



RESEARCH PAPER

Red foxes increase white spruce seed production at its northern range limit

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ABSTRACT

The northern boreal forest treeline is usually considered to be the result of climate limiting tree reproduction. Although climate also influences the cycling of nutrients, the effects of nutrient availability on the treeline have largely been ignored. Various animal activities can alter nutrient cycling, creating microsites of highly fertile soil. Red foxes (*Vulpes vulpes*) act as ecosystem engineers in the nutrient-poor northern boreal woodlands by concentrating soil nutrients through their denning activities, increasing white spruce (*Picea glauca*) tree growth. Here, we examined how denning activity affects reproduction in white spruce by determining the number cones per tree, seeds per cone (with or without endosperm, i.e., filled or not) and their viability. Overall, seed production in the study region was low, with an average of 3.7 filled seeds and 0.73 viable seeds per cone. Denning activity affected all stages of seed production, with trees on dens producing an average of two times more cones, three times more total seeds, four times more filled seeds, and 18 times more viable seeds than trees growing away from dens. While cone counts per tree were a good predictor of filled seeds per tree, they were less reliable at predicting viable seeds per tree. Additionally, the number of cones on a tree does not predict the number of filled seeds in a cone, making it difficult for granivores like squirrels and birds to assess food availability from cone abundance. Overall, these results suggest that nutrient availability can play a crucial role in tree reproduction at the treeline and denning activities can create hotspots of seed production and seed viability, acting as a potential food source for granivores and locations for tree reproduction.

Introduction

Climate is widely accepted as the dominant factor determining the position of the northern treeline by directly limiting tree growth and reproduction (Paulsen & Körner, 2004; Harsch et al., 2009). At the treeline, temperature is primarily thought to limit the conversion of photosynthates into growth (Sullivan et al., 2015). During the summer months at their northern range limit, tree growth is particularly influenced by climate (Girardin et al., 2005; Tardif et al., 2008; Mamet & Kershaw, 2013; Lang et al., 2022). For example, at the northern treeline, 60 % of growth in tamarack trees (*Larix laricina*) can be explained by temperatures between May and July (Girardin et al., 2005), and both summer temperature and precipitation positively influence growth in white spruce, *Picea glauca* (Lang et al., 2022).

Climate also directly impacts the reproductive potential of trees. The reproduction limitation hypothesis suggests that the treeline position is cumulatively determined by various reproduction-related mechanisms (Kambo & Danby, 2018; Sirois, 2000). These mechanisms include limited seed production, pre-dispersal seed damage, limited seed

dispersal, seed predation, and failure to germinate. At their northern range limit, tree density is typically low, which is thought to limit pollination success (Brown et al., 2019). Conifer reproduction relies on wind to disperse pollen and successful fertilization from wind pollination is generally limited by how many trees are located nearby (Kelly (1994); Robledo-Arnuncio and Gil (2005); LaMontagne and Boutin (2007); Friedman and Barret (2009); Krebs et al. (2012); Brown et al. (2019)). Unsuccessful fertilization can result in unfilled seeds, which have an external seed coat but no developed endosperm (Gruwez et al., 2013). At low tree density, self-fertilization is more likely to occur in conifers, which results in higher failed seed development compared to outcrossing (Smith et al., 1988, 2001). Within fertilized seeds, pre-dispersal seed damage from environmental conditions, predation, or infections can also hinder seed development, particularly in late embryo development (Gruwez et al. 2013; Kambo & Danby 2018). These seeds will be fertilized and filled with a developed endosperm but will not contain any live tissues and will not be viable for germination, thus not improving the fitness of the tree. However, non-viable filled seeds still represent a food source for granivorous animals like red squirrels,

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Tamiasciurus hudsonicus (Gruwez et al. 2013; LaMontagne et al. 2013). There can be considerable yearly variation in seed production through synchronous and intermittent production of large seed crops, known as mast-seeding (Kelly 1994), and regional variation with total seed counts and seed viability being lower near the northern and high elevation treelines (Sirois 2000; Roland et al. 2014; Kambo & Danby 2018; Lantz et al. 2019). This reduced seed production can limit tree regeneration at the treeline (Brown & Johnstone 2012) and, in combination with an increased fire frequency due to climate change, may result in an expansion of tundra rather than the advance of the treeline (Timoney 2023).

Not only does climate directly limit plant growth and reproduction, but it also indirectly affects them by restricting nutrient cycling and, consequently, nutrient availability to plants (Sullivan et al. 2015). In the boreal woodlands and on the tundra, the short summer period and shallow active layer limits the decomposition of organic material, slows nitrogen fixation, and promotes the immobilization of nitrogen and phosphorus, resulting in low nutrient availability for plants (Alexander & Schell 1973; Nadelhoffer et al. 1991; Jonasson et al. 1999; Blume-Werry et al. 2019). Limited access to essential nutrients can reduce tree growth and reproduction (Loewe-Muñoz et al. 2020). Although nutrient limitation can potentially contribute to the position of the treeline (Loomis et al. 2006; McNowen & Sullivan 2013; Sullivan et al. 2015), there is little information on the effect of nutrient availability on seed production at the northern treeline. Greater nutrient availability is expected with a warming climate but there are mixed results based on soil type (Robinson et al. 1998; Ernakovich et al. 2014; Pold et al. 2021).

While the effect of climate on nutrient cycling is well-documented, animals can also influence nutrient cycling through a variety of behaviours and activities (Gharajehdaghpour et al. 2016; Lang et al. 2021). Ecosystem engineering occurs when an organism creates, destroys, or otherwise significantly alters the physical habitat in its environment (Jones et al. 1994). Ecosystem engineers can have various effects on biogeochemical cycles, food-web dynamics, and energy transfer among trophic levels (Jones et al. 1997; Cuddington et al. 2009; Gharajehdaghpour & Roth 2018). These engineers can influence the physical properties and nutrient levels of soil through their foraging activities (Maisey et al. 2021), burrowing (Reichman & Seabloom 2002), excreta (Piló et al. 2023), and carcass remains (Quagiotto et al. 2019). Nutrient concentration can significantly alter plant growth and biodiversity in these microsites, having even greater ecological significance on the entire community (Gharajehdaghpour & Roth 2018; Fafard et al. 2020; Lang et al. 2021).

Red foxes (*V. vulpes*) act as ecosystem engineers in the sub-Arctic and low Arctic by concentrating nutrients in the soil at their den sites through urination, defecation, and prey remains (Lang et al. 2021). Arctic foxes (*Vulpes lagopus*) similarly act as ecosystem engineers on the tundra (Gharajehdaghpour et al. 2016). Soil disturbance through digging activities also helps cycle nutrients and increases the aeration and the pH of the soil through bioturbation (Godó et al. 2018; Lang et al. 2021). Den sites are used for many years and nutrient enrichment and soil disturbance by foxes can persist for many decades, long after the foxes are no longer present (Fafard et al. 2020). In the boreal woodlands, the soil organic layer on red fox den sites contains up to 81 % more inorganic nitrogen and 250 % more extractable phosphorus than reference sites (Lang et al. 2021). As a result, red fox den sites have a greater cover of erect woody shrubs, grasses, and weedy ephemerals (Lang et al. 2021), and white spruce tree growth on red fox den sites is greater than on reference sites (Lang et al. 2022). White spruce cone production was also greater on red fox den sites than on reference sites during a non-mast year (Kucheravy et al. 2021). However, we do not know if cone production is an accurate index of viable seed production. The mismatch between cone production and viable seed production may be particularly important in areas where a large proportion of ovules do not develop into seeds. It is common practice to use only cone counts as a measure of the reproductive output for coniferous trees, especially as a

measure of food availability to granivores, since cone counting is both labour and time-efficient (LaMontagne & Boutin 2007; LaMontagne et al. 2013). However, the number of cones may not reflect the true number of filled and viable seeds.

Here, we explored how the ecosystem engineering activities of red foxes alleviates nutrient limitation in white spruce at the northern treeline, increasing the production and viability of seeds. Given the harsh environmental conditions and the low tree density in this region, we aimed to test the assumption that cone counts sufficiently reflect reproductive output by also estimating the production and viability of seeds, which is rarely done in studies of conifer reproduction at their range limits. We hypothesized that at their northern range limit, reproduction of white spruce trees is limited by nutrient availability. Specifically, we predicted that red fox den sites have greater counts of total seeds, filled seeds, and viable seeds per cone, per tree, and at a landscape scale, compared to reference sites.

Materials and methods

Study area

Fieldwork occurred in July and August of 2021 in the boreal woodlands near Churchill, Manitoba, Canada (58°44'14.8"N 93°49'08.6"W). The landscape is predominantly fens and bogs, interspersed with gravel ridges deposited by glacial activity (Smith et al. 1998). Foxes den on upland habitats dominated by white spruce trees, with black spruce (*Picea mariana*) and tamarack making up <10 % of the tree abundance. The woodlands are sparse with low tree density and the understory primarily comprises ericaceous plants and lichens (Smith et al. 1998). Red fox dens have been previously identified in this area by the presence of burrows, tracks, disturbed soils, urine odor, prey remains, and shed hairs (Roth 2003). We selected ten previously studied red fox den sites in undisturbed areas of boreal woodlands, excluding any dens in proximity to anthropogenic disturbance (gravel pits, roads, and other human excavations) (Kucheravy et al. 2021). These were all the known red fox dens in the study area without anthropogenic disturbance and encompassed an area of 60 km². Den site centres were determined as the midpoint along a straight line connecting the two outermost burrows (Lang et al. 2021). The dens averaged 260 m² (measured as the area encompassing all the burrows at a den) and ranged from 60 to 419 m². Paired reference sites for each red fox den were located along the ridge, centered 50 m from the centre of the den sites, beyond any significant impact of red fox denning activity (Gharajehdaghpour et al. 2016; Lang et al. 2021). The reference sites were the same as previous studies (Lang et al. 2021, 2022; Kucheravy et al. 2021) and had similar elevation, slope, and soil type as the dens. Previous work on eight of these den sites found the trees were an average of 111 years old, and there was no difference in tree age on den and reference sites (Lang et al. 2022).

Experimental protocol

We took measurements from five permanently tagged white spruce trees located within 18 m of the centre of each den site and each reference site (Lang et al. 2021, 2022; Kucheravy et al. 2021). The sampled trees were >5 cm in diameter at breast height (DBH), the size that trees begin to produce cones in higher latitudes (LaMontagne & Boutin 2007). We recorded the DBH, tree height using a Nikon Forestry Pro rangefinder, and the density of trees > 5 cm DBH within 5 m of each tagged tree, averaged per site.

Cone counts took place in July prior to cone harvesting by red squirrels (Peters et al. 2003). The year 2021 was a non-mast year. We estimated the number of new female cones on each tree by taking three to six photographs of the crown on opposite sides of the tree (Kucheravy et al. 2021). We counted the total number of new cones, matching photographs from both sides so as not to double-count cones.

We then randomly collected up to twelve cones at varying heights from each of the tagged trees at each den site and paired reference site using a pruning pole. Cones from the trees on each site were pooled into a single sample. We measured the length of the collected cones from each site and let them dry at room temperature in paper bags until they opened to aid in seed removal. We dissected each cone to extract the seeds and floated the seeds in 100 % ethanol to determine how many were filled. The unfilled seeds floated in the ethanol and the filled seeds sank. The filled seeds were then soaked in water overnight before being cut laterally and soaked in a 0.2 % tetrazolium solution for eight hours to assess viability (Leadman 1984). To account for variability in tree density between sites, for each den and reference site, cone production per tree and seed production per cone was converted to cones and seeds produced per land area. This was done by taking the product of the mean number of seeds per cone, the mean number of cones per tree and the density of trees on each site, expressed on a per hectare basis.

Statistical analyses

Data analyses were performed in R version 4.4.0, using RStudio Version 2023.12.0 + 369. First, we conducted a preliminary analysis of the variables measured on our sites to detect which variables influence cone and seed production. We were unable to collect any new cones at one den site due to all the cones being out of reach, so that site and its paired reference site were excluded from analyses on cone size and seed production. We took the mean cone length of collected cones from each site and compared den and reference sites using a paired t-test. Counts of cones, total seeds, filled seeds, and viable seeds tended to be right skewed and highly dispersed. Therefore, we tested the effect of den sites versus reference sites with generalized linear mixed models using the nlme, MASS and lme4 packages. We ran the models using either Gaussian (both with and without log transformations), Poisson, or negative binomial distributions. We selected the most appropriate distribution by examining the distribution of residuals using DHARMA and Bolker's overdispersion function (<http://bbolker.github.io/mixedmodel-misc/glmmFAQ.html>). The inclusion of site ID as a random effect was based on the AIC values of the model. Because researchers use cone counts as an index of tree reproduction, we calculated Pearson correlations between cone numbers per tree and the number of filled and viable seeds per tree and per cone. Tree height and circumference were compared between den and reference sites using linear mixed models with site as a random effect. The circumference values were log

transformed to improve the homogeneity of variance.

Results

Across all sites, 8.7 % of the collected seeds were filled, of which 13.7 % were viable. Cones from den sites had 1.45 times more total seeds ($z = 2.57, p = 0.0101$ for a negative binomial model), 1.87 times more filled seeds ($z = 2.33, p = 0.0202$ for a Poisson model) and 9.19 times more viable seeds ($z = 2.40, p = 0.0166$ for a negative binomial model) than cones from reference sites (Fig. 1). Trees on den sites had 2.18 times more cones ($z = 0.2195, p = 0.0433$ for a log transformed Gaussian model), 3.00 times more total seeds ($z = 2.583, p = 0.0200$ for a log transformed gaussian model), 3.52 times more filled seeds ($z = 2.237, p = 0.0253$ for a negative binomial model), and 17.95 times more viable seeds ($z = 3.621, p = 0.0003$ for a negative binomial model) than trees from reference sites (Fig. 2). The inclusion of sites as a random effect did not improve the fit of any of the models. Across all sites, there were 665 ± 399 trees ha^{-1} (mean \pm SD) with no difference between the den and reference sites. Taking tree density into account at each site, the production of cones was $37,500 \pm 11,662 \text{ ha}^{-1}$ on den sites compared to $15,915 \pm 6,094 \text{ ha}^{-1}$ on reference sites. Total seed production was $1,583,867 \pm 548,820 \text{ ha}^{-1}$ on den sites compared to $670,256 \pm 301,280 \text{ ha}^{-1}$ on reference sites, filled seed production was $149,355 \pm 25,792 \text{ ha}^{-1}$ on den sites compared to $56,388 \pm 26,403 \text{ ha}^{-1}$ on reference sites, and viable seed production was $45,523 \pm 53,322 \text{ ha}^{-1}$ on den sites compared to $2,863 \pm 2,214 \text{ ha}^{-1}$ on reference sites. The mean number of cones per tree on a den or reference site was strongly correlated with the mean number of filled seeds per tree ($r = 0.908, p < 0.0001$), somewhat less correlated with the number of viable seeds per tree ($r = 0.614, p = 0.0051$), but showed no relationship to the number of filled seeds ($r = 0.400, p = 0.0897$) nor viable seeds ($r = 0.383, p = 0.1050$) per cone.

The linear mixed models with site as a random effect showed that the trees on den sites had significantly greater circumference at breast height (Den: $76 \pm 22 \text{ cm}$, Reference site: $59 \pm 15 \text{ cm}$, $p = 0.0040$) and were significantly taller than trees on reference sites (Den: $9.7 \pm 1.6 \text{ m}$, Reference site: $8.9 \pm 2.04 \text{ m}$, $p = 0.0014$). However, there was no correlation between a tree's circumference and the number of cones ($F_{1,98} = 0.9661, p = 0.7968$), nor between the height of a tree and the number of cones ($F_{1,98} = 0.9661, p = 0.3281$). Therefore, we did not include these parameters in the models of seed production (or they did not improve the model fits). Mean cone length per site did not differ significantly between den and reference sites (mean \pm SD, den sites =

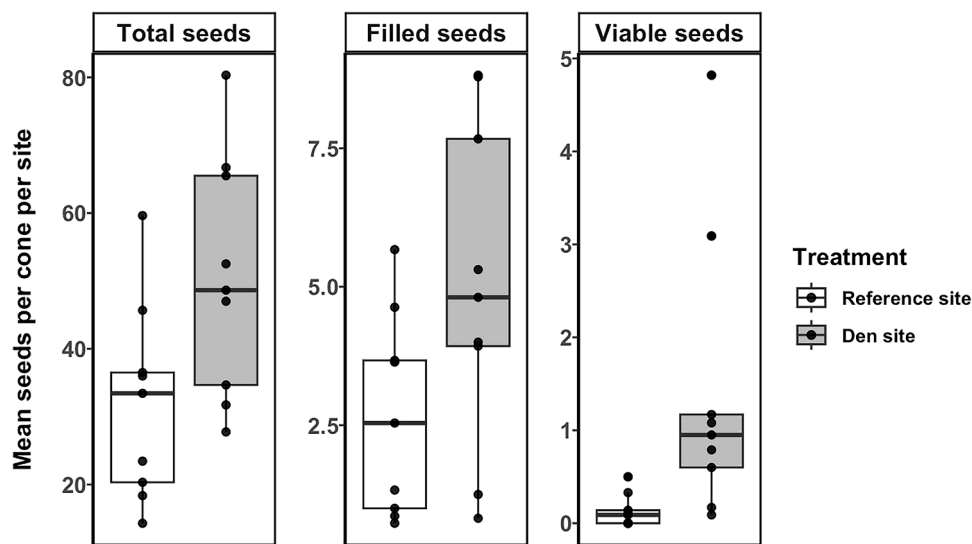


Fig. 1. The mean number of total seeds, filled seeds, and viable seeds per cone at each den site and reference site. Boxes are the interquartile range, bold black lines are the median, whiskers are 1.5x the interquartile range, and the black points are mean numbers at each site.

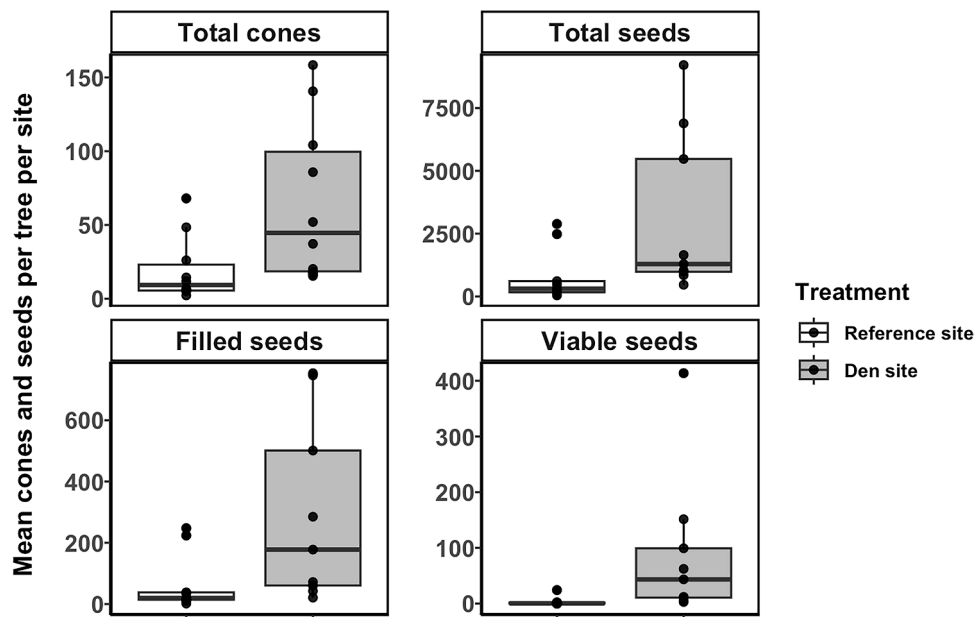


Fig. 2. The mean number of estimated cones, total seeds, filled seeds, and viable seeds per tree.

40.7 ± 4.57 mm, reference sites = 36.7 ± 6.20 mm; $t_8 = 1.4938$, $p = 0.17$).

Discussion

Our study demonstrates that the ecosystem engineering activities of red foxes influence the seed output of white spruce trees at their northern range limit. The increasing difference in our results between den and reference sites from cone numbers to total seeds, to filled seeds, to viable seeds largely supported our hypothesis of nutrient limitation and indicates that denning activities affect all stages of white spruce reproduction. This adds to our previous work showing that white spruce in this region have greater growth on den sites (Lang et al. 2022). These results also support the hypothesis that tree growth at the northern treeline is nutrient-limited (Sullivan et al. 2015), in addition to trees at their northern range limit producing few seeds. Under ideal conditions, conifers typically have at least half of their seeds filled (Smith et al. 1998). The proportion of total seeds that were either filled but non-viable or filled and viable was low, regardless of being on a den or not, indicating that the environmental conditions at the northern treeline restrict both fertilization and seed development. The low proportion of filled seeds we found and the fact that tree height had no significant effect on cone production are similar to what Sirois (2000) found in black spruce growing at the northern treeline.

Taller trees produced more cones on several of our sites prior to this study (Kucheravy et al. 2021). However, cone production in white spruce is highly variable from year to year. In red pines (*Pinus resinosa*), larger cone production was the result of greater light availability (Sutton et al. 2002). We found that tree height had no significant effect on cone production, suggesting that the low density and basal area of trees at the treeline likely reduces the effect of tree size on light availability, thus eliminating the relationship between tree size and reproduction. While the number of seeds per cone has been found to be positively correlated to cone size in conifers (Balekoglu et al. 2020), despite our larger sample of collected cones, our results show no significant difference in cone size between den and reference sites as was also found by Kucheravy et al. (2021).

We found strong relationships between the number of cones per tree and the number of total seeds and filled seeds per tree. However, the relationship between the number of cones per tree and the number of viable seeds per tree was weak, meaning that studies only using cone

counts may not truly reflect the tree's reproductive potential. Also, if many seeds are unfilled, the total number of seeds is not relevant in terms of a food source for animals or recruiting seedlings. Still, it does show the potential for reproductive output under ideal conditions. In denser forests with greater pollination success or at lower latitudes, the relationship between the number of cones per tree and the number of viable seeds per tree may be stronger (Kambo & Danby 2018). While other studies in less harsh environmental conditions, such as lower latitudes, could use cone counts as an index for reproductive output, studies at a species range limit cannot. Cone counts alone take much less manual labour and time, so there is merit in not extracting seeds if cone counts sufficiently estimate seed production. Whether or not the seeds are viable does not impact seed predators and the filled seeds contain nutrient-rich endosperm.

The highly localized seed production at den sites could have large ecological effects by creating hotspots of food availability for granivorous animals. This increase in food could affect the foraging behaviour and population dynamics of American red squirrels, a major consumer of white spruce seeds (Smith 1968; Hurlly & Lourie 1997; LaMontagne & Boutin 2007, 2013). The low portion of filled seeds in cones we found, creates a challenge for squirrels, which typically spend a large effort harvesting cones each fall. In addition, the lack of a relationship between the number of cones per tree and the number of filled seeds in a cone would imply that cone numbers cannot be used as a cue for balancing the effort put into cone harvesting versus the rewards of seed consumption. The low proportion of filled seeds within cones may explain why red squirrels in this region are much more reliant on consuming fungi than seeds (Alexandra Windsor, personal communication), whereas red squirrels are considered seed specialists in much of their range (Boutin et al. 2006). Other white spruce seed consumers include Northern red-backed voles, *Clethrionomys rutilus*, (Smith & Folkard 2001), birds (Hafthorn 1974; Holimon et al. 1998; Adkisson 1999; Smith & Folkard 2001), and several invertebrates (Svensson et al. 2018; Leeper & LaMontagne 2021). On the tundra, the increased plant biomass at Arctic fox den sites indirectly attracts one of the foxes' primary prey, collared lemmings (*Dicrostonyx groenlandicus*), through the increased insulative properties of deep snow drifts, along with numerous other potential prey (Gharajehdaghpour & Roth 2018; Zhao et al. 2022). While red squirrels, and songbirds are not common prey of red foxes, further research is needed to determine if squirrels could be attracted to den sites due to their increased seed production.

It is generally assumed that the northern boreal treeline is the result of a temperature limitation on seed development (Sirois 2000). Our results suggest that nutrients can play an important role in seed production in a harsh climate, and nutrient hotspots, such as red fox den sites, and increased nutrient availability, in general, may improve the resilience of conifers to disturbance. We suggest further research is needed into the effects of denning and other forms of animal redistribution of nutrients on plant performance in other nutrient-limited systems.

Conclusion

We investigated the effects of the ecosystem engineering activities of red foxes on the reproductive output of white spruce trees by examining the production and viability of seeds during a non-mast year. Our hypothesis that reproductive output was limited at the northern treeline due to nutrient deficiency was largely supported. We found that trees located at den sites produced significantly more filled seeds and viable seeds than control sites which represent greater reproductive output and an important food source for granivorous animals like red squirrels. The relationship between the number of cones per tree and the number of viable seeds per tree was weak, meaning that only using cone counts may not truly reflect the tree's reproductive potential at the range limit. These results suggest red foxes influence the reproduction of white spruce trees at all levels and could have larger effects on the rest of the ecological community. We suggest further exploration of the seed production between mast and non-mast years, investigating seed predation between den sites and reference sites, and the effects of red foxes on white spruce in the centre of their distribution range.

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Author contribution statement

JSB collected and analyzed most of the data and wrote most of the paper. JDR assisted with data analysis and contributed to the paper elaboration. JHM designed and supervised the study, collected, and analyzed part of the data, wrote part of the paper, and directed the projects that funded the study. All authors discussed the analyses, results, implications, and commented on the manuscript at all stages.

CRedit authorship contribution statement

Justin S. Benjamin: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **James D. Roth:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **John H. Markham:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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