

Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic

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Funding information

Natural Sciences and Engineering Research Council of Canada (RGPIN/386704-2011), University of Manitoba Field Work Support Program.

Co-ordinating Editor: Hans Henrik Bruun

Abstract

Questions: In most ecosystems, some organisms can be considered ecosystem engineers because they modify their physical environment in a way that can affect many other organisms. Nutrient deposition may be extremely important as an ecosystem engineering activity in nutrient-limited environments, but this mechanism remains understudied. In low-Arctic tundra, a region characterized by continuous permafrost, low-nutrient soils, and slow nutrient turnover, Arctic foxes (*Vulpes lagopus*) concentrate nutrients on their dens through faecal deposition and feeding their young. This nutrient concentration enhances productivity in patches on the landscape, likely creating a unique habitat for a variety of plants, and could have cascading effects on the distribution and diversity of vegetation on the tundra.

Location: Low-Arctic tundra in Wapusk National Park, Manitoba, Canada.

Methods: We quantified differences in vegetation composition between 20 fox dens and adjacent control sites.

Results: Plant growth form differed greatly between dens, which were dominated by deciduous grasses near the coast and erect shrubs farther from the coast, and control sites, which were dominated by evergreen prostrate shrubs. Dens also had more forb cover and less cover of lichens, mosses, and sedges. Species composition also varied greatly between control and den areas, with 17 of the 20 species found in at least 10% of the sampled sites being indicator species for dens or control sites.

Conclusions: By providing habitat for plants reliant on higher nutrient availability not typical of tundra heath, Arctic foxes enhance the biodiversity of the region. These erect plants may also help create new habitat by retaining snow on normally wind-swept beach ridges. Overall, this study illustrates the broader impacts of predators on diversity and community composition through mechanisms other than predation.

KEYWORDS

Arctic heath, denning activity, ecosystem engineering, *Leymus mollis*, nutrient addition, species diversity, *Vulpes lagopus*

1 | INTRODUCTION

Ecosystem engineers, organisms that create, modify, or maintain ecosystems through non-trophic interactions (Jones, Lawton, & Shachak, 1994), cause a physical state change in their environment through

direct modification of biotic or abiotic components of their environment. When considered at a scale that encompasses both modified and unmodified habitats, ecosystem engineering enhances species richness by increasing habitat diversity (Jones, Lawton, & Shachak, 1997). Nutrient deposition, in the form of faeces, has been explored

as a mechanism of ecosystem engineering in both terrestrial (Bruun, Österdahl, Moen, & Angerbjörn, 2005; Mohr, 1943; Thompson, Thomas, Readley, Williamson, & Lawton, 1993) and marine habitats (de Wilde, 1991; Reichelt, 1991; Roman & McCarthy, 2010). In addition to faecal deposition, predators can alter nutrient deposition by moving and/or failing to consume animal carcasses, which are rich sources of nutrients (Barry et al., 2019; Danell, Berteaux, & Bråthen, 2002). While these activities have a direct effect on autotrophs (Bonachela, Raghieb, & Levin, 2011; Comerford, 2005), they can also indirectly affect heterotrophs as well (Gharajehdaghpour & Roth, 2018).

The effects of ecosystem engineers are likely to be more pronounced when they affect limiting resources. For instance, kangaroo rat burrowing, which dries soil, increasingly affects soil moisture over a precipitation gradient. Consequently, burrows have a greater effect on nitrogen mineralization and plant species beta diversity as precipitation increases (Grinath, Larios, Prugh, Brashares, & Suding, 2019). Nutrient deposition therefore most likely affects communities when it occurs in nutrient-limited environments. Tundra ecosystems are typically nutrient-limited, with a relatively shallow active soil layer coupled with slow nutrient cycling (Henry & Molau, 1997; Jonasson, Michelsen, & Schmidt, 1999). Fertilization experiments have confirmed that tundra plant growth is often limited by nitrogen and/or phosphorus (Gough, Wookey, & Shaver, 2002; Jonasson, 1992; Kelley & Epstein, 2009), suggesting that nutrient deposition could be an important ecosystem service provided by ecosystem engineers in this biome (Gharajehdaghpour, Roth, Fafard, & Markham, 2016). Upland areas of the tundra are characterized by a heath vegetation of slow-growing dwarf shrubs, small forbs, graminoids, and stress-tolerant lichens and mosses (Ritchie, 1956). The ericoid mycorrhizal fungi associated with many heath plants allows them to access nutrients from recalcitrant organic sources, which cannot be accessed by other plants (Read & Perez-Moreno, 2003). Increased nutrient availability in heaths is therefore likely to increase the abundance of species more reliant on inorganic nutrients.

Arctic foxes (*Vulpes lagopus*) exhibit a number of behaviours that qualify them as ecosystem engineers. They use and maintain the same dens to rear young for decades, although dens may also go through periods when they are not used for raising pups (Roth, 2003; Tannerfeldt & Angerbjörn, 1998). Dens are the primary site of faecal deposition by pups and consumption of prey carcasses brought to them by the adults. This nutrient deposition on dens enhances soil nutrient concentrations and increases primary productivity (Bruun et al., 2005; Gharajehdaghpour et al., 2016). As nutrient cycling is slow in the Arctic (Jonasson et al., 1999), effects of nutrient-enriching activities by foxes may persist long after dens have been used for reproduction. The disturbed earth from tunnel excavation also provides colonization opportunities for disturbance-tolerant plant species (Huntly & Reichman, 1994).

Despite previous research into nutrient deposition as a mechanism of ecosystem engineering in both terrestrial and aquatic ecosystems (Bonachela et al., 2011; Bryce, Wal, Mitchell, & Lambin, 2013; Roman & McCarthy, 2010; Smith & Conway, 2007), the

effects on plant community dynamics are understudied, especially in tundra ecosystems (Jonasson, 1992; Kelley & Epstein, 2009; Yano, Shaver, Rastetter, Giblin, & Laundre, 2013). Denning activity by Arctic foxes has resulted in large changes in plant species composition in some studies (Bruun et al., 2005), but not in others (Anthony, 1996). Therefore, our objective was to quantify the potential effects of nutrient deposition by Arctic foxes on the upland heath plant community composition of the low-Arctic landscape by comparing plant assemblages on and off the dens. Our past work in the study area found that dens have higher soil N and P availability and greater plant biomass than non-den areas (Gharajehdaghpour et al., 2016). We hypothesized that Arctic foxes act as ecosystem engineers primarily by increasing nutrient availability on dens, supporting an assemblage of plant species that may not thrive elsewhere on the tundra heath. We also examined how recent fox reproduction affected soil moisture and the how proximity of dens to the coast, which influences the microclimate of dens, alters the impact Arctic foxes have on plant abundance.

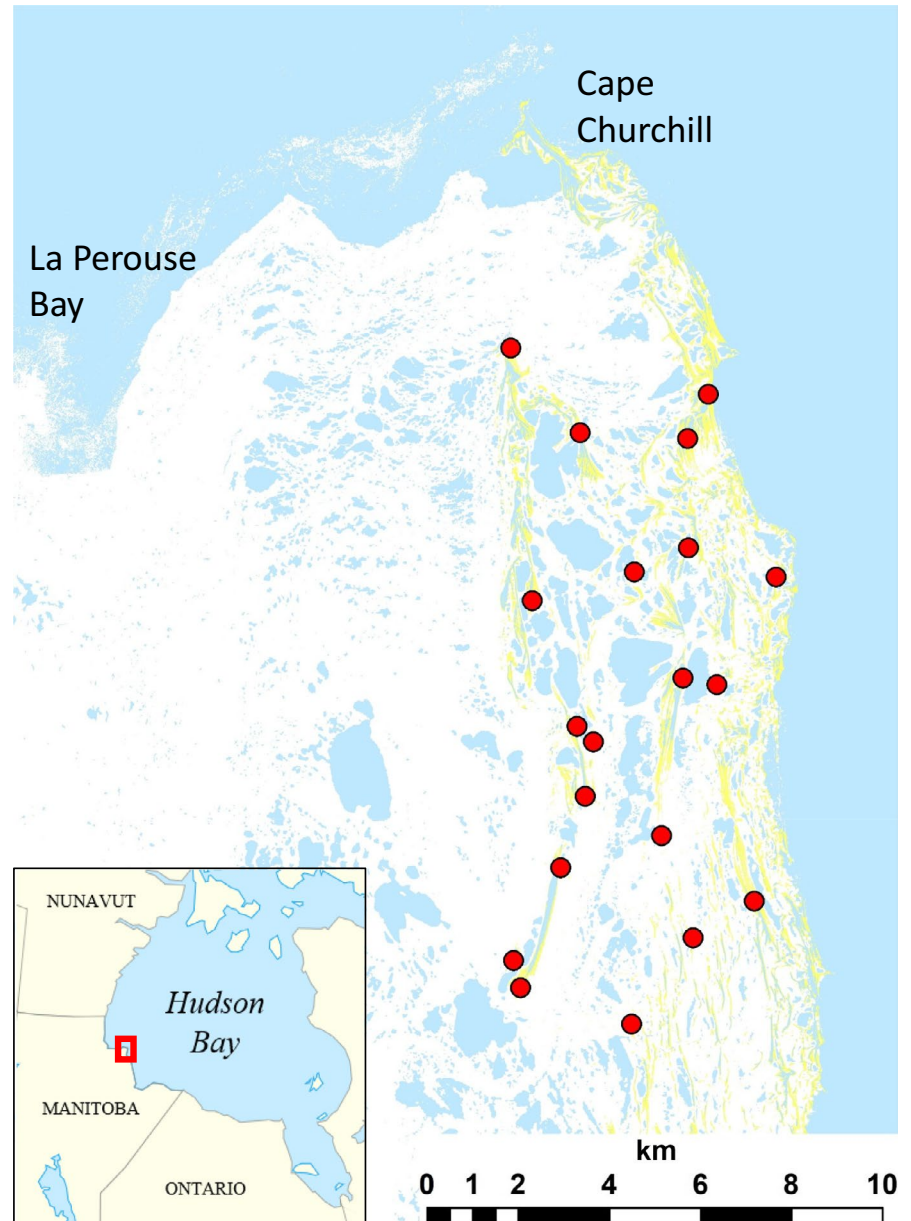
2 | METHODS

The study was located within Wapusk National Park, on the west coast of Hudson Bay in northern Manitoba (58°34' N, 93°11' W). The climate of the area is strongly influenced by Hudson Bay, which is frozen for seven to eight months of the year and exerts a cooling effect on the coast (Rouse, 1991). The landscape of the study area is a flat coastal plain consisting of alternating ancient beach ridges of limestone gravel and wet hollows running parallel to the coast (Johnson, 1987; Ritchie, 1956). These ridges are dominated by lichens and heath species and provide suitable denning habitat for Arctic foxes in the area (Roth, 2003).

Between 30 July and 5 August 2015, we sampled 20 fox dens and 20 adjacent control areas (Figure 1). Fox activity at dens was discerned through presence of cleared-out burrows, fresh scat, digging, and/or pups. Vegetation surveys were conducted on each den and control area using five 1-m² quadrats: one at the centre of the sampled area and one in each cardinal direction 5 m from the centre. All den quadrats were within the den perimeter, defined by the presence of burrows. Control areas were sampled 50 m along the beach ridge from the den centre, at a similar aspect, slope, and elevation to the dens. Within each quadrat, the presence of each vascular plant species and the percent cover of each growth form (erect shrubs taller than 25 cm, prostrate shrubs less than 25 cm, grasses, sedges, forbs, mosses and lichens) were estimated visually. Soil moisture was measured using a soil moisture probe (ML2x ThetaProbe, Delta T Devices Inc.) in each quadrant of each quadrat and measurements averaged. The distance to the ocean of each sampled area was determined using satellite imagery and the distance measurement tool in Google Maps (maps.google.com, accessed in 2015).

Each den and control area was considered a replicate. Therefore, the data analysis was based on mean values from the sampled quadrats in each den and control. Soil moisture and the

FIGURE 1 Map of study site in Wapusk National Park, Canada, indicating sampled Arctic fox (*Vulpes lagopus*) den locations [Colour figure can be viewed at wileyonlinelibrary.com]



number of species per quadrat and per site were compared using paired t tests. Mean cover of plant growth forms and number of species per growth form on den and control were compared using Wilcoxon signed rank tests with a Bonferroni adjustment (i.e., for the seven growth forms, the critical p -value was 0.0071). We also compared soil moisture and cover of growth forms between inactive dens and dens with pups, or dens with any sign of activity, using one-way ANOVAs. The effect of the soil moisture and distance to the ocean on the abundance of growth forms was examined using least squares using linear models. We used the frequency of species occurrence in the five quadrats in each area to conduct an indicator species analysis (Dufrêne & Legendre, 1997), which determines if species are associated with predetermined community subtypes, i.e., den or control areas. All data analysis was performed using JMP (version 10.0.0, 2012, SAS Inc.)

except for the indicator species analysis, which was done using the `labdsv` package in R (version 3.3.2; R Core Team, 2018).

3 | RESULTS

The abundance of all plant growth forms differed significantly between control and den areas (Figure 2). Control areas were dominated by typical Arctic heath prostrate shrubs, which made up 79.6% of all plant cover. The most frequently encountered shrubs were evergreen, mainly *Dryas integrifolia* and *Arctostaphylos alpina* (Appendix S1). Sedges, mosses and lichens were 11.6, 44.6 and 3.9 times more abundant, respectively, on heath controls than on den areas, although they made up a small portion of the vegetation cover. In contrast, den areas were dominated by grasses, erect

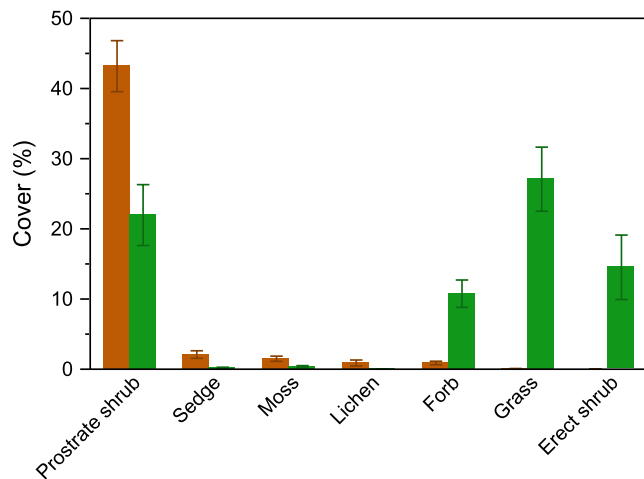


FIGURE 2 Cover (mean \pm SE) of plant growth forms on Arctic fox dens and control sites, calculated from mean cover of five quadrats per site. * $p < 0.0071$; ** $p < 0.0001$ [Colour figure can be viewed at wileyonlinelibrary.com]

shrubs (*Salix athabascensis* and *Salix glauca*, hereafter referred to as *S. athabascensis* as they were often difficult to distinguish) and forbs. The grass cover was overwhelmingly *Leymus mollis* growing over 1 m high, with an average cover of $27.1 \pm 3.0\%$, and found in 90% of the den sites. In comparison, *L. mollis* occurred in only 20% of the control sites, where individuals were <30 cm high and mean cover never exceeded 1%.

We found a total of 33 vascular plant species in the sampled quadrats (Appendix S1). Of these species, 17 were indicators for either den or heath areas (Table 1). Six of these species were unique to dens (*Chamerion angustifolium*, *Rubus acaulis*, *Salix athabascensis*, *Draba glabella*, *Stellaria longipes*, and *Cerastium alpinum*) and three were unique to the control areas (*Saxifraga oppositifolia*, *Oxytropis campestris* and *Physaria reediana*). Although the number of species per quadrat did not differ between den (4.6 ± 0.3) and control areas (5.1 ± 0.5 , $t = 1.071$, $p = 0.298$) the total number of species in the five quadrats was higher in den areas (9.5 ± 0.7) than heath areas (6.5 ± 0.6 , $t = 4.075$, $p = 0.0013$). This difference occurred because only dens had erect shrub species and dens had a higher number of forb species (4.7 ± 0.3 vs 2.0 ± 0.3 , $t = 5.067$, $p < 0.0001$) and grass species (1.9 ± 0.1 vs 0.3 ± 0.1 , $t = 5.922$, $p < 0.0001$) but fewer prostrate shrub species (1.9 ± 0.3 vs 3.2 ± 0.4 , $t = 3.158$, $p = 0.0052$).

At the time of sampling the soil was uniformly dry ($6.21 \pm 0.44\%$, mean \pm SE) with no difference in soil moisture between den and control areas ($t = 0.202$, $p = 0.842$). Eleven dens had signs of fox activity, three of which were occupied by pups. Soil moisture on dens was unaffected by the presence of pups ($F_{1,19} = 0.0003$, $p = 0.985$) or any sign of active use ($F_{1,19} = 1.048$, $p = 0.320$). Since dens and control areas were so different in their plant growth forms and species composition, we examined the effect of environmental variables on their vegetation composition separately. Grass cover was negatively affected by the distance to the ocean both on controls ($F_{1,18} = 5.027$, $p = 0.038$) and on dens ($F_{1,18} = 7.060$, $p = 0.016$). For the control areas, no grass was found farther than 2.4 km from the ocean, whereas all

TABLE 1 Indicator species for control and den areas. Indicator values are based on mean frequency of occurrence in sampled quadrats

Species	Indicator value	p-value
Control		
<i>Carex concinna</i>	0.7900	0.0001
<i>Dryas integrifolia</i>	0.6940	0.0001
<i>Saxifraga oppositifolia</i>	0.6000	0.0001
<i>Arctostaphylos alpina</i>	0.5802	0.0107
<i>Physaria reediana</i>	0.4000	0.0028
<i>Rhododendron lapponicum</i>	0.2842	0.0324
<i>Vaccinium uliginosum</i>	0.2769	0.0402
Den		
<i>Leymus mollis</i>	0.8299	0.0001
<i>Rubus acaulis</i>	0.7500	0.0001
<i>Chamerion angustifolium</i>	0.7500	0.0001
<i>Poa alpina</i>	0.7484	0.0010
<i>Salix athabascensis</i>	0.7000	0.0001
<i>Saxifraga tricuspidata</i>	0.5500	0.0015
<i>Pyrola grandiflora</i>	0.4667	0.0066
<i>Achillea nigrescens</i>	0.4219	0.0061
<i>Draba glabella</i>	0.4000	0.0037
<i>Stellaria longipes</i>	0.4000	0.0034

but one control location <2.4 km from the ocean had grass present (Figure 3a). On dens, grasses were found across the full range of distances from the ocean but cover decreased by 5.6% with every km from the ocean (Figure 3b). Erect shrubs on dens showed the opposite pattern (Figure 3c), with cover increasing with distance from the ocean ($F_{1,18} = 8.600$, $p = 0.0089$) and no dens within 2 km of the ocean having >10% cover of erect shrubs (no erect shrubs were found on control areas). Distance from the ocean did not affect cover of prostrate shrubs (control $F_{1,18} = 0.115$, $p = 0.738$; den $F_{1,18} = 0.001$, $p = 0.983$), sedges (control $F_{1,18} = 1.500$, $p = 0.237$; den $F_{1,18} = 0.120$, $p = 0.598$), mosses (control $F_{1,18} = 0.570$, $p = 0.460$; den $F_{1,18} = 0.238$, $p = 0.632$), lichens (control $F_{1,18} = 0.063$, $p = 0.805$; den $F_{1,18} = 0.005$, $p = 0.944$), or forbs (control $F_{1,18} = 0.447$, $p = 0.512$; den $F_{1,18} = 0.348$, $p = 0.563$). The only significant relationships between plant growth form and soil moisture were on control areas, where soil moisture was positively related to both moss ($r^2 = 0.304$, $F_{1,18} = 7.881$, $p = 0.012$) and lichen cover ($r^2 = 0.526$, $F_{1,18} = 19.94$, $p = 0.0003$).

4 | DISCUSSION

Overall, the mix of tall grasses, erect shrubs and forbs found on the dens is a unique vegetation assemblage, not only on the beach ridge heath, but in the entire region (see Ritchie, 1956, for a list of vegetation assemblages). Notably, all of the plants that were indicators of dens (except *Pyrola grandiflora* and *Saxifraga tricuspidata*) associate with arbuscular mycorrhizae. They therefore must

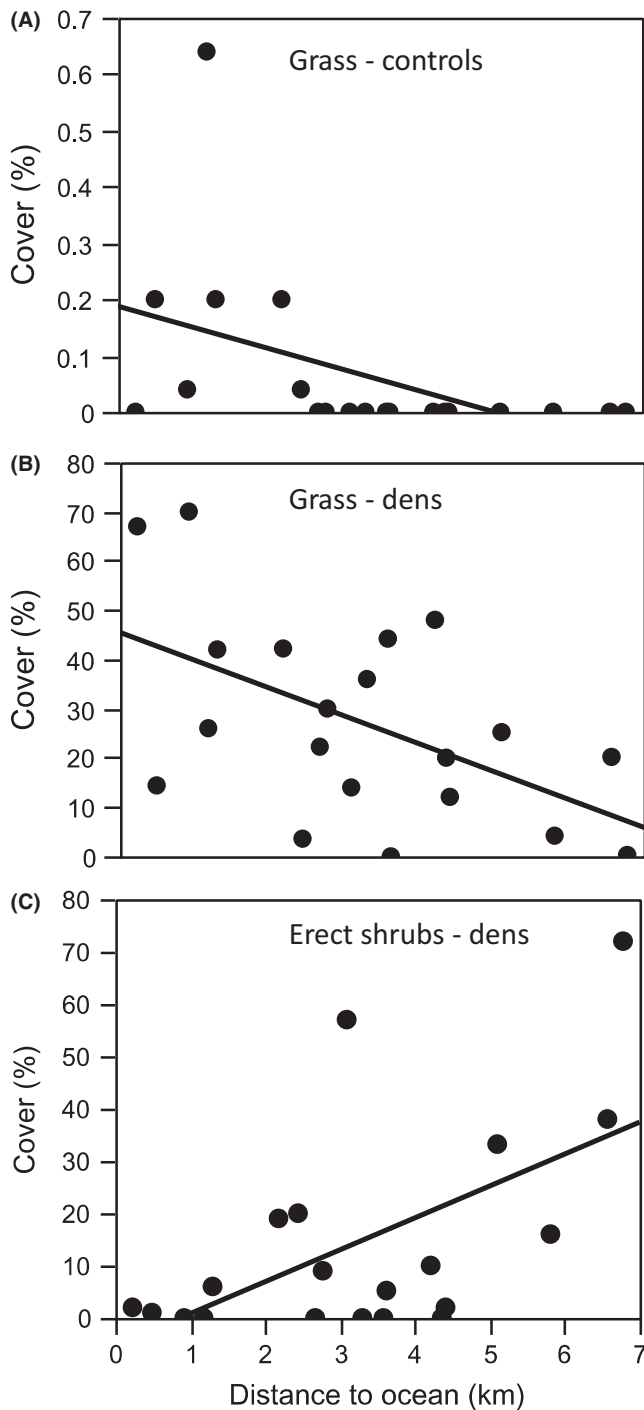


FIGURE 3 Relationship between abundance of plant growth forms and distance to the ocean for (A) grasses in control areas ($y = 0.187 - 0.037x$, $r^2 = 0.218$), (B) grasses on dens ($y = 45.55 - 5.65x$, $r^2 = 0.300$) and (C) erect shrubs on dens ($y = -5.30 + 6.10x$, $r^2 = 0.323$)

rely on uptake of inorganic nitrogen (Read & Perez-Moreno, 2003), suggesting their presence is driven by the increased nutrient availability we previously found (Gharajehdaghypour et al., 2016). Although heath plants have the ability to survive under conditions of low nutrient availability, faster-growing deciduous species are better able make use of an increased nutrient supply (Jonasson,

1992; Shaver & Chapin, 1980). Heath plants are therefore replaced by deciduous grasses and shrubs when nutrients become available (Aerts, 1990; Gutschick & Pushnik, 2005). The decrease in prostrate shrubs and increase in grasses and erect deciduous shrubs that we found on dens is similar to what was found on Arctic fox dens in northern Sweden (Bruun et al., 2005). However, that study found a much stronger decrease in dwarf shrubs, and the heath vegetation in that region had a much higher species diversity than our study area. Another study on fox dens in western Alaska, where species diversity was also low in fox habitats (pingos), showed a significant (30%) reduction in the frequency of only one of five prostrate shrubs found on the dens (Anthony, 1996). It is therefore likely that dwarf shrub displacement due to nutrient enrichment may be more pronounced in regions with a greater species pool.

The dominance of grass cover on dens is consistent with previous research in the Arctic showing grasses are better able to take advantage of increased nutrients compared to other species (Gough et al., 2002; Hargreaves, Horrigan, & Jefferies, 2009; Nilsson, Wardle, Zackrisson, & Jaderlund, 2002; Parsons et al., 1995). The shift from prostrate shrubs to grasses has also been found in fertilization experiments in alpine heaths in Italy (Brancaleoni, Gualmini, Tomaselli, & Gerdol, 2007). Additionally, the greater number of forb species on dens seen here and in another study (Bruun et al., 2005) may be due to foxes creating disturbed habitat.

While grasses were the dominant growth form on dens, they became less dominant away from the coast where erect shrubs became dominant. While the sharp decline in temperature and evapotranspiration near the coast (Rouse, 1991) could affect plant distributions, the increasing dominance of grass on dens near the coast may also be the result of the availability of propagules. In this region, dunes at the coast also have a large population of seed-bearing *L. mollis* whereas we see little seed production of *L. mollis* on inland heaths, except on the dens. This coastal population may therefore provide a seed source for den colonization. This seed source would also explain the existence of the grasses off the dens only being found near the coast.

Shrub expansion in the Arctic in response to climate change is well documented (Myers-Smith et al., 2011), and our results suggest denning activity by Arctic foxes may contribute to increased shrub cover. Erect shrubs can trap more snow in winter, maintaining higher ground temperatures, increased nutrient cycling (Sturm et al., 2005) and warmer winter habitat for small mammals (Reid et al., 2012). Besides retaining more snow, grasses growing on dens also have a higher leaf N, which could also attract herbivores to dens (Gharajehdaghypour & Roth, 2018). However, shrubs can also produce a litter that is more recalcitrant (Steinwandter, Schlick-Steiner, Steiner, & Seeber, 2019), offsetting any effect of increased winter temperature on nutrient cycling.

Although carnivores make up a small proportion of the biomass in ecosystems they can affect vegetation patterns through a number of processes. They can cause trophic cascades by suppressing herbivory (Beschta & Ripple, 2016). They can also affect ecosystem processes facilitated by prey. For example, predation on seabirds by

Arctic foxes introduced to the Aleutian archipelago severely reduced transport of nutrients from ocean to land, transforming affected islands from grasslands to tundra (Croll, Maron, Estes, Danner, & Byrd, 2005). In contrast, although Arctic fox dens occupy a small fraction of the landscape, by directly concentrating nutrients they provide a unique nutrient-rich habitat, and the resulting plant communities increase the community diversity across the landscape.

ACKNOWLEDGEMENTS

We would like to thank T. Gharajehdaghypour for help with field work, J. Kormish for feedback on a previous version of the manuscript, and C. Warret Rodrigues for creating the map. The Churchill Northern Studies Centre and Manitoba Conservation provided logistic support. Research was conducted under Parks Canada Research & Collection Permit WAP-2014-16142.

DATA AVAILABILITY STATEMENT

Data are available on Dryad: <https://doi.org/10.5061/dryad.8sf7m0ch7>.

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REFERENCES

- Aerts, R. (1990). Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oecologia*, 84, 391–397. <https://doi.org/10.1007/BF00329765>
- Anthony, R. M. (1996). Den use by arctic foxes (*Alopex lagopus*) in a subarctic region of Western Alaska. *Canadian Journal of Zoology*, 74, 627–631.
- Barry, J. M., Elbroch, L. M., Aiello-Lammens, M. E., Sarno, R. J., Seelye, L., Kusler, A., ... Grigione, M. M. (2019). Pumas as ecosystem engineers: Ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. *Oecologia*, 189, 577–586. <https://doi.org/10.1007/s00442-018-4315-z>
- Beschta, R. L., & Ripple, W. J. (2016). Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. *Biological Conservation*, 198, 93–103. <https://doi.org/10.1016/j.biocon.2016.03.031>
- Bonachela, J. A., Raghil, M., & Levin, S. A. (2011). Dynamic model of flexible phytoplankton nutrient uptake. *Proceedings of the National Academy of Sciences*, 108, 20633–20638. <https://doi.org/10.1073/pnas.1118012108>
- Brancaleoni, L., Gualmini, M., Tomaselli, M., & Gerdol, R. (2007). Responses of subalpine dwarf-shrub heath to irrigation and fertilization. *Journal of Vegetation Science*, 18, 337–344. <https://doi.org/10.1111/j.1654-1103.2007.tb02545.x>
- Bruun, H. H., Österdahl, S., Moen, J., & Angerbjörn, A. (2005). Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography*, 28, 81–87. <https://doi.org/10.1111/j.0906-7590.2005.04033.x>
- Bryce, R., van der Wal, R., Mitchell, R., & Lambin, X. (2013). Metapopulation dynamics of a burrowing herbivore drive spatio-temporal dynamics of riparian plant communities. *Ecosystems*, 16, 1165–1177. <https://doi.org/10.1007/s10021-013-9677-9>
- Comerford, N. B. (2005). Soil factors affecting nutrient bioavailability. In H. BassiriRad (Ed.), *Ecological Studies, Vol. 181: Nutrient acquisition by plants - An ecological perspective* (pp. 1–14). Berlin, Germany: Springer-Verlag Berlin Heidelberg.
- Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., & Byrd, G. V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science*, 307, 1959–1961. <https://doi.org/10.1126/science.1108485>
- Danell, K., Berteaux, D., & Bråthen, K. A. (2002). Effect of muskox carcasses on nitrogen concentration in tundra vegetation. *Arctic*, 55, 389–392. <https://doi.org/10.14430/arctic723>
- de Wilde, P. A. W. J. (1991). Interactions in burrowing communities and their effects on the structure of marine benthic ecosystems. In P. S. Meadows, & A. Meadows (Eds.), *The Environmental impact of burrowing animals and animal burrows* (pp. 107–118). London, UK: The Zoological Society of London; Oxford, UK: Clarendon Press.
- Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAAI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAAI]2.0.CO;2)
- Gharajehdaghypour, T., & Roth, J. D. (2018). Predators attract prey through ecosystem engineering in the Arctic. *Ecosphere*, 9, e20277. <https://doi.org/10.1002/ecs2.2077>
- Gharajehdaghypour, T., Roth, J. D., Fafard, P. M., & Markham, J. H. (2016). Arctic foxes as ecosystem engineers: Increased soil nutrients lead to increased plant productivity on fox dens. *Scientific Reports*, 6, 24020. <https://doi.org/10.1038/srep24020>
- Gough, L., Wookey, P. A., & Shaver, G. R. (2002). Dry heath arctic tundra responses to long-term nutrient and light manipulation. *Arctic, Antarctic and Alpine Research*, 34, 211–218.
- Grinath, J. B., Larios, L., Prugh, L. R., Brashares, J. S., & Suding, K. N. (2019). Environmental gradients determine the potential for ecosystem engineering effects. *Oikos*, 128(7), 994–1004. <https://doi.org/10.1111/oik.05768>
- Gutschick, V. P., & Pushnik, J. C. (2005). Internal regulation of nutrient uptake by relative growth rate and nutrient-use efficiency. In H. BassiriRad (Ed.), *Ecological Studies, Vol. 181: Nutrient acquisition by plants - An ecological perspective* (pp. 63–88). Berlin, Germany: Springer-Verlag Berlin Heidelberg.
- Hargreaves, S. K., Horrigan, E. J., & Jefferies, R. L. (2009). Seasonal partitioning of resource use and constraints on the growth of soil microbes and a forage grass in a grazed Arctic salt-marsh. *Plant and Soil*, 322, 279–291. <https://doi.org/10.1007/s11104-009-9915-2>
- Henry, G. H. R., & Molau, U. (1997). Tundra plants and climate change: The International Tundra Experiment (ITEX). *Global Change Biology*, 3(1–9 Suppl.), 1. <https://doi.org/10.1111/j.1365-2486.1997.gcb132.x>
- Huntly, N., & Reichman, O. J. (1994). Effects of subterranean mammalian herbivores on vegetation. *Journal of Mammalogy*, 75, 852–859. <https://doi.org/10.2307/1382467>
- Johnson, K. L. (1987). *Wildflowers of Churchill and the Hudson Bay region*. Winnipeg, MB: Manitoba Museum of Man and Nature.
- Jonasson, S. (1992). Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos*, 63, 420–429. <https://doi.org/10.2307/3544968>
- Jonasson, S., Michelsen, A., & Schmidt, I. K. (1999). Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. *Applied Soil Ecology*, 11, 135–146.
- Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386. <https://doi.org/10.2307/3545850>
- Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as ecosystem engineers. *Ecology*, 78, 1946–1957.
- Kelley, A. M., & Epstein, H. E. (2009). Effects of nitrogen fertilization on plant communities of nonsorted circles in moist nonacidic tundra, northern Alaska. *Arctic, Antarctic, and Alpine Research*, 41, 119–127. [https://doi.org/10.1657/1938-4246\(07-080\)\[KELLEY\]2.0.CO;2](https://doi.org/10.1657/1938-4246(07-080)[KELLEY]2.0.CO;2)

- Mohr, C. O. (1943). Cattle droppings as ecological units. *Ecological Monographs*, 13, 275–298. <https://doi.org/10.2307/1943223>
- Myers-Smith, I. H., Forbes, B. C., Wilmsking, M., Hallinger, M., Lantz, T., Blok, D., ... Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, 6, 045509.
- Nilsson, M. C., Wardle, D. A., Zackrisson, O., & Jaderlund, A. (2002). Effects of alleviation of ecological stresses on an alpine tundra community over an eight-year period. *Oikos*, 97, 3–17. <https://doi.org/10.1034/j.1600-0706.2002.970101.x>
- Parsons, A. N., Press, M. C., Wookey, P. A., Welker, J. M., Robinson, T. V., Callaghan, T. V., & Lee, J. A. (1995). Growth responses of *Calamagrostis lapponica* to simulated environmental change in the Sub-Arctic. *Oikos*, 72, 61–66. <https://doi.org/10.2307/3546038>
- R Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems: A journey towards relevance? *The New Phytologist*, 157, 475–492. <https://doi.org/10.1046/j.1469-8137.2003.00704.x>
- Reichelt, A. C. (1991). Environmental effects of meiofaunal burrowing. In P. S. Meadows, & A. Meadows (Eds.), *The environmental impact of burrowing animals and animal burrows* (pp. 33–52). London, UK: The Zoological Society of London, Oxford, UK: Clarendon Press.
- Reid, D. G., Bilodeau, F., Krebs, C. J., Gauthier, G., Kenney, A. J., Gilbert, B. S., ... Hofer, E. (2012). Lemming winter habitat choice: A snow-fencing experiment. *Oecologia*, 168, 935–946. <https://doi.org/10.1007/s00442-011-2167-x>
- Ritchie, J. C. (1956). The native plants of Churchill, Manitoba, Canada. *Canadian Journal of Botany*, 34, 269–320.
- Roman, J., & McCarthy, J. J. (2010). The whale pump: Marine mammals enhance primary productivity in a coastal basin. *PLoS ONE*, 5, e13255. <https://doi.org/10.1371/journal.pone.0013255>
- Roth, J. D. (2003). Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology*, 72, 668–676. <https://doi.org/10.1046/j.1365-2656.2003.00739.x>
- Rouse, W. R. (1991). Impacts of Hudson Bay on the terrestrial climate of the Hudson Bay Lowlands. *Arctic and Alpine Research*, 23, 24–30. <https://doi.org/10.2307/1551433>
- Shaver, G. R., & Chapin, F. S. I. I. (1980). Response to fertilization by various plant growth forms in an Alaskan tundra: Nutrient accumulation and growth. *Ecology*, 61, 662–675. <https://doi.org/10.2307/1937432>
- Smith, M. D., & Conway, C. J. (2007). Use of mammal manure by nesting burrowing owls: A test of four functional hypotheses. *Animal Behavior*, 73, 65–73. <https://doi.org/10.1016/j.anbehav.2006.05.012>
- Steinwandter, M., Schlick-Steiner, B. C., Steiner, F. M., & Seeber, J. (2019). One plus one is greater than two: Mixing litter types accelerates decomposition of low-quality alpine dwarf shrub litter. *Plant and Soil*, 438, 405–419. <https://doi.org/10.1007/s11104-019-03991-5>
- Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., ... Romanovsky, V. E. (2005). Winter biological processes could help convert arctic tundra to shrubland. *BioScience*, 55, 17–26. [https://doi.org/10.1641/0006-3568\(2005\)055\[0017:WBPCHC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2)
- Tannerfeldt, M., Angerbjörn, A., & Angerbjörn, A. (1998). Fluctuating resources and the evolution of litter size in the arctic fox. *Oikos*, 83, 545–559. <https://doi.org/10.2307/3546681>
- Thompson, L., Thomas, C. D., Readley, J. M. A., Williamson, S., & Lawton, J. (1993). The effect of earthworms and snails in a simple plant community. *Oecologia*, 95, 171–178. <https://doi.org/10.1007/BF00323487>
- Yano, Y., Shaver, G. R., Rastetter, E. B., Giblin, A. E., & Laundre, J. A. (2013). Nitrogen dynamics in arctic tundra soils of varying age: Differential responses to fertilization and warming. *Oecologia*, 173, 1575–1586. <https://doi.org/10.1007/s00442-013-2733-5>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Frequency of occurrence of vascular plants on den and paired control areas

How to cite this article: Fafard PM, Roth JD, Markham JH. Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. *J Veg Sci*. 2020;31:173–179. <https://doi.org/10.1111/jvs.12828>