

**Red foxes engineer the boreal forest: impacts of denning on vegetation near
the Arctic treeline**

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Abstract

Terrestrial predators are known for their role in controlling herbivore populations, but they can also influence vegetation by altering soil nutrients through excretions and redistributing prey remains. Added nutrients, specifically nitrogen and phosphorus, can modify plant assemblages by alleviating nutrient limitations in soils, thereby altering plant diversity and growth. Red foxes (*Vulpes vulpes* L.) are a top predator in the Subarctic, and their dens, which are reused over many years, could serve as biogeochemical hotspots for soil nutrients. If nutrient additions by red foxes alter the availability of resources for other organisms, such as plants, then red foxes can be considered ecosystem engineers. My thesis examined the impacts of denning on soils, plant assemblages and tree growth in the Subarctic boreal forest, near Churchill, Manitoba, Canada. I quantified and compared soil characteristics (inorganic nitrogen, extractable phosphorus, soil pH and respiration), understory vegetation composition (diversity and abundance) and the growth of white spruce (*Picea glauca* (Moench) Voss) between red fox dens and paired control sites. Red fox denning increased soil nutrients, pH and respiration (microbial activity), which could indicate higher rates of nutrient mineralization. By increasing soil nutrients and disturbance, red fox denning increased the cover of woody shrubs (*Salix* L. spp.), grasses (*Leymus mollis* (Trinius) Pilger) and weedy ephemerals on dens compared to control sites. Increased nutrients also promoted long-term radial growth of white spruce trees on dens, despite having stand characteristics otherwise similar to control sites. Denning by red foxes therefore creates distinct microhabitats near the Arctic treeline. Predators that engineer ecosystems can play critical roles in the structure of ecological food webs by modifying habitat resources in addition to trophic interactions, and can therefore influence a broad suite of other organisms.

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Thesis Format

This thesis is in manuscript format, with each chapter written as an individual manuscript. Each chapter therefore contains its own abstract, introduction, methods, results, discussion, references and figures. The introduction and conclusion provide background information and connect my research to broader ecological implications beyond what is described in each chapter.

I conducted all the fieldwork related to this research, with assistance from my colleagues for polar bear monitoring, assessing fox dens, collecting tree cores and tree height measurements. I performed all laboratory work, data analyses and the writing of this thesis with guidance from my committee members and France Conciatori, who provided guidance for dating, crossdating, measuring and validating my tree core measurements.

Thesis Introduction

Ecologists have long debated the factors that drive primary productivity. The ‘green world’ hypothesis proposed by Hairston *et al.* (1960) was among the first to spark the idea that predators have a role in regulating vegetation by depressing herbivore populations. Subsequently, the exploitative ecosystems hypothesis (Oksanen *et al.* 1981; Oksanen and Oksanen 2000) proposed that only when primary productivity is high do predators affect vegetation by controlling herbivores. Many studies have focused exclusively on predator-prey interactions to understand the functional role of predators within the community. These hypotheses assume predator abundance and effort are the primary determinants of the predator’s effect on vegetation composition and productivity. While predators have a clear role in modifying vegetation by consuming herbivores, they could also modify vegetation through alternative mechanisms (Schmitz *et al.* 2010).

Predators may influence vegetation by dispersing seeds, altering soil fertility and disturbing soils by digging. Mammals, including predators, can alter seed dispersal via various mechanisms, such as through epizoochory, where seeds adhere to fur (Couvreur *et al.* 2008; Kulbaba *et al.* 2009). Adherence and dispersal of seeds depend on morphological and ecological traits of both mammals and plant species (Couvreur *et al.* 2004; Kulbaba *et al.* 2009). For example, seed adhesion is typically higher in animals with longer fur (Couvreur *et al.* 2004; Quick *et al.* 2016). Predators could also disperse seeds in their feces by consuming vegetation (Willson 1993) or unintentionally through their prey (diploendozoochory) (Hämäläinen *et al.* 2017). For example, López-Darias and Nogales (2016) found considerable quantities of seeds from multiple weed species in pellets of raptors that consumed herbivores, despite raptors being obligate carnivores. Unlike the traditional hypotheses examining the role of predators on

vegetation by consuming herbivores, the impacts of diploendozoochory do not depend on the suppression of herbivore populations, but on the dietary preference of seeds consumed by herbivores, as well as the hunting efforts by predators.

By altering habitat conditions, such as by increasing soil nutrient concentrations, predators can also affect plant assemblages. Specifically, predators may create nutrient hotspots by transporting prey carcasses across or within landscapes to feeding sites and depositing organic waste (Schmitz *et al.* 2010; Leroux and Schmitz 2015). For example, Hilderbrand *et al.* (1999) examined nitrogen stable isotopes in white spruce (*Picea glauca* (Moench) Voss) needles and found that brown bears (*Ursos arctos* L.) facilitate the transport of nitrogen by consuming salmon and subsequently excreting feces and urine. Similarly, Ben-David *et al.* (1998) found that scent-marking by river otters (*Lontra canadensis* Schreber) increased nitrogen content in grasses and mosses by concentrating marine-derived nutrients at coastal latrine sites. Arctic foxes (*Vulpes lagopus* L.) also influenced soil nutrients by reducing seabird densities, and therefore guano input by seabirds, on the Aleutian Islands through predation (Croll *et al.* 2005). As a result of less fertile soils, islands with introduced Arctic foxes had lower vegetation biomass (Croll *et al.* 2005). Furthermore, in addition to the deposition of prey remains, food hoarding and caching have also been documented in a variety of predators, such as raptors, canids, mustelids and bears, as a strategy for maximizing food intake regardless of prey fluctuations (Collopy 1977; Smith and Reichman 1984). While most food items are typically retrieved shortly after being cached, some are never found (Collopy 1977), which could increase soil nutrients at cache sites.

Other behaviours, such as digging, can disturb soils and remove vegetation. Predators may dig to excavate burrows or search for subterranean prey, which can alter soil characteristics and composition, such as soil moisture and litter quality (Valentine *et al.* 2017). As predicted by

the intermediate disturbance hypothesis, plant diversity can increase in a given area if disturbance occurs at intermediate levels (frequency or intensity) by permitting species that thrive at both early and late successional stages (Connell 1978; Hobbs and Hueneke 1992). Typically, the mixing of soils from digging initially benefits the growth of weedy ephemerals, which are able to colonize rapidly after disturbance (Grime 1974; Grime 1979; Kurek *et al.* 2014). For example, digging by grizzly bears improved conditions for ephemeral species (Tardiff and Stanford 1998), which can increase species richness and diversity following initial recolonization (Doak and Loso 2003).

Red foxes (*Vulpes vulpes* L.) are typically known for their impacts on small mammal and waterfowl populations through predation, but increasing evidence suggests that red foxes could also influence vegetation through several of the aforementioned mechanisms. For example, Rosalino and Santos-Reis (2009) found that red fox feces in Mediterranean Europe contained seeds from as many as 35 fruit species, indicating foxes may consume fruit as part of their diet. Similarly, red fox feces collected from Kampinos National Park, Poland, contained both seeds and feathers, which was attributed to foxes being possible secondary seed dispersers through the consumption of herbivores (Kurek and Holeksa 2015). Although studies on epizoochory in red foxes are limited, Hovstad *et al.* (2009) found that red fox fur was capable of retaining seeds from several different plant species simultaneously. Prey caching has also been well documented in red foxes (MacDonald *et al.* 1994; Sklepkovych and Montevicchi 1996). Furthermore, red foxes occupy dens (Larivière and Pasitschniak-Arts 1996; Roth 2003; Gallant *et al.* 2012), which could serve as localized hotspots of high soil nutrient concentrations and distinct plant diversity. Since red foxes typically give birth to 3-6 pups that remain inside the dens for several weeks until fully weaned (Larivière and Pasitschniak-Arts 1996), dens may receive continual nutrient

input each year during breeding season from feces, urine and prey remains, as well as frequent soil disturbance by excavating burrows. Additionally, dens may also be hotspots for seeds dispersed via endozoochory and epizoochory processes. By modifying the quantity and quality of resources, red foxes could be considered as ecosystem engineers (Jones *et al.* 1994).

The effects of climate change, such as increasing temperatures, can significantly alter plant composition and distribution in northern ecosystems (Grace *et al.* 2002; Post *et al.* 2009; Bjorkman *et al.* 2018). In addition to occupying the largest distribution of any carnivore (Larivière and Pasitschniak-Arts 1996), red foxes are becoming more abundant at the northern edge of their distribution, possibly due to warmer temperatures in the Arctic (Bartoń and Zalewski 2007; Berteaux *et al.* 2015). As such, the impacts of denning on soil characteristics and vegetation in northern ecosystems could have repercussions for ecosystem function in an already sensitive area.

In this thesis, my objective was to identify and quantify the effects of red foxes as ecosystem engineers at the transition zone between Subarctic boreal forest and tundra. Specifically, I examined red fox dens located at Arctic treeline near Churchill, Manitoba, Canada. Treeline in this area is expanding towards the tundra (Tews 2004; Mamet and Kershaw 2012), which is likely due to changes in climate and availability of soil nutrients. More than twenty known red fox dens occur in this area (Roth 2003), yet many of these dens are situated close to the coast, where vegetation differs from the boreal forest, or in areas of high human disturbance, such as gravel pits, buildings or roads, which could lead to confounding influences on vegetation composition. To minimize this bias, I exclusively sampled at dens located in natural boreal forest, where human disturbance is minimal. I therefore excluded dens that are either in 1) highly disturbed areas (gravel pits, major roads) or 2) located outside of the boreal

forest (i.e. on the tundra along the coast.). In the first chapter, I quantified the denning impacts by examining soil characteristics, such as soil nutrients, as well as understory vegetation. The second chapter builds upon the first chapter and examines the long-term impacts of red fox denning on tree growth using dendroecological analyses of white spruce. Examining the role of red foxes can provide insight into the broader ecological importance of predators in structuring the spatial distribution and diversity of resources across the landscape, which can therefore influence a variety of other organisms through non-trophic interactions.

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Chapter 1. Foxes fertilize the forest: denning modifies Subarctic plant diversity and soil characteristics

Abstract

Ecosystem engineers modify habitats through processes other than trophic interactions, which ultimately influences the availability of resources for other organisms. Through denning, red foxes (*Vulpes vulpes* L.) could engineer local ecosystems by enhancing soil nutrients through excrements and prey remains, as well as mixing soils through digging. In the Subarctic boreal forest, where cold climates typically limit soil fertility and primary productivity, red fox denning could increase plant diversity and growth by providing nutrients to soils. I compared soil and vegetation characteristics between red fox dens and paired control sites near Churchill, Manitoba, Canada. Dens had 81% more inorganic nitrogen and 250% more extractable phosphorus in the soil organic layer, which was thick on both dens (mean \pm SE = 0.46 ± 0.04 m) and controls (0.31 ± 0.06 m). Denning also altered soil respiration and pH in the organic layer, suggesting improved soil quality and nutrient availability for plants. Vegetation was distinct on dens, with a greater coverage of willows (*Salix* L spp.), whereas control sites were dominated with prostrate shrubs, such as black crowberry (*Empetrum nigrum* Hagerup) and bog bilberry (*Vaccinium uliginosum* L.). By engineering the habitat through denning, red foxes increase plant diversity and richness regionally, creating heterogeneous patches of resources for other organisms. My research highlights the importance of considering predators through alternative mechanisms of interaction with other organisms besides their roles as predators consuming prey, and provides insight into the role of burrowing mammals in modifying plant diversity and productivity by concentrating nutrients and mixing soils through digging.

Introduction

Integrating non-trophic interactions, such as ecosystem engineering, into the study of food webs is essential to understanding the community structure and function of ecological networks (Sanders *et al.* 2014). First defined by Jones *et al.* (1994), ecosystem engineers are organisms that “directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials. In so doing, they modify, maintain, and/or create habitats”. As a result, ecosystem engineers can impact species abundance, diversity and the distribution of other organisms by modifying the distribution of their required resources.

While all organisms may play a role in structuring the physical environment of their habitats (Wright and Jones 2006; Berke 2010), the magnitude of impacts created by certain organisms may be more influential than others, which ultimately distinguishes ecosystem engineers from other ecological classifications. Specifically, ecosystem engineers typically influence the landscape via multiple processes (physical, chemical, etc.), and the resulting impacts should be significant and large (Reichman and Seabloom 2002). Ecosystem engineers create habitat conditions that are uncommon in the landscape, which can increase resource diversity and availability (Wright *et al.* 2002). For example, beavers (*Castor canadensis* Kuhl) are well-known ecosystem engineers whose dams significantly influence aquatic and terrestrial resources, leading to the growth of herbaceous plants that are otherwise absent in the landscape (Wright *et al.* 2002).

Red foxes (*Vulpes vulpes* L.) are found in almost all terrestrial biomes across the globe (Larivière and Pasitshniak-Arts 1996), yet few studies have examined the impacts of red fox denning on plant composition, which can be altered by influencing soil nutrient concentrations

and disturbance. Although previously limited by harsh climate, warming temperatures in Arctic and Subarctic regions over the last century may have facilitated the range expansion and increasing prevalence of red foxes in the North (Bartoń and Zalewski 2007; Berteaux *et al.* 2015). Vegetation in northern ecosystems has also rapidly changed as a result of climate change, resulting in increased plant productivity and shrub abundance on the tundra, as well as decreased productivity or ‘browning’ in many regions of the boreal forest (Post *et al.* 2009; Beck and Goetz 2011; Buermann *et al.* 2014; Bjorkman *et al.* 2018). Soil microbial activity in northern ecosystems is typically restricted by cold soil temperatures, which therefore also limits nutrient uptake by plants and plant growth (Foster and Bhatti 2006). Consequently, Subarctic soils could be especially sensitive to the impacts of red foxes if denning alters microhabitat characteristics, resulting in changes to nutrient availability and plant productivity.

I examined the impacts of red fox denning near the Arctic treeline. My first objective was to examine the influence of denning activity on soil characteristics (nutrient concentrations, soil respiration, depth of organic matter, and pH) that can influence plant growth and diversity. I hypothesized that red foxes modulate soil nutrients on dens through the addition of urine, feces, and prey remains. Specifically, I predicted that soils sampled from red fox dens would have higher concentrations of inorganic nitrogen and extractable phosphorus, the main nutrients taken up by plants for growth and metabolism (Schachtman *et al.* 1998; Nordin *et al.* 2001). Since increased nutrient availability can increase rates of soil microbial activity (Hartley *et al.* 2010), I also predicted that soils on red fox dens would have higher rates of soil respiration.

My second objective was to evaluate if denning subsequently influenced plant composition (diversity and abundance) in the Subarctic boreal forest by altering soil characteristics. I hypothesized that red foxes modulate vegetation composition (diversity and

abundance) by altering soil disturbance and nutrient concentrations. When nutrient limitations are alleviated, plant diversity can change by permitting the establishment and persistence of species that are better competitors for other resources, such as access to sunlight or soil moisture, or species that do not tolerate low-nutrient concentrations (Grime 1974; Grime 1979; Suding *et al.* 2005). In addition to nutrient additions by red foxes, localized soil disturbance created through digging could also influence plants by creating available niches for new plants by removing community biomass and disrupting soil layers. Digging may therefore facilitate the growth of colonizer plant species (Grime 1979). I predicted that soil conditions on red fox dens would favor the growth of erect shrubs due to increased nutrient availability, as well as colonizer species, such as weedy ephemerals, where soil has been disturbed, such as around burrows.

Methods

My fieldwork was conducted in July 2018 in the Coastal Hudson Bay Lowland ecoregion (Hudson Plains ecozone) near Churchill, Manitoba (58°46'09"N and 94°10'09"W; **Figure 1.1**), at the transition zone between the northern boreal forest and the tundra (Smith *et al.* 1998). Between 1981 and 2010, annual precipitation averaged 452.5mm and monthly mean temperature ranged between -26°C and 12.7°C (Environment and Climate Change Canada 2011). The landscape is generally flat with elevated crests (Ritchie 1957; Tews 2004) due to isostatic uplift and glacial retreat following the last glacial period (Smith *et al.* 1998). These ridges provide suitable sites for fox dens, since they have well-drained soils and greater depth to permafrost, which facilitates digging and prevents spring flooding in burrows (Gallant *et al.* 2012). Permafrost is continuous throughout the study area (Smith *et al.* 1998). Vegetation on these dry upland sites is dominated by patchy stands of white spruce (*Picea glauca* (Moech) Voss) and

tamarack (*Larix laricina* K Koch) (Smith *et al.* 1998; Tews 2004). Understory vegetation includes erect shrubs (woody deciduous shrubs with upright stems greater than 15cm in height) such as willows (*Salix* L. spp.) and dwarf birch (*Betula glandulosa* Michaud), prostrate shrubs (short trailing shrubs with woody stems below 15cm in height), such as black crowberry (*Empetrum nigrum* L.) and bog bilberry (*Vaccinium uliginosum* L.), as well as various forbs and graminoids (Johnson 1987).

Fox dens in the study area were previously identified by assessing fox activity, using signs of tracks, digging, vocalizations, urine odor and prey remains as indicators (Roth 2003). Using direct sightings and the presence of red fox guard hairs (red, black or gray with striations), I was able to determine if the dens were occupied by red foxes. All dens have been periodically occupied by red foxes each year since 1994 (Roth unpublished). Each den consists of multiple burrows (typically between 2 and 10), and all burrow entrances are located within a few meters of one another. Red fox dens can have extensive burrow systems, up to 22 meters in length and 1.2m in depth below the surface (Saunders 1988).

At each den (n=8), I determined the centre of the den, defined as the midpoint along a straight line connecting the two outermost burrows, and designated a paired control site, with the centre 50m from the centre of the den, to ensure the control site was well outside the area of all burrows and denning activity (Kurek *et al.* 2014; Gharajehdaghpour *et al.* 2016), while also maintaining a similar habitat type (i.e. similar elevation, slope, soil type etc.). Since fox dens are typically located along gravel ridges, I randomly selected one of two directions running parallel along the ridge, maintaining a constant elevation and slope relative to the den, to determine the control site.

To sample each den and control site, I used five 1-m² quadrats placed at the site centre and 5m from the centre in each cardinal direction (den quadrats were all within the area of the outermost burrows). In each quadrat, I visually estimated vegetation percent cover, by assigning a percentage (1-100%) from the following cover classes: 0%, 1% (trace amount, occurring once or twice), 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 100% (full coverage). A sample of each species was collected as a voucher specimen to be preserved in the University of Manitoba Vascular Plant Herbarium. While I included seedless plants (Bryophyta, Lycopodiophyta and Marchantiophyta) and lichens in my analysis, some could not be identified to species level due to the lack of identifying features in my samples. I also recorded the number of woody stems in each quadrat (stem density) for all erect shrubs.

I collected soil samples from both organic and mineral layers at each quadrat by collecting roughly 250ml of soil using a 0.15m soil auger. If the quadrat landed on a burrow or in areas with extensive digging, creating mixed soil layers, no organic soil was collected. I recorded the depth of the organic layer from each quadrat where I collected organic soil. All soil samples were air dried and stored at room temperature in sealed bags until analysis.

I determined concentrations of inorganic nitrogen (NO_3^- and NH_4^+) and extractable phosphorus (PO_4^{3-}) in a subsample of each soil sample. Soil nutrients were examined in the mineral and organic soil layers separately. I extracted inorganic nitrogen by shaking samples in a 2M NaCl solution. Total inorganic nitrogen was measured using a modified microdiffusion protocol, which included two incubation periods: the first converted NH_4^+ to NH_3 and the second reduced NO_3^- to NH_4^+ and then to NH_3 . These were followed by colorimetric titration of a pH indicator with sulfuric acid (Kahn *et al.* 2000). Phosphorus was extracted using a Bray extraction

(Kuo 1996). I measured concentrations of extractable phosphorus using the Murphy-Riley protocol (Kalra and Maynard 1991).

A subsample of the remaining soil from each quadrat was used to evaluate microbial soil respiration. For each sample, I added deionized water and incubated samples in airtight containers for four hours (Wardle 1993). Using a CO₂ sensor, I examined the change in CO₂ concentrations for each sample (Wardle 1993). I also measured the pH of each soil sample (mixed with deionized water to form a soil slurry).

To compare soil and vegetation characteristics at den and control sites, I used paired t-tests after averaging measurements from the 5 quadrats at each site. To satisfy the assumptions of normality and homoscedasticity, I square root transformed inorganic nitrogen and extractable phosphorus concentrations, but no other variables required transformation (organic layer depth, soil respiration, pH, percent cover of each plant species, species richness (number of species at each site) and stem density). I compared plant diversity between dens and control sites by calculating Shannon-Wiener diversity index values. I used an indicator species analysis (Dufrêne and Legendre 1997) to determine if specific plant species were indicative of den or control sites using the `lapsdv` package in R (Roberts 2016). I also grouped species by functional growth forms (erect shrub, prostrate shrub, forb, sedge, grass, seedless plants and lichen), and compared growth forms using a Monte Carlo Simulation test (Rubinsten 1981), which can be used to examine data that does not follow a normal distribution (e.g. percent cover data which is bound by 0% and 100%). The Monte Carlo Simulation test randomly assigns data to a group, and then shuffles the data over many repetitions to generate a null distribution used to examine a test statistic (Gotelli and Ellison 2004). Specifically, I examined the difference between percent cover of each growth form from dens and controls over 10,000 repetitions.

Results

Depth of the organic layer did not differ between dens (mean \pm SE = $0.46 \pm 0.04\text{m}$) and controls ($0.31 \pm 0.06\text{m}$; $t_7 = -1.919$, $p = 0.096$). In the organic soil layer, dens had 81% more total inorganic nitrogen compared to control sites ($t_7 = -3.288$, $p = 0.013$), but in the mineral layer, total inorganic nitrogen did not differ (**Figure 1.2A**; $t_7 = -1.551$, $p = 0.165$). Similarly, the organic layer on dens had 250% more extractable phosphorus compared to control sites ($t_7 = -5.282$, $p = 0.001$), but in the mineral layer, extractable phosphorus did not differ between dens and controls (**Figure 1.2B**; $t_7 = 0.271$, $p = 0.795$).

Dens had higher soil respiration compared to controls in the organic layer (**Figure 1.3**; $t_7 = -3.351$, $p = 0.012$), but soil respiration did not differ between dens and controls in the mineral layer ($t_7 = -0.890$, $p = 0.401$). The organic layer on dens was more basic (**Figure 1.4**) compared to control sites ($t_7 = -2.677$, $p = 0.032$). The mineral layer was overall more basic than the organic layer for both dens and controls but the mineral layer did not differ in pH between dens and controls (**Figure 1.4**; $t_7 = 1.147$, $p = 0.289$).

Species richness (total number of species) was significantly higher on dens (mean \pm SE = 17.38 ± 0.73) compared to controls (13.13 ± 0.67 ; $t_7 = -6.298$, $p < 0.001$). Dens had higher plant diversity (Shannon $H' = 2.63$) compared to controls (Shannon $H' = 2.30$). Stem number tended to be higher on dens (7.35 ± 2.58) compared to control sites (1.55 ± 0.82 ; $t_7 = -2.164$, $p = 0.067$).

Indicator species for dens included tall willows (*Salix glauca* L. and *Salix athabascensis* Raup), fireweed (*Chamaenerion angustifolium* L.), sea lyme-grass (*Leymus mollis* (Trinius) Pilger) and large-flowered wintergreen (*Pyrola grandiflora* Radius). Indicator species for control sites included black crowberry (*Empetrum nigrum*), bog bilberry (*Vaccinium uliginosum*), white

mountain-avens (*Dryas integrifolia* Vahl), and star reindeer lichen (*Cladonia stellaris* L.) (**Table 1.1**).

Dens had significantly higher cover of erect shrubs ($p < 0.001$), grasses ($p = 0.007$) and forbs ($p < 0.001$) compared to control sites, but lower cover of prostrate shrubs ($p = 0.006$) and lichens ($p = 0.003$) (**Figure 1.5**). Dens and controls did not differ in cover of seedless plants ($p = 0.145$) or sedges ($p = 0.450$).

Discussion

My results demonstrate that red foxes have enriched the soils on their dens by concentrating nutrients in the organic layer, whereas denning did not affect nutrient concentrations in the mineral layer. Higher microbial activity (soil respiration) on red fox dens could result in greater availability and uptake of nutrients by plants compared to control sites. Through the combined effects of nutrient additions and soil disturbance, which was absent on control sites, red foxes may increase microhabitat heterogeneity on dens (Wijesinghe *et al.* 2005) resulting in higher plant species richness and atypical dominating vegetation growth forms at the Arctic treeline.

The organic layer is essential for storing nutrients and maintaining moisture required by plants (Firlotte and Staniforth 1995; Craswell and Lefroy 2001) and is likely where nutrient additions by red foxes are predominately held. While the organic layer is generally acidic in the boreal forest (Moore 1980; Vance and Chapin III 2001), the organic layer on dens was more basic compared to control sites. Similarly, Kurek *et al.* (2014), found that soil mounds produced by burrowing red foxes and badgers (*Meles meles* L.) were also more basic compared to the surrounding topsoil, which they attributed to the mixing of soil layers. By excavating burrows,

red foxes mix a portion of the mineral layer into the organic layer, but it is unlikely that red foxes similarly influence mineral soils given the unidirectional nature of excavating burrows. Red foxes could therefore increase pH in the organic layer without increasing soil nutrient concentrations or decreasing soil pH in the mineral layer. Alternatively, since red fox feces are typically slightly basic (Green and Flinders 1981), the deposition of feces, as well as urine, may also increase basicity in the organic layer.

Microbial activity is closely linked to soil characteristics, such as soil pH (Wardle 1993; Vance and Chapin III 2001). Specifically, acidic soils typically have lower soil respiration, which is indicative of lower microbial activity (Persson *et al.* 1989; Vance and Chapin III 2001). Since the den organic layer had both higher soil respiration and pH compared to control sites, red foxes may improve substrate conditions for microbial activity through denning. Improved soil conditions in the den organic layer could lead to a greater uptake of nutrients by plants compared to control sites. In comparison, soil respiration is lower in the mineral layer compared to the organic layer, and I did not find a difference in respiration between den and control mineral layers. Microbial activity predominantly occurs in the organic layer relative to the mineral layer (Lee *et al.* 2013; Yu *et al.* 2018), so soil respiration should be lower in the mineral layer compared to the organic layer regardless of whether the soil came from a den or control site.

While nutrient additions and increased microbial activity could result in increased decomposition (Facelli and Pickett 1991; Hartley *et al.* 2010) and therefore a shallower organic layer, the organic layer depth did not differ between dens and controls. These results may be explained by the feedback between vegetation biomass on dens compared to controls. Although I did not specifically measure vegetation biomass, dens were dominated by large erect shrubs, which suggest greater aboveground plant biomass. Higher standing biomass generally leads to

greater litter accumulation, if all other processes that reduce litter accumulation or biomass, such as herbivory, are equal (Facelli and Pickett 1991). Therefore, it is possible that the differential rate of decomposition on litter/organic matter depth are negated by the increased plant biomass found on dens compared to controls, resulting in no apparent difference in organic layer depth between dens and controls.

Soil pH, nutrient concentrations and nutrient uptake all affect plant growth and diversity. As soil nutrient concentrations increase, competition for alternative resources may alter plant diversity (Grime 1974; Grime 1979; Suding *et al.* 2005). My results show a clear shift of plant functional traits on dens, which are dominated by erect shrubs, grasses, and forbs, compared to control sites, which are dominated by lichens and trailing prostrate shrubs. The presence of tall, erect shrubs may explain the marginal difference in stem density on dens compared to controls.

Indicator species, which reflect environmental conditions of a particular habitat, for den sites included tall willows (*Salix L. spp.*), fireweed (*Chamaenerion angustifolium*), sea lyme-grass (*Leymus mollis*) and large-flowered wintergreen (*Pyrola grandiflora*). Tall willows and sea lyme-grass are common on moist or wet soils, and are mainly found close to the coast or near water bodies (Johnson 1987). Large-flowered wintergreen also prefers moist areas, growing underneath taller shrubs, such as willows, that provide ample shading (Johnson 1987). Sea lyme-grass and fireweed are both common in areas of high disturbance and sandy soils (Johnson 1987) such as in burn areas, gravel pits or alongside roads. Indicator species for control sites included black crowberry (*Empetrum nigrum*), bog bilberry (*Vaccinium uliginosum*), white-mountain avens (*Dryas integrifolia*), which are small trailing plants, as well as star reindeer lichen (*Cladonia stellaris*). Black crowberry, bog bilberry and reindeer lichen generally grow in acidic

soils (Hall *et al.* 1964; Johnson 1987), while white-mountain avens is common throughout the Churchill area on most terrains (Johnson 1987).

Overall, plant communities observed on red fox dens were distinct from control sites, reflecting different microhabitat and soil conditions. Previous studies have shown that foxes preferentially select den sites based on favourable habitat characteristics, such as areas where prey are more abundant (Kurek *et al.* 2014; Márton *et al.* 2016). Red fox den selection in the Subarctic is especially limited given the necessity of selecting elevated ridges due to abundant wetlands, so foxes likely select existing den sites or available spaces along ridges to construct new dens where prey is abundant, regardless of soil fertility and plant diversity. As such, the impacts on vegetation composition are more likely the result of denning impacts, as opposed to pre-existing conditions prior to den construction. Additionally, since the dens in my study are at least 25 years old, the continual soil disturbance and excretions by foxes over multiple decades have influenced community structure, resulting in the current distinct vegetation composition, regardless of pre-existing soil conditions.

Similar impacts have also been observed by red foxes in other regions. For example, Kurek *et al.* (2014), found that red fox dens in a temperate forest in Poland had higher available phosphorus and plant diversity relative to reference sites. In a separate study by Godó *et al.* (2018), red foxes increased soil nutrients through denning on grassland kurgans in Hungary, but decreased vegetation cover, species richness and litter depth, which created favourable growing conditions for invasive plants and weeds. Although increased soil nutrients and disturbance on red fox dens are consistent in other studies, the response of vegetation may have varied across different ecosystems due to the available species composition in the soil seed bank.

Similar impacts of denning have also been documented in an ecologically similar predator species. Specifically, Arctic fox (*Vulpes lagopus* L.) dens on the tundra also had high cover of willows (*Salix* spp.), sea lyme-grass (*Leymus mollis*) and fireweed (*Chamaenerion angustifolium*) (Gharajehdaghypour *et al.* 2016; Fafard *et al.* 2019). Red foxes have encroached onto the tundra in recent years, where they now occupy dens created by Arctic foxes (Roth unpublished). While the ecological impacts by Arctic and red foxes on the tundra have not been compared, the similarity of impacts I documented in the boreal forest suggest that red foxes could also alter plant diversity and soil dynamics on the tundra as well. Despite red foxes having larger bodies, they have smaller litters (mean 3-6 compared to 6-12 pups in Arctic foxes) (Larivière and Pasitschniak-Arts 1996; Audet *et al.* 2002) and defecate less on dens than Arctic foxes (Friesen 2013). Furthermore, compared to the tundra, the boreal forest has higher soil nutrients and vegetation biomass (Thompson *et al.* 2004; Orlova *et al.* 2013). Overall, nutrient additions by either species would likely have a larger impact on the tundra than in the boreal forest, and dens occupied by Arctic foxes may have higher nutrient concentrations given the larger litter sizes and abundance of feces compared to red foxes. Further exploration of red fox dens on the tundra could provide a better understanding of denning as an ecosystem engineering process, the role of ecosystem type in determining the response of vegetation to denning, and the possible consequences of red fox range expansion onto the tundra.

In conclusion, foxes engineer landscapes on a local scale through denning, and their impacts can have important roles in providing services at the ecosystem level. Carcass sites, which generally have nutrient enriched vegetation, often become foraging sites for herbivores (Towne 2000). Red foxes could also provide ecosystem services to herbivores by enhancing vegetation composition, like Arctic foxes on the tundra (Gharajehdaghypour and Roth 2018). By

denning at the transition zone between the boreal forest and tundra, red foxes may influence resources used by both boreal forest and tundra organisms. In addition, while the impacts of denning occur at a local scale, the lifespan and collective impacts of all dens could result in implications for long-term landscape and ecosystem function.

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Figures

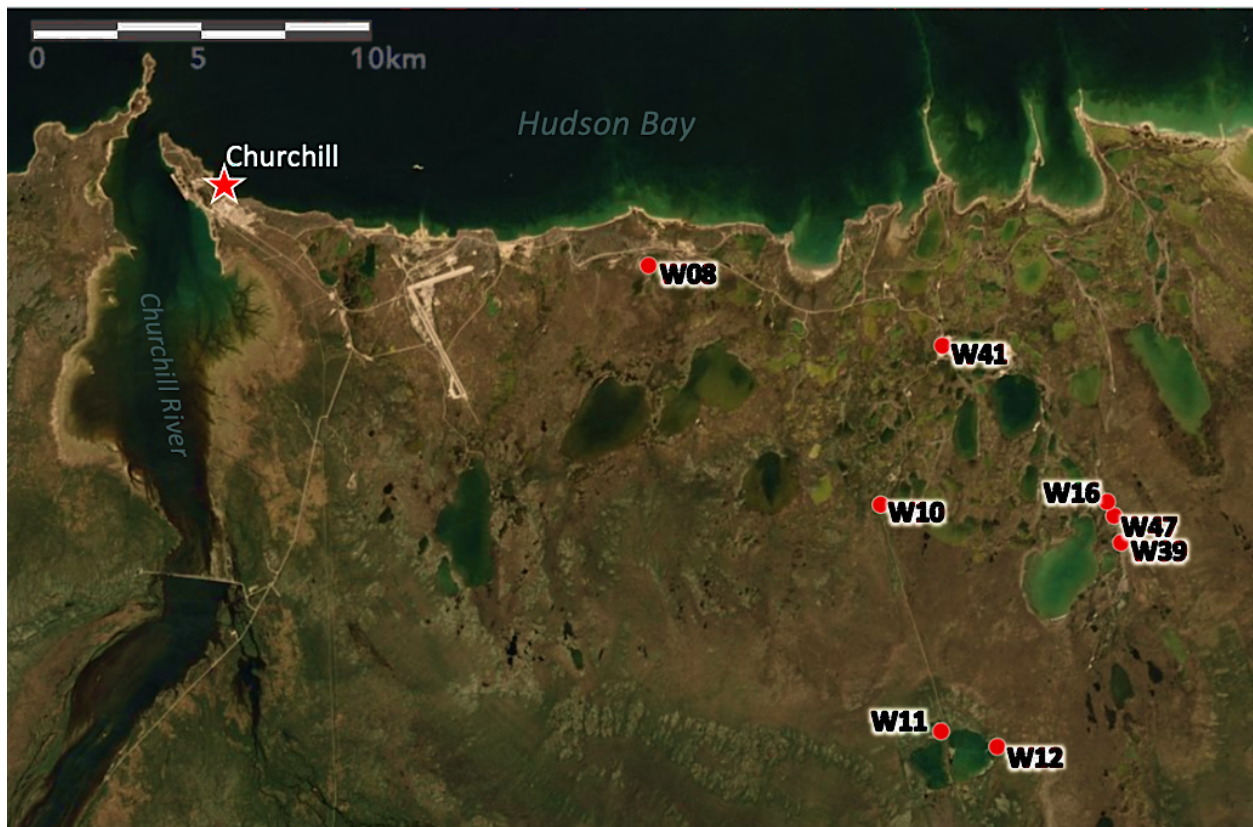


Figure 1.1. Map of Churchill, Manitoba, Canada ($58^{\circ}46'09''\text{N}$ and $94^{\circ}10'09''\text{W}$) and surrounding area indicating red fox dens examined in this study (red circles, $n=8$).

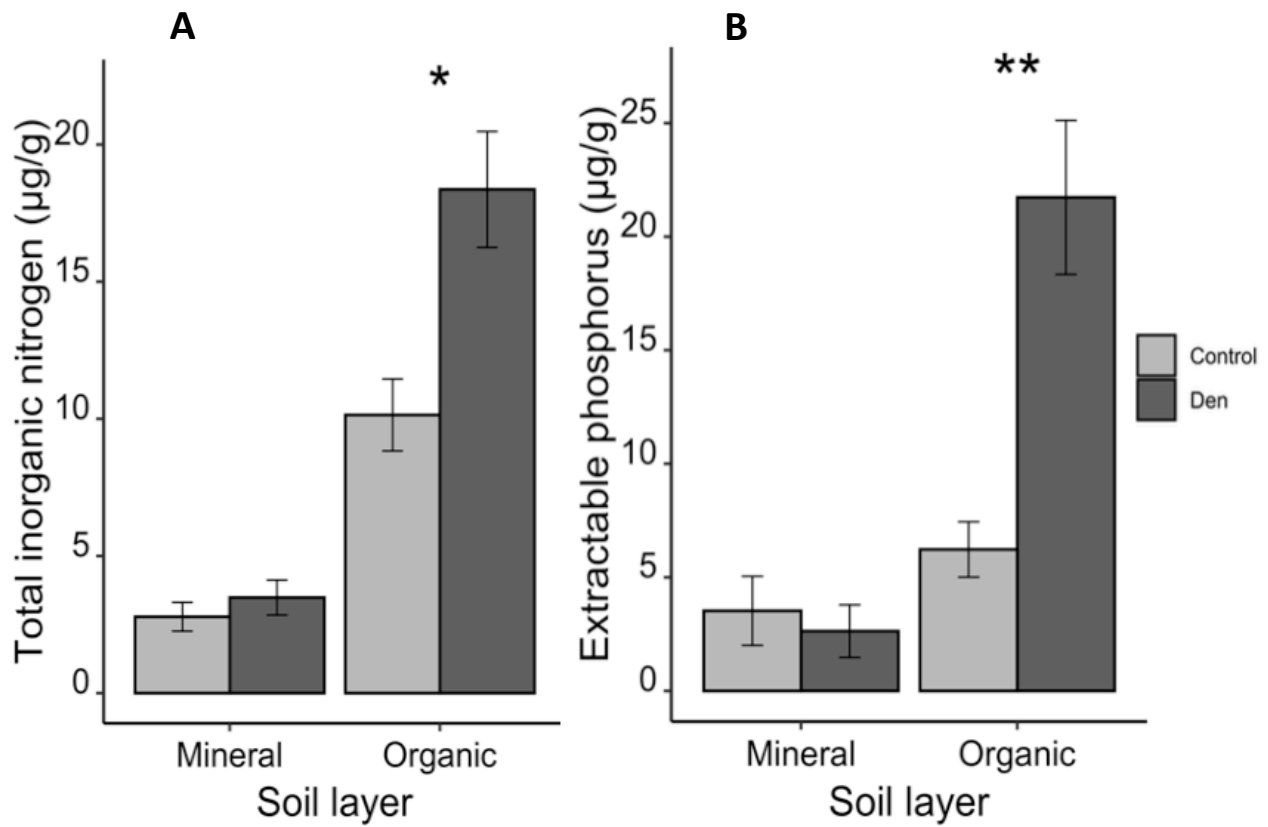


Figure 1.2. Concentrations (mean \pm SE) of (A) inorganic nitrogen and (B) extractable phosphorus in the organic and mineral soil layers from red fox dens and paired control sites (n=8) near Churchill, MB, Canada, in July 2018. (*) $p < 0.05$, (**) $p < 0.01$.

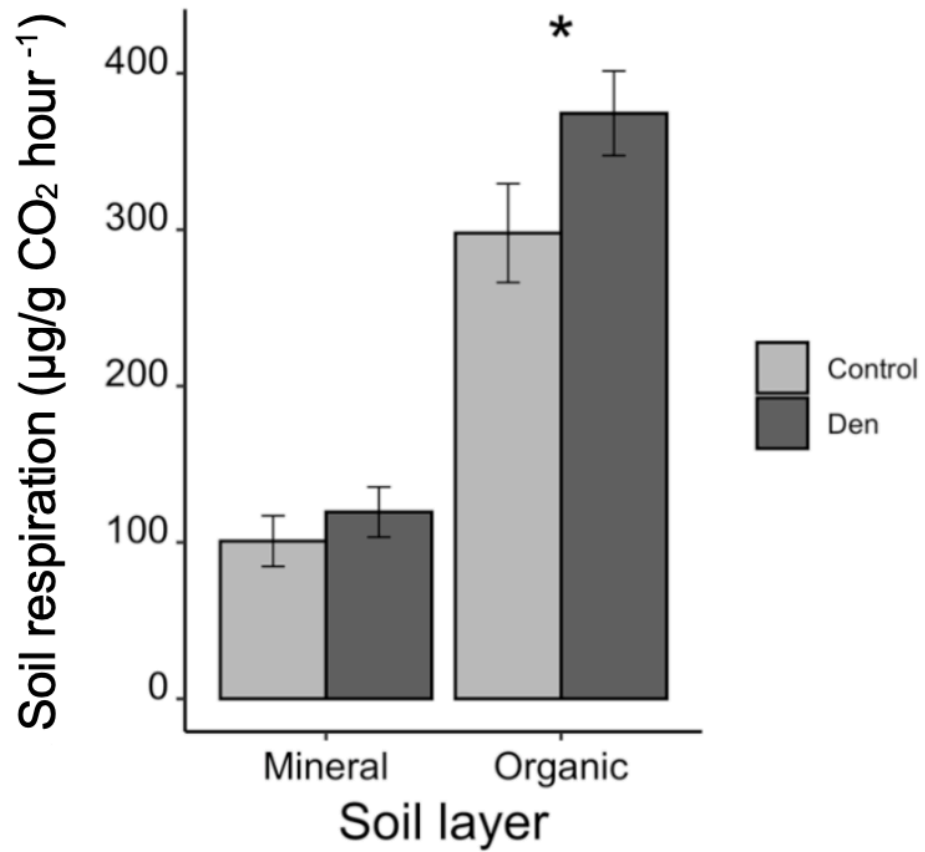


Figure 1.3. Soil respiration (mean \pm SE) in the organic and mineral soil layers from red fox dens and paired control sites (n=8) near Churchill, MB, Canada, in July 2018. (*) $p < 0.05$.

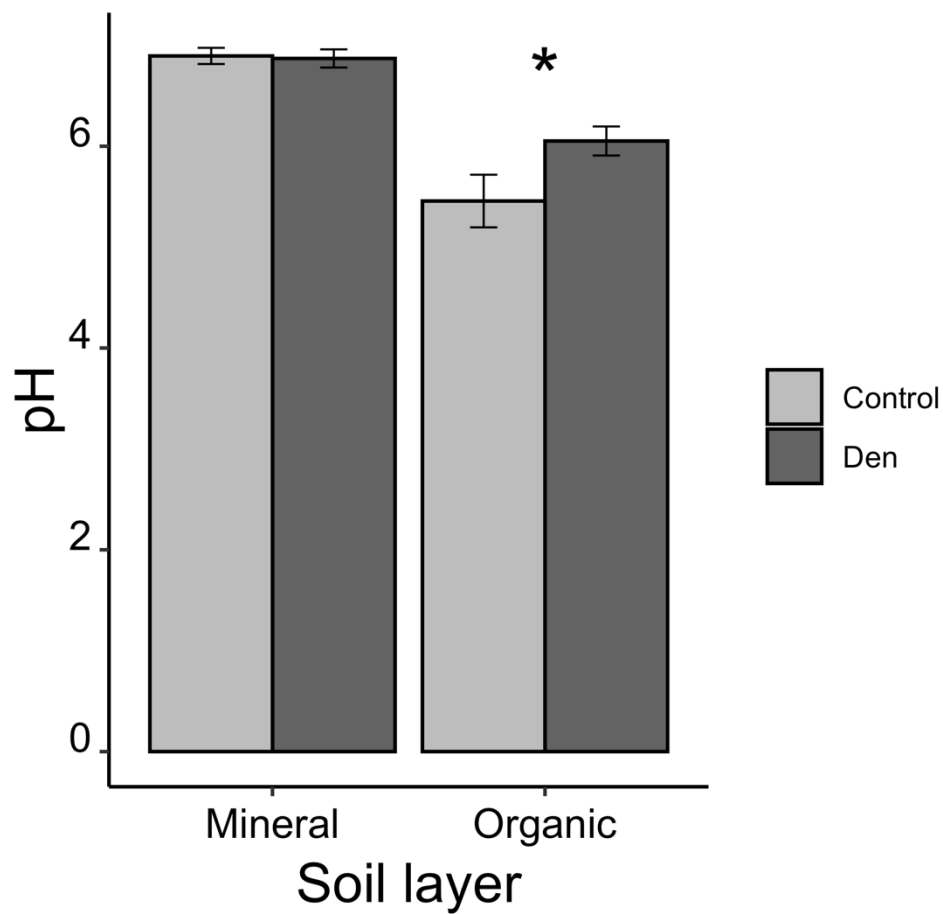


Figure 1.4. Soil pH (mean \pm SE) in the organic and mineral soil layers from red fox dens and paired control sites (n=8) near Churchill, MB, Canada, in July 2018. (*) $p < 0.05$

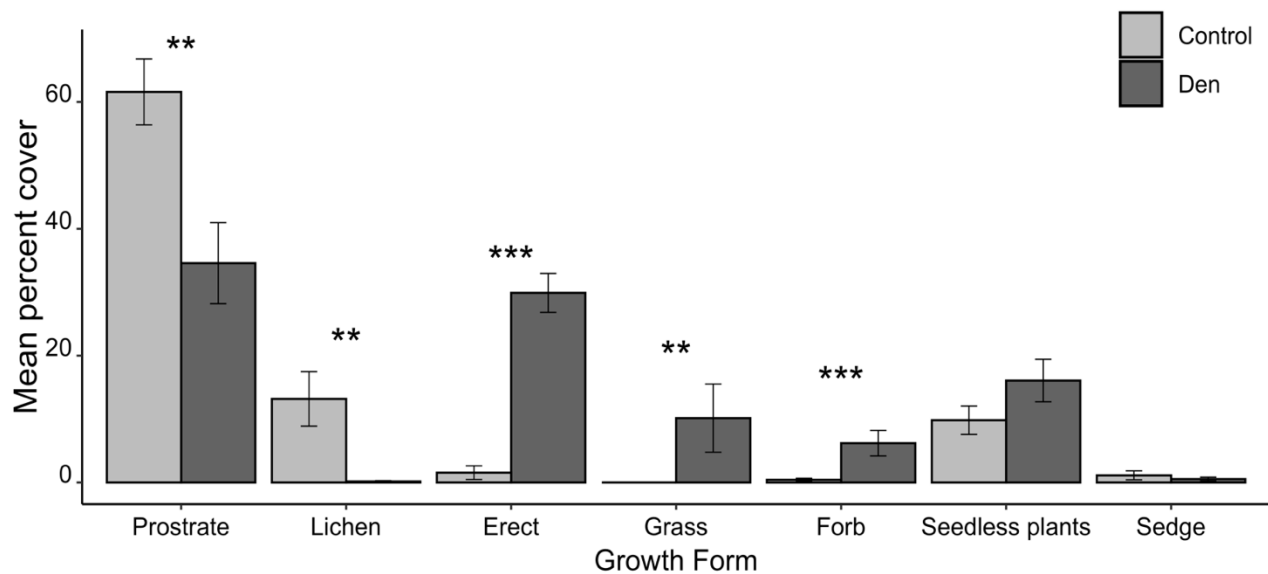


Figure 1.5. Cover of vegetation growth forms (mean \pm SE) from red fox dens and paired control sites near Churchill, MB, Canada, in July 2018. Growth forms include prostrate shrubs, lichens, erect shrubs, grasses, forbs, seedless plants (Bryophyta, Lycopodiophyta and Marchantiophyta), and sedges. (**) $p < 0.01$ and (***) $p < 0.001$ using a Monte Carlo Simulation test.

Table 1.1. Relative abundance (percent cover) and indicator analysis for plant species on dens and controls. Significant indicators are bolded ($p < 0.05$).

Plant species	Control percent cover (mean \pm SE)	Den percent cover (mean \pm SE)	Control indicator values	Den indicator values	P-value
Prostrate shrubs					
<i>Andromeda polifolia</i>	0.5 \pm 0.4	0.0 \pm 0.0	0.250	0.000	0.462
<i>Arctous^a</i>	2.2 \pm 1.1	5.6 \pm 2.0	0.210	0.630	0.185
<i>Dryas integrifolia</i>	3.0 \pm 1.4	0.0 \pm 0.0	0.625	0.000	0.025
<i>Empetrum nigrum</i>	27.9 \pm 4.3	10.5 \pm 2.8	0.727	0.273	0.004
<i>Rhododendron tomentosum</i>	4.6 \pm 3.0	1.9 \pm 1.5	0.353	0.074	0.355
<i>Rubus acaulis</i>	0.0 \pm 0.0	0.8 \pm 0.6	0.000	0.375	0.194
<i>Salix reticulata</i>	0.2 \pm 0.2	1.8 \pm 1.3	0.041	0.556	0.269
<i>Shepherdia canadensis</i>	5.5 \pm 2.4	3.0 \pm 2.2	0.565	0.177	0.240
<i>Vaccinium uliginosum</i>	14.4 \pm 1.8	6.9 \pm 2.7	0.678	0.322	0.041
<i>Vaccinium vitis-idaea</i>	2.0 \pm 0.4	4.1 \pm 1.2	0.327	0.673	0.116
Erect shrubs					
<i>Betula glandulosa</i>	0.9 \pm 0.6	4.7 \pm 1.8	0.062	0.627	0.055
<i>Juniperus communis</i>	0.1 \pm 0.1	1.6 \pm 1.6	0.009	0.116	1.000
<i>Salix^b</i>	0.5 \pm 0.5	23.2 \pm 3.4	0.003	0.979	0.000
<i>Ribes hudsonianum</i>	0.0 \pm 0.0	0.4 \pm 0.3	0.000	0.250	0.471
Forbs					
<i>Achillea millefolium</i>	0.0 \pm 0.0	0.3 \pm 0.2	0.000	0.375	0.203
<i>Anemone richardsonii</i>	0.0 \pm 0.0	0.5 \pm 0.3	0.000	0.375	0.200
<i>Bartsia alpina</i>	0.0 \pm 0.0	0.0 \pm 0.0	0.125	0.000	1.000
<i>Bistorta vivipara</i>	0.3 \pm 0.3	0.0 \pm 0.0	0.125	0.000	1.000
<i>Chamaenerion angustifolium</i>	0.3 \pm 0.0	0.7 \pm 0.2	0.005	0.843	0.004
<i>Fragaria virginiana</i>	0.0 \pm 0.0	0.7 \pm 0.4	0.000	0.500	0.076
<i>Geocaulon lividum</i>	0.1 \pm 0.1	0.8 \pm 0.5	0.008	0.352	0.205
<i>Kalmia procumbens</i>	1.4 \pm 1.4	0.0 \pm 0.0	0.125	0.000	1.000
<i>Moneses uniflora</i>	0.0 \pm 0.0	0.3 \pm 0.3	0.000	0.125	1.000
<i>Mitella nuda</i>	0.0 \pm 0.0	0.2 \pm 0.1	0.000	0.375	0.202
<i>Pedicularis flammea</i>	0.3 \pm 0.3	0.0 \pm 0.0	0.063	0.063	1.000
<i>Pyrola grandiflora</i>	0.0 \pm 0.0	1.7 \pm 0.7	0.002	0.739	0.011
<i>Solidago multiradiata</i>	0.0 \pm 0.0	1.2 \pm 0.1	0.000	0.500	0.077
<i>Stellaria longipes</i>	0.0 \pm 0.0	0.1 \pm 0.0	0.063	0.063	1.000

Plant species	Control percent cover (mean ± SE)	Den percent cover (mean ± SE)	Control indicator values	Den indicator values	P- value
Grasses					
<i>Leymus mollis</i>	0.0 ± 0.0	10.1 ± 5.4	0.000	0.625	0.025
<i>Poa arctica</i>	0.0 ± 0.0	0.1 ± 0.1	0.000	0.375	0.199
Sedges					
<i>Carex concinna</i>	0.5 ± 0.3	0.0 ± 0.0	0.125	0.000	1.000
<i>Carex scirpoidea</i>	0.6 ± 0.6	0.3 ± 0.2	0.171	0.157	1.000
<i>Carex vaginata</i>	0.0 ± 0.0	0.3 ± 0.3	0.000	0.125	1.000
Seedless plants (Bryophyta, Lycopodiophyta and Marchantiophyta)					
<i>Dicranum</i> spp.	2.0 ± 1.3	1.4 ± 1.0	0.221	0.309	0.892
<i>Lycopodium annotinum</i>	0.0 ± 0.0	0.3 ± 0.3	0.000	0.125	1.000
<i>Moss</i> sp. 1	0.0 ± 0.0	2.0 ± 2.0	0.002	0.123	1.000
<i>Plagiochila</i> spp.	0.0 ± 0.0	0.1 ± 0.0	0.000	0.125	1.000
<i>Pleurozium schreberi</i>	7.8 ± 2.3	12.3 ± 1.7	0.340	0.611	0.141
Lichens					
<i>Cladonia</i> ^c	1.0 ± 0.0	0.0 ± 0.0	0.125	0.000	1.000
<i>Cladonia bacilliformis</i>	0.1 ± 0.1	0.0 ± 0.0	0.250	0.000	0.465
<i>Cladonia stellaris</i>	12.3 ± 4.3	0.2 ± 0.1	0.988	0.003	0.001
<i>Flavocetraria nivalis</i>	0.3 ± 0.2	0.0 ± 0.0	0.500	0.000	0.071
<i>Lichen</i> spp.	0.5 ± 0.5	0.0 ± 0.0	0.125	0.000	1.000
<i>Peltigera</i> spp.	0.0 ± 0.0	0.8 ± 0.0	0.000	0.250	0.456
Trees					
<i>Larix laricina</i>	7.3 ± 6.1	0.0 ± 0.0	0.500	0.000	0.079
<i>Picea glauca</i>	3.3 ± 1.8	1.2 ± 0.4	0.461	0.164	0.472

^a Given the absence of berries, I was unable to distinguish between *Arctous rubra* and *A. alpina*.

^b Both *Salix glauca* and *S.athabescensis* were identified on dens, and were often mixed together.

^c I was unable to distinguish between *Cladonia fimbriata* and *C. chlorophaea*

Chapter 2. Red fox denning enhances long-term tree growth near the Arctic treeline

Abstract

Northern ecosystems are experiencing some of the most pronounced ecosystem modifications in response to climate change, including the expansion of the Subarctic boreal forest onto the tundra. While climate variables primarily determine the range and growth of trees in the Subarctic, organisms may also influence trees by modulating essential resources that could impact tree growth. Red foxes (*Vulpes vulpes* L.) are a globally common species that has responded to warming temperatures and are becoming more abundant at the northern edge of their distribution. They are also considered ecosystem engineers by enriching soil nutrients and plant diversity through denning. Increased soil nutrients through prey remains, feces and urine, could benefit tree growth in the Subarctic by alleviating soil nitrogen and phosphorus limitations. Using dendroecological methods, I examined radial growth in white spruce (*Picea glauca* (Moench) Voss) trees growing on red fox dens and paired control sites near Churchill, Manitoba, Canada, near the Arctic treeline. Radial growth was 53% higher for trees on dens than control sites between 1897 and 2017, despite similarities in tree ages, densities and regional climate across all sites. By promoting tree growth near the treeline, red foxes may have a role in influencing the position of the treeline. Although the impacts on tree growth largely depend on the spatial distribution of dens and predator activity in the boreal forest, my results highlight the role of predators in creating distinct microhabitats via ecosystem engineering processes, leading to increased productivity that can persist for several decades.

Introduction

Impacts associated with climate change, such as increasing air temperatures, CO₂ concentrations and nutrient availability, are resulting in largescale changes to vegetation in northern ecosystems (Grace *et al.* 2002; Post *et al.* 2009; Bjorkman *et al.* 2018). Specifically, northern plant assemblages are experiencing greater plant growth and earlier growing seasons, as well as the northward shift of woodland species onto the tundra (Sturm *et al.* 2001; Post *et al.* 2009; Jeong *et al.* 2011; Bjorkman *et al.* 2018). Furthermore, the expansion of treeline in response to warming temperatures and increasing availability of soil nutrients has been well documented (Post *et al.* 2009; Pearson *et al.* 2013; Greenwood and Jump 2014). Treeline expansion can have numerous impacts at the ecosystem level, including a shift in community diversity and altered biogeochemical cycles (Greenwood and Jump 2014).

Climate, specifically temperature and precipitation, largely determines the distribution and growth of trees in any biome (Woodward *et al.* 2004; Girardin *et al.* 2005). Yet trees at the edge of the Arctic can also be influenced by terrestrial vertebrates. For example, foraging by mammals can remove outer bark, phloem and cambial tissues, resulting in structural damage and decreased growth (Payette 1987; Sullivan *et al.* 1993). In particular, snowshoe hares (*Lepus americanus* L.) may reduce rates of treeline expansion by browsing white spruce (*Picea glauca* (Moench) Voss) saplings (Olnes *et al.* 2017).

Some vertebrates also modify vegetation through non-trophic interactions by influencing the physical environment, thereby creating habitat characteristics that alter plant composition or growth. The distribution of red foxes (*Vulpes vulpes* L.) is widespread throughout the world (Larivière and Pasitschniak-Arts 1996), and red foxes are considered ecosystem engineers by concentrating soil nutrients through organic waste and leaving prey carcasses at denning sites

(Thesis chapter 1). Previous studies have found that increased soil nutrients were common on red fox dens, though the response of vegetation to denning activity can vary in different habitats (Kurek *et al.* 2014; Godó *et al.* 2018). For example, while the growth of weeds and ruderal species was common on other sites, red fox denning increased species richness in Kampinos National Park, Poland, but decreased richness and cover on grassland burial mounds in Hungary (Kurek *et al.* 2014; Godó *et al.* 2018). Red fox dens can persist in the landscape for several decades (Gallant *et al.* 2012; Roth unpublished), and the continual impacts of digging and fertilization could persist over long periods of time. By fertilizing soils through nutrient additions over multiple decades, red foxes could influence long-term tree growth. Yet the duration of effects of denning has not been well documented.

In the Subarctic, red fox dens have been characterized by soils high in nitrogen and phosphorus (Thesis chapter 1), which could benefit the growth of trees. Nitrogen limits plant growth from temperate to Arctic climates (Tamm 1991), and added nitrogen typically increases tree biomass and radial growth by promoting earlywood growth, including in trees damaged by insects (Kytö *et al.* 1999; Lupi *et al.* 2013). However, the effects of nitrogen fertilization may also depend on the concentration of nitrogen added, as well as application frequency. Specifically, if nitrogen becomes saturated, then other resources can become limiting and constrain tree growth (Aber *et al.* 1989; Gress *et al.* 2007; Lupi *et al.* 2013).

The objective of this study was to examine the long-term influence of red fox denning on tree growth. I used tree ring analyses from white spruce to assess tree growth on red fox dens and paired control sites. I predicted trees located close to or on dens would have larger radial growth increments (ring width) compared to trees on controls.

Methods

My study area is located in the Hudson Bay Lowlands ecoregion, east of the town of Churchill, Manitoba, Canada (58°46'09"N and 94°10'09"W; **Figure 1.1**). Local climate is affected by the Hudson Bay, resulting in short and cool growing seasons (Smith *et al.* 1998). Air temperature varies highly throughout the year, and the highest mean monthly temperature typically occurs in July, averaging around 12.7°C (Environment and Climate Change Canada 2011). Monthly precipitation ranged from 16.6mm in February to 69.9mm in September between 1980 and 2010 (Environment and Climate Change Canada 2011). The landscape is dominated by gravel ridges deposited by glacial activity, interspersed by fens and bogs (Smith *et al.* 1998). Red foxes typically den on gravel ridges (Roth 2003; Gallant *et al.* 2012).

Both climate and topography in the region strongly influence vegetation composition. Gravel ridges are dominated by open coniferous forest stands, while lowlands support greater sedge, moss, and lichen cover (Ritchie 1957). Tree stands in the Subarctic boreal forest are patchy with open canopies (Smith *et al.* 1998) and host three main tree species: white spruce, which are mainly found on dry upland sites, black spruce (*Picea mariana* (Mill) Britton), which are found farther inland and are common in wet areas, and tamarack (*Laricina larix* (Du Roi) K. Koch), which are dispersed throughout the region in black and white spruce stands (Ritchie 1962; Brook 2001; Girardin *et al.* 2005). The forest-tundra transition zone forms a boundary between the mature boreal forest and the tundra, which is located north/northeast of the boreal forest (Ritchie 1962; Dredge 1992). Treeline is expanding onto the tundra in the region (Tews 2004; Mamet and Kershaw 2012).

In July 2018, I collected tree cores from white spruce trees, the dominant tree on dry upland sites, from 8 red fox dens and paired control sites. The den centre was estimated as the

midpoint between the two outermost burrows and control sites were located 50m from the den centre in one of two directions that maintained constant elevation and slope along the gravel ridge. I collected the cores from the 5 white spruce (diameter > 10cm) closest to the centre of each site (total = 40 den trees, 40 control trees). I extracted tree cores using an increment borer, which was used perpendicular to the tree and taken at a height of 30cm above the base of the tree. Collecting cores at this height enabled us to maximize tree age estimates (Fraver *et al.* 2011). I collected two cores, one from each side (~180° difference) of the 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 2012). I also recorded tree height and circumference at coring height for every cored tree. To estimate stand density, I examined the total number of trunks with a diameter > 10cm at breast height within a 15m radius around the centre of 7 dens and paired control sites. The circumference of each tree was converted to tree cross-sectional area, which I converted to basal area (total stem area/hectare) for each site.

I mounted all air-dried cores and then sanded each core with increasingly finer sandpaper until rings were clearly visible (Girardin *et al.* 2005; Tardif *et al.* 2008). I used a VELMEX UniSlide stage micrometer to measure the ring widths of each core (Tardif *et al.* 2008) and matched ring width patterns to visually crossdate the cores. I then validated the accuracy of the measurements and crossdating using the program COFECHA (Holmes 1983). The pith was missing from many of the cores, so the determined tree ages were minima. Although almost identical, radial growth often deviated slightly between paired cores within a given tree (two cores taken from opposite sides) due to uneven mechanical stress (i.e. growing on a slope, stronger wind on one side etc.) (Speer 2012). I therefore averaged radial growth measurements from the two matching cores to provide a single growth series for each tree.

To compare annual radial growth for dens and controls between 1897 and 2017, I used a linear mixed effects model with den or off-den (i.e. control sites) as a fixed effect using the nlme package in R (Pinheiro *et al.* 2019). I selected this time frame since 1897 corresponds to the earliest year where I had a minimum of 10 cores from both dens and control sites (den = 14 cores, control = 10 cores). Radial growth estimates were log-transformed to meet the assumptions of the model. Tree cambial age (ring number from the pith) and calendar year were included as covariates since tree growth slows with maturity (Szeicz and Macdonald 1994; Black *et al.* 2008; Mamet and Kershaw 2013) and can vary due to yearly climate and long-term climate trends (Mamet and Kershaw 2013). Tree ID nested in den ID was included as a random effect to control for the possibility that trees located on or near the same den are more similar to one another than they are to trees at other sites or trees at random. I also included the corAR1 autocorrelation structure, since tree growth at any given year depends on tree growth of the year before within a single tree (Speer 2012).

To examine the response of trees to denning at different ages, I separated the radial growth data from all sites into three age classes; young (45 - 90 years old), medium (91 - 125 years old) and old (126 - 180 years old). The age classes were selected to maximize sample size for both den and control sites. I ran separate linear mixed effects models for each age class, with den and off-den (control) as a fixed effect and year as a covariate, tree ID nested in den ID as a random effect, and the corAR1 autocorrelation structure.

Climate is known to have a strong influence on radial growth each year, and white spruce in the Churchill area are particularly influenced by climate during June and July (Girardin *et al.* 2005; Mamet and Kershaw 2013), which may correspond to the optimal period for earlywood growth. Using climate data from Churchill weather station A (Environment and Climate Change

Canada 2017) between 1935 and 1998, I also 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, which replaced year. Tree ID nested in den ID was used as a random effect, and the corAR1 autocorrelation structure was included in the model.

To compare stand characteristics between den and control sites, I used linear mixed effects models to separately compare tree age, height, height growth rate (height divided by age), and stem cross-sectional growth rate (cross-sectional area divided by age) between dens and controls (den or off-den as fixed effect), with tree ID nested in den ID as a random effect. Height and stem cross-sectional growth rates were log-transformed to satisfy assumptions. I used paired t-tests to respectively compare density, basal area and distance from tree to site centre (averaged for each den and paired control).

Results

Trees on dens had larger annual radial growth (ring widths) than controls (**Figure 2.1**), although results varied among sites (**Appendix**). Annual ring widths between 1897 and 2017 were strongly influenced by denning (den or off-den; $F_{1,78} = 17.856$, $p < 0.001$), age ($F_{1,7050} = 13.443$, $p < 0.001$), and year ($F_{1,7050} = 11.285$, $p < 0.001$). During this time period, annual radial growth was 53% higher for trees on dens (mean \pm SE = 0.98 ± 0.014 mm/year) compared to trees on control sites (0.64 ± 0.01 mm/year).

When separated into age classes, den or control was an important predictor for radial growth for all age classes compared to controls; young age class (**Figure 2.2**; $F_{1,22} = 10.089$, $p = 0.004$), medium age class (**Figure 2.3**; $F_{1,19} = 10.097$, $p = 0.005$) and old age class (**Figure 2.4**;

$F_{1,24} = 9.050$, $p = 0.006$). Year was also an important predictor for radial growth in the medium age class ($F_{1,1875} = 74.254$, $p < 0.0001$) and the old age class ($F_{1,3329} = 52.051$, $p < 0.001$), but was not significant in the young age class ($F_{1,1410} = 0.228$, $p = 0.633$).

When climate covariates are included in the model instead of year as fixed effects between 1935 to 1998, den or control ($F_{1,78} = 11.431$, $p = 0.001$), cambial age ($F_{1,4350} = 34.698$, $p < 0.001$), July mean temperature ($F_{1,4350} = 197.572$, $p < 0.001$), June mean temperature ($F_{1,4350} = 79.121$, $p < 0.001$), and July total precipitation ($F_{1,4350} = 32.011$, $p = 0.001$) were all important in determining ring width.

The minimum age of den trees ranged from 37 to 209 years, whereas the minimum age of control trees ranged from 47 to 239 years. Tree age did not significantly differ between dens (mean \pm SE = 104 ± 8) and controls (121 ± 7 ; $F_{1,78} = 2.884$, $p = 0.093$) (**Figure 2.5A**). Similarly, tree height did not differ between dens (9.6 ± 0.3 m) and controls (8.9 ± 0.3 m; $F_{1,78} = 2.600$, $p = 0.111$) (**Figure 2.5B**). Height growth rate was 38% higher on dens (0.11 ± 0.01 m/year) than controls (0.08 ± 0.01 m/year; $F_{1,78} = 9.208$, $p = 0.003$) (**Figure 2.5C**). Similarly, the cross-sectional growth rate was 90% higher on dens (630.7 ± 67.3 mm²/year) than on controls (331.9 ± 37.1 mm²/year; $F_{1,78} = 24.644$, $p < 0.001$) (**Figure 2.5D**).

Stand density did not differ between dens (362 ± 61 trees/ha) and controls (320 ± 52 trees/ha; $t_6 = -0.451$, $p = 0.668$). Likewise, basal area did not differ between dens (11.6 ± 2.2 m²/ha) and controls (7.5 ± 1.9 m²/ha; $t_6 = -1.210$, $p = 0.272$). Distance of each tree to den/control centre did not differ between dens (8.8 ± 0.9 m) and controls (8.3 ± 0.9 m; $t_7 = -0.399$, $p = 0.702$).

Discussion

My results demonstrated that red fox denning has a positive and sustained effect on the growth of white spruce trees at the Arctic treeline. Radial tree growth is determined by complex interactions between environmental variables, stand characteristics, and microhabitat conditions (Fritts 2001; Vaganov *et al.* 2006). Consistent with other studies, temperature and precipitation influenced tree growth in my study area (Girardin *et al.* 2005; Mamet and Kershaw 2013), but trees on red fox dens also grew faster than on control sites, despite similarities in climate, age, stand density and stand basal area. Denning was a significant predictor of ring width in each of the models. By increasing soil nitrogen and phosphorus on dens (Thesis chapter 1), red foxes create distinct microhabitat characteristics from surrounding Subarctic soils, leading to favorable growing conditions for trees. Enhanced tree growth from nutrient deposition has also been documented by other terrestrial predators in other regions. For example, brown bears (*Ursus arctos* L.) also promote tree growth by providing nutrients via salmon remains and excretions (Hilderbrand *et al.* 1999; Quinn *et al.* 2018).

Overall, radial growth increments were consistently higher on dens compared to controls between 1897 and 2017 across all sites. Other studies have also used dendroecological methods to examine long-term predator denning activity. For example, Scott and Stirling (2002) used tree cores from black spruce to determine the year of den construction and subsequent denning activity by polar bears (*Ursus maritimus* Phipps) based on the timing and location of tree damage. Similarly, it is possible that the impacts of red fox denning began before 1897, given that tree growth appears higher on dens compared to controls as early as 1865, but my sample size was limited prior to 1897 (**Figure 2.1**). Although the exact ages of the fox dens in my study are not known, most dens were first identified in 1994 (Roth 2003), often found through local

knowledge, but may be several decades older. Red fox dens may persist for many decades, but are not always occupied by foxes consistently each year (Roth unpublished). Yet the effects of denning on tree growth rate was sustained over multiple years. Gharajehdaghipour *et al.* (2016) found that soil nutrient concentrations from Arctic fox dens were consistently higher relative to control sites, regardless of whether the dens were occupied that year. If radial growth can also be used as indicator of red fox denning, then the impacts of denning activity in the study area were present as early as 1897, with subsequent denning activity maintaining high radial growth and growth rates, though the exact age of the dens likely differs among sites (**Appendix**).

Although annual radial growth was higher for trees on dens, tree height did not differ between dens and controls. Taller trees have a competitive advantage for light access, but it is also more energetically costly to transport water and nutrients throughout the tree (King 1990). As such, trees continue to expand radially throughout the lifespan of a tree, but vertical growth slows considerably with maturity (Kira 1978; King 1990). As such, maximum individual height is typically similar among trees throughout the forest stand. Despite added resources from red foxes, like nutrient additions, morphological constraints prevent trees from growing infinitely tall. Although overall tree height did not differ between dens and controls, height growth rate was higher compared to control trees, and therefore den trees may reach a maximum height faster (i.e. at a younger age) than control trees. The leading edge of the treeline or transition zone is typically dominated by stunted krummholz trees, which have delayed cone production due environmental stressors, such as wind, snow, and nutrient limitations (Scott *et al.* 1993; Grace *et al.* 2002). By growing more rapidly on fox dens, den trees may be able to produce cones at younger ages relative to control sites. Nitrogen addition has been shown to increase cone production in conifers (Puritch 1977), therefore denning could also promote greater cone

production and yield. While I did not find a difference in density of trees larger than 10cm in diameter, my study did not examine saplings, and our youngest tree was 37 years old. Further investigation is needed to examine the influence of red fox denning on tree recruitment and cone production near the Arctic treeline. Additionally, since thicker trees (higher width to height ratio) may be less susceptible to breaking from wind (Wang *et al.* 1998), den trees may be better at persisting in the harsh Subarctic climates at treeline edge due to higher radial growth. Consequently, red foxes could ultimately have a role in the recruitment of trees if cone production is improved by fertilization effects and the position of treeline at the edge of the Arctic, though impacts vary according with density and location of fox dens.

In conclusion, my study highlights the importance of predators in the Subarctic beyond trophic impacts, through their role as ecosystem engineers. As ecosystem engineers, the impacts of denning by red foxes may persist for several decades. The interactions between predators, nutrients and their impacts on tree growth are a critical linkage to understanding ecosystem function, which can have important implications for forest and tundra resources at the transition zone between these ecosystems.

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Figures

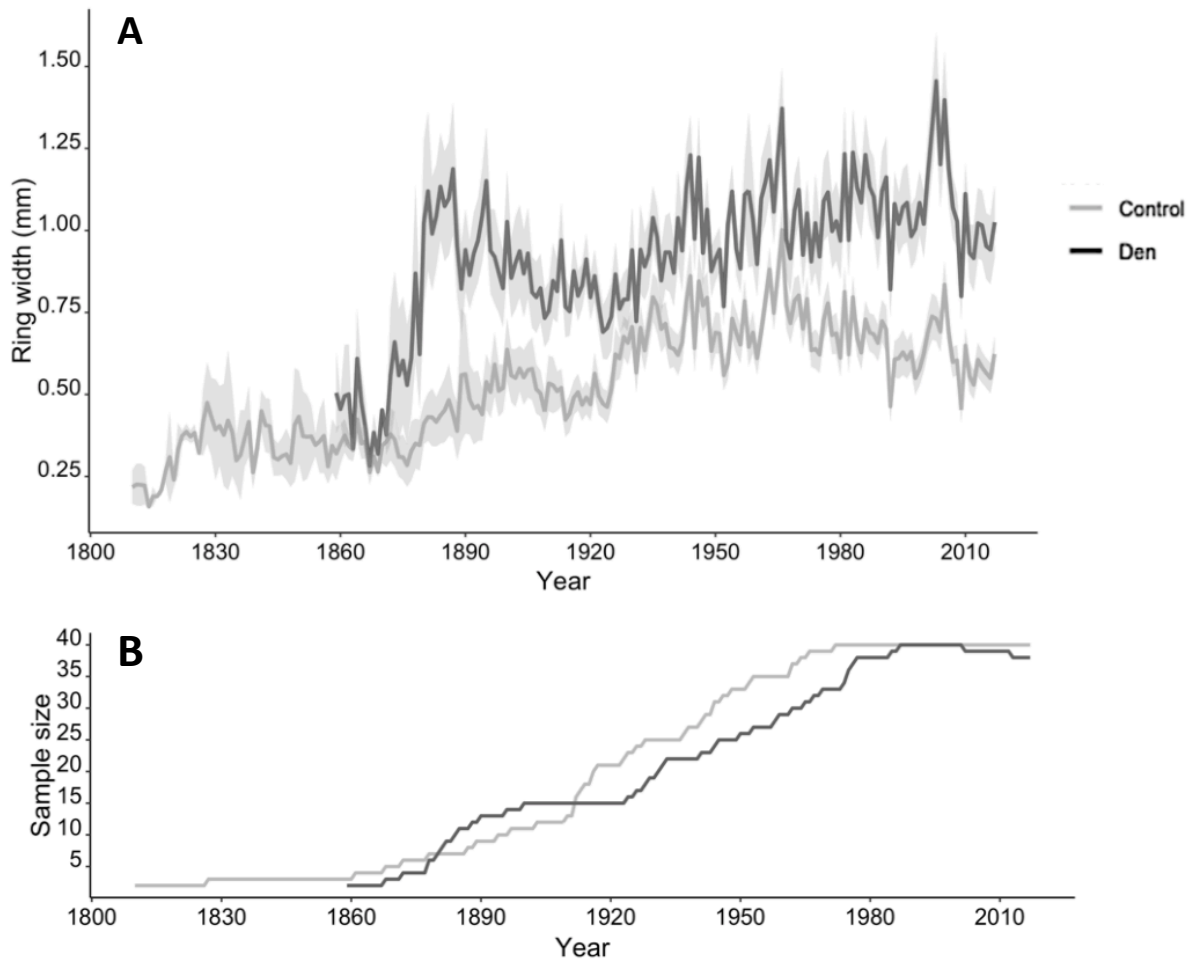


Figure 2.1. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1808 and 2017 from white spruce on red fox dens and paired control sites near Churchill, MB, Canada.

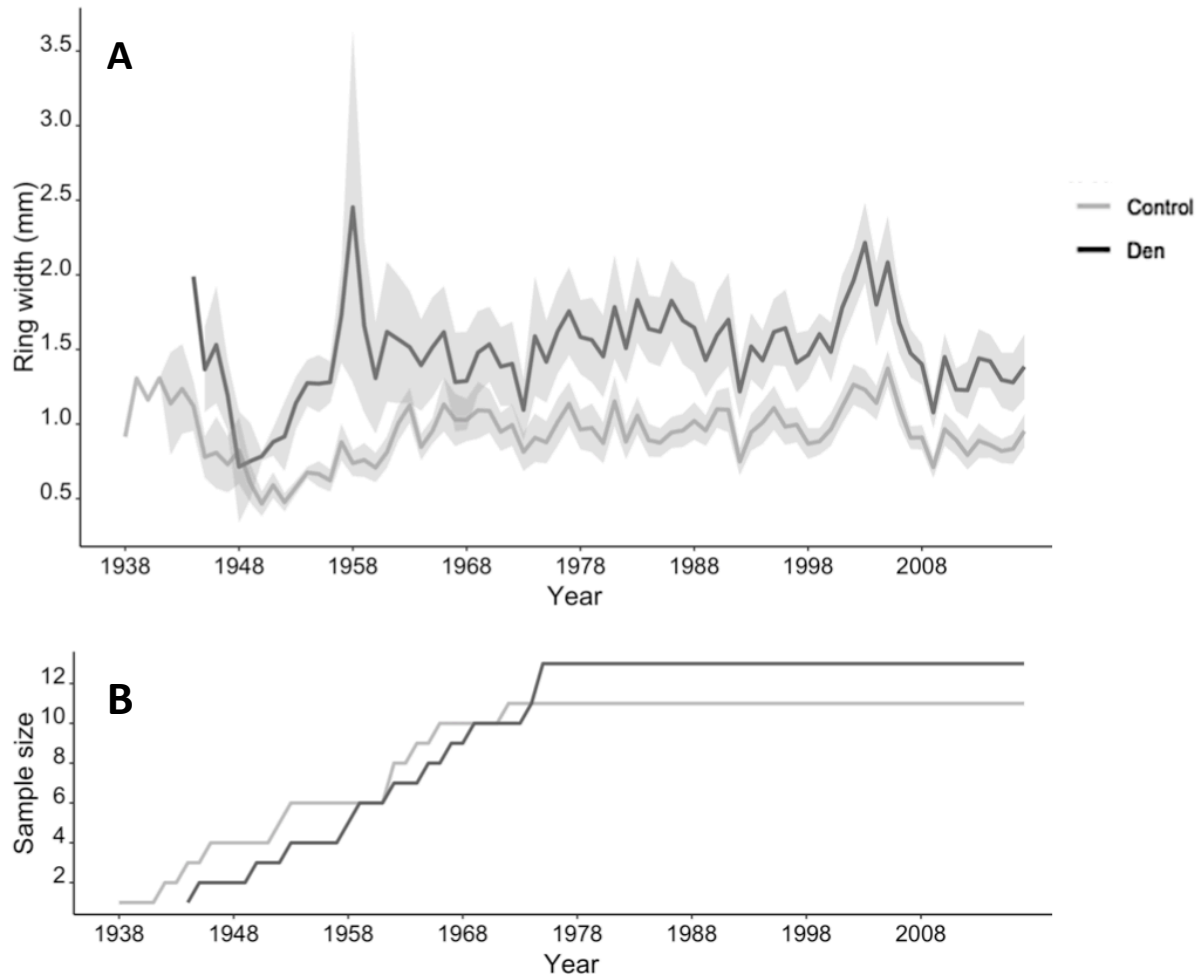


Figure 2.2. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) from young white spruce trees (45 to 90 years old) from red fox dens and paired control sites near Churchill, MB, Canada.

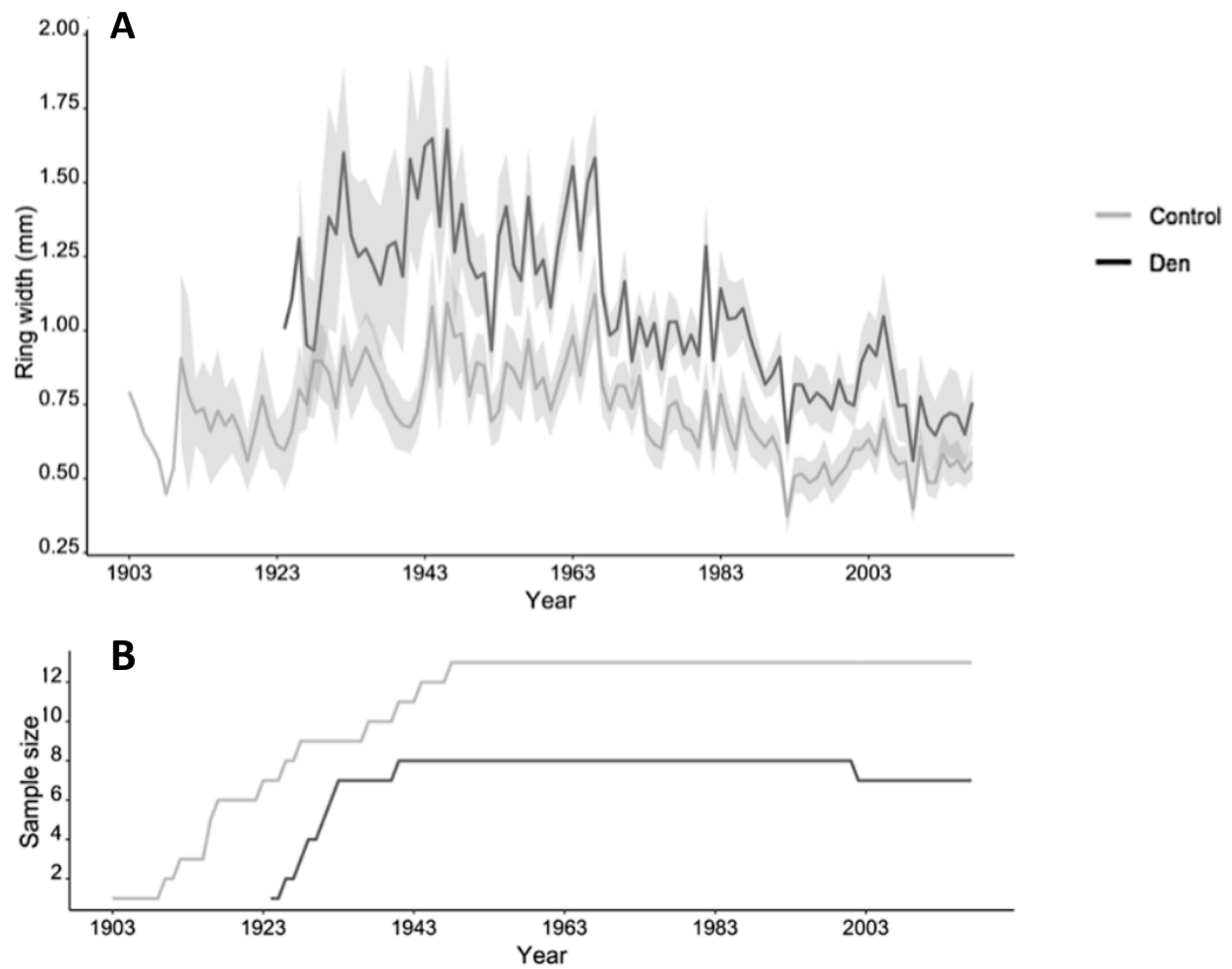


Figure 2.3. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) from medium-aged white spruce trees (91 to 125 years old) from red fox dens and paired control sites near Churchill, MB, Canada.

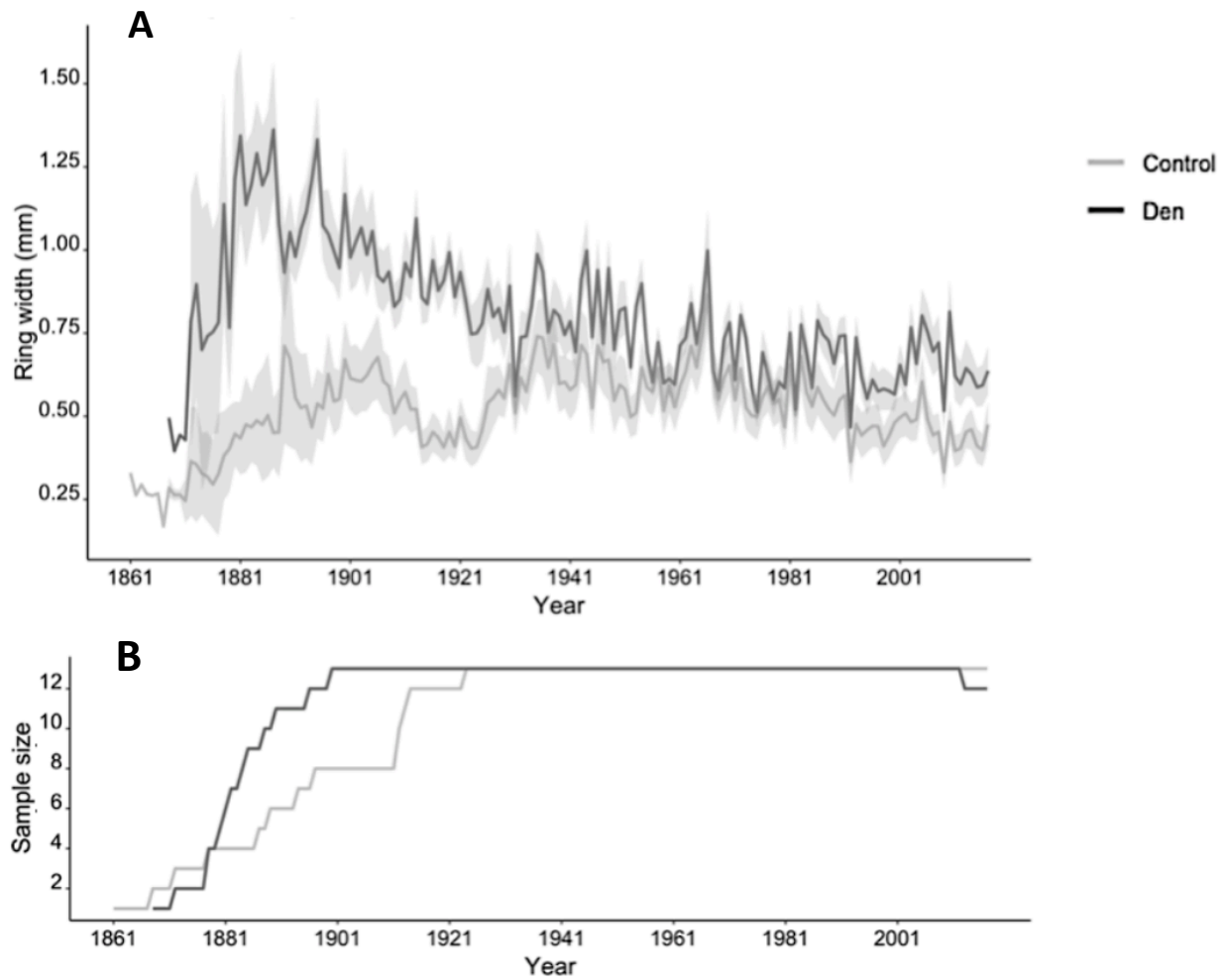


Figure 2.4. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) from old white spruce trees (126 to 180 years old) from red fox dens and paired control sites near Churchill, MB, Canada.

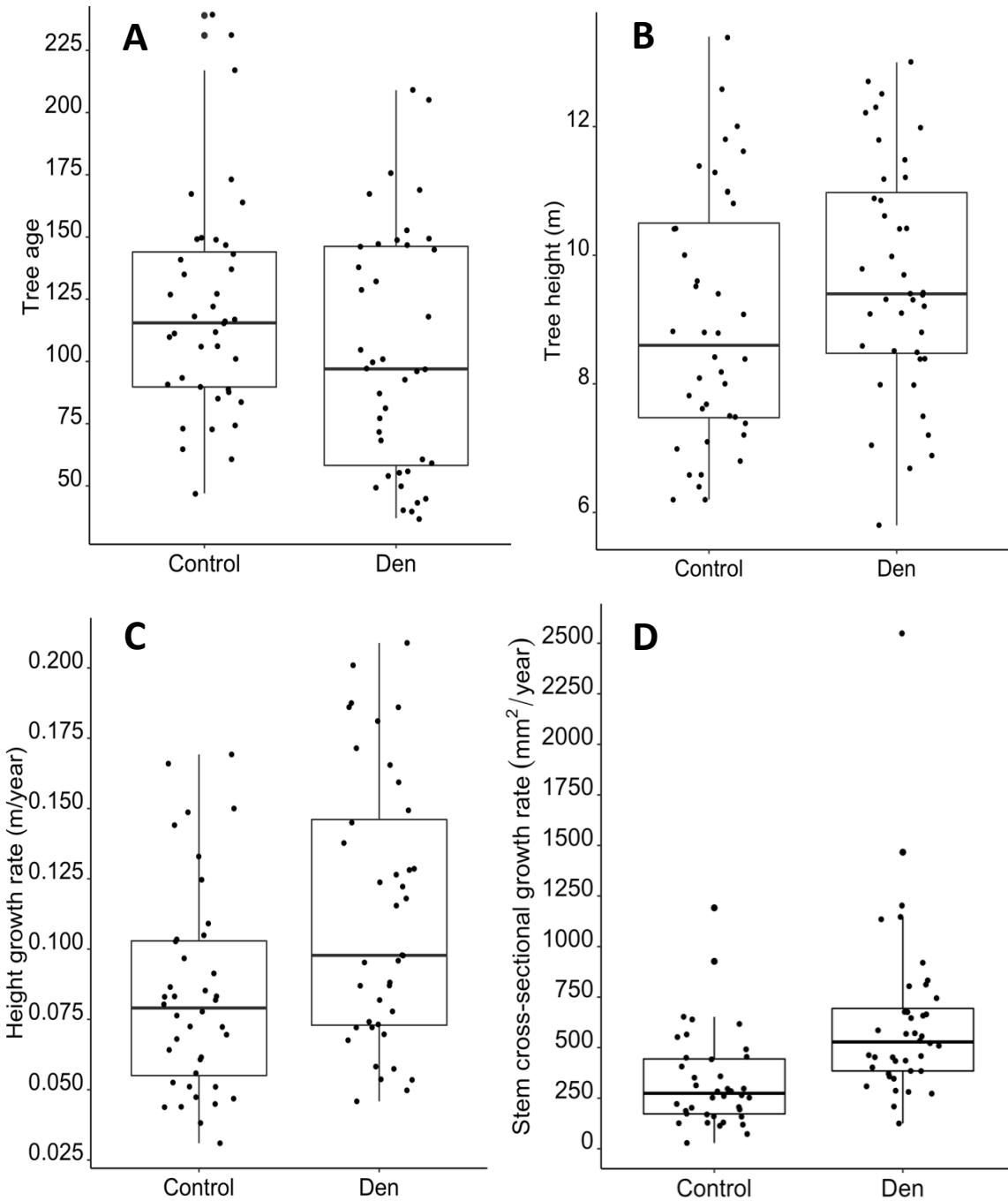


Figure 2.5. Box plots of tree (A) age in years (B) height (C) height growth rate and (D) stem cross-sectional growth rate of white spruce on red fox dens (40 trees) and paired control sites (40 trees) near Churchill, MB, Canada, in July 2018. Box represents the interquartile range and horizontal line represents the median.

Thesis Conclusion

My research demonstrates that, in addition to their role as predators, the functional role of red foxes (*Vulpes vulpes* L.) can also be conceptualized using an ecosystem engineering framework. Through denning, red foxes create distinct microhabitats in the boreal forest by concentrating soil nutrients (nitrogen and phosphorus) and creating small-scale soil disturbance through digging, resulting in atypical vegetation on dens. Although not specifically examined in this thesis, plant assemblages found on red fox dens may also be influenced by the impacts of animal-mediated seed dispersal by red foxes, by carrying seeds attached to their fur or through the subsequent defecation of seeds via consumed herbivores and/or plants (Hovstad *et al.* 2009; Rosalino and Santos-Reis 2009; Kurek and Holeksa 2015). Plants may also grow from seeds already present in soils that are unable to germinate under non-denning conditions. Staniforth *et al.* (1998) found that vegetation along the coast near Churchill was dominated by ruderals due to frequent disturbances, but additional species were found in the soil seed bank. By influencing soil respiration, pH, and nutrients, as well as disturbing soils through digging, red foxes create heterogeneous soil conditions on dens, allowing for the germination of plants that may otherwise remain dormant. In addition to facilitating the growth of vegetation less commonly found on dry upland sites in the boreal forest, such as willows (*Salix* L. spp) and sea lyme-grass (*Leymus mollis* (Trinius) Pilger), red foxes increase overall plant diversity.

Modifications to northern plant assemblages by red foxes indirectly influence the availability and quality of vegetation used by other organisms. Previous studies examining Arctic fox dens have found that tundra herbivores, such as caribou (*Rangifer tarandus* L.) feed on the vegetation found on dens, which may offer improved foraging resources compared to surrounding habitat (Zhao 2015). Similarly, despite being the main prey source of Arctic foxes,

lemmings preferentially selected to nest on Arctic fox dens given the improved habitat quality from enhanced vegetation (Gharajehdaghypour and Roth 2018). The vegetation found on red fox dens may also attract herbivores, such as snowshoe hare (*Lepus americanus* L.), ptarmigan (*Lagopus* L. spp.), and voles (*Microtus* L. spp.) (Wolff 1978; Thomas 1984; Shaw *et al.* 2013), which are known to forage on shrubs, such as willows, which were common on fox dens. By promoting tree growth, red foxes may also improve habitat quality for arboreal species, such as red squirrels, which may benefit from improved tree growth (Sullivan and Sullivan 1982; Flaherty *et al.* 2012). Additionally, Lewis and Starzomski (2015) found that passerine bird species richness increased with greater vegetation biomass, which may improve opportunities for perching, foraging and nesting. As such, red foxes could influence avian distribution by influencing tree growth at Arctic treeline. Since dens are reused by foxes (Gallant *et al.* 2012), the impacts of denning can also persist for long periods of time. I found higher radial growth in white spruce trees growing on or near red fox dens beginning by 1897 in the study area, despite similarities in regional climate, tree age, and forest stand density between dens and controls. Consequently, red foxes may have influenced resource quality and availability over extensive periods of time for both boreal and tundra species by denning at the transition zone between ecotones.

Despite ecological differences (litter size, body mass, and fecal deposition patterns) between Arctic and red foxes (Larivière and Pasitschniak-Arts 1996; Audet *et al.* 2002; Friesen 2013) and habitat differences (boreal forest vs tundra), there are similarities between vegetation found on red fox dens in the boreal forest and on Arctic fox dens in the tundra (Gharajehdaghypour *et al.* 2016). Dens from both species had higher soil nutrient concentrations and were dominated by shrubs and grasses (Gharajehdaghypour *et al.* 2016). Furthermore,

willows and fireweed were common indicator species found on both Arctic and red fox dens (Fafard *et al.* 2019), indicating commonalities in microhabitat conditions. Unlike the tundra study, my results demonstrated that the presence of an organic layer was particularly important on dens in the boreal forest, since differences in soil nutrients, pH and respiration were only present in the organic layer. In contrast, differences in soil nutrients could only be observed in the mineral layer on Arctic fox dens (Gharajehdaghipour *et al.* 2016), given the absence of a true organic layer in the tundra heath habitat. Compared to the tundra, boreal forests typically have a thicker organic layer (Lafleur *et al.* 2010), higher soil nutrients (Orlova *et al.* 2013) and a higher density of trees. While ecosystem engineering can alter habitat structure and function, the magnitude of impacts also depends on the capacity of the ecosystem to respond to changes (Grinath *et al.* 2019). In habitats where nutrient availability is low, which is common of both the boreal forest and tundra, denning can alleviate nutrient limitations in soils, resulting in increased primary productivity. The similarity of impacts I documented from red fox dens in the boreal forest and the ecosystem response to nutrient additions in the tundra suggest that red foxes could have similar impacts on the tundra as well.

While the role of predators in maintaining ecosystem function through predation is well known, predators also provide essential non-trophic interactions by modifying habitat characteristics. Denning predators can increase environmental heterogeneity of resources by concentrating soil nutrients and mixing soils through digging, though effects at the landscape level largely depend on the spatial and temporal distribution of dens and predators. Consequently, predators have critical roles in providing habitat resources and conditions for other organisms, and many predators can be considered ecosystem engineers. Certain predators may have larger impacts than others, such as those that influence resources and conditions over

long periods of time. Feedback with environmental variables also determines the impacts of an ecosystem engineer, and impacts are greater when they provide a limiting resource (Crain and Bertness 2006; Grinath *et al.* 2019). Further exploration on the feedback between denning predators and ecosystem response could provide additional insight into the specific processes driving environmental heterogeneity across a landscape, as well as provide a more complete view of the functional role of predators beyond exclusively trophic interactions.

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Appendix - Radial tree growth (ring width) of white spruce trees separated by site (den ID) near Churchill, Manitoba, Canada

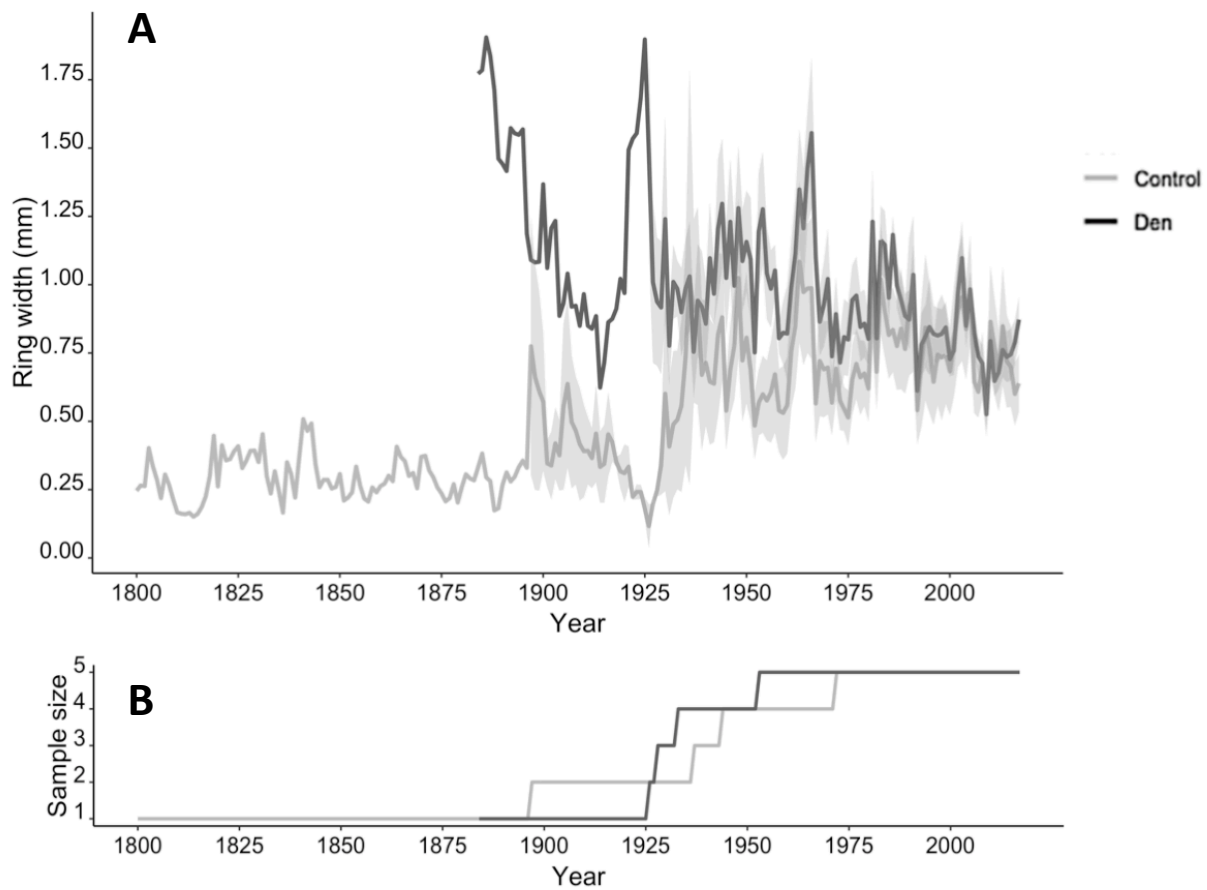


Figure A.1. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1884 and 2017 from white spruce from red fox den W08 and paired control site near Churchill, MB, Canada.

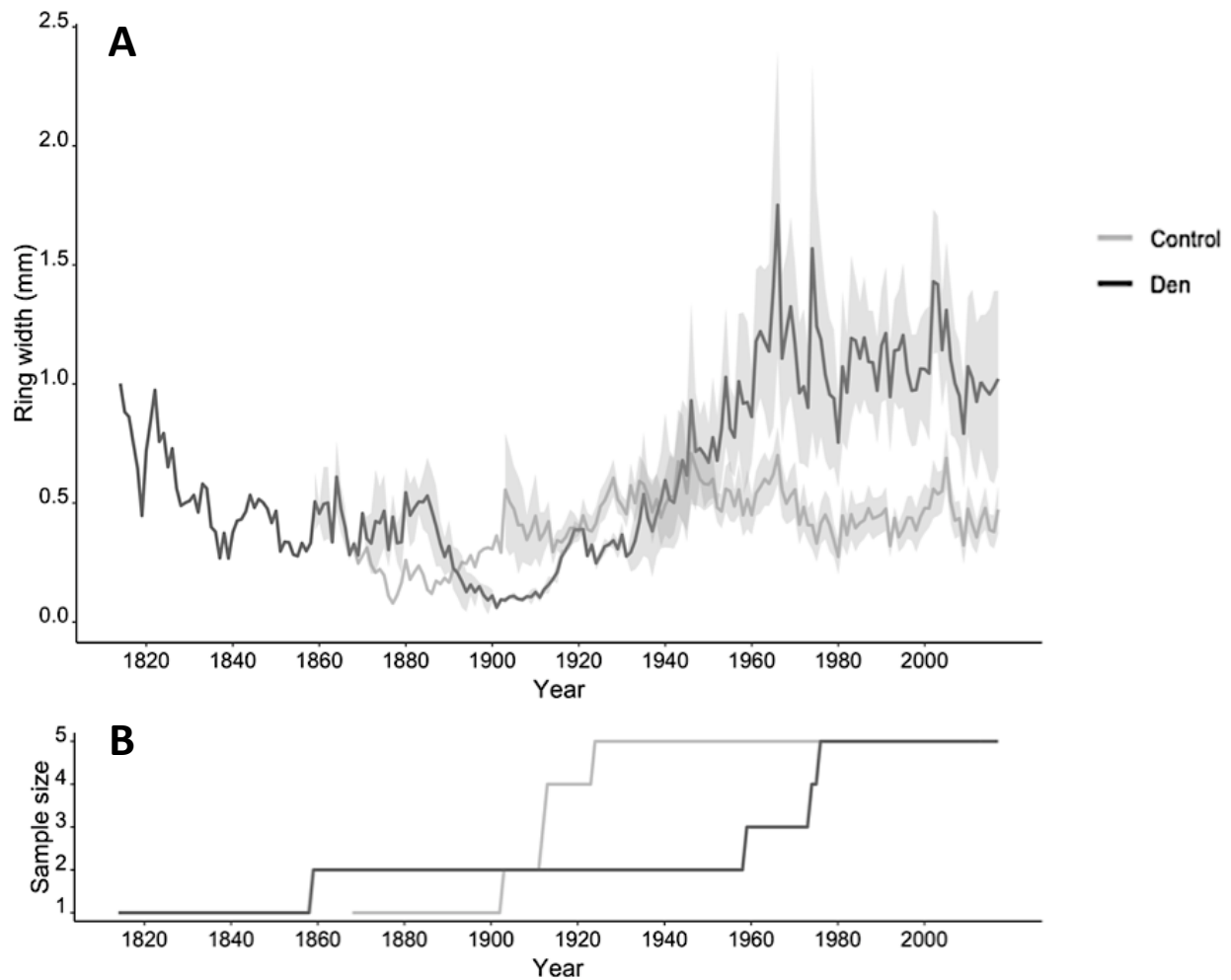


Figure A.2. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1814 and 2017 from white spruce from red fox den W10 and paired control site near Churchill, MB, Canada.

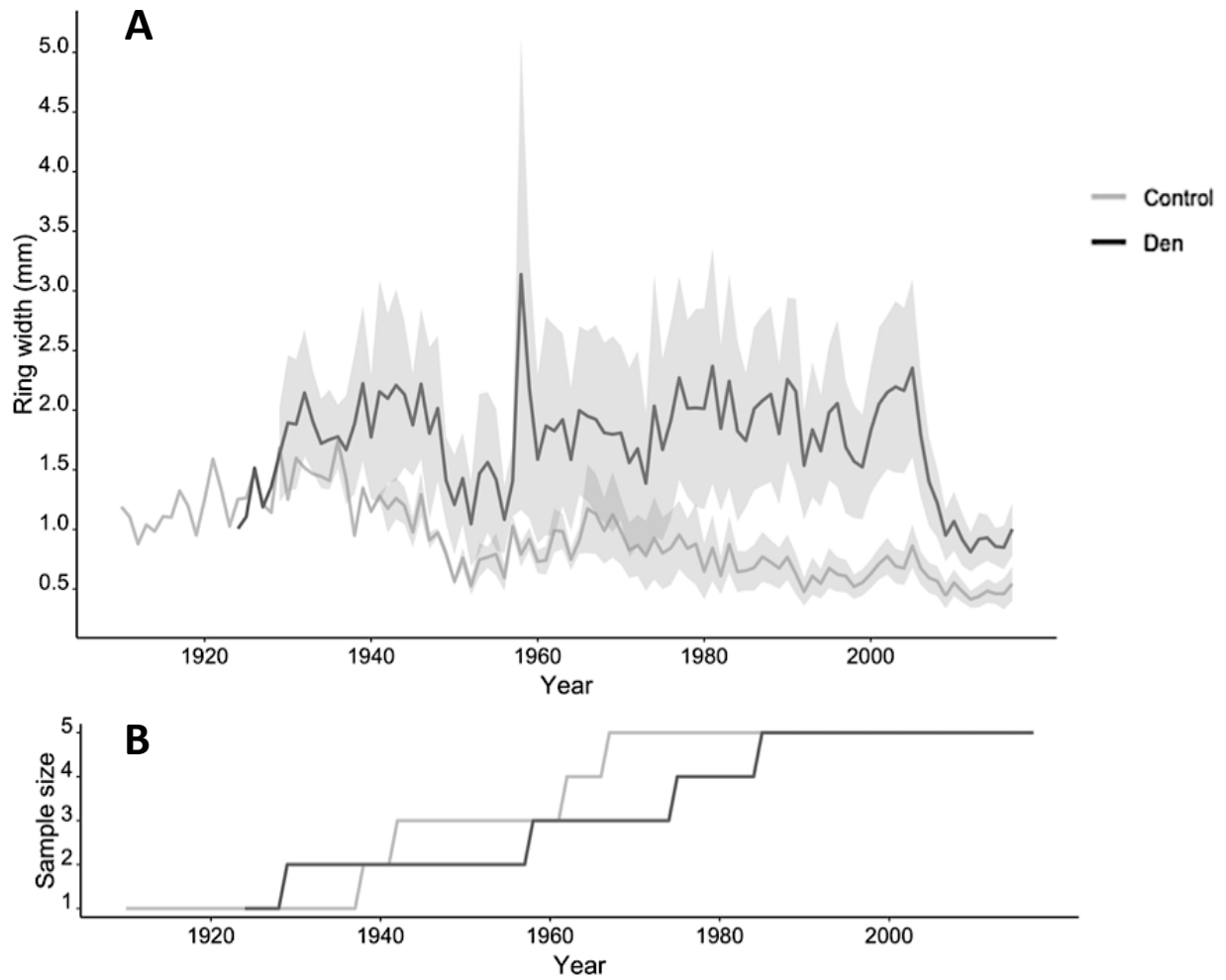


Figure A.3. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1910 and 2017 from white spruce from red fox den W11 and paired control site near Churchill, MB, Canada.

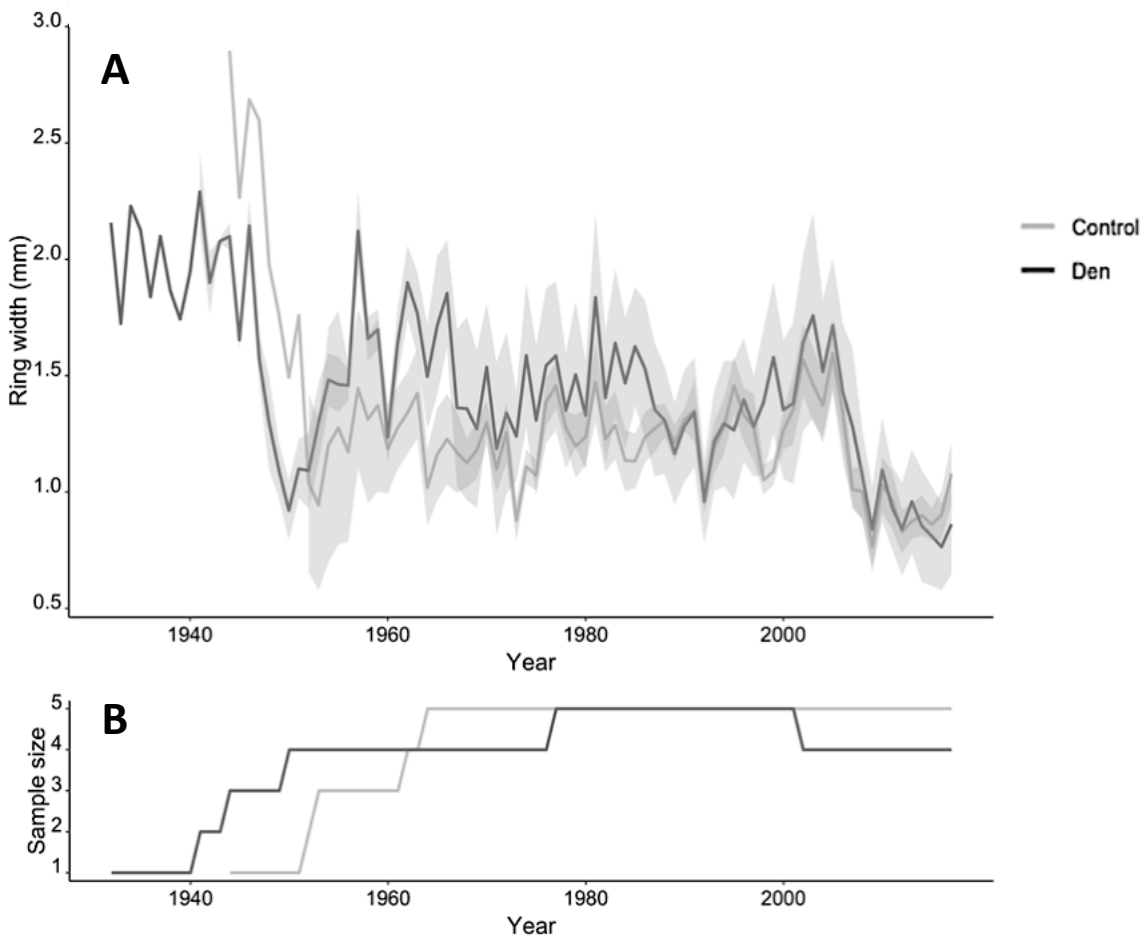


Figure A.4. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1932 and 2017 from white spruce from red fox den W12 and paired control site near Churchill, MB, Canada.

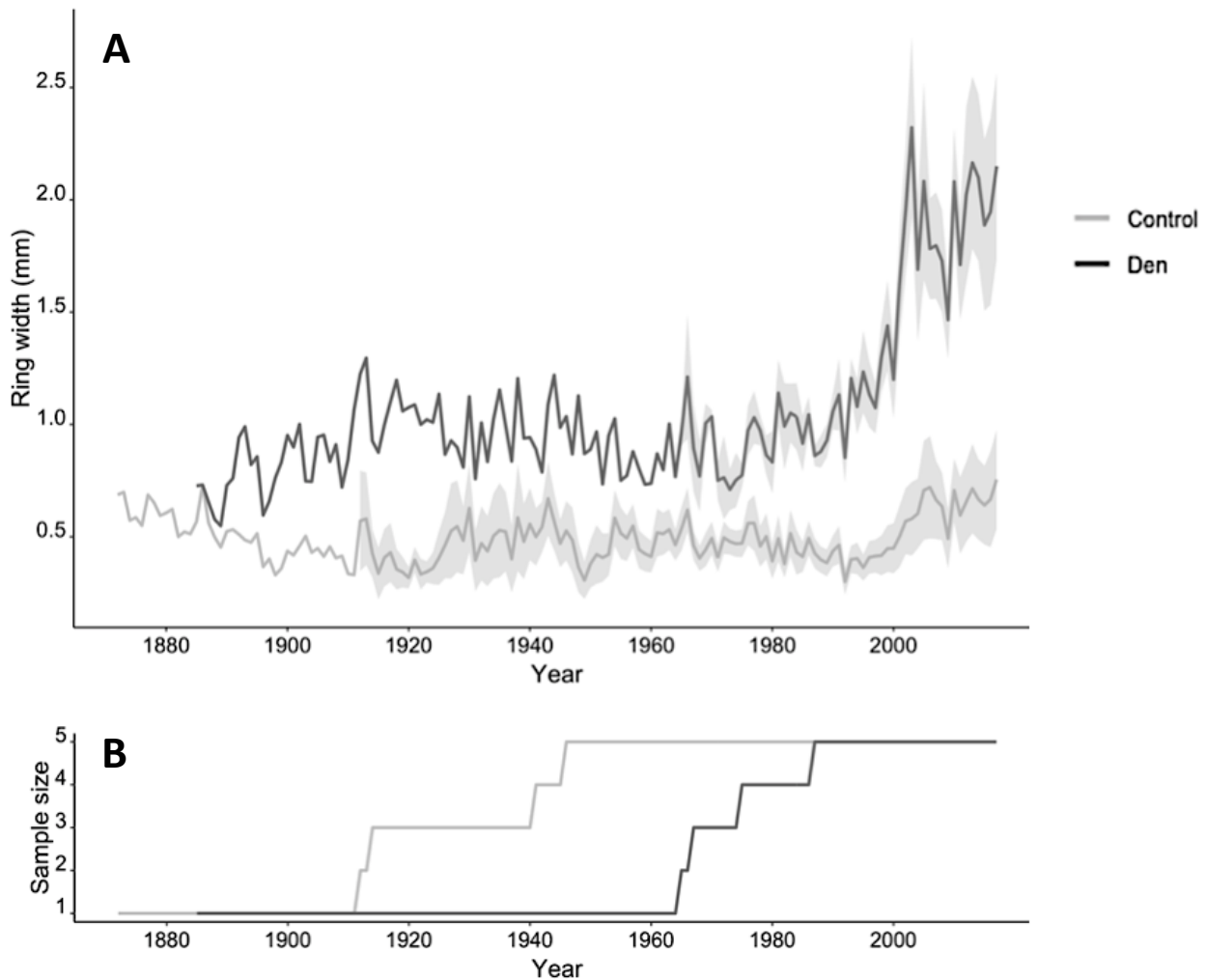


Figure A.5. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1872 and 2017 from white spruce from red fox den W16 and paired control site near Churchill, MB, Canada.

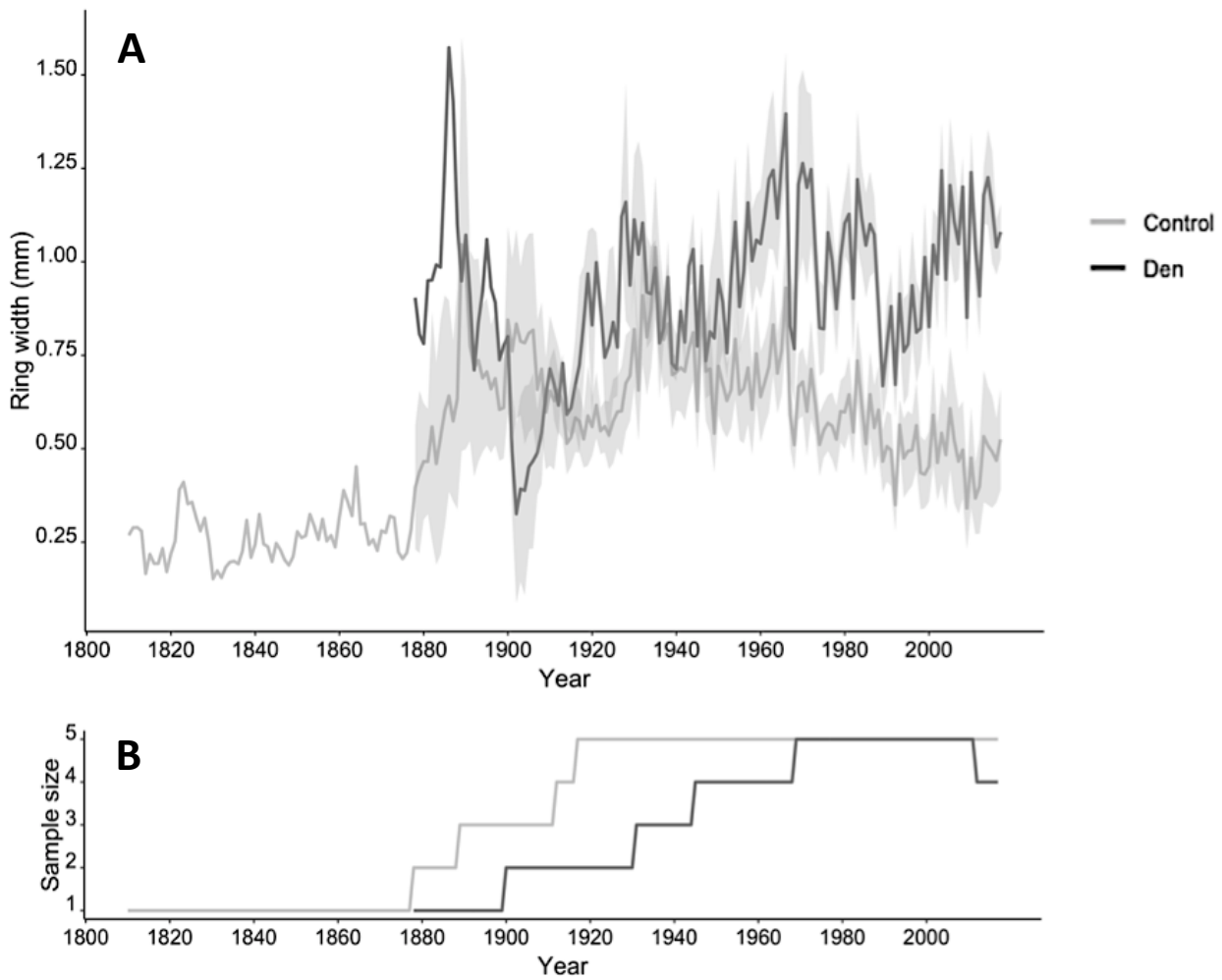


Figure A.6. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1810 and 2017 from white spruce from red fox den W39 and paired control site near Churchill, MB, Canada.

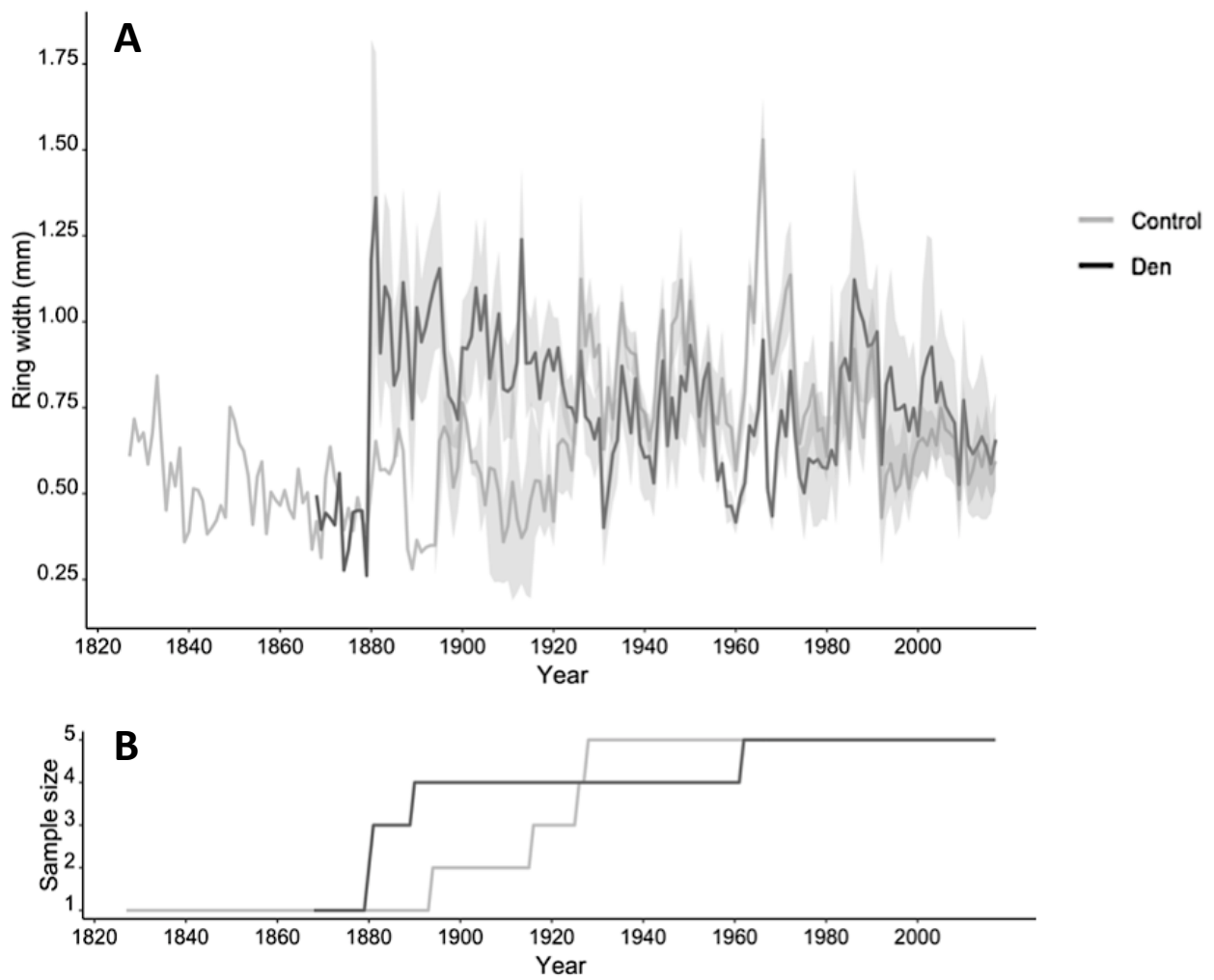


Figure A.7. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1827 and 2017 from white spruce from red fox den W41 and paired control site near Churchill, MB, Canada.

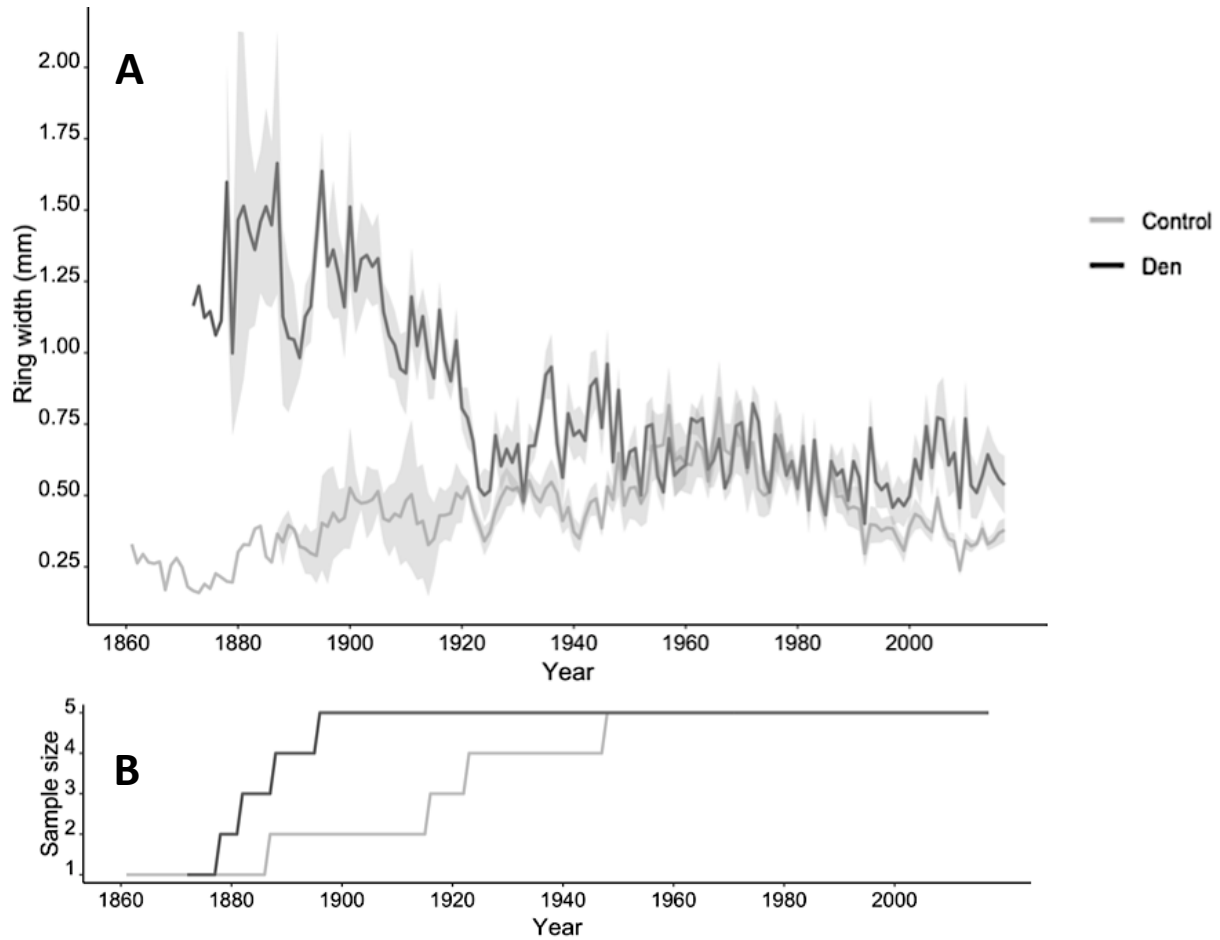


Figure A.8. A) Ring width increments (mean \pm SE) and B) corresponding tree sample size (sample depth) between 1861 and 2017 from white spruce from red fox den W47 and paired control site near Churchill, MB, Canada.