

ARTICLE

Red foxes enhance long-term tree growth near the Arctic treeline

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Funding information

Canadian Botanical Association; Laurie
Consaul Northern Studies Award;
Churchill Northern Studies Centre;
Northern Research Fund; NSERC;
Discovery Grants; University of Manitoba;
Fieldwork Support Program; Wildlife
Society (Canadian Section and Manitoba
Chapter Student Travel awards)

Handling Editor: Rebecca J. Rowe

Abstract

Recent climate warming is expected to increase tree growth and productivity, substantially altering ecological function and boundaries in northern ecosystems. Although climate largely determines the range and growth of trees in any biome, variations in microsite conditions can influence growth on a finer scale. Red foxes (*Vulpes vulpes*) are found in most terrestrial ecosystems and are considered ecosystem engineers through their denning activities. Added soil nutrients from prey remains, feces, and urine could benefit tree growth on dens in subarctic regions by alleviating soil nutrient limitations. We examined growth in white spruce (*Picea glauca*) trees growing on eight red fox dens and paired control sites at the Arctic treeline. Radial growth was 55% higher for trees on dens than on control sites between 1897 and 2017, despite similarities in tree ages and densities. This enhanced growth was more pronounced in younger trees, consistent with the decrease in growth with age among all trees. By promoting tree growth near the treeline, red foxes may act as hotspots for tree reproduction. Although the impacts on tree growth largely depend on the spatial distribution of dens, predators can create distinct microhabitats across the landscape, leading to increased vegetation productivity, persisting over many decades.

KEYWORDS

boreal forest, dendroecology, ecosystem engineer, *Picea glauca*, tree rings, *Vulpes vulpes*

INTRODUCTION

Vegetation structure and function in northern ecosystems have changed considerably over the past few decades in response to climate warming. Increasing atmospheric temperatures have been associated with greater plant growth, earlier growing seasons, and thawing permafrost, all of which may be contributing to an increased abundance of shrubs in the tundra (Bjorkman et al., 2018;

Kropp et al., 2021; Post et al., 2009). Although climate warming has been projected to advance northern treelines (Greenwood & Jump, 2014; Pearson et al., 2013), recent remote sensing studies suggest that tree migration overall has been highly variable across different regions (Rees et al., 2020; Sniderhan et al., 2021; Timoney & Mamet, 2020). Localized shifts in the treeline can occur at sites where tree growth is enhanced, resulting in regional heterogeneity at the edge of the treeline. In particular,

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since boreal and subarctic terrestrial ecosystems are N limited, increased N availability can increase tree performance at the northern range limit (Sullivan et al., 2015). There is also a growing body of evidence suggesting that plants in these systems acquire the majority of their nitrogen through their mycorrhizal associations (Hobbie & Hobbie, 2006) and that mycorrhizal fungi can be quite variable in their ability to access organic nitrogen (Clemmensen et al., 2021; Hobbie et al., 2013). Therefore, a better understanding of the factors influencing tree growth near the treeline is needed.

At the global scale, temperature and precipitation primarily determine the growth of trees (Rees et al., 2020; Woodward et al., 2004). However, the effects of environmental factors on tree growth often act in combination with one another, making their impacts on tree performance difficult to predict. While temperature influences the duration of the growing season, it also alters rates of soil organic matter decomposition and evapotranspiration (Jarvis & Linder, 2000; Sveinbjörnsson et al., 2002), thereby affecting tree growth through several mechanisms. Tree growth can also be affected at finer scales due to microsite variability in soil organic matter or nutrient availability. Consequently, any factors contributing to microsite variation can influence tree performance within a particular set of climatic conditions.

Animal abundance and activity can modify tree growth at a local scale through a variety of mechanisms (Sveinbjörnsson et al., 2002). By consuming the outer bark, phloem, and cambial tissues of trees, mammals physically damage trees (Holtmeier, 2012; Payette, 1987; Sullivan et al., 1993), which can reduce tree growth and survival. In particular, snowshoe hares (*Lepus americanus*) may reduce rates of northern treeline expansion by browsing white spruce (*Picea glauca*) saplings (Olnes et al., 2017). Large ungulates also negatively impact treelines by rubbing on trees, trampling, wallowing, and bedding, leading to soil erosion and disturbance (Holtmeier, 2012). Some vertebrates also alter plant composition or growth indirectly by consuming herbivores or influencing habitat conditions and resources. Vertebrate disturbance can also have positive effects on tree recruitment by exposing the mineral soil for seeding establishment (Tremblay & Boudreau, 2011). By consuming leaf-damaging insects, some insectivorous bird species indirectly improve tree growth (Marquis & Whelan, 1994). By manipulating soil conditions, such as nutrient concentrations, some animals may also create favorable growing conditions for trees. For example, brown bears (*Ursos arctos*) may promote tree growth by providing nutrients via salmon remains in terrestrial habitats (Hilderbrand et al., 1999; Quinn et al., 2018).

Red foxes (*Vulpes vulpes*) are widely distributed worldwide (Larivière & Pasitschniak-Arts, 1996) and are considered ecosystem engineers by concentrating soil nutrients through organic waste, depositing prey remains, and disturbing soils at den sites (Godó et al., 2018; Kurek et al., 2014; Lang et al., 2021). These activities alter vegetation composition on dens compared to the surrounding habitat. Previously, we examined the impacts of red fox denning at the Arctic treeline, quantifying soil nutrient concentrations, soil respiration, depth of the organic soil layer, and vegetation composition on red fox dens and paired control sites (Lang et al., 2021). Soils on dens had 81% more inorganic nitrogen, 250% more extractable phosphorus, and elevated CO₂ production. Dens were also dominated by nutrient-demanding plant species that associate with arbuscular mycorrhizae, whereas non-den areas had stress-tolerant ericaceous species. In addition to affecting plant composition, plant growth may also be influenced by improved soil characteristics. As fox dens can persist in the landscape and are reused over many decades (Gallant et al., 2012; Nakazono & Ono, 1987), the continual effects of denning may have long-term effects on plant communities.

Our objective was to examine the long-term impacts of red fox denning on tree growth. We examined tree rings from white spruce, which forms the Arctic treeline across the North American boreal forest, on red fox dens and paired control sites. We predicted trees near dens would benefit from nutrient additions to dens. Examining the duration of fertilization effects by red foxes can not only provide better insight into the functional role of red foxes as ecosystem engineers but can also be used to understand the role that nutrient limitation has on tree performance at the forest–tundra ecotone.

METHODS

Our study area is located in the Hudson Bay Lowlands ecoregion (58°46' N and 94°10' W) in the forest–tundra transition zone, which forms an ecological boundary at the north/northeast edge of the boreal forest (Dredge, 1992). The local climate is affected by Hudson Bay, resulting in short and cool growing seasons (Smith et al., 1998). The landscape is dominated by fens and bogs, interspersed with gravel ridges deposited by glacial activity (Smith et al., 1998). Red foxes den on these gravel ridges (Roth, 2003), which are dominated by open coniferous forest stands, while lowlands have greater sedge, moss, and lichen cover (Ritchie, 1957). Tree stands have open canopies and are composed of three main tree species: white spruce dominates upland sites where red foxes den; black spruce (*Picea mariana*) dominates wet areas;

and tamarack (*Larix laricina*) are dispersed throughout (Girardin et al., 2005).

In July 2018, we collected tree cores from white spruce trees at the same den and paired off-den sites (controls) examined in Lang et al. (2021). The den center was estimated as the midpoint between the two outermost burrows, and off-den sites were located 50 m from the den center. Despite clear differences in vegetation and soil on the red fox dens, both den and off-den sites were otherwise ecologically comparable (i.e., similar elevation, slope, distance to water, and surrounding vegetation outside the sampling sites). These sites are most of the known woodland fox dens within an 8000-ha area and were selected because they are not associated with human disturbance.

We extracted cores from the five closest white spruce trees to the den and control site centers that were greater than 10 cm diameter at breast height (dbh), for a total of 40 den trees and 40 control trees. All cores were taken at 30 cm above the base of the tree, for maximum tree age estimates (Fraver et al., 2011). We collected two cores on opposite sides of each tree to facilitate cross-dating and obtain an accurate ring count in the event of suppressed/compressed rings on one side of the tree (Speer, 2010). We also recorded tree circumference at coring height. Tree density was estimated using the total number of trees >10 cm dbh within a 15-m radius around the center of the dens and paired control sites in August 2019. We then used the tree cross-sectional areas and densities to determine the basal area, that is, total stem area per hectare.

All cores were prepared following standard dendrochronological methods (Speer, 2010). Using a VELMEX UniSlide stage micrometer and the program MeasureJ2X, we measured the ring widths of each core (Tardif et al., 2008). Prior to measuring, we matched ring width patterns to visually cross-date the cores using both the list method (Phipps, 1985) and pointer years (i.e., narrow rings, pale latewood rings) previously identified for the region (Girardin et al., 2005; Tardif et al., 2008). We then validated the accuracy of the measurements and cross-dating using the program COFECHA (Holmes, 1983). Since the pith was missing from some cores, the determined tree ages were minima. As radial growth often deviates slightly between paired cores from any given tree due to uneven mechanical stress (Speer, 2010), we averaged radial growth measurements for the overlapping years from the two matching cores to provide a single growth series for each tree. The oldest regions of the cores, where no overlapping portion was present, were excluded from the analysis.

We compared annual radial growth for dens and controls between 1897 and 2017 (the period over which we had cores from at least 10 trees from den and control sites) using general linear mixed-effects models in the nlme

package in R (Pinheiro et al., 2019). Den versus control sites was a fixed effect. Tree cambial age (ring number from the pith) was included as a covariate since tree-ring growth slows with maturity (Mamet & Kershaw, 2013). Tree ID nested in den ID was included as a random effect. We also included the corAR1 autocorrelation structure into the model since, within a tree, growth in any given year depends on growth in the previous year (Speer, 2010). Models with and without autocorrelation were compared using likelihood ratio tests. Radial growth measurements (in millimeters) were log-transformed to meet model assumptions (linearity and homoscedasticity). To examine the response of trees of different ages to denning, we separated the trees from all sites into young (45–90 years), medium (91–125 years), and old (126–180 years) age classes. These classes were selected to maximize the sample size for both den and control sites. For each model, we calculated variation within trees as the difference between conditional and marginal R^2 as a proportion of the conditional R^2 .

White spruce growth in the Churchill area is particularly influenced by climate during June and July (Girardin et al., 2005; Mamet & Kershaw, 2013; Tardif et al., 2008). Using climate data (adjusted and homogenized surface air temperature and total precipitation) from Churchill weather station A (<https://www.canada.ca/en/>) between 1932 and 2011, we examined annual radial tree growth during this time period using a linear mixed-effects model with den and off-den (control) as a fixed effect, as well as cambial age and climate variables (June mean temperature, July mean temperature, and July total precipitation) as covariates. Years with missing climate data (1999, 2000, 2001, and 2010) were excluded from the analysis. Tree ID nested in den ID was used as a random effect, and the corAR1 autocorrelation structure was included in the model. We also compared the mean annual increment (stem cross-sectional area divided by age) between den and control sites using a linear mixed effects model with tree ID nested in den ID as a random effect. This same model was used to compare tree age and distance to the center of the site between den and control sites. We used paired t tests to compare tree density and basal area between the den and off-den sites.

RESULTS

Trees on dens had larger annual radial growth than trees on control areas over the entire radial growth chronology, that is, from 1897 to 2017 ($F_{1,78} = 26.190$, $p < 0.0001$ for the treatment effect; Figure 1; Appendix S1: Table S1). Within-tree variation accounted for 58.8% of the total variation in the model. Averaging individual tree annual growth over time, trees on dens had 55% higher growth

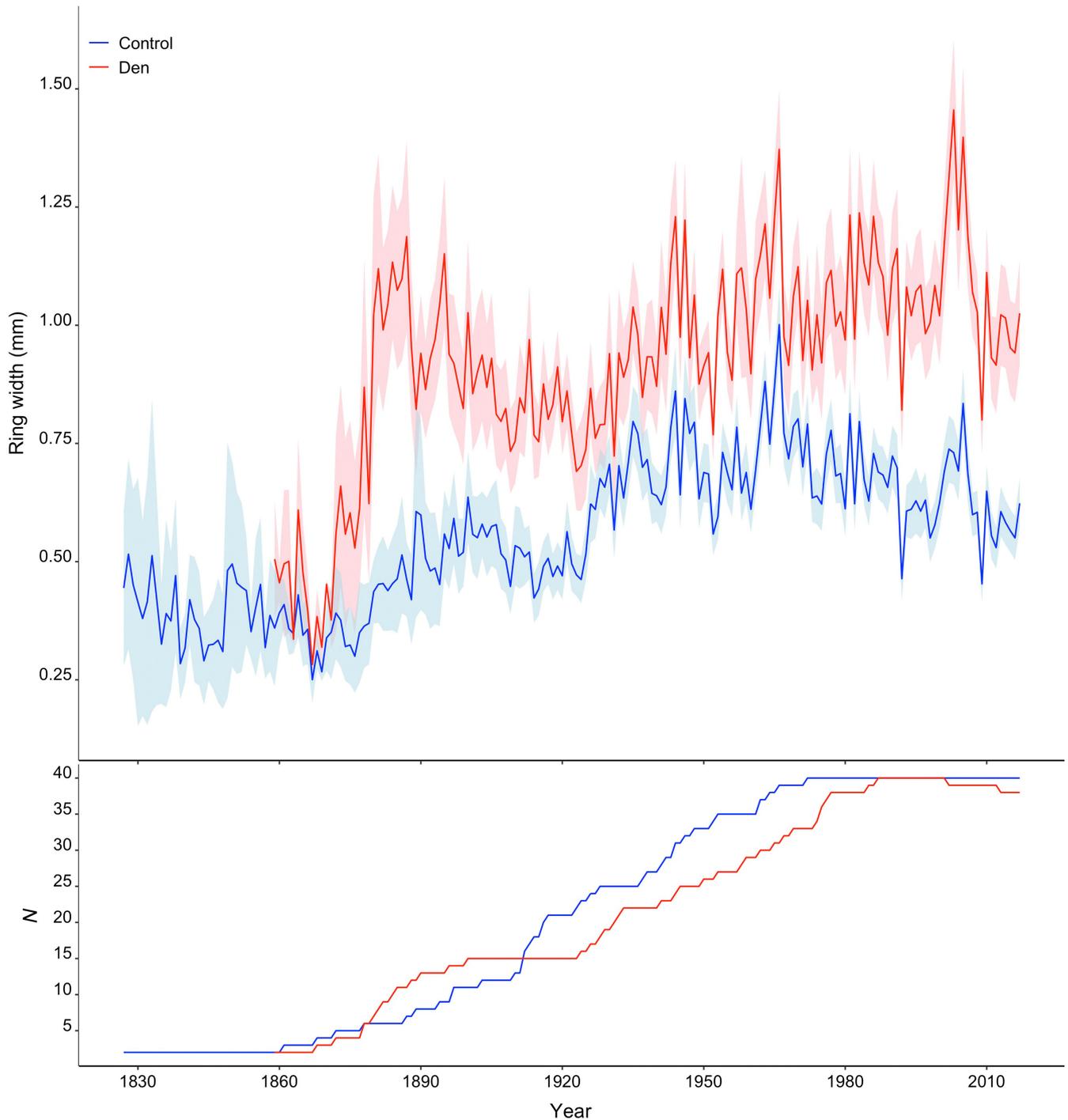


FIGURE 1 Ring width increments (mean \pm SE) and corresponding tree sample size (N) between 1808 and 2017 from all sampled white spruce on red fox dens and paired control sites near Churchill, Manitoba, Canada.

(1.02 ± 0.01 mm/year, mean \pm SE) than trees on control sites (0.66 ± 0.01 mm/year). Similarly, when growth was averaged over the life of the tree, the annual increment was 90% higher on dens (629.9 ± 67.2 mm²/year) than on controls (331.9 ± 37.1 mm²/year; $F_{1,78} = 24.633$, $p < 0.0001$). Annual radial growth significantly declined with age ($F_{1,7051} = 74.183$, $p < 0.0001$), whether or not the trees were located on fox dens. Tree age did not

significantly differ between dens (104 ± 8 years) and controls (121 ± 7 years; $F_{1,78} = 2.881$, $p = 0.0936$). The minimum age of trees on dens ranged from 37 to 209 years, compared to 47–239 years on control sites.

When separated into age classes, trees on dens had 61.2% higher growth in the young age class ($F_{1,22} = 10.100$, $p = 0.0044$), 49.9% higher growth in the medium age class ($F_{1,19} = 11.837$, $p = 0.0027$), and 47.9% higher growth in

the old age class ($F_{1,24} = 10.893$, $p = 0.0030$; Figure 2). Cambial age was a significant predictor of growth in the medium age class ($F_{1,1875} = 78.514$, $p < 0.0001$) and the old age class ($F_{1,3333} = 53.337$, $p < 0.0001$), but not the young age class ($F_{1,1410} = 0.038$, $p = 0.8451$). Separating trees into age classes had little effect on the proportion of

model variation associated with individual trees, with 61.5%, 43.9%, and 61.8% in the young, medium, and old age classes, respectively, associated with individual trees.

When climate covariates were included in the model as fixed effects, denning ($F_{1,78} = 23.622$, $p < 0.0001$ for the treatment effect), June mean temperature

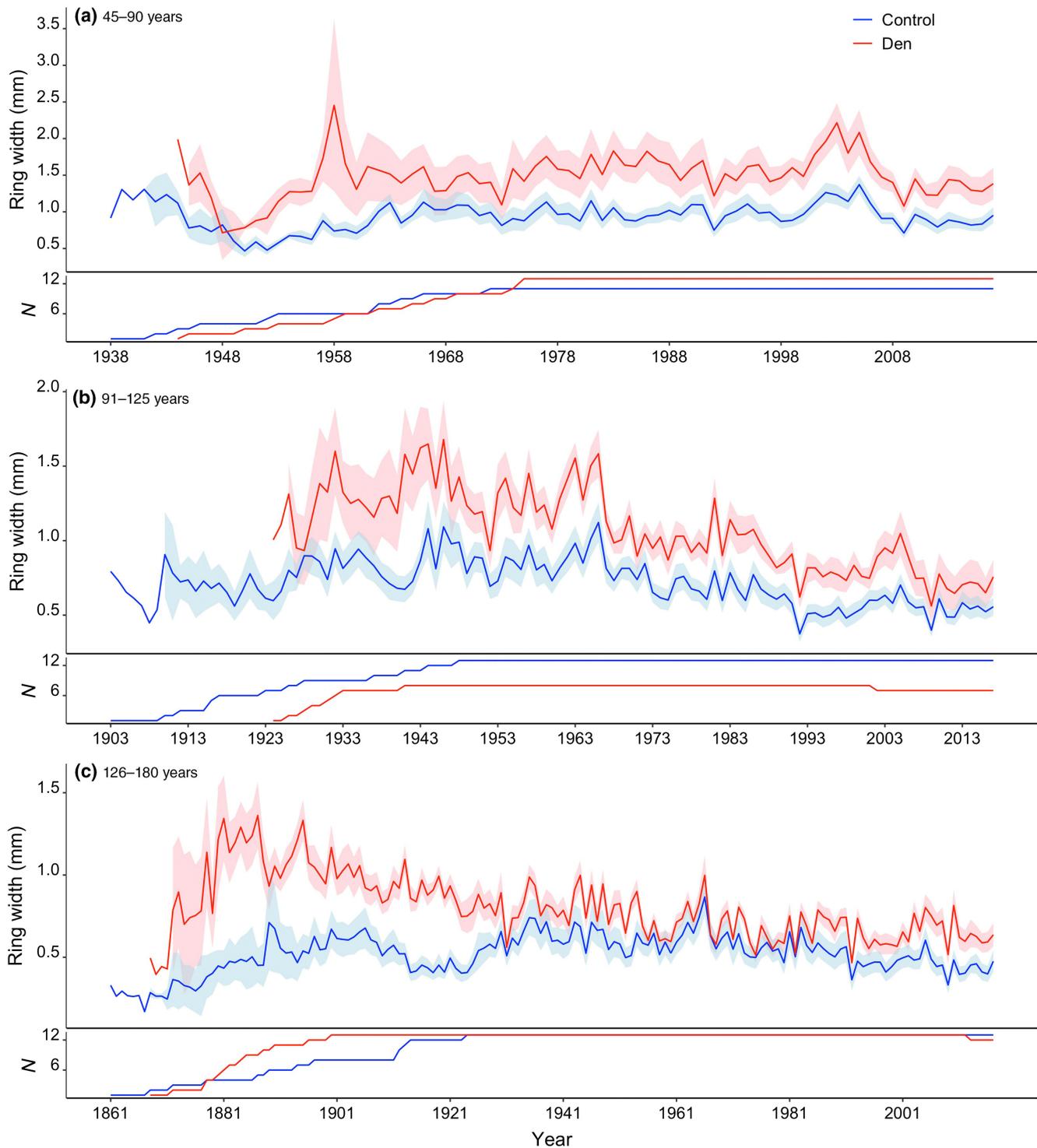


FIGURE 2 Ring width increments (mean \pm SE) and corresponding tree sample size (N) for white spruce divided into (a) young, (b) medium, and (c) old age classes.

($F_{1,5109} = 170.260$, $p < 0.0001$), July mean temperature ($F_{1,5109} = 283.386$, $p < 0.0001$), and July total precipitation ($F_{1,5109} = 10.800$, $p = 0.0010$) all positively influenced radial growth, while age negatively affected growth over time ($F_{1,5109} = 167.091$, $p < 0.0001$), as growth slows with maturity. Including the autocorrelation structure significantly improved all the models of annual radial growth ($p < 0.0001$ according to likelihood ratio tests).

Basal area did not significantly differ between dens (11.6 ± 2.2 m²/ha) and controls (7.5 ± 1.9 m²/ha; $t_6 = -1.210$, $p = 0.2719$). However, increasing our sample size from 8 to 15 paired sites would have achieved sufficient power (0.800) to detect a significant difference in basal area, with the same effect size (0.768). This power analysis suggests that basal area may be greater on dens given the higher radial growth than control sites. Tree density did not differ between dens (362 ± 61 trees/ha) and controls (320 ± 52 trees/ha; $t_6 = -0.451$, $p = 0.6680$). Likewise, the distance of each tree to the site center did not differ between dens (8.8 ± 0.6 m) and controls (8.4 ± 0.7 m; $F_{1,76} = 0.237$, $p = 0.6279$).

DISCUSSION

Our study demonstrates that red fox denning has a positive and sustained effect on the growth of white spruce trees at the Arctic treeline. Tree radial growth is determined by complex interactions between environmental variables and stand characteristics (Vaganov et al., 2006). Consistent with other studies, temperature and precipitation positively increased tree growth in our study region (Boonstra et al., 2008; Girardin et al., 2005; Mamet & Kershaw, 2013). Yet, tree growth can also be largely influenced by smaller scale habitat conditions and resources (Fitzpatrick et al., 2020). In each of our models, denning was a significant predictor of ring width, with higher radial growth in white spruce on dens between 1897 and 2017 at treeline, despite similarities in tree densities, climate, and age across all sites. Our previous work found that red fox dens were dominated by tall, erect shrubs, grasses, and forbs, whereas control sites are mainly dominated by prostrate shrubs, which we attributed to the higher nutrient concentrations on dens (Lang et al., 2021). The nutrients added by red foxes likely also resulted in the higher radial growth observed in white spruce. A similar response was found in a fertilization experiment by Boonstra et al. (2008), where white spruce radial growth increased by 9%–48% relative to control sites. That study also found a positive growth response to summer temperature, consistent with our study. Despite the enhanced radial growth by NPK fertilization, Boonstra et al. (2008) found continual fertilization

was required to maintain enhanced radial growth, as ring width declined immediately after supplemental fertilization ended.

Although foxes frequently use the same den sites for decades, they may be absent from dens in some years. Gharajehdaghipour et al. (2016) found that soil nutrient concentrations on Arctic fox (*V. lagopus*) dens remained consistently higher than control sites even in years when foxes did not occupy dens. This finding suggests nutrient enrichment can carry over from one year to the next. Therefore, tree cores may be limited in their ability to provide year-to-year information on red fox denning activity. Red foxes have been present in the area since at least 1733 (Robson, 1752). The dens in this study were first identified in 1994 (Roth, 2003), but our results indicate that trees growing on den sites have had higher growth as far back as 1897, suggesting the dens may have been occupied, at least periodically, since then.

Harsh environmental stressors, such as wind, snow, and nutrient limitations, typically restrict tree growth at the Arctic treeline, leading to stunted trees with delayed cone production (Grace et al., 2002; Kambo & Danby, 2018). Enhanced growing conditions by red foxes may increase the recruitment and establishment of new trees at the Arctic treeline. Kucheravy et al. (2021) found that trees on dens produced more cones in non-mast years compared to trees on control sites. As cone production is positively correlated with tree height (Bronson, 2020), higher growth rates may also facilitate cone production at younger ages on den sites. Although we did not find a difference in the density of mature trees, further investigation into the presence and growth of saplings on red fox dens may provide additional insight into the role of red foxes in tree recruitment at the Arctic treeline. If improved tree performance at the Arctic treeline results in increased sapling recruitment and establishment, then red foxes could ultimately have a role in advancing the treeline. As the effects of denning are highly localized, the location and density of red fox dens in the region have a large role in determining if and where treeline position could be affected. Impacts to treeline position would therefore likely be greatest in areas where red fox dens are more abundant.

By denning at the transition zone between two ecosystems, red foxes consistently influence soil resources. While denning affects plant composition and growth, it also likely affects other community members. For example, passerine bird species composition may be positively affected near subarctic treeline with increased vegetation species richness and volume (Lewis & Starzomski, 2015). Increased tree growth at den sites could therefore improve habitat and resource conditions by improving foraging, perching, and nesting opportunities for birds, as well as other arboreal species.

Our study highlights the importance of predators in the Subarctic, beyond trophic impacts, through their role as ecosystem engineers. Ecosystem engineers are often considered for the spatial extent of their impacts, yet the temporal scale should be equally considered when evaluating their impacts (Hastings et al., 2007; Petrosillo & Zurlini, 2016). Similar to beavers (*Castor canadensis*), where the effects of dam construction can permanently shift forest riparian zones into meadow ecosystems, despite dams only being occupied for an average of 4 years (Hastings et al., 2007), the impacts of red fox denning can extend far beyond the lifespan of one individual fox. Both the spatial distribution of predator denning activities across the landscape and the duration of their impacts are important factors that should be considered to better understand ecosystem function, particularly at the Arctic treeline. Given the increased performance of trees on den sites, further research is needed to determine if den sites act as hot spots for tree recruitment and the expansion of the treeline.

ACKNOWLEDGMENTS

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada (Discovery Grants to James D. Roth, Jacques C. Tardif, and John H. Markham, and a Canadian Graduate Scholarship [Masters] to Jessica A. Lang), Canadian Botanical Association (Laurie Consaul Northern Research Fund to Jessica A. Lang), the University of Manitoba (Fieldwork Support Program to James D. Roth and John H. Markham and Graduate Fellowship and Oakes-Riewe Aboriginal-Environmental Studies Research Award to Jessica A. Lang), the Churchill Northern Studies Centre (Northern Research Fund), and the Wildlife Society (Canadian Section and Manitoba Chapter Student Travel awards). The authors thank France Conciatori for help in the dendroecology lab and the Churchill Northern Studies Centre staff for help throughout the field season.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R code (Lang et al., 2022) are available from Dryad: <https://doi.org/10.5061/dryad.34tmpg4mq>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lang, Jessica A., James D. Roth, Jacques C. Tardif, and John H. Markham. 2022. "Red Foxes Enhance Long-Term Tree Growth near the Arctic Treeline." *Ecosphere* 13(9): e4236. <https://doi.org/10.1002/ecs2.4236>