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Highlights

- Over many decades, red foxes increase nutrient concentrations and affect vegetation diversity on their dens in the boreal woodlands, a nutrient-poor environment.
- Denning activity also affects the growth and reproduction of white spruce, a mast-seeding conifer.
- White spruce on fox dens are taller and produce more cones in non-mast years than trees off dens.
- The effects of denning are subject to the mast-seeding cycle, as cone production in mast years was not elevated on dens.

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Red foxes increase reproductive output of white spruce in a non-mast year

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Abstract

Predators may act as ecosystem engineers by modifying their physical environment through non-trophic interactions. Red foxes (*Vulpes vulpes*) are ecosystem engineers in the boreal woodlands, a nutrient-poor environment, where their denning activity increases soil nutrient concentrations, affecting the diversity of vegetation around dens. Since dens can persist for many decades and tree growth is enhanced on dens, dens can be used to study the long term impacts of nutrient additions on community and ecosystem processes. We examined the reproductive output of a mast-seeding conifer, white spruce (*Picea glauca*), on 10 red fox dens and paired control sites at the boreal treeline near Churchill, Manitoba, in July 2019. We estimated cone production in both the current non-mast year (2019), and the previous mast year. The number of cones produced per tree and per hectare was significantly higher on dens than control sites in the non-mast year, but did not differ between in the mast year. Higher cone production on dens was partly driven by trees being larger on dens. These results suggest that red fox ecosystem engineering activity affects white spruce reproduction, since increased soil nutrients on dens allows for higher cone production, but the effect of red fox denning is limited by interactions with mast-seeding mechanisms. For example, weather cues may override the effects of denning in mast years, while trees on dens may be able to allocate more resources to

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reproduction in non-mast years, but store the same amount of resources as trees off dens to produce similarly large cone crops in mast years. Altered resource availability in this nutrient-limited landscape could have additional ecological implications, by affecting the foraging patterns of seed predators and spruce range expansion.

Keywords: Ecosystem engineering, spruce cones, mast-seeding, boreal woodlands, denning activity, *Vulpes vulpes*, *Picea glauca*

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Introduction

Organisms can help shape their habitat through interactions with the biotic and abiotic components of the ecosystem. Recently, there is a greater recognition of how indirect and non-trophic interactions influence food web dynamics and ecosystem functioning (Olff et al., 2009; Sanders et al., 2014). For example, predators not only affect prey species through predation, but also by modifying habitats and impacting the abundance of prey species through ecosystem engineering (Sanders et al., 2014). Ecosystem engineers are organisms that create, modify, or otherwise shape habitats through non-trophic interactions (Jones, Lawton & Shachak, 1994). These modifications can cause physical state changes and control resource flow, which may result in the heterogenous distribution and availability of resources across a landscape (Jones, Lawton & Shachak, 1997). In turn, ecosystem engineering activities influence the diversity and abundance of other organisms in the ecosystem, and may generate positive or negative feedbacks for the engineering species (Jones et al., 1997).

Ecosystem engineers can be found in both terrestrial and aquatic environments. For example, corals engineer marine ecosystems by generating the limestone base of the reef, providing habitat for themselves and thousands of other organisms (Jones et al., 1994). Arctic foxes (*Vulpes lagopus*) act as ecosystem engineers on the tundra by digging and depositing nutrients on their dens, which over many years increases plant productivity on the den and results in unique plant assemblages that include faster-growing, nitrogen-dependent deciduous species (Gharajehdaghipour, Roth, Fafard, & Markham, 2016; Fafard, Roth, & Markham, 2020). The increase in vegetation subsequently attracts herbivorous prey species to the dens (Gharajehdaghipour & Roth, 2018).

Red foxes (*Vulpes vulpes*) also act as ecosystem engineers in the boreal forest through denning activities. Red foxes occupy an expansive range in a variety of habitats (Larivière & Pasitshniak-Arts, 1996). In Manitoba, the northern extent of their denning range coincides with the treeline of the boreal forest (Roth, 2003). Soils in the forest-tundra ecotone are generally nutrient-poor (Sveinbjörnsson, Hofgaard, & Lloyd, 2002). Red foxes dig burrows, defecate, urinate, and deposit prey remains on dens (Lang, 2019). Over long periods, red fox activity on dens has led to higher concentrations of inorganic nitrogen and extractable phosphorous in the organic layer, higher soil respiration and pH, and greater understory species richness compared to surrounding areas (Lang, Roth, & Markham, *in revision*). White spruce (*Picea glauca*) on dens have greater tree ring widths than trees off dens, suggesting that the denning activity of red foxes promotes enhanced tree growth that persists for decades (Lang, 2019).

Although red foxes influence the productivity of vegetation on dens, the impact of red fox activity on the reproductive output of vegetation has yet to be explored. White spruce trees are one of the most common and widely distributed conifers in the boreal forest, and can often be found surrounding red fox dens (Smith, Veldhuis, Mills, Fraser, & Lelyk, 1998). White spruce are monoecious and produce both male and female cones yearly, with female (seed-bearing)

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cones maturing in late summer and shedding of seeds occurring from late August to September (Waldron, 1965; Owens & Molder, 1979). White spruce are mast-seeding trees, and reproductive output varies greatly between mast years and non-mast years (Lamontagne & Boutin, 2007; Krebs, LaMontagne, Kenney, & Boutin, 2012).

Mast seeding is the synchronous, intermittent production of large seed crops, a phenomenon commonly observed in northern tree species (Kelly, 1994). Although mast seeding has long been observed in perennial plants, the underlying mechanisms that drive mast seeding are still not well understood (Crone & Rapp, 2014; Pearse, Koenig, & Kelly, 2016). Several ultimate-level hypotheses (which explain the evolutionary advantage) have been proposed to explain mast seeding, with the most popular being predator satiation (including seed dispersal) and pollination efficiency (Kelly, 1994). Proximate-level hypotheses (the immediate mechanism) stem from two main explanations: environmental constraints and weather cues (Crone & Rapp, 2014; Pearse et al., 2016). The role of resources – an environmental constraint – in mast seeding is widely debated, and various resource budget and resource matching models have been proposed (Kelly, 1994; Kelly & Sork, 2002). In reality, mast-seeding patterns are likely the result of the interaction between resource availability, weather, and ultimate fitness benefits (Pearse et al., 2016). Nitrogen fertilizers have been shown to increase seed production in mature mountain beech (*Nothofagus solandri*) and Monterey pine (*Pinus radiata*), as well as red and black oak (*Quercus rubra* and *Q. velutina*) acorn abundance in non-mast years, but not mast years (Griffin, Crane, & Cromer, 1984; Davis, Allen, & Clinton, 2004; Callahan, Del Fierro, Patterson, & Zafar, 2008; Smaill, Clinton, Allen, & Davis, 2011). These findings suggest that nutrient addition can alter annual seed production in mast-seeding species.

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In white spruce, seed production has also been linked to climatic variables in prior years. Mast-seeding patterns have been associated with July and August temperatures of years *t – 1* and *t – 2* and May precipitation of year *t – 2,* while increased seedfall has been correlated with warmer temperatures, lower precipitation in year *t – 1* and low snowfall in year *t* (Krebs et al., 2012; Krebs, O'Donoghue, Taylor, Hofer, & Boutin, 2017; Roland, Schmidt, & Johnstone, 2014). Mast-seeding intervals in white spruce can vary from 2-6 years, and regional synchrony is negatively related to distance (Waldron, 1965; Lamontagne & Boutin, 2007; McAdam, Boutin, Dantzer, & Lane, 2019). White spruce cone production and germination rates generally decrease as individuals approach the northern treeline due to low summer temperatures, a short growing season, low pollen viability, and low genetic diversity resulting in low seed viability (Elliott, 1979; Fowler & Park, 1983; Walker, Henry, McLoed, & Hofgaar, 2012; Roland et al., 2014). However, little research has been done on the effects of nutrient addition on white spruce reproduction in unmanaged or undisturbed areas.

Increased nutrient availability may allow for greater allocation of nutrients to reproductive tissues. Similarly, the increased growth of white spruce on red fox dens may have a synergistic effect to increase reproductive output, since larger trees are generally more productive (Davi, Cailleret, Restoux, Amm, Pichot, & Fady, 2016). Therefore, the enriched soil surrounding red fox dens may increase the seed production of white spruce trees surrounding the den. If so, the activity of red foxes as ecosystem engineers might not only influence the growth and reproduction of vegetation on den sites, but could also influence greater ecosystem dynamics such as foraging behaviour and abundance of seed predators (Ostfield & Keesing, 2000).

We hypothesized that the nutrients added to the soil by red foxes in the forest-tundra ecotone will increase the reproductive capacity of conifers in the area surrounding den sites.

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Specifically, the enriched soil on den sites should increase the number and size of cones found on trees at den sites, with cone crop as a proxy for seed crop (Lamontagne & Boutin, 2007). Thus, as a result of their denning activities, red foxes alter the surrounding environment by alleviating the limiting growth factor of nutrients and allowing vegetation to increase reproductive output, which could ultimately affect the distribution of trees at the treeline.

The objective of this study was to determine the impact of red foxes on the reproductive output of white spruce trees by measuring the production of cones on trees on den sites as compared to off-den sites, and the difference in effect between a mast year and a non-mast year. We predicted that a greater number of cones would be produced on den sites than on off-den sites, cones produced on den sites will be larger than those produced on off-den sites, and the effect of additional nutrients will differ between mast years and non-mast years.

Materials and Methods

Study area

The study was located in the boreal woodlands near Churchill, Manitoba. The Coastal Hudson Bay Lowland ecoregion is a transition zone between the boreal forest and the Arctic tundra, and represents the range periphery of red fox dens and major white spruce populations (Scott, Hansell, & Fayle, 1987; Smith et al., 1998; Roth, 2003). Red fox dens in the study area have been previously identified by the presence of burrows, using tracks, digging, prey remains, and shed hairs to determine current or prior red fox activity (Roth, 2003; Lang et al., *in revision*). Most dens in the study area were identified in 1994 and thus are at least 25 years old, though radial tree growth patterns on dens suggest that the impacts of denning may have begun as early as 1897 (Roth, 2003; Lang, 2019). Dens are occupied periodically, which sustains the observed effects of consistently higher soil nutrients on dens than control sites even in years when dens are

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not being occupied (Gharajehdaghipour et al., 2016; Lang et al., *in revision*). Patches of vegetation including white spruce, black spruce (*Picea mariana*), tamarack (*Larix laricina*) and a variety of understory species are found on a landscape characterized by glacial retreat (Smith et al., 1998). Although white spruce trees typically drop their cones over winter, in our study area the prior year's cones were still found on trees in the following summer. Therefore, when fieldwork was conducted in late July and early August, both the prior year's and current year's cones were present on the trees. Based on relative abundance and local expertise (L. Fishback, personal communication, June 4, 2019), we treated the prior year (2018) as a mast year and the year of study (2019) as a non-mast year.

Experimental Protocol

We selected 10 red fox dens based on the presence of white spruce trees and minimum human disturbance. Some dens not included in the study were in close proximity to gravel pits, which could influence soil and growing conditions, while for others white spruce were too sparse, with no trees near the den centre. The centre of the den was determined by identifying the midpoint of a straight line connecting the two outermost burrows (Lang et al., *in revision*). A paired control site for each den was centered 50 m from the den centre, which appeared to be beyond the visible effects of denning on the surrounding vegetation and similar in elevation, slope and soil type to the red fox den (Lang et al., *in revision*). These dens have an average of 81% more total inorganic nitrogen, an average of 250% more extractable phosphorous, and higher respiration in the organic soil layer than the paired control site, but tree age does not differ between den sites (mean ± SD; 104 ± 49 years) and control sites (121 ± 49 years; Lang 2019; Lang et al., *in revision*).

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At each den and paired control site, we selected trees for sampling as the 5 white spruce trees closest to the centre that were >5 cm diameter at breast height (approximately 1.4m), the size at which white spruce begin to produce cones (LaMontagne & Boutin, 2007). All sampled trees were within 18 m of the site centre. For each tree, we measured the height using a Nikon Forestry Pro rangefinder and circumference at breast height using a measuring tape. To assess the number of cones produced by each tree, we stood approximately 20m from the tree (or as far as possible with an unobstructed view) and took 4-6 photographs down the length of the tree on one side, and another set of photographs from the side directly opposite. Using these photographs, we counted both current year (non-mast year) and prior year (mast year) female cones, matching up photographs to avoid double-counting cones (Fig. 1). We estimated basal area of white spruce surrounding the site by measuring the circumference of each white spruce tree within 15 m of each site center (Krebs, 1999). Plot size was amended in two circumstances due to one site being adjacent to a road and another being on the edge of a gravel pile. Finally, we collected up to 5 cones from 2 trees on each site, which were dried and stored in a cool environment before transport. We measured the length and mass of each cone.

Statistical analysis

Statistical analyses were performed in R version 3.6.1. First, we conducted a preliminary analysis of the variables measured on den sites to detect possible variables influencing cone production. We used paired t-tests to determine if mean tree height, mean tree circumference, and basal area differed between dens and controls. Basal area and tree circumference were log-transformed for normality. Cone counts were right-skewed and highly dispersed. Therefore, we used a negative binomial mixed model to assess white spruce cone production for the current year (non-mast year) and the prior year (mast year), with treatment (den or control) as a fixed

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effects variable and site ID as a random effect. Tree height was included in the model as a covariate to account for the effect of individual variation in tree height on cone production. We calculated cone production per land area for each den and control site in both years as the mean number of cones per tree (the average of the five trees sampled on the site) multiplied by the density of trees on the plot, converted to hectares. We used a paired t-test to determine if cone production per hectare differed between dens and controls. Non-mast year cone production per hectare was log-transformed for normality. Finally, we used paired t-tests to compare the length and mass of cones from dens and controls. Cone mass was log-transformed for normality.

Results

Dens and controls differed in tree height (mean ± SE, den = 9.52 ± 0.22 m, control = 8.69 ± 0.41 m; $t_9 = 2.86$, $P = 0.019$) and circumference (den = 0.66 ± 0.03 m, control = 0.56 ± 0.02 m; $t_9 = 3.42$, $P = 0.007$), but not basal area (den = 14.79 ± 4.39 m^2/ha, control = 13.60 ± 2.44 m^2/ha; $t_9 = 0.19$, $P = 0.19$). As tree height and circumference were correlated ($r = 0.76$, $P < 0.001$), circumference was excluded from further analyses to avoid multicollinearity.

The negative binomial mixed model indicated that in the non-mast year, the number of cones per tree was greater on dens than controls ($z = 2.60$, $P = 0.009$) and was positively related to tree height ($z = 2.25$, $P = 0.022$) (Fig. 2). In the mast year, the number of cones also increased with tree height ($z = 3.06$, $P = 0.002$) but did not differ between dens and controls ($z = -0.89$, $P = 0.37$) (Fig. 2). Therefore, denning activity increased the number of cones produced in a non-mast year, but not in a mast year (Fig. 3). Likewise, cone production per hectare was greater on dens in the non-mast year (den = 47,373 ± 16,649 cones/ha, control = 18,328 ± 7,836 cones/ha; $t_9 = 2.86$, $P = 0.018$) but not in the mast year (den = 145,548 ± 32,816 cones/ha, control = 129,132 ± 18,518; $t_9 = 0.38$, $P = 0.71$) (Fig. 3). Cones from dens and controls did not differ in length (den

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= 28.0 ± 1.52 mm, control = 27.4 ± 1.12 mm; $t_9 = 0.30$, $P = 0.77$) or mass (den = 608.2 ± 51.1 mg, control = 625.4 ± 49.7 mg; $t_9 = -0.26$, $P = 0.80$).

Discussion

The increased production of cones on white spruce trees at den sites compared to control sites in the non-mast year suggests that the enriched soil on dens from red fox activity may alleviate, to some extent, the nutrient limitation on reproduction, allowing a greater cone yield. Coniferous boreal forest productivity is typically nitrogen limited, particularly at the treeline (Mahendrappa, Foster, Weetman, & Krause, 1986; Sveinbjörnsson et al., 2002). These findings suggest that heightened soil nutrients on fox dens allow white spruce a greater reproductive output, in addition to increased growth (Lang, 2019), consistent with our first prediction. Steinbrenner, Duffield, and Campbell (1960) found that nitrogen fertilization increased both cone yield and length in Douglas fir (*Pseudotsuga menziesii*). In our study, white spruce cone size (mass and length) did not differ between den and control sites. However, the nutrient input of red foxes would be significantly lower than that of a fertilizer experiment, and our study was conducted at the range limit of white spruce, potentially accounting for the differing cone size results. In this study, cone size similarity between treatments suggests that in non-mast years, trees allocate a greater amount of resources to producing more cones, but not larger cones.

In both the non-mast year and the mast year cone yield was positively related to tree height, consistent with other studies relating cone crop to tree size (both height and circumference) (Sutton, Staniforth, & Tardif, 2002; Messaoud, Bergeron, & Asselin, 2007; Ayari, Zubizarreta-Gerendiain, Tome, Tome, Garchi, & Henchi, 2012; Davi et al., 2016). However, there was no difference in cone production between den and control sites in the mast

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year, suggesting that the enriched soil on fox dens impacts cone production only in non-mast years.

With two years of data available, it is difficult to understand the interaction between white spruce mast-seeding patterns and increased nutrient availability. Despite these challenges, proximate-level hypotheses of mast seeding may help to explain why cone production would differ between dens and controls in a non-mast year but not in a mast year. First, weather cues and climate variables, such as prior years' summer temperatures and precipitation, can influence mast-seeding patterns and annual cone crop in white spruce (Krebs et al., 2012, 2017; Roland et al., 2014). The influence of climatic variables may be moderate in most years, but in mast years these cues could outweigh the effects of nutrient addition, resulting in a similar reproductive output between trees on dens and control sites.

On the other hand, the resource budget model of mast seeding proposes that in a given year, a portion of acquired resources will be allocated to growth, a portion to reproduction, and a portion will be stored for later reproduction. Once the stored level of resources exceeds the threshold for reproduction, plants will produce a large seed crop (Isagi, Sugimura, Sumida, & Ito, 1997). In this case, it is possible that trees on dens and off dens allocate the same amount of resources to storage each year, resulting in a comparable cone crop in mast years. Since most trees in the boreal woodlands have limited acquisition of resources in a given year, they allocate less to reproduction annually resulting in small cone crops between mast years, while trees on red fox dens have greater access to nutrients from year to year and produce larger cone crops between mast years. The resource budget model also implies that a mast-seeding event depletes resources stored in tissues, as observed by Sala, Hopping, McIntire, Delzon, and Crone (2012), where mast seeding depleted tissue nitrogen and phosphorus in whitebark pine (*Pinus*

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albicaulis). Depletion of tissue resources could make reproduction difficult in the year following a mast year. It is important to note that although cone crop is often assumed to infer seed crop, this assumption may be misleading in areas with low spruce density and low seed viability. Low rates of viable seed have been observed in white spruce at the treeline, and may occur more frequently in this zone due to low stand density and unfavorable climatic conditions (Kambo & Danby, 2018; Brown et al., 2019; Lantz, Moffat, Fraser & Walker, 2019). Due to this potential discrepancy, future studies should consider the production of viable seed in addition to cone crop.

Altered seed production on dens could have further ecological implications, particularly in the low productivity environment of the boreal woodlands. For example, high or low seed production could affect the foraging behaviour and demography of seed predators, such as North American red squirrels (*Tamiasciurus hudsonicus*). White spruce seeds are a primary source of nutrition for red squirrels, and their reproductive success is often linked to white spruce cone crop (Smith, 1968; Klenner & Krebs, 1991; McAdam et al., 2019). In non-mast years, as was observed in this study in 2019, low cone production may force seed predators to rely less on white spruce seeds as a primary food source and supplement their diet with other available food sources (Smith, 1968; Fletcher et al., 2010). However, high localized seed production in non-mast years by white spruce on dens could create foraging hotspots and may potentially lead to a slight increase in recruitment.

Similarly, although the boreal treeline has been predicted to expand northward with climate change, empirical observations of this response are mixed. Poor conditions beyond the treeline may limit seedling recruitment and therefore treeline advancement (Kambo & Danby, 2018; Brown et al., 2019). Brown et al. (2019) suggest that the sequence of occurrence of

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growing degree days during the developmental period of reproductive structures, as well as increased conspecific density (to reduce pollen limitation), affect the proportion of viable seed produced. The density of white spruce at the forest-tundra ecotone has increased with warming temperatures (Lantz et al., 2019). Despite the proportion of viable seed produced by white spruce at the treeline being generally low (Roland et al., 2014; Lantz et al., 2019), it is possible red fox activity, combined with warming temperatures and increasing conspecific density, may contribute to treeline advancement on to the tundra through increased seed production at the forest-tundra ecotone.

In conclusion, this study suggests that red foxes influence the reproductive output of white spruce through ecosystem engineering activities in the boreal forest. By concentrating nutrients on dens over many decades, red foxes have created patches of increased resource availability on the landscape that can elevate reproduction for surrounding vegetation.

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Figures

Fig. 1. Sample images of white spruce trees possessing cones from both the current non-mast year (2019) and the previous mast year (2018). Image (A) shows current year cones are a lighter, reddish-brown colour with closed scales, while prior year cones are darker brown in colour with open scales. Image (B) demonstrates how cones were marked with different colours to avoid double counting on the photographs. Images taken with a Nikon DSLR camera on red fox dens near Churchill, Manitoba in July or August 2019. (Colour image)

Fig. 2. Relationship between number of white spruce cones per tree and tree height in (A) a mast year (2018) and (B) a non-mast year (2019) for 10 red fox dens and paired control sites near Churchill, Manitoba (n = 5 trees per site).

Fig. 3. White spruce cone production in (A) number of cones per tree, and (B) number of cones per hectare from a mast year (2018) and non-mast year (2019) for 10 red fox dens and paired control sites near Churchill, Manitoba (mean ± SE).

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Fig. 1

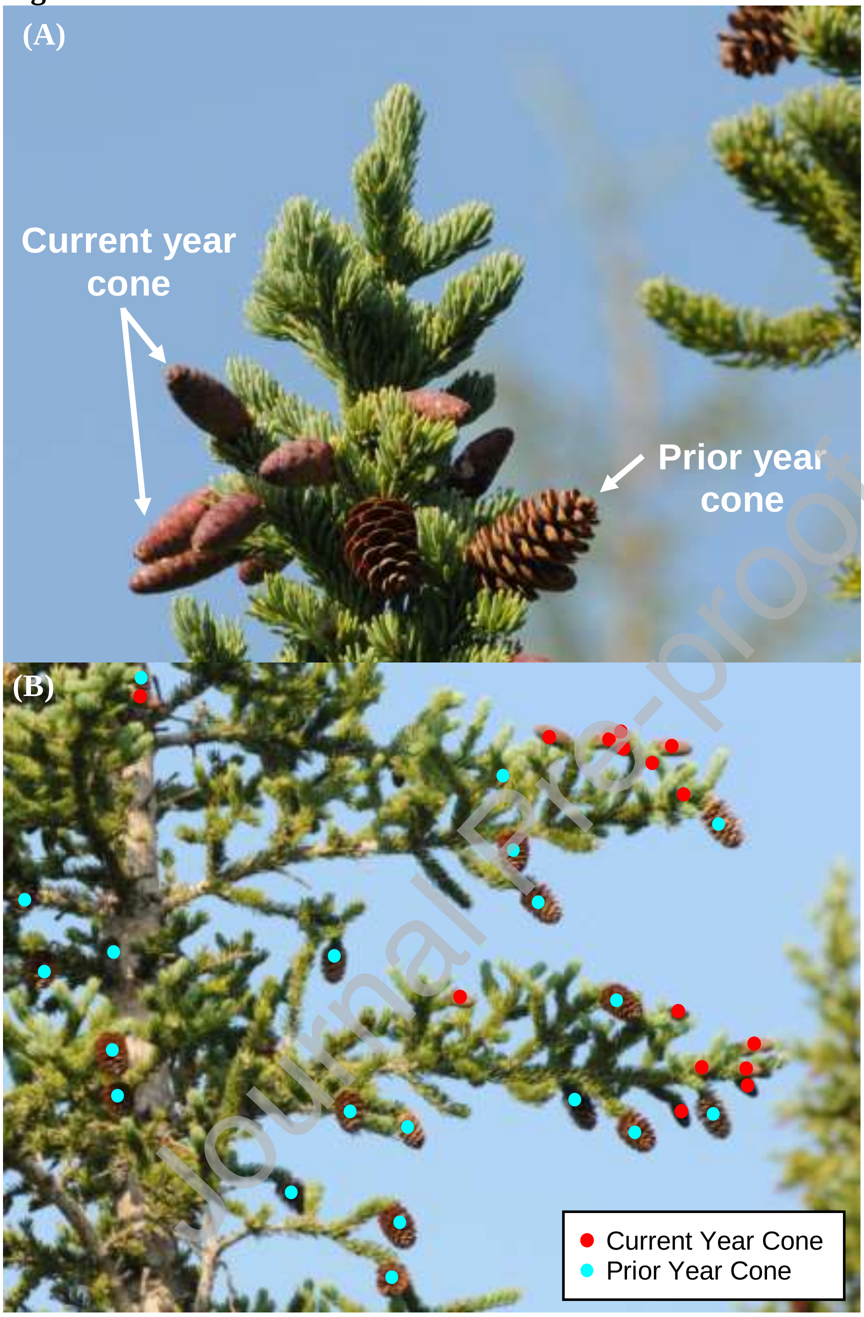

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Fig. 2

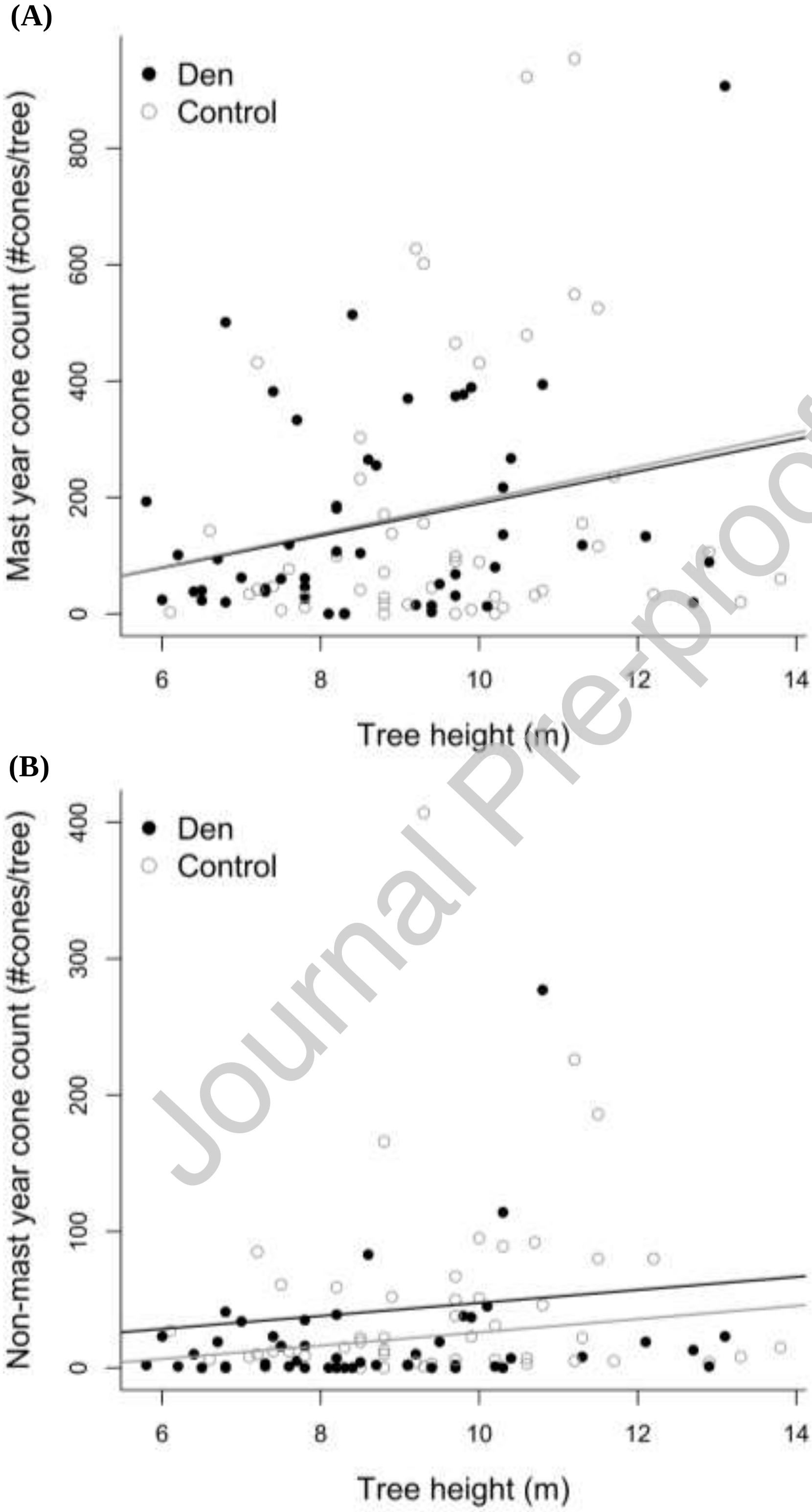

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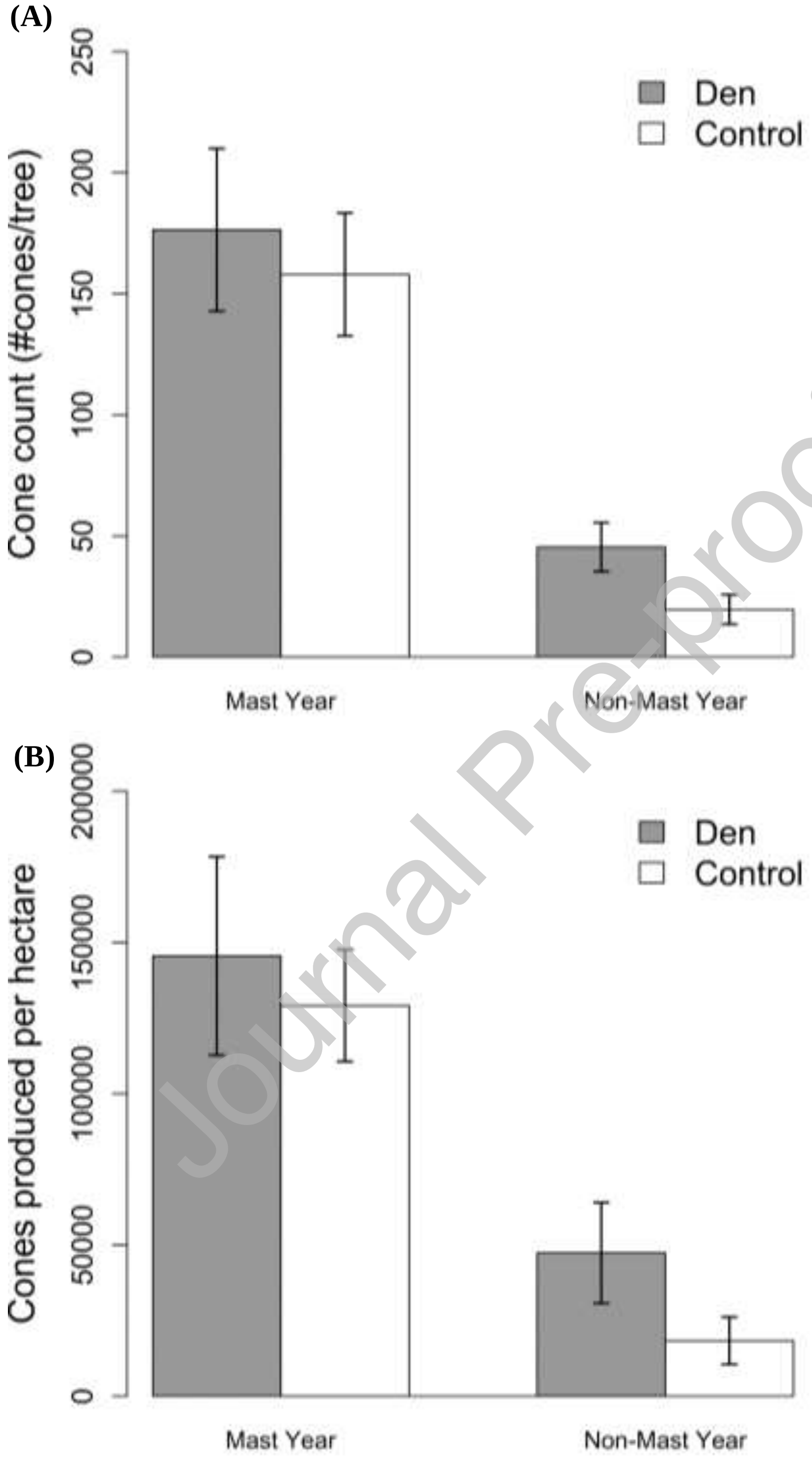
Fig. 3



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