A recruit was defined as any pine tree present in the plot which was below four meters in height. The target number of recruits per plot was 30. Recruits were marked with numbered flags, starting in the first sector around the seed tree, decided as North-East. If the number of recruits in the first sector was below 30, the counting would proceed to the next sector in clockwise order, until completion of the plot. If the sum of the inspected sector reached 30, the count was continued until exhaustion of the sector, hence the number of recruits recorded might exceed 30 (Figure 3). Each recruit was then measured for height, diameter at the base and the eventual presence of pinecones in the canopy. The height was measured from the ground to the highest living part of the recruit. For the dendrological sample, the sample size was limited to 15 recruits per seed tree. If the total sum of all the sectors was below or equal to 15, all recruits were sampled. If the sum was instead higher than the threshold, a randomizer app was used to select 15 recruits out of the pool. In the majority of cases, recruits were harvested and the section above the root collar was cut using pruning shears or a hand saw, and labelled with a unique ID. If the recruit stem was thick enough to obtain a core sample (>50mm), a non-destructive approach was preferred. In these cases, the sample was obtained using a short version of the standard 5mm increment bore (Figure 4). All cores were stored in plastic sheets with 9mm channels and labelled with a unique ID.

Target not reached
(2+3+4+2 = 12 recruits).
All sectors surveyed.

Target reached after two sectors
(15+17 = 32 recruits).
White sectors not surveyed.
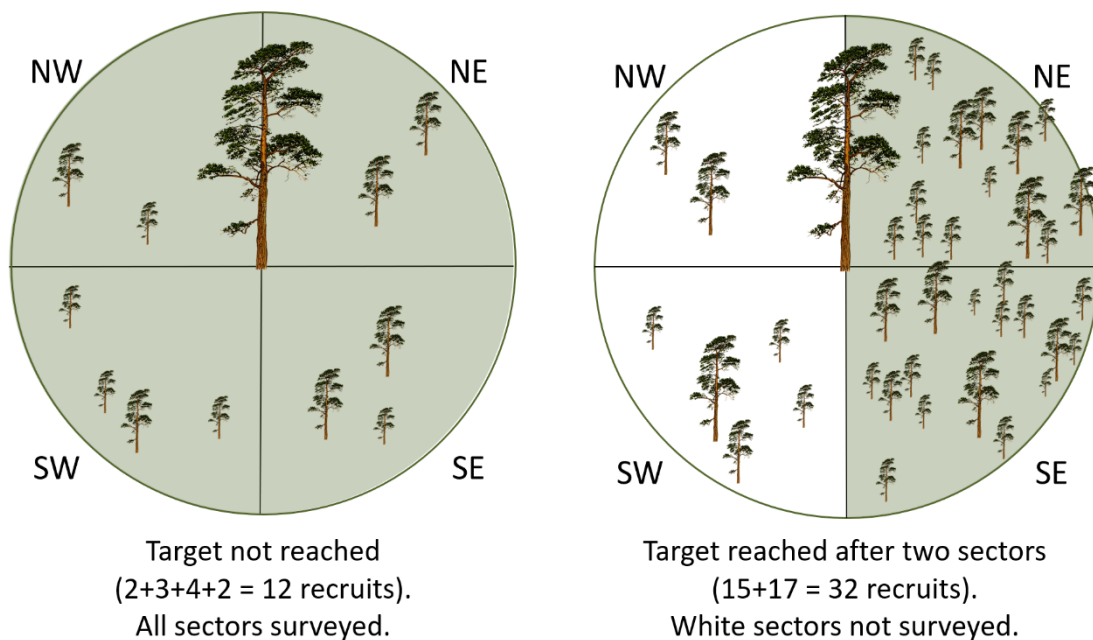
Figure 3 Representation of plot design with recruit counting, shaded sectors are surveyed. Plot on the right did not reach 30 recruits, hence the survey proceeded for the whole plot. In the case on the right, the counting was stopped at the second sector as the 30-recruit limit was reached. Counting and measuring was carried out for all the 32 recruits.

Dendroecological samples preparation and reading

All samples were allowed to dry during the field season and subsequently stored carefully in paper bags in a dry and ventilated area to avoid rotting. In order to precisely read the year rings of the recruit samples, these were prepared into permanent microscope slides. To do so, the samples were sized down and fitted in a sliding microtome. Where possible, a section of the whole disk was prepared, while for wider recruits (>12mm diameter) just a section at least containing pith and one side with bark were preserved. Core samples for recruits could be fit in the microtome through an adapter. The slides were prepared according to the procedure from Gartner et al. (2015), adapted to my purpose. The steps were the following:

Preparation of the sample: Create a continuous and smooth surface on the sample by repeatedly slicing the surface with a gain of 10μm to 20μm. Using a brush, gently apply water to the sample to help soften the sample and upkeep the sharp edge of the blade.

Slicing of the microsection: Using a flat narrow brush, apply a layer of corn starch solution (10g corn starch, 8ml water and 7g of 100% glycerol). Move the sample around 15μm forward and slowly push it onto the blade, obtaining a thin slice. Repeat, while helping the slice move with a moist brush, until a complete slice is obtained (Figure 4). Application of water on the cutting point of the blade helps avoiding curling of the sample, facilitating sliding forward. Thickness of the slice to achieve a complete section may vary. Transfer the slice to a microscope slide with the help of the brush.

The following steps, Sample staining and Slide preparation, were performed in a fume hood.

Sample staining: Rinse the microsection with water to remove the glycerol and eventual wood fragments. Add a few drops of Safranin solution (1g Safranin powder, 100ml water) and Astrablue (0.5g Astrablue powder, 2ml 100% acetic acid, 100ml of water). This will allow to distinguish between lignified and non-lignified structures but also enhance the contrast visually. Let rest for 2 minutes and proceed to rinse with water. Dehydrate the sample by rinsing first with a solution 75% ethanol and then with 100% ethanol.

Slide preparation: To create a permanent slide, first rinse the sample with xylene. This completely dehydrates the sample. When the xylene stays transparent instead of becoming milky, it means the sample is now ready. This step is necessary as the most stable embedding medium, Canada balsam, need to be used in combination with xylene. Apply one or two drops of 100% Canada balsam and cover with a cover glass which at least covers the microsection. Carefully push eventual bubbles out. Place the slides in heat resistant plastic, place some weights on top of the sheets and transfer in an oven at 60°C for 24

hours. When cooled to room temperature, use a razor blade to remove eventual leaked Canada balsam from the glass surface.

High-resolution (46383dpi) scans of all the samples were created using a microscope Zeiss AXIO and the software "MicroVisioneer" (Microvisioneer, 2022).

The year ring count and width measurement was carried out using software "CooRecorder" (Larsson, 2022b), following the suggested procedures suggested by Maxwell and Larsson (2021). When the pith was not visible in the samples, the distance and number of rings missing were estimated using the bult-in function of the program. The measurements were then processed through the software "CDendro" (Larsson, 2022a) to organize and export the data for statistical analysis.

Figure 4 On the left, the coring near the base of a young tree with an increment borer. On the right the slicing of a sample using a microtome. Photos: Author

Climate data

The climatic data was included in the project to address site specific climate trends, with the aim of comparing these with the recruitment and growth patterns in the different study areas. Due to the broad design and the scarcity of weather stations which are sufficiently local to capture site differences, gridded climatic data with resolution 1x1Km for the whole Troms and Finnmark region was obtained from the Norwegian Meteorological Institute ("seNorge", 2023). Three variables were fetched in the available time range 1961-2019: average temperature for the months of July and January, plus the yearly total precipitation. The data was then ingested in R studio using the "terra" package and extracted for the 6 sites (summary in Table 2). The site area was obtained by grouping the coordinates for the seed trees in each region and using a 500m buffer.

Figure 5 depicts the mean annual temperatures for the months of January and July in each of the six study areas. The recordings manifested a positive linear trend for the air temperatures in July across all sites and locations, with an increase varying from 1.4°C in the West-Core to 1.74°C in East-Core. Likewise, a similar positive trend was also recorded for the temperatures in January with an increase varying from 0.6°C in West-Edge up to 1.7°C in East-Edge.
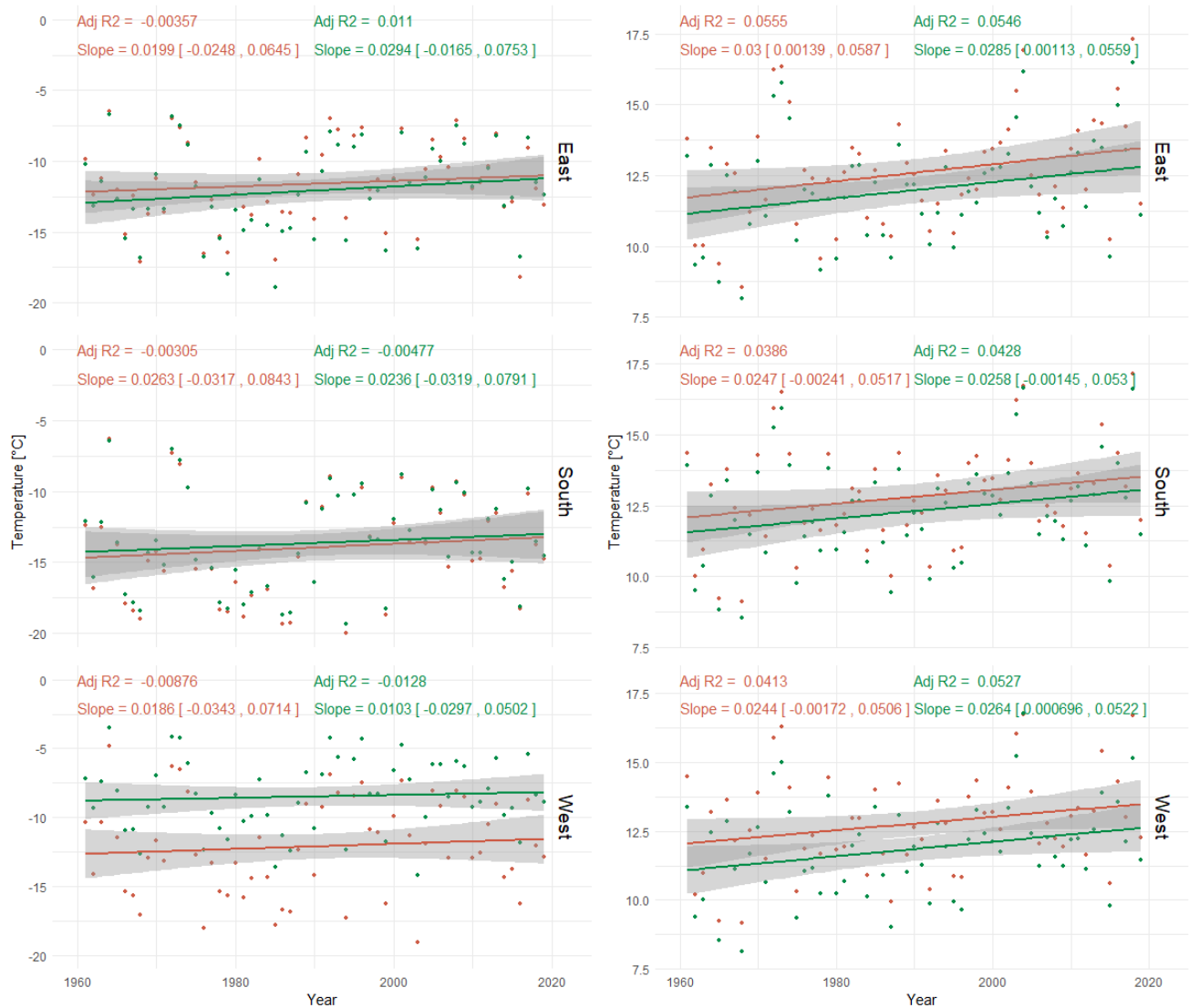
Figure 5 Air temperature for the different combinations of location and sites in the period 1961-2019. On the left column are temperatures for January, on the right are temperatures for July. In each location, red indicates Core sites while green indicates Edge sites. Also noted are the slope for the linear regression with confidence intervals and the adjusted R square value.

The trends for precipitation in the study areas depicted in figure 6, resulted not as uniform as the temperatures trends. Precipitation in the 59-year period presented predicted values with local increase for the sites West-Edge (+172mm), South-Edge (+143mm), East-Core(+126mm) and a small increase in East-Edge (+46mm). The precipitation average in South-Core remained unchanged while in West-Core there was a decrease of 97mm.
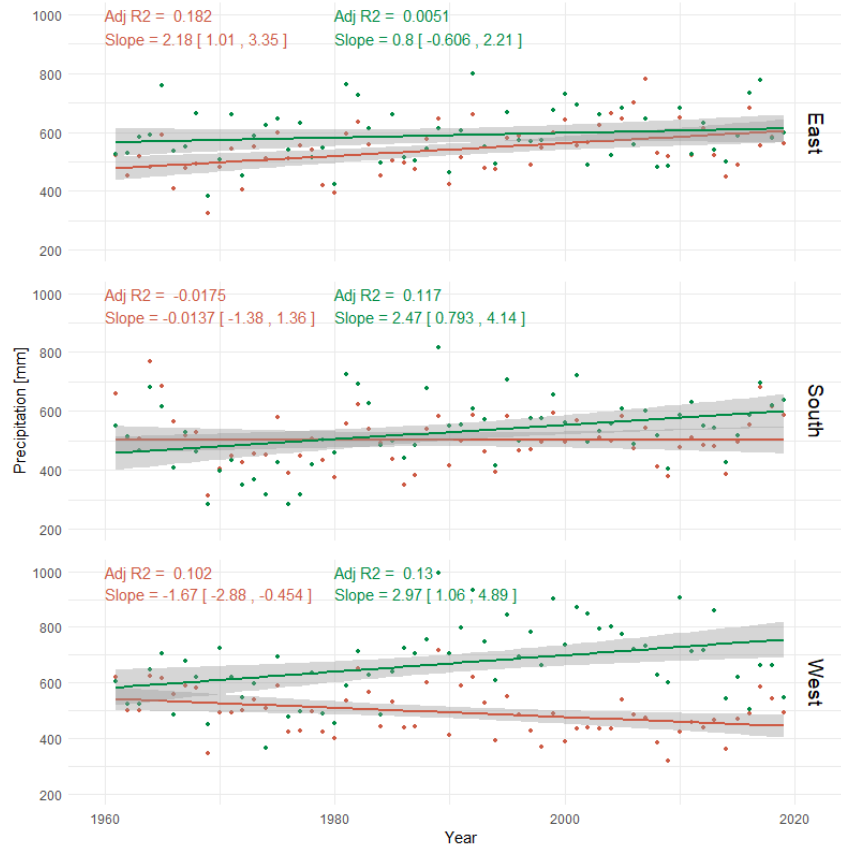
Figure 6 Linear precipitation trends for the yearly precipitation in the study areas over the period 1961-2019. Noted are the adjusted R squared and the slope with confidence intervals. Red indicates Core sites, green indicates Edge sites. Also noted are the slope for the linear regression with confidence intervals and the adjusted R square value.

Table 2 Summary climatic values for the six study areas for the period 1961-2019. Number in parentheses represent the standard deviation.

Study area	January mean [°C]	July mean [°C]	Yearly precipitation [mm]
East core	-11.6(±2.9)	12.6(±1.9)	541.0(±84.5)
East Edge	-12.1(±3.0)	12.0(±1.8)	589.2(±92.1)
South Core	-14.3(±3.8)	12.8(±1.8)	503.1(±88.7)
South Edge	-14.0(±3.6)	12.3(±1.8)	529.0(±116.5)
West Core	-12.1(±3.4)	12.8(±1.7)	492.8(±83.7)
West Edge	-8.5(±2.6)	11.9(±1.7)	669.1(±134.1)

Statistical analysis

All data was analysed in the software R (version 4.1.2) (R Core Team, 2021). The dendrochronological data was handled using the dendrochronological analysis package "dplR" (Bunn et al., 2022).

To explore the differences in age distribution between location and sites, a Generalized Linear Mixed-Effect Model (GLMM) with negative binomial distribution was fitted using the *"glmer"* function from the "lme4" package (Bates et al., 2015). This was chosen as the response variable being the recruits age, a model fitting the nature of the data was necessary. Generalized Linear Models are optimal in the case of designs with hierarchical data as they allow the incorporation of random effects accounting for correlation among observations. The negative binomial distribution is preferred in this case as it allows for a stronger approach on ecological data than a Poisson distribution due to the increased flexibility to heterogeneity and overdispersion. This is possible as it uses an additional parameter controlling the variance independently from the mean, while the simpler Poisson assumes the two to be equal. The fixed effect were the site and location, and in addition the interaction between the two was included, as the locations are different and independent. The seed tree to which each recruit belonged was added as a random factor, as individuals belonging to the same tree are not independent from each other.

The determination of specific years where the recruitment was particularly high was done by determination of number and position of modes in the age distribution of recruits for each study area. The number of modes in the age distribution within each location and site combination was done by sequentially using the "modetest" function from the R package "multimode" (Rodriguez-Casal, 2021) with the default test method "ACR" (Ameijeiras-Alonso et al., 2018) . The test proceeds by presenting a p-value which rejects or accepts the null hypothesis that the number of modes equals to the value *mod0*. The alternative hypothesis is that the number of modes is greater than mod0.If the null hypothesis is rejected, the test is repeated with a higher *mod0* value until the null hypothesis cannot be rejected. The starting value for mod0 was set as one and increased by one at each necessary iteration. To ensure repeatability, a specific seed (1548) for random number generation was used throughout the analysis.

The location of the modes was determined with the function "*locmodes*". The function *locmodes*, given the number of modes *mod0*, fits a kernel density estimation with gaussian kernel and the critical bandwidth is calculated using the Silverman method. The output from *locmodes* also provides the position of antimodes, identified as the valleys between two modes in the distribution. These can be useful to identify additional trend in the distribution.

The position of the modes in the age distributions was approximated by grouping the recruitment years in three-years intervals. The use of age classes rather than the row age distribution was chosen for two reasons: (1) account for eventual errors in the age determination, (2) the particularly high recruitment period is likely to be the result of more consecutive favourable years. Both high recruitment and particularly low recruitment episodes were highlighted. Detailed information on the output of the *modetest* and *locmodes* can be found in Appendix (Table A.1).

To determine if there are any relevant differences in the growth of the recruits between the different study areas, Generalized Linear Mixed-Effect Model (GLMM) with gamma distribution and log link function was fitted to predict the mean radial growth of recruits in the first 10 years of life of the recruits. The gamma distribution was suitable for this application as it treats positive continuous variables with non-normal distributions. As the aim was to investigate possible differences between the study areas as in response to variable local conditions, the fixed effect were location and site, while using the seed tree as random effect.

To assess the statistical relevance of the difference in the height distribution within location, a Wilcoxon singed-rank test was performed between Core and Edge sites of each location. This was chosen over the parametric t-test due to the non-normal data distribution. The same test was repeated for the presence of *E. nigrum* (as en_hits).

Results

Across the six sampling areas, a total of 146 seed trees were located and sampled. This resulted in the counting and measuring of 1656 recruits, of which 1150 were selected for dendrological sampling (Table 3). The number of seed trees recorded was 25 for each area, apart from the West-Core site, where it was only 21 because of logistical reasons during the field work. Despite having the lowest number of seed trees, the West-Core site provided the most recruits, with a total of 384. Core sites in general had more recruits, apart from the South location, where the total was equal.

Table 3 Total number of seed trees and recruits by locations and sites. In parentheses is the number of recruits selected for dendrological analysis.

Seed trees	Core	Edge		Recruits	Core	Edge
East	21	25		East	366(229)	296(182)
South	25	25		South	218(189)	218(187)
West	25	25		West	384(236)	173(126)

Age distribution

The age distribution of the recruit across all sites shows a low frequency of young recruits, an overall mean age of 28.66 years. One sample was removed from the analysis as it resulted 156 years old, this was clearly an outlier and could have strongly impacted the summary statistics and modelling outputs.

Recruit ages in the six areas resulted different (Figure 7). The area with the oldest recruit population was East-Core, with an average age of 41.68 years (sd = ±20.71), with a strong difference from the East-Edge with average age 20.38 (±15.15). The other two location showed a weaker but similar pattern: South-Core with 29.07 years(±16.68) and South-Edge with 23.17 years(±14.60), West-Core with 29.30 years(±15.22) and West-Edge 24.29 years(±10.98).
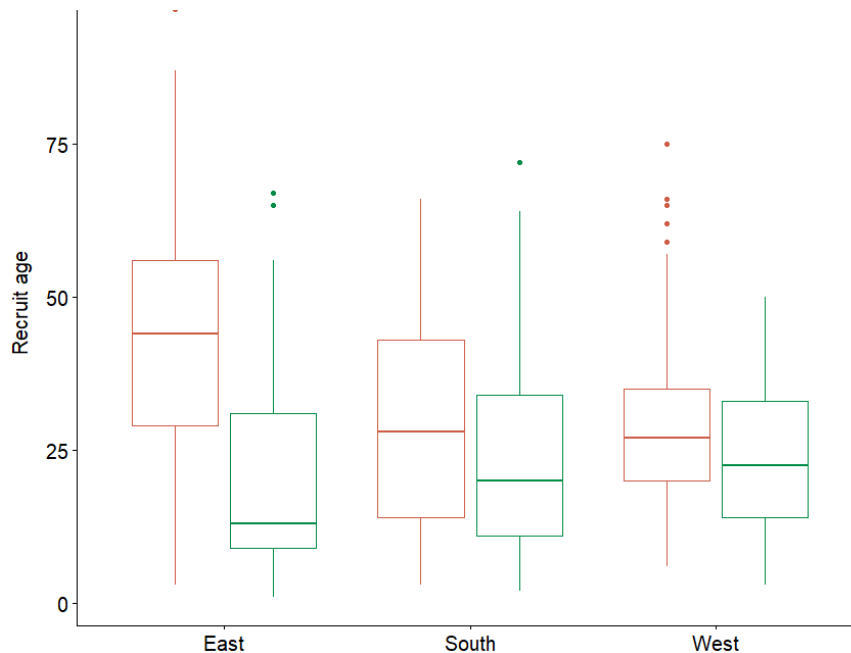
Figure 7 Box plot showing the age distribution and quartiles of the different combinations of site and location. Red represents core sites, green represents Edge sites.

The GLMM used to test the hypothesis of a difference in age distribution among locations and the expectation of a general older age in Core sites showed that Core sites resulted older than Edges. As the values in Table 4 show, East-Edge was significantly younger compared to the East-Core location. The different Core sites proved significantly different in age distribution as well, with age distribution being lower than the East-Core in both the South and the West). The interaction between locations and sites also proved highly significant result of an increase in age in both South and West Edges compared to the East-Edge site.

Table 4 Results from the generalized linear mixed effect model used to determine the effect of site and location on the age distribution.

	Estimate	Std. Error	p-value
Intercept	3.70473	0.08916	< 2e-16 ***
Site (Edge)	-0.95223	0.13139	4.24e-13 ***
Location (South)	-0.40694	0.12531	0.001165 **
Location (West)	-0.40215	0.12601	0.001416 **
Site (Edge) x Location (South)	0.69750	0.18339	0.000143 ***
Site (Edge) x Location (West)	0.85181	0.18686	5.15e-06 ***

The mode analysis revealed different patterns and recruitment periods among the different study areas (Figure 8). The recruit population the East-Core and East-Edge showed a recruitment peak in the age classes of 6-8 yrs. and 9-11 yrs., respectively. While the peak years for the East-Edge (and the two adjacent classes) contains over 54% of the observations, the latest peak in the East-Core just contains 15% of the local population, while over 81% (186 recruits) of it is older than 20 years, indicating a more abundant and continuous recruitment period in the vicinity of the second peak in its distribution, the age class 45-47 yrs. Despite the analysis for the modes in EE resulted in just one peak, the near-significance of the p-value(p=0.056) suggests the possibility for the presence of a second peak. In the South-Edge and Core, the recruitment periods are similar, but the Core with presents a slight delay in the recruitment compared to the Edge for both peaks. The Core presented peaks for the age classes 12-14 and 42-44, in contrast to the peaks for the 9-11 yrs. and 33-35 yrs. age classes in the Edge site. The west location presents very different age distributions compared to the other two locations. West-Core resulted in a unimodal distribution, with a single peak corresponding to the age class 24-26 yrs. and markedly no young recruits. The West-Edge site Showed a peculiar distribution, with three rather sharp peaks representing over 37% (47) of the recruits. It also was the only site with no recruit older than 50 years. The p-value of the modality test for West-Core was 0.076, close to rejecting mod0=1, but visually the use of one mode seems correct.
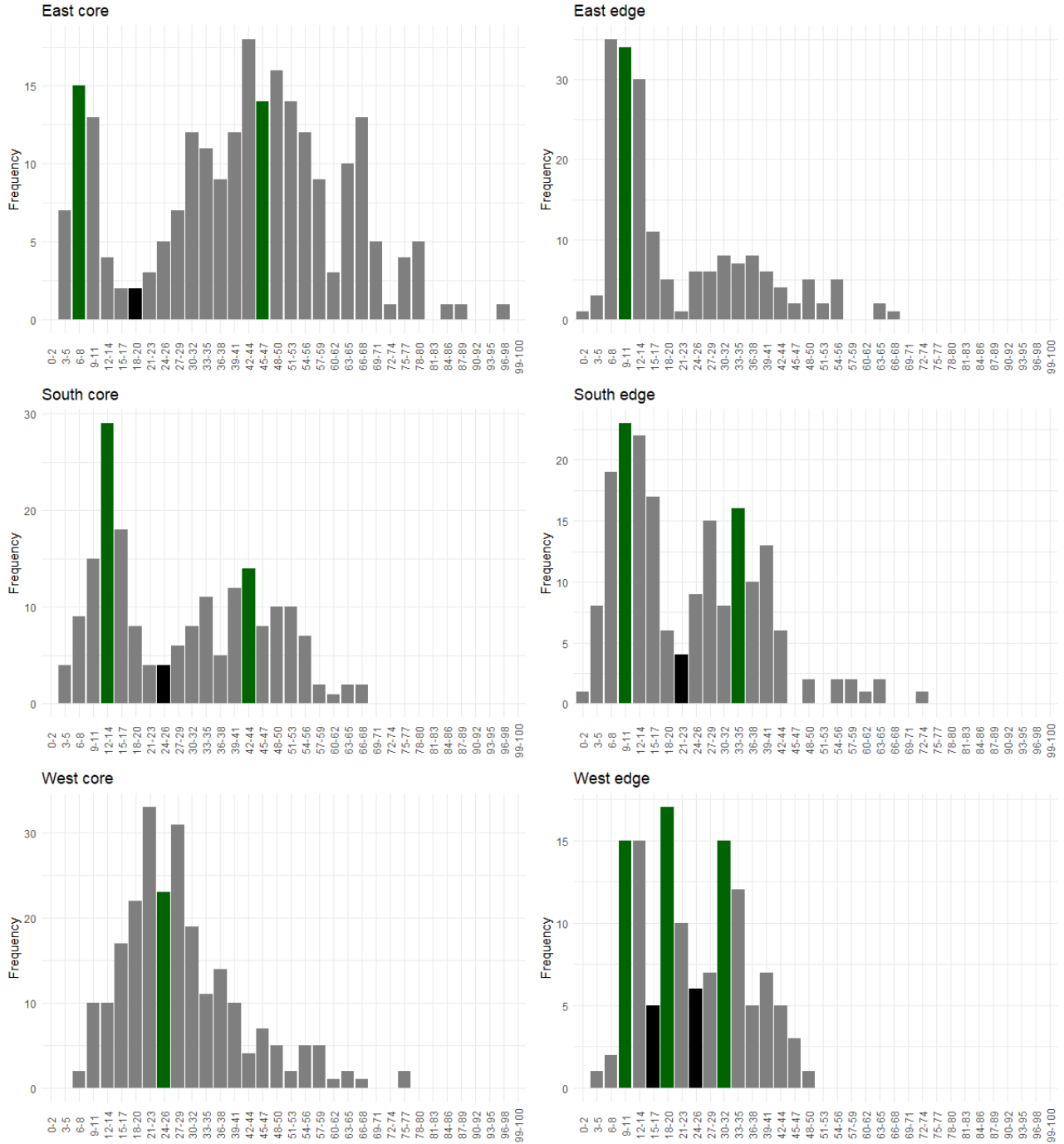
Figure 8 Age distribution of Scots pine recruits in the six study areas, aggregated in into 3-year age classes. Modes in the distribution are in green. Black bars represent age classes corresponding to the antimodes positions. On the x-axis are the age classes, all classes were kept in the plot to better depict differences among sites.

Growth

The mean radial growth for the first 10 years can be seen in Figure 9. The model fit to determine the general effect of the study area on the mean growth in the first years of the recruit showed a significant positive effect of East-Edge site (Table 5). The interactions between site and location were not significant. Thus, there was no evidence that the west and south locations showed a different effect of Edge than the east location. The negative effect of the West location on the mean growth was near significant.
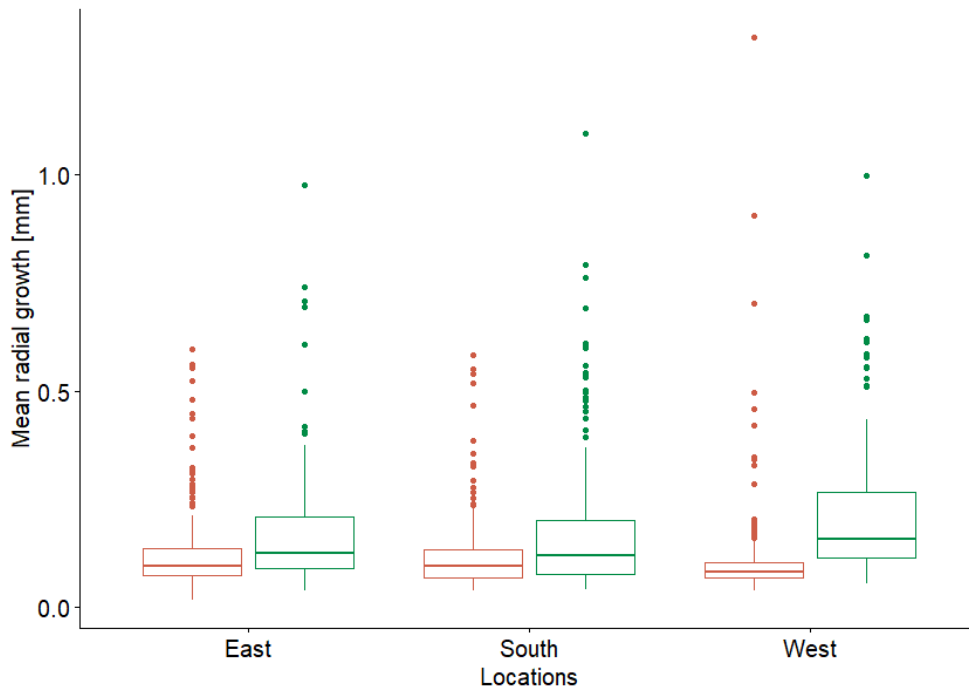
Figure 9 Boxplot showing the average radial growth for the first 10 years of recruits from the different study areas. Red represents Core sites, green represents Edge sites.

Table 5 Results from the generalized linear mixed effect model used to determine the effect of site and location on the mean growth of recruits in their first 10 years from establishment.

	Estimate	Std. Error	P-value
Intercept	-2.05420	0.10125	< 2e-16 ***
Site (Edge)	0.32661	0.15301	0.0328 *
Location (South)	0.01252	0.14061	0.9290
Location (West)	-0.27194	0.14262	0.0566
Site (Edge) x Location (South)	-0.07844	0.21051	0.7094
Site (Edge) x Location (West)	0.32833	0.21537	0.1274

Height for recruits were significantly different between Core and Edge site within all locations (Figure 10). The Wilcoxon ranked test for non-parametric distributions returned the following p-values were obtained: East = 5.131e-14, South= 0.01888, West= 0.002958. Across all locations the Edge sites showed a higher vertical growth by age trend, well visible for the East and West locations but not as clear for the South location. The West location recorded both the highest and lowest vertical growth rates, with an estimated growth rate for Edge recruits over two times greater than the rate observed at the Core site.
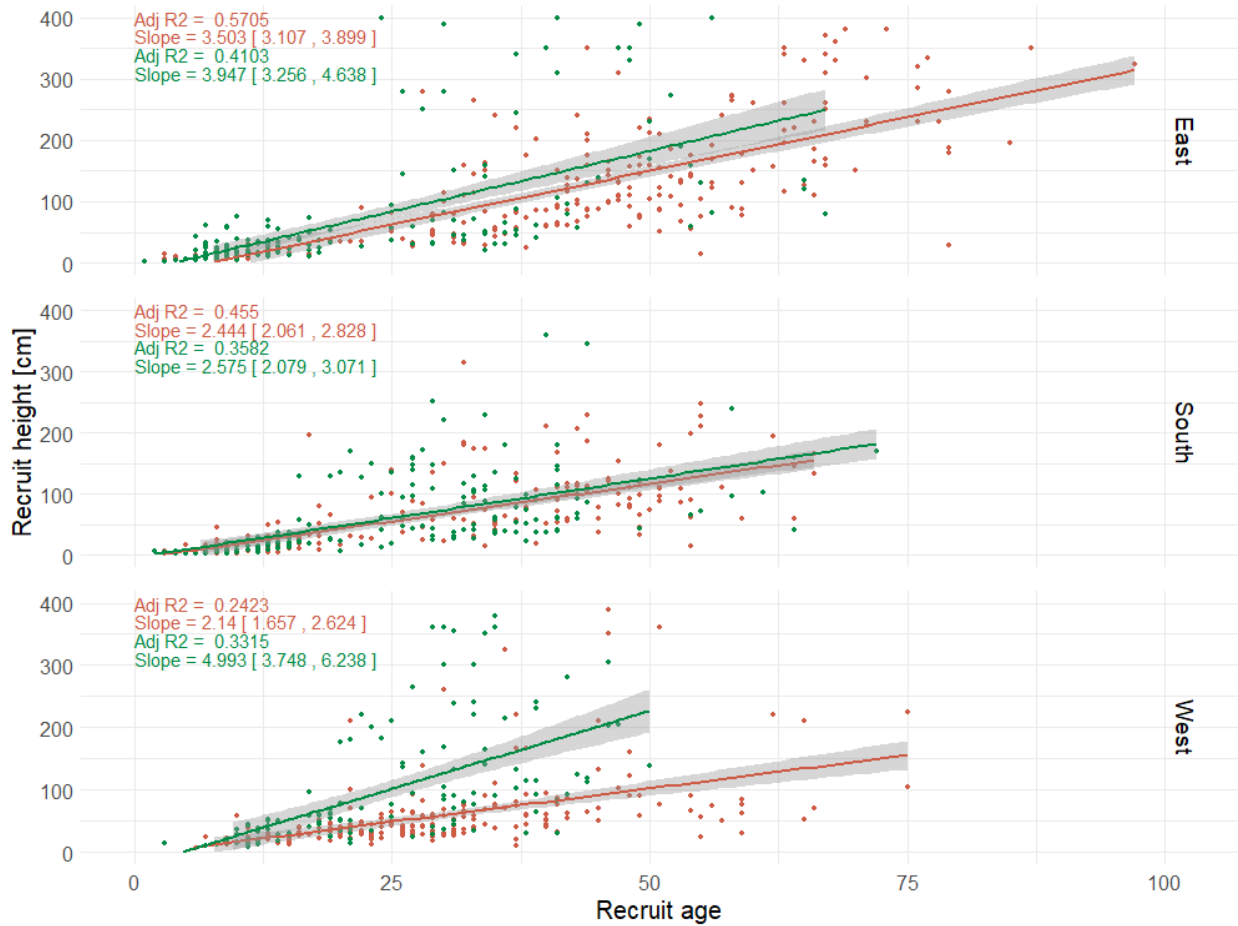
Figure 9 scatterplot with linear fit for each site across the three locations (on the right). Green represents Edge sites, red represents Core sites. Gray shaded area represents the confidence intervals. Also noted are the slope for the linear regression with confidence intervals and the adjusted R square value.

Additional factors

Across all sites, 198 recruits out of 1155 had cones. The East-Core had the highest incidence of recruits with cones on the canopy, with 20.7% of the total East-Edge was the second highest site were 14.4% of the recruits showed cones. In the South location, 10.1% of the recruits in the Edge site had cones, while

only 8.5% in the Core. Just 9.5% of the recruits had cones in the West-Edge, but the lowest occurrence was in the West-Core site, with 7.4%. The youngest dated recruit bearing cones was harvested in the South-Edge and marked 19 years old, with a height of 130cm. The shortest cone-bearing recruit was instead samples at the East-Edge site, at a height of 40cm at 39 years since establishment.

Figure 11 shows the proxy for density of E. nigrum as in hits using the point intercept method, and its height in the different study areas. The highest presence was recorded in the East-Edge, and generally maintained higher in Edge sites than in Core sites. Height resulted significantly different for all locations using the Wilcoxon ranked test which resulted in the following p-values: East = 2.2e-16, South= 6.978e-08, West= 4.173e-12. The height was more constant and did not follow the same dynamic as the presence. Height was rather similar in all areas, but lower in East-Core.
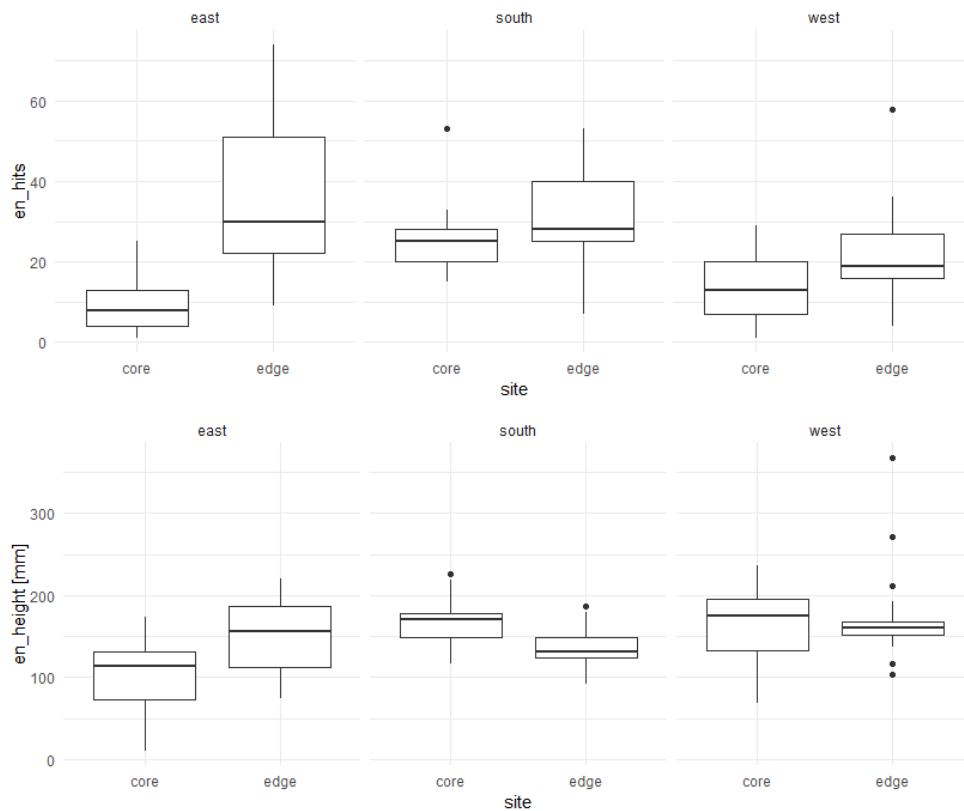
Figure 10 Boxplot showing the presence expressed as hits from the point intercept method (top) and height (bottom) of Empetrum nigrum in the different study areas.

Discussion

As expected, the age distribution showed a generally older recruit population in Core sites than in Edge sites. This was true across all locations, with a most marked difference in the East. The younger population in the Edge sites could be a symptom of the satisfaction of minimum requirements for pine establishment just in later years, with a seed tree population which was established during particularly favourable years and/or in microsite facilitation (Holtmeier, 2011; Hörnberg et al., 1997). No obvious difference was found in the age distribution patterns of the recruits within locations, possibly highlighting the complexity of recruitment processes in forest stands. Unexpectedly, radial growth in the first years after establishment was higher in Edge sites, but significant difference was found on the effect of sites on growth just in one location. Vertical growth was also, contrary to expectations, higher in Edge sites than in Core sites, perhaps indicating that the impact of resource competition in older stands might be higher than the positive climate conditions. Low number of very young recruits are most likely caused by the difficulty to spot small recruits on the ground, especially in the study area, where ground vegetation was often covering most of the soil. This might lead to underestimation of the regeneration rates of pine stands and the influence of mortality in the first years of pine recruits. The lower recruit count in Edge sites, considering the higher occurrence of *Empetrum* across all locations, might also be the result of recruit smothering or allelopathic interference (Nilsson & Zackrisson, 1992; Nilsson, 1994; Zackrisson et al., 1995).

Age structures

The age structure found in the study is in line with the characteristic regeneration pattern at distributional Edges due to climatic thresholds, with intermittent regeneration pulses with marked peaks and valleys (Agren & Zackrisson, 1990; Hörnberg et al., 1995; Zackrisson et al., 1995). The recruitment peak in the 1970s was also recorded from other studies (Agren & Zackrisson, 1990; Zackrisson et al., 1995), while the apparent peak in the late 2000s is not yet mentioned in the main literature.

As seed production and recruit establishment are mostly sensitive to summer temperatures and precipitation (Juntunen et al., 2006) , periodically high pine recruitment is expected to be the result of climate oscillation above or below the abiotic regeneration requirements for Scots pine. However, the evidence collected during this project does not completely support that hypothesis. This is most true for the summer temperatures influence, as all sites show very similar values and trend, while temporal differences in recruitment spurs across sites are clear. In support of this findings, the study from Kullman

(2007) postulates that viable seed production has shown a noticeable increment following the summer temperature increase in Fennoscandia, and no longer constitutes a limiting factor for pine regeneration. The variation in recruitment patterns among my study sites could hence be less linked to the macroscale climate trend than previously thought, but be highly influenced by the range of biotic and abiotic factors in a local scale (Juntunen et al., 2006; Kullman, 2010; Matías & Jump, 2012). Despite this, on some occasions temperature and precipitation might still exercise a strong influence on the germination: the West-Edge site presents the lowest average summer temperature and the lowest recruit count. Here, the recruitment spurs are very sudden and intense, and this might be caused by particularly favourable germination conditions which allowed high establishment in circa 10-year intervals. This could be an indication of the local climatic factors being close to marginal regeneration conditions, where small changes can have great effects on the regeneration rates resulting in strong recruitment episodes (Juntunen et al., 2006; Nilsson & Zackrisson, 1992; Wieser et al., 2009). However, this consideration needs to be taken cautiously as over 60% of the recruits in the site belong to just six seed trees, hence the pattern of the whole site might be heavily influenced by specific plot-level conditions.

Wave-like and bell-shaped age structures could be indicative of recovery from disturbance (Parker & Peet, 1984), and this might be the case for the West-Core. The bell-shaped age structure resulting from this site is unusual among the study areas. A possible explanation might come from the characteristics of the study area: during the collection of samples, the stand appeared to not be under management at current time but has possibly been impacted by logging or thinning. This anthropogenic disturbance in the forest stand may have reduced the vitality and density of the ground vegetation, which in turn could be an explanation for this unusual age distribution. The area is also close to a military training ground, and the site showed clear signs of both recent and past activities such as trenches and ruins (from the 1940s). Hence, the stand cannot be considered fully natural in its form. Only a few seed trees in West-Core were found in seemingly completely natural stands. Disturbance in various forms seem to have shaped both the age structure and the topography of the area. In addition, the area recorded the lowest yearly precipitation, with a marked reduction in the period 1961-2019, which might have particularly reduce the germination rate (Gunnarsson & Rydin, 1998).No particular signs of disturbance were noticed in the other areas, as these should have been avoided in principle by the protocol. Excluding site-broad disturbance and fluctuation in the climate allowing only episodic reproduction, the wave-like patterns are likely to be the result of variations in mortality rates.

The first years of a recruit are characterized by high mortality (Liu et al., 2021), hence constitute a bottleneck in the recruitment. Mortality was not measured during this study, but it is known to heavily influence stand regeneration capabilities and hence age structures. With winter frost, herbivory and pathogens being the most common mortality causes (Matías & Jump, 2012), the evaluation of their impact without proper assessment is difficult.

Winter desiccation was suggested to be especially damaging for pines with height in the range 80-150cm as they surpass the maximum winter snow cover, with an overall reduced mortality over that threshold (Kullman, 1981). East-Core recruits are significantly older than recruits at other sites, and the high rate of survival to older age might be linked to the height being generally the lowest, with 55% of the recruits measuring under one meter, including individuals dated up to 79 years. Recruit survival might also be hindered by frost damage, especially since the winter temperature showed a common increasing trend in the analysed period for the studies areas. This correlates with an increase of winter melt days, which can cause considerable damage to the vegetation (Bokhorst et al., 2009).

Seed predation (Ellingsen et al., 2016; Nilson & Hjältén, 2003) and ungulate browsing (Danell et al., 1991; Heikkilä & Härkönen, 1996) can also severely decrease the recruitment and survival rates. Seeds in low growing ground vegetation have a higher probability of predation than ones in taller vegetation. In addition, lower vegetation is common in the close distance from adult trees as a result of resource competition (Kuuluvainen & Pukkala, 1989). These two factors combined with the low-distance transportation of viable seeds mentioned in the introduction, could cause very high rates of seed predation. Browsing in low productivity environments is especially high from moose, as the pine needles are more palatable under such conditions (Nilson & Hjältén, 2003). This might be part of the explanation for the unusually low recruit presence recorded in the South-Edge, where many signs of browsing were encountered (Figure 12). Intraspecific competition between recruits of different age and size classes might be relatively more important in denser stands, where regeneration is suppressed from a robust recruit cohort which monopolizes the available resources (Agren & Zackrisson, 1990). One more aspect to consider is that the regeneration potential increases as more recruits reach the reprodctive stage. For example, the three sites with the most recruits bearing cones also show very high recruitment levels in past few

Figure 11 Pine recruit severely damaged by browsing. Photo: Jane U. Jepsen

years. While the lowest percentage of recruits recorded in West Core might help explain the lowest levels of young recruits found across all sites.

Growth

Contrary to my expectations, the effect of location and site on the growth in the first years of age of the recruits did not show major differences. Only the East-Edge area showed a significant increment in growth compared to the East-Core but this might be more due the singularity of the latter. East-Core stood out as site due the very high recruit presence (366, second just to West-Core) and old age (average close to 42 years), together with a slow vertical growth. The stands in the site were quite dense and homogeneous, scarce presence of ground vegetation, which possibly favoured pine establishment. The high recruit number and the closed canopy might have hindered the individual growth due to shading (Carlisle & Brown, 1968) and resource competition (Kuuluvainen & Pukkala, 1989). This is possibly true also for the other Core sites, as the reduced radial and vertical growth were characteristic across all locations. The expected hindering effect of *Empetrum* on growth was not observed, as Edges presented the significantly higher concentration of the dwarf shrub, but also recorded the steepest vertical growth and fastest radial growth in the first years. This result was somewhat similar to the observations from Grace and Norton (1990), where growth at the treeline distributional limit was higher than below the treeline. Despite that, the treeline individuals still presented an irregular shape, while in this case the vertical growth was higher for Edge recruits despite the expectation of a lower and wider form in the distributional limit (Körner, 2012). This observation is however in line with the modelling results from Matías et al. (2017), predicting increase growth in the northern distributions in function of increased temperatures, but with water availability limitations. Possibly the openness of the canopy and the lower competition for both nutrients and water allowed this behaviour. Soil dryness was in fact demonstrated by Oberhuber and Kofler (2000) to be the main driver between differences in growth at small spatial scales, highlighting how edaphic conditions can influence radial growth once climatic variability is reduced to zero. This could be extended at a site level, where the climate can be considered uniform among plots, but small-scale soil conditions can influence radial growth. As a possible result, the increased openness and diversity in microtopography of Edge sites in addition to being closer to marginal growth conditions could be linked with the larger range in ring growth mean.

Higher vertical growth rate was also recorded at all Edge sites, with the highest being in West-Edge. This site has particularly oceanic climate, with milder winters and the highest yearly precipitation of all sites. On the opposite end of the scale, the West-Core presented the lowest vertical growth rate across all

sites. The climatic features of the site are particular, as it is the only site where a decrease in precipitation over the period 1961-2019 was recorded. Notably, in all Edge locations the precipitation was higher than their Edge counterparts, and so was the vertical growth. This contrast could indicate an influence of precipitation on the vertical development of young trees. The difference in vertical growth in the South region was less visible, but this could be caused by the high number of damaged recruits due to browsing, as previously mentioned. When the apical shoot of saplings is lost, the delay to reach a determinate height and maturity can be severely delayed (Matías & Jump, 2012).

Conclusion and recommendations

The overall results of this study seem to suggest that while climate variation can play an important role on large scale, similar climatic conditions can still produce highly differentiated responses in both recruitment and growth. Site specific conditions such as competition for resources and water, browsing and seed predation, and allelopathic influence can influence the age distribution, recruitment patterns and growth dynamics of pine recruits.

Given the absence of apparent climatic effects on a site scale, future projects should investigate the climate-growth relationship in a more comprehensive manner. This could be done firstly by separating the temporal from the spatial effects of climate on the actual year by year ring width (e.g. Oedekoven et al. (2017)). In this way a site- and time-specific growth response could then be obtained, with the aim to produce a model the response based on location and climatic variability in a similar way of the study proposed by Matías et al. (2017), but in a smaller and higher resolution northern distribution context.

Alternatively, an approach similar to the one from Hannerz et al. (2002) could be adequate. This could be done by exploring the potential regeneration capacity of the different sites combining seed productivity and calculation of degree days by use of on-site temperature and precipitation loggers, and then compare the potential and the effective regeneration. This could be a first step into better understanding of the regeneration and stand densification dynamics, to then possibly explore in more depth the different aspects regulating the difference between potential and real recruitment and survival rates.

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Appendix

Table A.1 Table reporting the values of the *modetest* function with ACR calculation and the positions of modes and antimodes obtained from the function *locmodes.*

	mod0=1		mod0=2		mod0=3			
locsite	Excess mass	p-value	Excess mass	p-value	Excess mass	p-value	nmodes	modes positions
EE	0.054	0.056	/	/	/	/	1	10.65
EC	0.076	2.20E-16	0.029	0.202	/	/	2	8.25 ; 46.57
SE	0.076	0.004	0.036	0.160	/	/	2	11.19 ; 33.22
SC	0.088	0.002	0.028	0.752	/	/	2	13.65 ; 43.01
WE	0.079	0.034	0.070	2.20E-16	0.070	0.354	3	11.51 ; 19.60 ; 30.92
WC	0.042	0.076	/	/	/	/	1	23.97