

Arctic foxes as ecosystem engineers: benefits to vegetation and collared lemmings through
nutrient deposition

By

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A Thesis submitted to the Faculty of Graduate Studies of

The University of Manitoba

In partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg

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Abstract

One approach to further understanding an organism's broader role in an ecosystem is to determine how they create, modify or maintain habitats for other organisms by changing the flow of resources or physical surroundings. We estimated the non-trophic effects of arctic fox (*Vulpes lagopus*) denning activities on soil nutrient dynamics, vegetation production and quality, snow cover thickness, and their primary terrestrial prey, collared lemmings (*Dicrostonyx richardsoni*), near Churchill, Manitoba in April, June and August 2014. Arctic foxes increased soil inorganic nitrogen and extractable phosphorous concentration on their dens. This increase in soil nutrient levels resulted in greater vegetation quantity (measured as biomass and cover) and quality (measured as nitrogen content) on dens. Increased vegetation cover, specifically *Salix* sp. and *Leymus mollis* cover, positively affected snow cover thickness on dens by trapping blowing snow. Increased snow cover thickness made arctic fox dens attractive nesting sites to collared lemmings (measured as lemming nest counts). In addition, dens with lemming nests had greater snow cover thickness compared to dens without lemming nests. Greater vegetation quantity and quality on dens could also attract lemmings to arctic fox dens for winter nesting. Our research suggests that arctic foxes engineer their ecosystems at local scales: arctic foxes provide enhanced nutrient cycling as an ecosystem service, and thereby benefit both fast-growing dominant plant species and their primary prey populations by creating suitable habitats for them. We suggest that considering both trophic and non-trophic impacts of arctic foxes is necessary for gaining a more accurate view of the effect of this species in the arctic tundra.

Acknowledgments

I would like to express my gratitude to my advisor, Jim Roth, for his patience, and for teaching me the skill of disciplined critical thinking by letting me design this project whilst consistently providing me with invaluable improvements. I would also like to thank my graduate committee members, John Markham and Ryan Brook. Their knowledge and guidance helped me immensely throughout this project. A warm thank you to Alyssa Eby, Wapusk National Park staff (especially J. Larkin and K. Burke) and students in Arctic Field Ecology course (offered by University of Manitoba in summer 2014) for field assistance in June 2014, and to Ian Burrton, for his assistance in the lab. The Natural Sciences and Engineering Research Council of Canada (NSERC), the University of Manitoba Fieldwork Support Fund, Parks Canada, and Churchill Northern Studies Centre (CNSC) Northern Research Fund have all funded this project.

I would also like to thank Christa Szumski, Danielle Fox, Michelle Ewacha, Bonnie McCullagh, Jennifer Sojka, Dane Burstahler, Dawn Wood, Dylan Pond, Kelsey O'Brien, Jackie Verstege, Kyle Ritchie, Elaine Anjos, Annemarie Van Der Marel and Miles Zhang for their encouragements and feedback on my work. To Christa, Danielle, Dane, Michelle, Bonnie and Jen, your friendship is one of the greatest gifts I have received, and without your support, this project would have been infinitely harder to finish. A special thanks goes out to Paul Fafard. His genuine friendship, kind view on life and enthusiasm for nature made me love fieldwork even more! In the lab, his dedication and great taste in music was very much appreciated.

Above all, my deepest love and naturally gratitude is always for my wonderful parents, Mahnaz Ghazvini and Daryoush Gharajehdaghypour, for making my life more beautiful with their unconditional love, for reminding me to keep perspective in life... for everything, for making me who I am.

Dedication

This thesis is dedicated to my

mom, Mahnaz, for her unending love, and energy to tackle life

dad, Daryoush, for teaching me not to be afraid to be different

and grandmother, Ferdous, for showing me that knowledge is power.

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Thesis Format

This thesis is in manuscript format. I wrote each chapter as individual manuscripts containing their own abstract, introduction, methods, results, discussion, references, and figures. The first chapter was submitted to the journal of *Scientific Reports* (Gharajehdaghipour T, Roth JD, Fafard PM, Markham JH. *Submitted*. Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. *Scientific Reports*). The thesis introduction outlines the background for my research, and the thesis conclusion ties my research to the ecosystem engineering body of research and provides implications beyond what is included in the manuscripts.

I participated in all of the fieldwork related to this research, including visits to fox dens and sample collection, and taking aerial photos. I prepared all vegetation samples for stable isotope analysis and performed all other laboratory analyses, including soil nutrient measurements, and vegetation biomass and cover analysis, with the assistance of undergraduate students working in our lab. I conducted all data analyses and wrote the entire thesis with guidance from my committee.

Thesis Introduction:

One way to further understand the broader role of organisms in ecosystems, particularly outside the context of trophic interactions, is to determine their role in the creation, modification and maintenance of habitats. Organisms who create or modify habitats by altering physical surroundings or changing the flow of resources are ecosystem engineers (Jones 1994). The concept of ecosystem engineering incorporates the joint influences of two coupled direct interactions: the ecosystem engineering process, and the ecosystem engineering consequence. The first is the way organisms alter the abiotic environment, and the latter is how these abiotic changes influence biota (Jones & Gutiérrez 2007). By definition, ecosystem engineering is a ubiquitous process, since essentially all organisms engineer their environments to some extent at least in certain phases of their life. While some have equated ubiquity of this process with nonutility (Reichman and Seabloom 2002a, 2002b), ubiquity is the strength of this concept, making it relevant to many species, across many habitats. Similar to the ubiquity attribute, focusing on the processes rather outcomes makes the concept applicable to all organisms. Intrinsic to the process-based vs. outcome-based attribute, is the issue with scale. Most researchers prefer a definition that offers the concept more breadth. That means a process-based, scale-independent definition is desired. With such characterizations, models on any scale can contain engineering as a process, from individual-level effects (such as behavioral or fitness) and single species level effects (such as population dynamics) to ecosystem level effects (such as energy transfer). Thanks to its breadth, the ecosystem engineering concept has even been used to change food web studies to also include non-trophic interactions (i.e. interaction webs), for both theoretical and practical reasons (Sanders *et al.* 2014).

The consequences of ecosystem engineers are variable spatially and temporally; for example, caterpillars increase arthropod diversity via leaf rolling at both leaf and plant level (i.e. local scale) up to a year (Vieira & Romero 2013), whereas shell beds dominated by molluscs have altered benthic community composition on regional and global scales over geological time scales (Erwin 2008).

As with all common processes, the challenge is to determine which engineers have roles important for ecosystem processes and ultimately functions. Furthermore, because maintenance of ecosystem functions has maximum conservation priority (Balvanera *et al.* 2001), identifying when, where and which types of engineers maintain or influence ecosystem functions is a sensible objective for conservation actions. Crain & Bertness (2006) suggested that important ecosystem engineers are species that alter the limiting resources or constraining variables in the system. In physically stressful habitats, even small alterations in physical parameters could make such habitats hospitable for species that would otherwise be incapable of tolerating such limiting physical conditions. For example, in semiarid areas, where vegetation establishment is limited by low moisture levels in soils, shrubs that trap moisture by shading soils are important ecosystem engineers, since they play the main role in facilitating the growth of grasses and ultimately maintaining a vegetative community (Aguilar and Sala 1994).

Knowledge about the biology of individual species within a system usually exceeds that of processes driving that system (Schwartz 1999). There has been a developing realization that the traditional focus on a single species without considering their ecosystem as a web of trophic and non-trophic interactions and abiotic constituents typically results in a myopic and incomplete view on the role of species and in limited, if any, conservation gains (Simberloff 1998). In the case of predators, the nature of scientific investigation on their role has evolved from focusing

solely on the prey–predator relationships, to trying to understand the impact of predators on both the whole community of species and the abiotic constituents within their system (Ray 2005). For example early research on the ecology of the arctic fox (*Vulpes lagopus*) concentrated on the distinct cyclic population fluctuations of foxes in response to abundance of small mammals, particularly lemmings (*Lemmus* and *Dicrostonyx* spp.), their primary terrestrial prey in their continental range (Macpherson 1969, Angerbjorn *et al.* 1999, Elmhagen *et al.* 2000). Ecological research on this species has gradually acquired a larger scale view; for example Roth (2002) has shown that in years with low lemming abundance, arctic foxes depend on sea ice formation (an abiotic constituent of the arctic ecosystem) to access marine-derived resources (such as ringed seal (*Phoca hispida*) pups and seal carcasses killed by polar bears (*Ursus maritimus*)) as alternative food sources during winter. Another example is the effect of this species as an introduced species on the Aleutian Islands, where due to their excessive predation pressure on birds, and therefore lower guano input into soil, the vegetation community has shifted from grassland to tundra on the landscape scale (Croll *et al.* 2005).

Both the early descriptive studies and more recent community-level studies on ecology of arctic foxes in tundra areas have noted that arctic fox dens are notably greener than the background landscape (Garrot *et al.* 1983, Smits *et al.* 1988, Bruun *et al.* 2005), suggesting that the denning activities of foxes could change the tundra nutrient dynamics. Given this widespread effect of foxes on the vegetation community through non-trophic interactions, and the lack of knowledge about the magnitude of and processes involved in driving such an effect and the consequences on herbivore community, we suggest that studying arctic foxes in an ecosystem engineering framework, which by definition is process-based and focused on non-trophic interactions, is suitable.

Top predators can offer important ecosystem services such as nutrient cycling, and their impact can be even greater in environments with low nutrients and low primary productivity, such as arctic tundra. Thus investigating the broader role of arctic foxes and as ecosystem engineers is not only suitable but also necessary. The necessity for such studies is more stressed in arctic ecosystems where low species diversity makes these ecosystems highly susceptible to disturbances such as climate warming and human activities. At the same time low species diversity makes ecosystem engineering studies more feasible in arctic communities (Meltote *et al.* 2013).

In the following chapters, our goal was to identify and quantify the effects of arctic foxes as ecosystem engineers in the subarctic tundra. In the first chapter we focused on quantifying the impacts of arctic fox denning activities on soil nutrient dynamics and vegetation biomass. The second chapter is built upon the first chapter, and focuses on the engineering effects of arctic foxes on collared lemmings (*Dicrostonyx richardsoni*) through changes in snow thickness and vegetation quality. Results from this research suggest that arctic foxes provide enhanced nutrient cycling as an ecosystem service and their effects extend beyond predator-prey trophic interactions.

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Chapter 1: Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens

Abstract

Top predators can provide fundamental ecosystem services such as nutrient cycling, and their impact can be even greater in environments with low nutrients and low productivity, such as arctic tundra. We estimated the effects of arctic fox (*Vulpes lagopus*) denning activities on soil nutrient dynamics and vegetation production near Churchill, Manitoba in June and August 2014. Soils from fox dens contained much higher nutrient levels in June (86% more inorganic nitrogen, 1195% more extractable phosphorous) and in August (250% more inorganic nitrogen and 191% more extractable phosphorous) than adjacent control sites. Pup production the previous year, which should enhance nutrient deposition (from urine, feces, and prey brought to dens), did not affect soil nutrient concentrations, suggesting the impact of arctic foxes persists >1 year. Dens supported 2.8 times greater vegetation biomass in August, but $\delta^{15}\text{N}$ values in sea lyme grass (*Leymus mollis*) were unaffected by denning. By concentrating nutrients on dens arctic foxes provide enhanced nutrient cycling as an ecosystem service and thus engineer arctic ecosystems on local scales. The enhanced productivity in patches on the landscape could have prominent cascading effects on the distribution and diversity of vegetation and the dispersion of herbivores on the tundra.

Introduction:

Ecosystem engineering can happen at any scale, and due to its ubiquity, at any trophic level (Berke 2010). In some cases, physical modification of the environment by ecosystem

engineers is relatively large compared to other physical processes operating in the ecosystem (e.g. dam building by beavers). However in most instances, ecosystem engineers are working at a more refined scale. Therefore, separating the effects of an ecosystem engineer from other biotic and abiotic factors is challenging. For example, factors such as species diversity, changes in species distribution, and numerous species interactions within an ecosystem make distinguishing between different biotic influences on soil processes difficult (Jones *et al.* 2006).

Low food web complexity of arctic biomes, which is primarily due to bottom-up effect of decreased vegetation diversity and productivity, makes ecosystem engineering easier to study in arctic communities (Meltofte 2013). Simultaneously, having low species diversity makes arctic ecosystems highly susceptible to disturbances such as climate warming and human activities (Meltofte 2013). The loss (or introduction) of even a single species can cause drastic and cascading effects in arctic ecosystems (Post *et al.* 2009). Therefore, studies on species' role as ecosystem engineers in arctic biomes are also necessary.

Top predators can drastically change nutrient dynamics of an ecosystem through mechanisms such as decoupling carcass distribution from live-prey distribution. For example brown bears (*Ursus arctos*) feeding on salmon (*Oncorhynchus* spp.) redistribute marine-derived nutrients to terrestrial ecosystems, increasing the forest's total inorganic nitrogen pools threefold (Holtgrieve *et al.* 2009). Carcasses of moose (*Alces alces*) killed by grey wolves (*Canis lupus*) also create hot spots with up to 6 times more inorganic soil nutrients (Bump *et al.* 2009). Similarly, carcasses of muskoxen (*Ovibos moschatus*) create nitrogen-rich plant growth on the surrounding tundra (Danell *et al.* 2002).

The arctic fox (*Vulpes lagopus*) has a native circumpolar tundra distribution, ranging from northern Greenland (88°N) to the southern edge of Hudson Bay, Canada (53°N). Arctic

foxes are top predators, and within their continental range their main prey are microtine rodents including lemmings (*Dicrostonyx* and *Lemmus* spp.) and voles (*Microtus* and *Myodes* spp.) (Macpherson 1969, Angerbjorn *et al.* 1999, Elmhagen *et al.* 2000). In years with low lemming density, arctic foxes rely on geese and their eggs during summer (Bety *et al.* 2002), and ringed seal (*Phoca hispida*) pups and carcasses of seals killed by polar bears (*Ursus maritimus*) during winter (Roth 2002).

Arctic foxes depend on well-established dens to shelter pups from the harsh arctic climate and predators (Tannerfeldt *et al.* 2003). Suitable denning sites for the arctic fox are mostly on elevated topographical features (e.g. ridges, banks, mounds, moraines) composed of coarse well-draining sediments, and greater depth to permafrost, allowing for easier excavation (Smits *et al.* 1988, Szor *et al.* 2008). Development of a good den can take many years, with some dens estimated to be hundreds of years old (Macpherson 1969). However, high-quality den sites are limited (Smits and Slough 1993), and digging new dens is energetically costly and mainly done during peak population years (Dorogoi 1987). Climate, soil type, and permafrost also further limit excavations of new dens spatially and temporarily (Smits *et al.* 1988, Tannerfeldt *et al.* 2003).

Arctic fox litter size averages 8-10 pups in Canada (Tannerfeldt *et al.* 2003), so active den sites receive high amounts of nutrients due to urine and faeces deposits as well as nutrient release from the remains of decaying prey items. Due to this nutrient addition, in many arctic areas, arctic fox dens have lush green vegetation and are readily spotted across the tundra landscape (Smits *et al.* 1988, Garrott *et al.* 1983, Bruun *et al.* 2005) (Fig 1.1). Despite the obvious differences in vegetation growth on arctic fox dens, studies examining arctic fox effects on soil are rare. Smith *et al.* (1992) found higher soil total nitrogen (N) levels at den sites

compared to off-den areas, but no difference in soil total phosphorous (P). On the Aleutian islands, where the arctic fox is an introduced species, predation of sea birds by arctic foxes results in lower guano input, thus fox-inhabited islands have lower soil total N and extractable P (plant available P extracted with Bray extractant) percentages compared to fox-free islands (Croll *et al.* 2005, Maron *et al.* 2006). A more thorough analysis of the effect of arctic foxes as chemical ecosystem engineers on soil nutrient dynamics is necessary for better understanding their functional role in nutrient cycling processes in their native range. Specifically, by analysing soil inorganic N and extractable P (as opposed to the total N and P) and seasonal changes in these nutrients, our objective is to estimate the effect of arctic fox denning activities on local nutrient dynamics.

Primary productivity usually varies more within a tundra site than among sites. This high local variation in primary productivity suggests that soil condition is one of main determinants of primary production in arctic tundra ecosystems (Kielland and Chapin III 1992). Primary productivity during short growing seasons in tundra ecosystems is often strongly limited by inorganic N availability in the soil, and followed closely by P, as shown by plant tissue analyses (Ulrich and Gersper 1978) and fertilization experiments (Henry *et al.* 1986, Robinson *et al.* 1998). Measuring concentrations of the inorganic forms of N and P is necessary for a better understanding of the pool of nutrients available to plants in arctic tundra where, because of cold temperatures and extremely high or low moisture levels, the decomposition rate of organic material is severely restricted (Nadelhoffer *et al.* 1992). Although Arctic soils are often rich in organic material and some Arctic plants can make use of the organic form of N, Arctic soils are still fairly poor medium for plant growth due to the fact that organic N in Arctic soil is mostly in

insoluble form, and only a small proportion of the soluble organic N occurs in a form that is useable by Arctic plants (Atkin 1996).

We predicted that, due to nutrient addition by arctic foxes, inorganic N and extractable P levels at den sites would be higher than control sites, and as a result vegetation biomass would be higher at den sites. Additionally, we predicted that due to receiving nutrients from marine and allochthonous resources in arctic fox diet (such as geese and seals), $\delta^{15}\text{N}$ values would be elevated in plants growing on fox dens, whereas plants on control sites would have lower $\delta^{15}\text{N}$ signatures, indicative of locally fixed N sources (Dawson *et al.* 2002, Schindler and Lubetkin 2004). We also predicted that dens with pups in the previous year would have higher inorganic N and extractable P levels than dens that did not have pups.

Methods:

Our study was conducted in the western Hudson Bay coastal habitat within Wapusk National Park, Manitoba, Canada. This region is close to the southern boundary of arctic fox distribution in North America (Banfield 1977). Retraction of the ice load, followed by post-glacial rebound of the land have made sand or gravel north-south oriented beach ridges one of the main landform features in this region (Bahr 1989, Dredge 1992). These elevated beach ridges are separated by many depressed shallow lakes and ponds (Bahr 1989). Greater depth to permafrost compared to the surrounding lowlands, and xeric moisture levels due the sandy texture of the soil, make these beach ridges suitable arctic fox denning habitat (Chesemore 1969, Macpherson 1969, Smits *et al.* 1988, Dalerum *et al.* 2002). Vegetation on beach ridges is typical of low-growing heath communities (Johnson 1987); specifically *Dryas* heath due to the major dominance of *Dryas integrifolia* (Brooke and Kenkel 2002, Elliott 2009). However, arctic fox

dens are usually covered with lush green vegetation, dominated by *Leymus mollis*, a perennial graminoid that can colonize subarctic coastal dunes (Imbert and Houle 2000), and *Salix planifolia*, a perennial deciduous shrub, a native colonizer of primary succession tundra (Kershaw and Kershaw 1987). Since 2010 we have visited all known dens in the area in April, June, and August each year to examine them for signs of fox activity. Fresh prey items, tracks, faeces, signs of digging and numerous cleared out burrows reflect the presence of pups in August (Roth 2003).

Soil samples were collected from fox dens in June and again in August, 2014. We collected 5 samples from each den: 1 sample was collected from the centre of the den (the midpoint of a straight line connecting the two farthest open burrows) and 4 samples were collected 5 meters from the centre, in opposite directions (2 parallel to the beach ridge and 2 perpendicular to the beach ridge). For each den site a paired control area was chosen at a similar elevation, slope and aspect. The centre of the control area was designated 50 m away from the centre of the den to ensure that control area was well outside of the fox denning area. For each control site, 5 samples were collected following the same protocol as den samples. Each sample was a 10 cm deep cone of soil (approximately 200 cm³ in volume) kept frozen until analysis. To estimate productivity we collected vegetation biomass samples in August. Although not all plant species in our area are deciduous, variation in vegetation biomass should reflect variation in productivity. At each sampling location, a 1 m² quadrat was placed centred on the soil sampling hole, and the above ground live plant biomass was collected from the northeast quarter of the quadrat. For *D. integrifolia*, however, we collected this species from only 13 sampling locations, estimated its percent cover from those locations, and used the relationship between biomass and percent cover (biomass = -1.730 + 0.597* percent cover, F_{1,11} = 86.418, p < 0.0001,

$R^2=0.887$) to estimate biomass at the remaining sampling locations based on percent cover.

When possible, *L. mollis* samples were also collected from den and paired control sites for stable isotope analysis.

Each soil sample was thawed in the lab and homogenized, and a subsample was air dried. Total inorganic N concentrations [$\text{NH}_4^+ + \text{NO}_3^-$] were measured using the accelerated microdiffusion method (Khan *et al.* 1997) and extractable P concentrations [PO_4^-] were determined from sodium bicarbonate extracts using the Murphy Riley technique (Kalra and Maynard 1991). To estimate productivity, vegetation biomass samples were dried to constant weight. *L. mollis* samples collected for stable isotope analysis were also dried to constant weight and homogenized with a ball mill. $\delta^{15}\text{N}$ values were measured in 3 mg subsamples using an elemental analyzer and a continuous flow isotope ratio mass spectrometer at the Chemical Tracers Laboratory, Great Lakes Institute for Environmental Research, University of Windsor.

To compare soil inorganic N and P concentrations between 17 and 11 den and control pairs respectively, and between seasons (June vs. August), we performed linear mixed effect analysis in R (R Core Team 2015), using lme4 package (Bates *et al.* 2013). Site (den vs. control) and season (without the interaction term) were entered as fixed effects into the model. As a random effect, we let intercepts vary for site id. To satisfy the normality and homoscedasticity assumptions, inorganic N and P concentrations for the 5 samples at each site were averaged and square-root transformed. To obtain p-values for each fixed effect, likelihood ratio tests of the full model against reduced models without the effect in question were used. Marginal R^2 (proportion of variance explained by the fixed factors) and conditional R^2 (proportion of variance explained by both the fixed and random factors) values were calculated based on Nakagawa & Schielzeth (2013) using lme4 (Bates *et al.* 2013) and arm (Gelman, A. and Yu-Sung 2015) packages.

Vegetation biomass measurements were averaged for each site and then compared between 18 den and control pairs using paired t-test. To determine if dens receive N from allochthonous sources, $\delta^{15}\text{N}$ values were averaged for each site, and then compared between 15 den and control pairs, using paired t-test. To investigate the effect of pup presence on soil inorganic N ($n = 34$) and P ($n = 22$) concentrations a linear mixed effect model was constructed; season and pup presence were entered as fixed factors and site id as a random factor. Inorganic N and P values were square root transformed to satisfy the normality and homoscedasticity assumptions. The full model was then compared to the reduced model (i.e. model without pup presence as a factor) using a likelihood ratio tests.

Results:

Den sites had 86% more soil inorganic N than control sites in June. In August, the difference in inorganic N concentration between den and control sites increased threefold, to 250% (Fig 1.2a). The mixed effect analysis on inorganic N data indicated that site and season both had a significant effect ($\chi^2_{\text{site (1)}} = 25.37$, $p_{\text{site}} < 0.0001$; $\chi^2_{\text{season (1)}} = 9.05$, $p_{\text{season}} = 0.0026$). Inorganic N concentration in soil was higher on dens compared to control sites ($\beta = 1.880$), and higher in June compared to August ($\beta = 0.949$). In the full model, marginal $R^2 = 0.385$ and conditional $R^2 = 0.470$.

Extractable P levels in soils were 1195% higher on dens compared to control sites in June, and 191% higher in August. However, unlike inorganic N levels, extractable P levels were higher in August than in June (Fig 1.2b). Mixed effect analysis results suggest that extractable P concentration also differed between sites and seasons ($\chi^2_{\text{site (1)}} = 32.89$, $p_{\text{site}} < 0.0001$; $\chi^2_{\text{season (1)}} = 19.15$, $p_{\text{season}} < 0.0001$). Extractable P concentration was greater on dens than control sites ($\beta =$

0.826) and lower in June compared to August ($\beta = -0.428$). Marginal R^2 and conditional R^2 value were 0.657 and 0.770 respectively for the full model.

The presence of fox pups the previous summer did not affect soil inorganic N ($\chi^2_{(1)} = 0.092$, $p=0.76$) or P concentrations ($\chi^2_{(1)} = 0.306$, $p = 0.58$).

$\delta^{15}\text{N}$ values of *L. mollis* did not differ between dens (Mean = 2.78, SE = 0.94) and their paired control sites (Mean = 3.56, SE = 0.958) ($t_{(14)} = -0.555$, $p = 0.37$).

Den sites (Mean = 191.251 g, SE = 23.667) were more productive than control sites (Mean = 68.907 g, SE = 10.925) ($t_{(17)} = 4.531$, $p = 0.0002$). Dens on average supported 2.8 times more vegetation biomass than controls (Fig 1.3).

Discussion:

Enriched inorganic N and extractable P levels in soil and increased plant biomass at den sites compared to control sites indicate that arctic fox denning activity provides vegetation with the limiting factor for their growth. Average total inorganic N concentrations on control sites in both June and August were comparable to background concentrations reported for similar *Dryas* heath tundra ecosystems (Stewart 2010) (Fig 1.2a). Decreasing inorganic N levels from June to August suggest that the growing vegetation is using the available inorganic N in the soil and some of the inorganic N is gradually leaching away. Furthermore, in similar arctic ecosystems, inorganic N peaks early in spring immediately or slightly after snowmelt, and then progressively declines throughout the summer (Edwards *et al.* 2006).

Even after uptake of N by plants in August, den areas still have higher inorganic N content than control sites. Furthermore, in August the difference in inorganic N concentrations between den and control sites is greater than in June (Fig 1.2a). These findings suggest that the

nutrient enriching effects of arctic foxes as ecosystem engineers is strong enough to support vegetation biomass 2.8 times as high as control sites (Fig 1.3), and simultaneously elevate unused inorganic N concentrations on dens far above concentrations on controls.

Our estimates of the difference in annual plant productivity between den and control areas are conservative. Unlike *L. mollis* and willow species, *D. integrifolia* is an evergreen species (Philipp and Siegismund 2003), thus not all the above-ground *D. integrifolia* biomass collected is produced in one growing season. Furthermore, *L. mollis* dominates on the den sites but it is almost non-existent on control sites, whereas *D. integrifolia* dominates on the control areas (Elliott 2009) and is not commonly found in high proportions on den sites (Fafard unpubl. data). Therefore, the effect of arctic fox nutrient deposition on plant biomass is most likely even greater than our estimates.

Average extractable P concentrations on control sites were similar to concentrations suggested in previous studies (Edwards *et al.* 2006) (Fig 1.2b). A number of studies on P dynamics in arctic ecosystems have concluded that one of the largest pools of potentially available P in arctic soils is the microbial biomass, which immobilizes P during the growing season (Giblin *et al.* 1991). Microbial biomass can contain up to about 35% of total P pool, compared to only ~3.5% of total N pool. Therefore, lower levels of microbial immobilization of P is likely the reason for higher concentration of extractable P in August than in June.

By constantly depositing nutrients, arctic foxes maintain the higher inorganic N and extractable P concentrations on den sites compared to control sites. This effect could be carried on for multiple years, considering that dens with and without pups did not differ in inorganic N and extractable P concentrations. Furthermore, the enhancing effect of foxes on nutrient levels does not seem to be restricted to the growing season, since we found fox urine on about 80% of

these dens in April (Roth, unpubl. data), suggesting that dens are visited regularly throughout the year.

Nitrogen to phosphorus (N:P) ratios in plant tissues are regularly used as reliable indicators of nutrient limitation for both vascular plants (Güsewell and Koerselman 2002) and bryophytes (Jiroušek *et al.* 2011). N:P ratios greater than 16 suggest P limitation, whereas N:P ratios less than 14 indicate N limitation and N:P ratios between 14 and 16 indicate N and P co-limitation (Güsewell and Koerselman 2002, Koerselman and Meuleman 1996). However, due to homeostatic regulation by plants, N:P ratios in plants are not equal to N:P ratios in soil. Homeostatic regulation coefficients (the inverse slope of the log-log relationship between soil and plant N:P) can vary from 1.7 to 4.6 (Güsewell 2004), and based on our measured soil N:P ratios, control sites are likely P limited in June, and N limited in August. Den sites, however, are likely to be N limited in both seasons.

$\delta^{15}\text{N}$ values in grass samples from den and control areas were not different, contrary to our predictions. One possible explanation is the discrimination against the heavier N isotope during N mineralization process (and other soil N transformations) (Nadelhoffer *et al.* 1996). Studies have also found that if the N pool is large enough, mineralization and uptake rate do not affect its size, and the discrimination against ^{15}N plant uptake processes is more pronounced (Evans 2001). Inorganic N levels only decreased by 26% from June to August on den soils, and compared to control sites, inorganic N levels are maintained at a high level throughout the growing season on dens. As a result, ^{15}N discrimination during plant uptake could be more pronounced on dens than control sites, where even after the minimal vegetation growth, inorganic N decreases by 62%. As heavier N isotopes from consumed prey usually get incorporated in the predator's body, with lighter isotopes flushed out in urine (Gannes *et al.*

1998), our results could also suggest that deposition of urine by arctic foxes is potentially a more important source of nutrients for vegetation growth than decomposing prey items such as geese (with high $\delta^{15}\text{N}$ values) in arctic areas, where decomposition rates are slow.

In conclusion, our study shows that arctic foxes engineer arctic ecosystems on local scales: through nutrient deposition, arctic foxes change the soil N and P dynamics. Increased inorganic N and P concentrations on arctic fox dens improved conditions on the tundra for plant growth, sustaining high vegetation biomass. Nutrient cycling is considered to be one of the most important ecosystem services (Costanza *et al.* 1997), and our results suggest that by generating spatial heterogeneity in nutrient distributions, arctic foxes, as top predators, exert strong positive influences on ecosystem nutrient dynamics. These positive influences feed upward to increase vegetation productivity and landscape heterogeneity. By enhancing nutrient dynamics locally, arctic foxes could have an important role in providing ecosystem services in arctic tundra landscape. Range contraction of arctic foxes due to climate warming and the encroachment of red foxes (*Vulpes vulpes*) could result in the loss of the ecosystem services they provide, and could have cascading effects on tundra ecosystems (Schmitz *et al.* 2010).

Besides increasing vegetation biomass, the nutrient enhancement on fox dens could also affect plant biodiversity and potentially could attract herbivores to arctic fox den sites. In fact lemming droppings and reindeer droppings have been observed at arctic fox dens sites in Alpine tundra (Bruun *et al.* 2005). As mammalian herbivores in arctic tundra can elevate soil nitrogen and phosphorous concentrations through deposition of their waste products (McKendrick *et al.* 1980), their use of arctic fox dens could further enhance local nutrient dynamics. Additional exploration of the influence of arctic foxes on herbivore communities through mechanisms other

than predation would broaden the scope of understanding the role of arctic foxes as ecosystem engineers.

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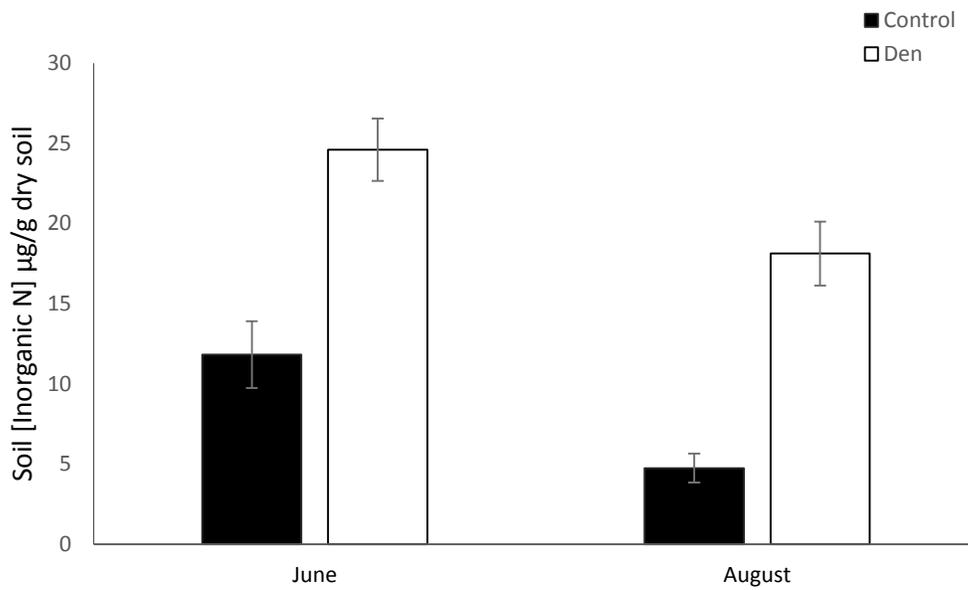
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Figures



Figure 1.1: Aerial photo of an arctic fox den in Wapusk National Park, Canada, in August 2014, showing the contrast between the lush green vegetation on dens (dominated by *Leymus mollis* and *Salix planifolia*) and the background *Dryas* heath on beach ridges. For scale, a 1 x 1 m quadrat can be seen in the middle of the den.

(a)



(b)

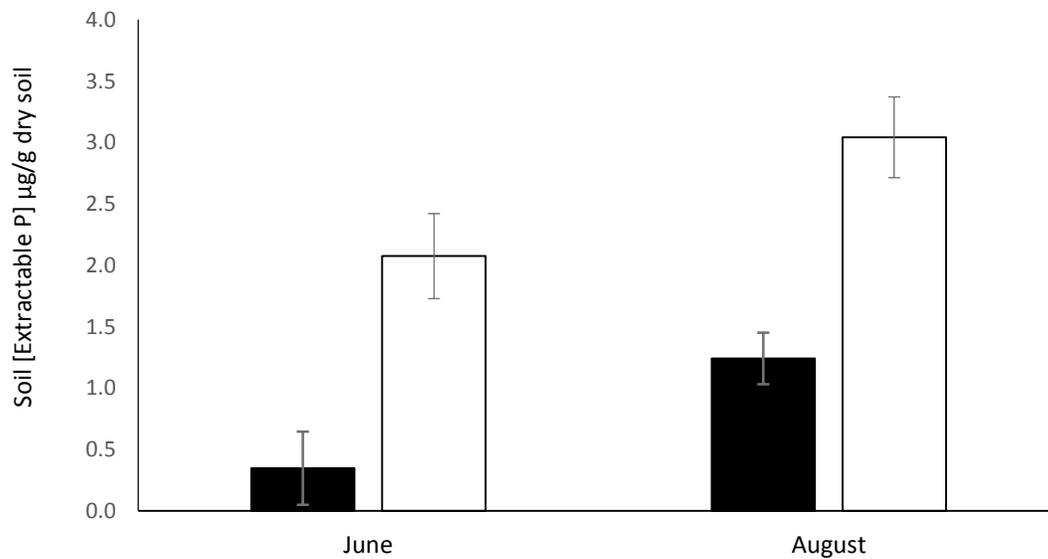


Figure 1.2: Nutrient concentrations (mean \pm SE) of soil samples collected from fox dens and control sites in Wapusk National Park, Canada, in June and August 2014. (a) Inorganic N (n=17) (b) Extractable P (n=11).

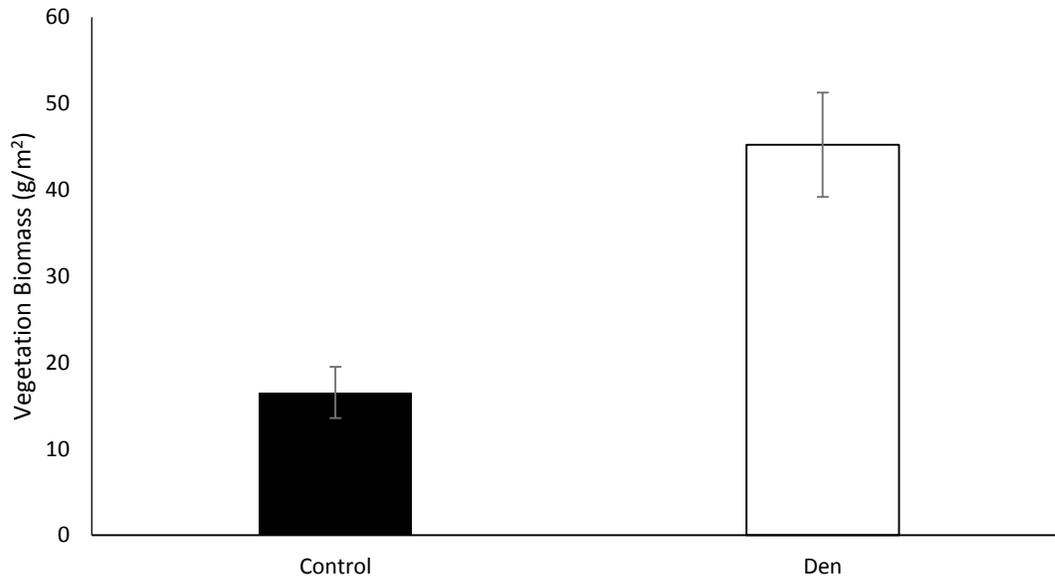


Figure 1.3: Vegetation biomass on fox dens and control sites in Wapusk National Park, Canada, in August, 2014 (mean \pm SE) (n=18).

Chapter 2: Arctic foxes benefit collared lemmings through ecosystem engineering

Abstract

Predators can mediate chains of reactions in the ecosystem through mechanisms other than predation. One way to further understand their broader role is to determine how they create, modify or maintain habitats for other organisms by changing the flow of resources or physical surroundings. By increasing soil nutrient concentrations, and therefore creating suitable habitats for nutrient-demanding plants, arctic fox (*Vulpes lagopus*) denning activities lead to increased vegetation productivity in tundra ecosystems, and potentially increased nutrient content in plants as well. Greater vegetation quantity and quality could attract herbivores to arctic fox dens. During a survey of arctic fox dens near Churchill, Manitoba in June 2014, we found collared lemming (*Dicrostonyx richardsoni*) nests, which are built and used under the snow in winter and revealed after snow melt, on 68% of fox dens, whereas control sites did not have any nests. Fox activity on dens in April did not affect the presence of lemming winter nests. We examined three mechanisms by which lemmings could be attracted to fox dens: increased vegetation quantity (% cover), quality (nitrogen content), and thickness of snow cover, which provides thermal insulation in winter. Due to nutrient addition by arctic foxes, dens had 2 times greater vegetation cover in August than control sites, and sea lyme grass (*Leymus mollis*) samples collected from dens had 50% greater nitrogen content than control samples. Snow thickness in April was about 4 times greater on dens than control sites, and dens with lemming nests had about 1.4 times thicker snow than dens without winter nests. Snow cover thickness was positively related to vegetation cover on dens, but snow cover thickness and vegetation cover were unrelated on

control sites. These results suggest that although arctic foxes negatively impact collared lemmings through predation, arctic foxes could also positively impact lemmings through engineering the tundra ecosystem and increasing local biological productivity, providing a refuge that could buffer the effects of deteriorating snow conditions on lemming populations. This juxtaposition of positive and negative effects of predators on herbivores through different mechanisms illustrates how ecosystem engineers potentially could alter food web interactions and highlights the importance of integrating these bodies of theory in attempts to understand food web dynamics.

Introduction

Predators often have strong impacts on ecological communities by regulating the abundance and changing the dynamics of species in lower trophic levels (Soule *et al.* 2005). One of the most prominent generalist predators of the Arctic is the arctic fox (*Vulpes lagopus*) (Banfield 1974). Arctic fox population dynamics often follow the multiannual, high-amplitude cyclic population dynamics of lemmings (*Dicrostonyx* and *Lemmus* spp.), particularly in regions such as Canadian Arctic, Northern Alaska and Fennoscandia where lemmings are their primary terrestrial prey (Chesemore 1969, Macpherson 1969, Angerbjörn *et al.* 1995, Elmhagen *et al.* 2000). Predators can also enhance ecosystem nutrient cycling strongly enough to increase vegetation productivity (Schmitz *et al.* 2010). For example, arctic fox dens can support lush green vegetation due to nutrient addition by arctic foxes (Chapter 1, Smits *et al.* 1988, Bruun *et al.* 2005), and the greater vegetation productivity on dens compared to surrounding areas could attract herbivores to these dens (Chapter 1). Lemming latrines can occur in vicinity of arctic fox dens on alpine tundra (Bruun *et al.* 2005), and lemming winter nests have been observed on

arctic fox dens in the Hudson Bay region of Canada (Roth, unpubl. data). The presence of lemming winter nests and latrines suggests that lemmings make use of arctic fox dens during winter despite the higher predation risk, and that arctic fox as predators could positively influence one of their main prey items, lemmings, through their engineering activities.

Another potential reason for lemmings to nest on arctic fox dens could be higher quality of vegetation. Herbivores, including lemmings, typically prefer to consume plants with higher nitrogen content [N] (Mattson 1980, Rodgers and Lewis 1985). Arctic foxes concentrate nutrients on their dens, leading to much higher nutrient levels in soils on fox dens than surrounding tundra (Chapter 1). These nutrient additions could also translate to higher quality vegetation on dens that make them attractive nesting and feeding sites for lemmings in winter. Therefore, we predicted that vegetation on dens would not only be more abundant, but also would have higher N content than vegetation on surrounding areas.

The greater vegetation productivity on fox dens could lead to improved thermal insulation in winter, which could be another reason for lemmings to choose arctic fox dens for nesting during winter. Lemmings remain active during winter and commonly reproduce (Millar 2001, Gruyer *et al.* 2010), and conditions that promote reproduction in winter (which can last up to 9 months in arctic regions) could be critical for the occurrence of regular peaks in these species' population dynamics (Reid and Krebs 1996, Kausrud *et al.* 2008). In winter, lemmings inhabit a layer of lightly-packed snow crystals close to the soil surface called the subnivean space (Korslund and Steen 2006), and use of this space provides thermal insulation against the harsh arctic ambient air temperatures, protection against predators and access to food (Scott 1993). In the subnivean space, lemmings make winter nests from vegetation, which they use for further thermal insulation (Chappell 1980, Casey 1981), breeding and raising litters (MacLean *et*

al. 1974, Krebs *et al.* 1995, Sittler 1995, Duchesne *et al.* 2011a). Winter nests are typically found in locations forming a thick snow cover, providing lemmings with better thermal insulation (Reid & Krebs 1996). At snow thickness above the hiemal threshold (20-30 cm) air and ground temperatures are no longer coupled, and the environment at the soil surface becomes more stable and suitable for lemmings compared to the highly fluctuating air temperatures (Pruitt 1970, Huryn and Hobbie 2012). If arctic fox dens offer better thermal insulation to lemmings during winter, we predicted that arctic fox dens would have a greater snow cover thickness than surrounding areas, and that dens with lemming winter nests on them would have greater maximum snow cover thickness than dens without lemming nests. We also hypothesized that if lemmings avoid dens currently occupied by arctic foxes, we would be less likely to find lemming winter nests on dens with signs of recent fox use.

On the tundra, areas with thick snow accumulation usually occur on the lee side of topographical features such as slopes, banks and ridges where wind-blown snow drifts deposit (Fuller *et al.* 1975, Reid and Krebs 1996, Kane *et al.* 1991, Duchesne *et al.* 2011b). Vegetation stands can also increase snow cover thickness by decreasing wind speed (Benson & Sturm, 1993). Shrub presence, for example, can increase snow cover thickness up to about 30% independent of local topographic heterogeneity (McFadden *et al.* 2001). Nutrient addition by foxes (Chapter 1) could increase vegetation cover on dens. Thus we predicted dens would support greater vegetation cover than control areas. Denser vegetation on dens could trap blowing snow. Therefore, we also predicted that snow cover thickness would be positively related to vegetation cover on dens.

Methods

Our study was conducted on the tundra adjacent to western Hudson Bay, within Wapusk National Park in Manitoba, Canada. Arctic fox dens in this area are almost exclusively found on north-south oriented beach ridges (Roth 2003), one of the main landform features in this region that are made by post-glacial rebound of the land (Bahr 1989, Dredge 1992). Low moisture levels due to the sandy soils and greater depth to permafrost make these beach ridges suitable denning habitats for arctic foxes (Chesemore 1969, Macpherson 1969, Smits *et al.* 1988, Dalerum *et al.* 2002,). Vegetation on beach ridges is characteristic of low-growing heath communities (Johnson 1987), specifically *Dryas* heath (Brook & Kenkel 2002, Elliott 2009), due to the dominance of *Dryas integrifolia*. However, arctic fox dens are usually covered with lush green vegetation, dominated by fast-growing species such as *Leymus mollis* and *Salix planifolia* (Fafard unpubl. data). Based on trapping efforts (Roth 2002), the only lemming species inhabiting this area is the collared lemming (*Dicrostonyx richardsoni*).

In April 2014 we measured snow thickness on 60 dens and paired control sites. Using an avalanche steel probe, we measured snow thickness at the point on the den with highest elevation and at four additional points 5 meters from the centre, approximately in the four cardinal directions (2 parallel to the beach ridge and 2 perpendicular to the beach ridge). For each den a paired control area was chosen 50 m from the centre of the den at a similar elevation, slope and aspect, and 5 snow thickness measurements were taken following the same protocol as den measurements. We also assessed the activity status of each den based on the presence of burrows (i.e. active dens had tunnels dug by foxes through the snow to the den).

In June 2014 we surveyed a subset of dens for the presence of lemming winter nests. For each den site, we also surveyed a paired control site with a similar area, elevation, slope and aspect. The centre of the control site was designated 50 m away from the centre of the den (the

midpoint of a straight line connecting the two farthest open burrows) to ensure that control area was not overlapping with the fox denning area.

In August 2014 we estimated vegetation cover by taking aerial photos from den and control pairs with a DJI Phantom 2 Vision⁺ drone. Centres of dens and paired control sites were designated following the same protocol as in June. To ensure the visibility of den and control centers in aerial photos, a stake and a 1 m² quadrat were placed at the centre of each den and control site. To compare the vegetation quality on and off dens, *L. mollis* samples were collected from den and surrounding areas when possible.

To compare snow depth between den and control pairs, we used linear mixed effect analysis in R (R Core Team 2015), using lme4 (Bates *et al.* 2015) and arm (Gelman & Yu-Sung 2015) packages. Site (den vs. control) was entered as a fixed effect into the model. As a random effect, we let intercepts vary for site id. The measurements for each site were averaged and Log₁₀-transformed to meet the normality and homoscedasticity assumptions. Likelihood ratio test of the full model against a null model was used to obtain a p-value for the fixed effect. Marginal R² (proportion of variance explained by the fixed factor) and conditional R² (proportion of variance explained by both the fixed and random factors) values were calculated based on Nakagawa & Schielzeth (2013).

To compare the maximum snow cover thickness measurements (taken in April) between dens with and without lemming winter nests, we used Welch's t-test. To test if fox activity affects lemming winter nest presence on dens, we used Fisher's exact test.

Vegetation dominated by *S. planifolia*, *L. mollis* and *D. integrifolia* and total vegetation cover estimates were calculated from aerial photos using Photoshop[®] CS6. For each aerial photo, the length of one side of the 1 m² quadrat visible in each photo was measured in pixels (L), the

photo was then cropped into a circle with a diameter of $10 \times L$ and centred on the stake (placed on the centre of den or control site). The total area of the circle was measured in pixels. The number of pixels belonging to *S. planifolia*, *L. mollis* and *D. integrifolia* were measured using the lasso and color range tools. We chose the same level of sensitivity (“Fuzziness”) of the color range tool for all species. The cover for each species was then measured by dividing the number of pixels of each species by the total area of the circle. For photos with only one plant species, the barren ground (including dead vegetation) area was determined and subtracted from the total area. Measurements were then compared between den and control sites using paired t-tests. To test if *S. planifolia*, *L. mollis* and *D. integrifolia* trap snow and result in thicker snow cover, we ran a multiple linear regression analysis for den and control sites separately. Snow cover measurements were Log_{10} -transformed to meet the normality and homoscedasticity assumptions.

L. mollis samples were dried to constant weight, and a portion of each was homogenized with a ball mill. Nitrogen content (%N based on mass) was measured in 3 mg sub-samples using an elemental analyzer at University of Windsor. N content of plants were compared between dens and controls using a paired t-test.

Results

We found lemming winter nests on 68% of the dens surveyed (26 out of 38, Mean = 1.47, SE = 0.25), but no nests on control areas. Fox activity did not affect the presence of lemming nests on dens (Fisher’s exact test, $N = 38$, $p = 0.484$).

Total vegetation cover differed between den and control areas ($N = 18$, $t_{17} = 4.363$, $p = 0.0002$), with dens having nearly twice as much vegetation cover as control sites (Fig. 2.1). *S. planifolia* and *L. mollis* were not found on control sites. *D. integrifolia* cover was about 3 times

greater on control sites than den sites ($N = 18$, $t_{17} = -3.535$, $p = 0.001$). N content in vegetation was significantly greater on dens than on control sites ($N = 14$, $t_{13} = 8.185$, $p < 0.0001$) (Fig. 2.2).

Snow cover was about 4 times thicker on den sites than control sites (Fig. 2.3) ($\chi^2_{(1)} = 115.616$, $p < 0.0001$, $\beta = 0.657$). The full model had a marginal $R^2 = 0.599$ and conditional $R^2 = 0.728$. Furthermore, dens with lemming winter nests had higher maximum snow thickness than dens without lemming winter nests ($N = 35$, $t_{25.5} = 2.426$, $p = 0.023$) (Fig. 2.4).

Snow thickness on den sites was affected by vegetation cover ($N = 18$, $F_{3, 14} = 41.632$, $p < 0.0001$, $R^2_{\text{Adjusted}} = 0.877$) according to this equation:

$$\text{Log}_{10} \text{Snow cover} = 0.006 \times S. \textit{planifolia} \text{ cover} + 0.003 \times L. \textit{mollis} \text{ cover} - 0.0002 \times D. \textit{integrifolia} \text{ cover} + 1.301$$

Snow thickness on dens increased with *S. planifolia* cover ($t_{17} = 8.89$, $p < 0.0001$) and *L. mollis*: cover ($t_{17} = 4.30$, $p = 0.0007$) but *D. integrifolia* had no effect ($t_{17} = -0.17$, $p = 0.869$) (Fig 2.5a). Likewise, *D. integrifolia* cover did not affect snow cover thickness on control sites ($N = 18$, $F_{1, 17} = 0.005$, $p = 0.947$) (Fig. 2.5b).

Discussion

The much greater snow thickness on arctic fox dens compared to control sites suggests den sites offer more thermal insulation against the harsh arctic climate than control sites, making them attractive sites for lemmings during winter. Furthermore, 90% of the den sites (compared to only 10% of the control sites) had average snow thickness greater than the hiemal threshold. Thus dens sites not only provide better thermal insulation but they also offer maximal dampening of the diurnal temperature fluctuations at ground level compared to ambient air. The influence of snow on lemmings' choice of winter habitat is further supported when snow thickness on dens

with and without nests are compared; dens with winter nests had greater snow cover thickness, therefore providing lemmings with better thermal protection than dens without nests.

Besides improving thermal insulation, thick snow cover has also been suggested to limit predation attempts on lemmings or reduce success rates (Gilg *et al.* 2006), but a recent study found that thick snow cover did not provide lemmings protection against ermine predation, only weakly limited fox predation attempts made by jumping through the snow, and did not affect attempts made by digging (Bilodeau *et al.* 2013). Our results are consistent with Bilodeau *et al.* (2013), as fox activity did not affect lemming nest presence on dens, suggesting that better protection against predators is not the primarily reason for lemmings' choice of areas with thick snow cover.

Deeper snow also increases soil temperature, which in turn results in greater over-winter nitrogen mineralization rates and available nitrogen in tundra ecosystems by causing increased microbial activity (Schimel *et al.* 2004). Thus dens have greater inorganic nitrogen concentrations because of both deposition of nutrients by foxes (Chapter 1) and deeper snow. Higher amounts of nutrients in turn increase plant biomass (Chapter 1) and cover (this study), as well as changing the plant community towards more nutrient-demanding species such as *L. mollis* and *S. planifolia* (Fafard unpubl. data). As our results demonstrate, snow cover thickness increases as the cover of *S. planifolia* and *L. mollis* increases, confirming that vegetation on dens can trap the blowing snow and increase snow cover thickness in a positive feedback cycle. *D. integrifolia* did not affect snow thickness on dens or on control sites, possibly because it is a shrub species that is only found dwarfed in our study area (Johnson 1987) and therefore would not trap any significant amount of snow. Our results are consistent with studies on the effects of height of erect shrubs such as willows on the amount of snow accumulation in tundra areas

(McFadden *et al.* 2001). However based on our model, *L. mollis*, which is a perennial grass, also traps snow (even on dens where willows are absent). Due to its extensive rooting system, *L. mollis* acts as a stabilizer in subarctic coastal dunes (Gagné and Houle 2002), and therefore, the dense *L. mollis* cover on arctic fox den could resist the wind during winter and trap the blowing snow.

N content of vegetation on dens was higher than control sites, suggesting that the greater inorganic N in soil on den sites also increases vegetation quality. N content of plant species was positively correlated with the diet preference of *Dicrostonyx groenlandicus* (Rodgers and Lewis 1985), a closely related species to *D. richardsoni*. Higher quality and quantity of food in addition to better thermal insulation could make arctic fox dens attractive nesting sites for lemmings. Moreover, collared lemmings have a preference for *Salix* species (Batzli and Pitelka 1983), which are commonly found on dens (Fafard unpubl. data). *S. palnifolia* and *L. mollis* are both perennial species, and their higher N content makes them valuable food sources during winter. Additionally elevated catechin (a plant secondary metabolite) concentrations in *Dryas* spp. negatively affect the consumption rates of these species by collared lemmings (Berg 2003). Control areas where *D. integrifolia* is the dominant vegetation could therefore could be considerably less attractive lemming feeding sites than den areas.

In conclusion, arctic foxes engineer arctic ecosystems on local scales: by enhancing the nutrient dynamics foxes create a vegetation community with more erect species that trap snow during winter. Increased snow cover thickness can in turn increase the availability of nutrients to plants by increasing the mineralization rates. Higher concentration of nutrients in soil also increases vegetation biomass and cover on dens. Our results suggest thicker snow in combination with increased quantity and quality of food attracts lemmings to arctic fox den sites during

winter, regardless of fox activity on dens, and the main value of choosing sites with thick snow cover is for thermal insulation rather than predator avoidance. As mammalian herbivores in arctic tundra can elevate soil nitrogen and phosphorous concentrations through deposition of their waste products (McKendrick *et al.* 1980), lemming use of arctic fox dens could further enhance local nutrient dynamics.

Arctic foxes as predators can negatively affect lemming populations through predation, but our study illustrates that by creating suitable winter habitats for lemmings, arctic foxes could positively influence lemming populations. Arctic fox den sites could be local refugia for collared lemmings whose population cycles have dampened due to climate change effects such as increasing temperatures and changing snow characteristics in a number of arctic areas (Ims *et al.* 2008, Kausrud *et al.* 2008). Arvicoline rodents such as lemmings support a number of mammalian and avian predators in the Arctic (Korpimäki *et al.* 2005, Gilg *et al.* 2006, Gauthier *et al.* 2011). Thus arctic fox engineering activities could also indirectly affect other predators. Combining both trophic and non-trophic impacts of arctic foxes (as both top predators and ecosystem engineers) into interaction webs would give a better representation of the role of this species in tundra ecosystems than focusing solely on food web interactions.

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Figures

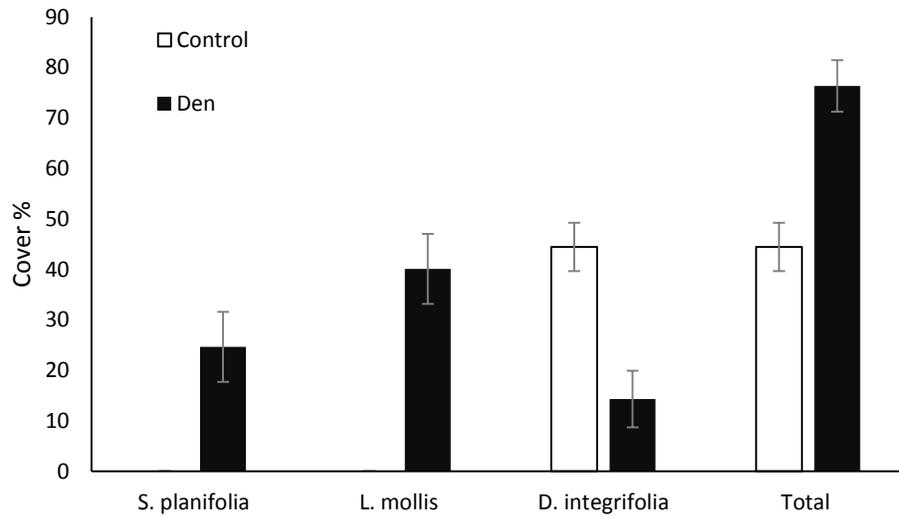


Figure 2.1: Vegetation cover percentage (mean \pm SE) on 18 fox dens and paired control sites in Wapusk National Park, Canada, in August 2014.

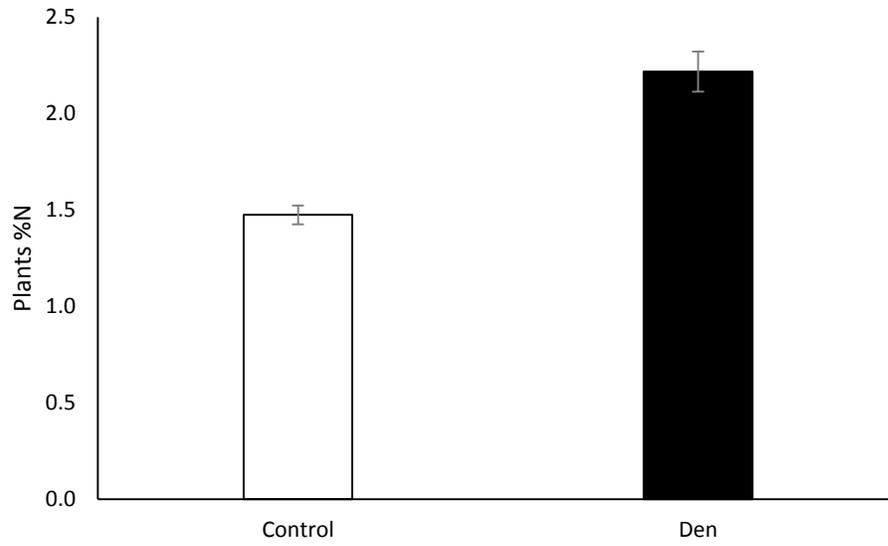


Figure 2.2: Percent nitrogen in *Leymus mollis* leaf samples collected from 14 fox dens and surrounding areas in Wapusk National Park, Canada, in August 2014.

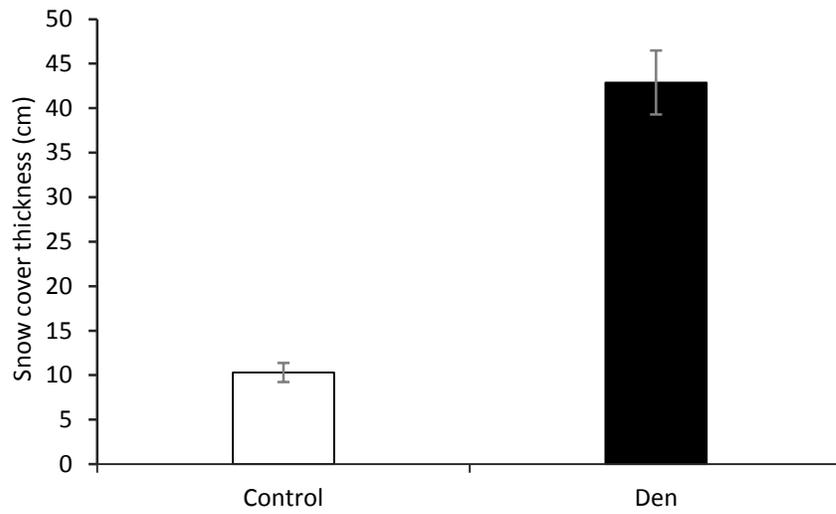


Figure 2.3: Snow thickness (mean \pm SE) on 60 fox dens and paired control sites in Churchill Wildlife Management Area, Canada, in April 2014.

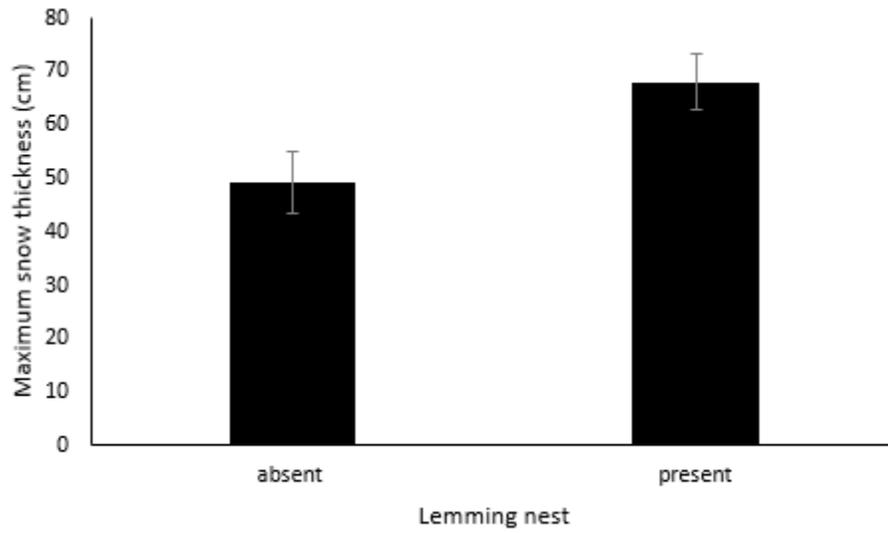


Figure 2.4: Maximum snow thickness (mean \pm SE) on fox dens with (n=24) or without (n=11) lemming winter nests in Churchill Wildlife Management Area, Canada, in April 2014.

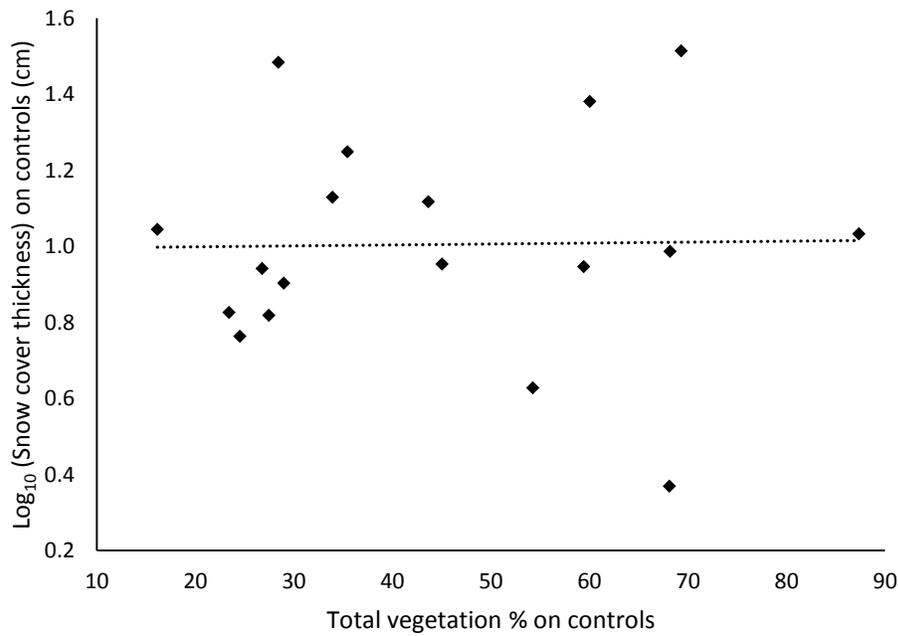
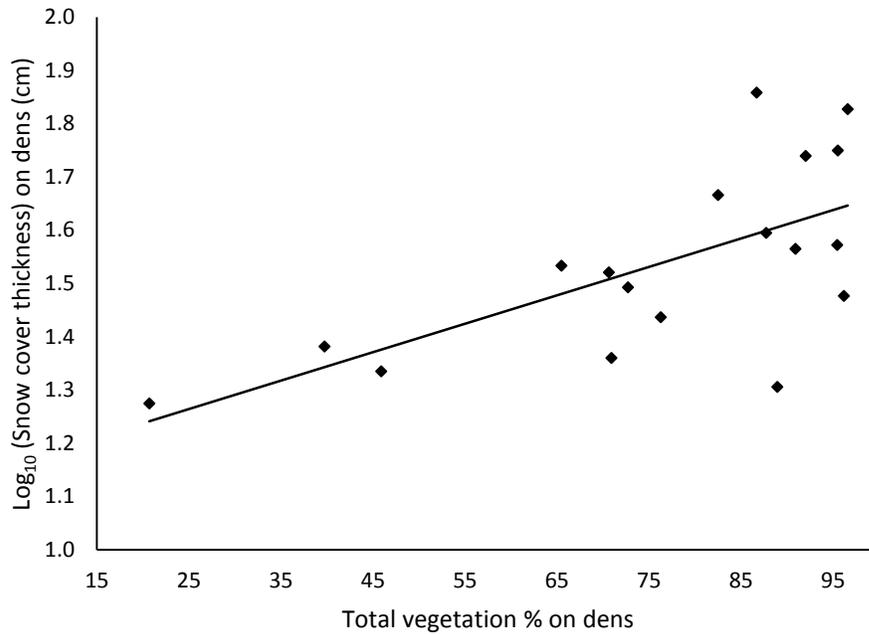


Figure 2.5: Relationship between snow cover thickness and vegetation cover on (a) fox den sites and (b) on control sites (n=18 sites in each category).

Thesis Conclusion

Our studies demonstrate that arctic foxes' influence on the arctic tundra, in the context of non-trophic interactions, can be effectively conceptualized in the ecosystem engineering framework. Both types of ecosystem engineering interactions were investigated: the role of foxes in elevating nutrient levels in mineral soil and snow thickness illustrated the effects of this species on the abiotic components of its environment, i.e. the ecosystem engineering process. The positive effects on vegetation biomass and cover, and lemming winter nest density illustrated the biotic engineering effects of arctic foxes, i.e. the ecosystem engineering consequence.

The increase in soil nutrient levels due to nutrient addition by foxes increased vegetation quantity (biomass and cover) and quality (nitrogen content). Increased vegetation cover, specifically *Salix* sp. and *L. mollis* cover, positively influenced snow cover thickness on dens by trapping blowing snow. Thicker snow cover could positively feed back to soil nutrient levels by providing microbial communities with higher ground temperatures, thereby increasing the nutrient mineralization rates. The increased snow cover thickness made dens attractive nesting sites for lemmings by providing them with better thermal insulation during the harsh arctic winter. Prevention of local lemming extinction can feed back upward to increase arctic foxes' fitness. Higher quality and biomass of vegetation could also attract lemmings to den sites, leading to another positive feedback to arctic foxes. Additionally, lemming latrines have also been observed on fox dens (Bruun *et al.* 2005, Roth unpubl. data) and could possibly further enhance soil nutrient levels (McKendrick *et al.* 1980).

While the ecosystem engineering concept has always excluded trophic interactions (the direct consumption or provision of tissue) as an engineering process, some later studies have

proposed to explicitly exclude all assimilatory and dissimilatory processes (such as deposition of nutrients through urine and feces) from the concept (Jones and Gutierrez 2007). Using this restricted definition, nutrient deposition by arctic foxes falls outside the ecosystem engineering framework. However, the mounting number of studies on the engineering role of organisms via assimilation and dissimilation processes shows that most researchers favor the original, more inclusive definition of the ecosystem engineering concept (Caraco *et al.* 2006, Volkenborn *et al.* 2007, Berke *et al.* 2010). Berke (2010) has developed a functional classification of ecosystem engineers and included the assimilation and dissimilation processes in the concept. Arctic fox nutrient deposition into soil would be considered as chemical ecosystem engineering under this classification system. Chemical ecosystem engineers create biogeochemical gradients (physically or physiologically) in their environment.

Past studies have suggested that the lush green vegetation on arctic fox dens could be to some extent the result of foxes digging burrows on their dens. These burrows can act as ventilation ducts leading to greater depth to permafrost and soil temperature on fox dens compared to surrounding areas and ultimately better soil chemical and physical conditions for plant growth (Smits *et al.* 1988, Smith *et al.* 1992). Therefore, arctic foxes may also change the abiotic and biotic components of their environments through physically-mediated interactions. Thus, under the functional classification proposed by Berke (2010), arctic foxes could also be considered as bioturbators.

The most important engineers in physically stressful environments (such as the arctic tundra) are those that relieve environmental limitations and support ecosystem functions with either their physical presence or activities (Crain & Bertness, 2006). Primary productivity in arctic ecosystems is limited by nitrogen and to a lower degree phosphorous availability (Ulrich &

Gesper 1978, Henry *et al.* 1986). Arctic fox denning activities increase nitrogen and phosphorous levels in the soil, providing vegetation with the limiting factors for their growth (Chapter 1). Furthermore, increased vegetation cover results in thicker snow cover which in turn provides a suitable nesting site for lemmings by providing them with thermal insulation. Thus the limitation on the survival of lemmings due to very low temperatures is also alleviated through years of fox denning activities (Chapter 2). Low temperature and nutrient alleviation by arctic foxes suggests that this species is an important ecosystem engineer in arctic tundra areas supporting ecosystem functions such as nutrient cycling.

Another operational approach for identifying important engineers is to consider the temporal and spatial scales of engineering impacts: The impacts of important ecosystem engineers can persist longer than the organisms itself, or in other words “engineering can outlive the engineer”, and that the spatial scale of such impacts is larger than the scale of biotic processes involved (Hastings *et al.* 2007). Temporally, development of high-quality arctic fox dens can take many years, with some dens estimated to be hundreds of years old (Macpherson 1969). Furthermore, pup presence during the previous year does not affect soil nutrient concentrations, suggesting the impact of arctic foxes persists >1 year (Chapter 1). Arctic fox dens are variable in size (average area 30-277 m²) depending on the age and habitat (Tannerfeldt *et al.* 2003). In coastal tundra habitats of northern Canada, well-established dens average to 123-130 m² in area (Tannerfeldt *et al.* 2003), spatially much larger than the fine-scale biotic processes involved (for example decomposition and nutrient mineralization by microbial processes). Den sites in our area are patches with enhanced ecosystem nutrient dynamics, vegetation productivity and lemming density, distributed on the landscape level. Thus the

impacts of arctic foxes ecosystem engineering are temporally and spatially large enough that arctic foxes could be considered important engineers.

Northern expansion of red foxes (*Vulpes vulpes*) into arctic areas has been correlated with climate warming (Hersteinsson and Macdonald 1992). Bottom-up increase in productivity, milder winter temperatures, and longer reproductive seasons, are all possible climate warming consequences hypothesized to increase the abundance of red foxes (Gallant *et al.* 2012). Due to their largely overlapping ecological niches, arctic and red foxes compete intensely for resources such as suitable den sites and food. In interference competition, red foxes dominate over arctic foxes due to their larger body size. The larger body size and higher resting metabolic rate, however, means that red foxes have higher energetic burden. Contrary to earlier hypotheses, results from den surveys in northern Yukon, where climate warming rate has been the fastest in North America, suggests that the negative effects climate warming on food availability (such as decrease in snow cover duration, therefore lower lemming winter survival rates, and increase in duration of ice-free season, therefore restricted accessibility to seal carcasses) has prevented the dominance of red foxes in this area (Gallant *et al.* 2012). Gallant *et al.* (2012) also suggest that in areas where red foxes have successfully dominated over arctic foxes, allochthonous food subsidies (for example increased ungulate densities or anthropogenic activities) sustain red foxes through the winter. In our study area, red foxes are present, but dens located on the tundra are mostly occupied by arctic foxes, and red foxes are mostly found in forested areas. Increase in anthropogenic activities in these sub-arctic tundra areas (for example Keeyask hydroelectric development project in Split Lake Resource Management Area, Manitoba Hydro 2014) could increase the winter survival rate of red foxes and ultimately facilitate their dominance over arctic foxes.

There are behavioral differences in denning activities between red and arctic foxes. Brunn (2005) has shown that the differences in plant species composition between arctic fox dens and the surrounding area in alpine tundra is more due to nutrient enrichment than due to soil disturbance. Red foxes defecate less on dens compared to arctic foxes (probably as a defense mechanism to decrease parasite infections, Friesen 2013). Additionally, red foxes have smaller litter sizes than arctic foxes (Cypher 2003). Furthermore, red foxes have 90% larger home ranges than arctic foxes (Hersteinsson and Macdonald 1992) and show more inter and intra specific aggression (Cypher 2003). Thus it is possible that fewer dens would be used if red fox expand more into tundra areas. Due to all the reasons above, concentration of soil nutrients measured on arctic fox dens could gradually decrease over the years when these dens are used by red foxes. Lower nutrient input on dens could lead to decrease in vegetation quality and quantity, vegetation cover and ultimately snow cover thickness on dens. For lemmings, whether the benefits associated with use of fox dens would still be greater than the predation risk, would require more investigation. Further research on the behavioral differences in denning activities between sympatric arctic fox and red foxes in arctic tundra is needed to accurately predict the consequences of red fox den use on beach ridge vegetation community and herbivores.

Lemmings in the arctic tundra are preyed upon intensely by a diverse group of raptors during summer (Pitelka *et al.* 1955). Diurnal raptors have the ability to detect UV and because microtine rodent waste products are visible in UV light, diurnal raptors can concentrate their hunting activities where microtine rodents defecate and urinate. In tundra areas, collared lemmings (*Dicrostonyx groenlandicus*) use underground latrines in their burrows to reduce the risk of predation by diurnal raptors (Boonstra *et al.* 1996). However, since lemmings' odor is concentrated in latrines and arctic foxes have an acute olfactory sense (Banfield 1974), predation

risk by foxes could increase (Boonstra *et al.* 1996). We found that in our study area, collared lemmings (*Dicrostonyx richardsoni*) build winter nests on fox dens, where fox predation risk is higher. This behavior in addition to latrine building could mean that lemmings might not have the same degree of antipredator adaptations against foxes compared to avian predators. Future research on the ability of lemmings to detect signs of fox presence (for example, fox urine) would be useful in further understanding the behavioral ecology of lemmings under environmental pressures caused by climate warming.

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Appendix A: Annual variation in soil inorganic nitrogen concentrations of arctic fox dens and paired control sites

Introduction

The impacts of important ecosystem engineers can persist longer than the engineer itself (Hastings *et al.* 2007). While long term soil nutrient concentrations data of arctic fox (*Vulpes lagopus*) dens and adjacent control sites are not available, the persistence of the distinct fast-growing lush plant species such *Leymus mollis* and *Salix planifolia* even on dens that have not produced pups in recent years (Roth, unpubl. data) suggests that the nutrient enriching effects of arctic foxes can last for multiple years. Presence of pups during the previous year does not affect soil inorganic nitrogen (N) concentrations, suggesting the effects of arctic foxes carry on for more than 1 year (Chapter 1). Here we compared the inorganic N concentration of the same dens and approximately the same control sites between August 2013 and 2014. If the nutrient enriching of arctic foxes persists more than a year, we predicted that den sites would have higher inorganic N levels compared to control sites in both years and that there would be no significant annual variation in inorganic N levels.

Methods

Soil samples were collected from arctic fox dens and paired control sites located on the tundra adjacent to western Hudson Bay, within Wapusk National Park in Manitoba, Canada. In August 2013, soil samples from 8 dens and paired control sites were collected (10 samples from each den and control site). Sampling locations on each den were chosen haphazardly. Two Control sites were chosen for each den towards north and south directions. The centre of each

control site was located 50 m from the edge of the den (based on the dramatic change in vegetation). One sample was collected from the centre and 4 more samples were collected 2 meters from the centre, in opposite directions (2 parallel to the beach ridge and 2 perpendicular to the beach ridge). In August 2014, soil samples were collected from these same dens as described in Chapter 1. Soil samples were kept frozen until analysis, then thawed in the lab and homogenized, and a subsample was air dried. Total inorganic N concentration [$\text{NH}_4^+ + \text{NO}_3^-$] was determined using the microdiffusion method (Saghir *et al.* 1993) for 2013 soil samples and the accelerated microdiffusion method (Khan *et al.* 1997) for 2014 soil samples (see Chapter 1).

To compare soil inorganic N between den and control pairs, and between years (2013 vs. 2014), we performed linear mixed effect analysis in R (R Core Team 2015), using lme4 package (Bates *et al.* 2013). Site (den vs. control) and year (without the interaction term) were entered as fixed effects into the model. As a random effect, we let intercepts vary for site id. Inorganic N measurements at each site were averaged and square-root transformed to satisfy the normality and homoscedasticity assumptions. We obtained p-values for each fixed effect using likelihood ratio tests of the full model against reduced models without the effect in question. Marginal R^2 (proportion of variance explained by the fixed factors) and conditional R^2 (proportion of variance explained by both the fixed and random factors) values were calculated based on Nakagawa & Schielzeth (2013) using lme4 (Bates *et al.* 2013) and arm (Gelman, A. and Yu-Sung 2015) packages.

Results

Den sites had 97% more inorganic N than control sites in 2013, and 199% more 2014 (Fig A.1). Mixed effect analysis results indicate that inorganic N concentration differed between

sites ($\chi^2_{\text{site (1)}} = 16.935$, $p_{\text{site}} < 0.0001$) but not between years ($\chi^2_{\text{year (1)}} = 0.485$, $p_{\text{year}} = 0.486$).

Soil inorganic N concentration was higher on dens compared to control sites ($\beta = 1.359$). The full model had a marginal $R^2 = 0.426$ and a conditional $R^2 = 0.453$.

Discussion

Higher inorganic N concentration on dens compared to control sites in August 2013 and 2014 suggest that the difference between dens and controls can persist at least more than one year (Fig A.1). Furthermore, lack of annual variation in inorganic N levels is consistent with our previous results that pup presence does not affect inorganic N levels (Chapter 1).

While both methods use the same reagents, and have high accuracy and precision, accelerated microdiffusion uses gentle heating to reduce the time needed for complete recovery of inorganic N (Khan *et al.* 1997, Saghir *et al.* 1993). Thus slight differences between microdiffusion and accelerated microdiffusion methods could potentially affect our results. To assure that such effects are accounted for, we suggest that future studies compare results obtained from microdiffusion and accelerated microdiffusion methods by analysing the same samples with both methods.

Monitoring soil nutrient levels and pup presence on a long term basis is necessary for a more accurate estimation of persistence of arctic fox effects, especially since arctic foxes have experienced a range contraction due to climate warming and the encroachment of red foxes (*Vulpes vulpes*). Furthermore, through nutrient deposition, arctic foxes create habitats for collared lemmings (*Dicrostonyx groenlandicus*) (Chapters 2), therefore a better understanding of the persistence of arctic foxes' engineering effects could be important in predicting the consequences of climate warming on lemmings' local population dynamics.

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Figures

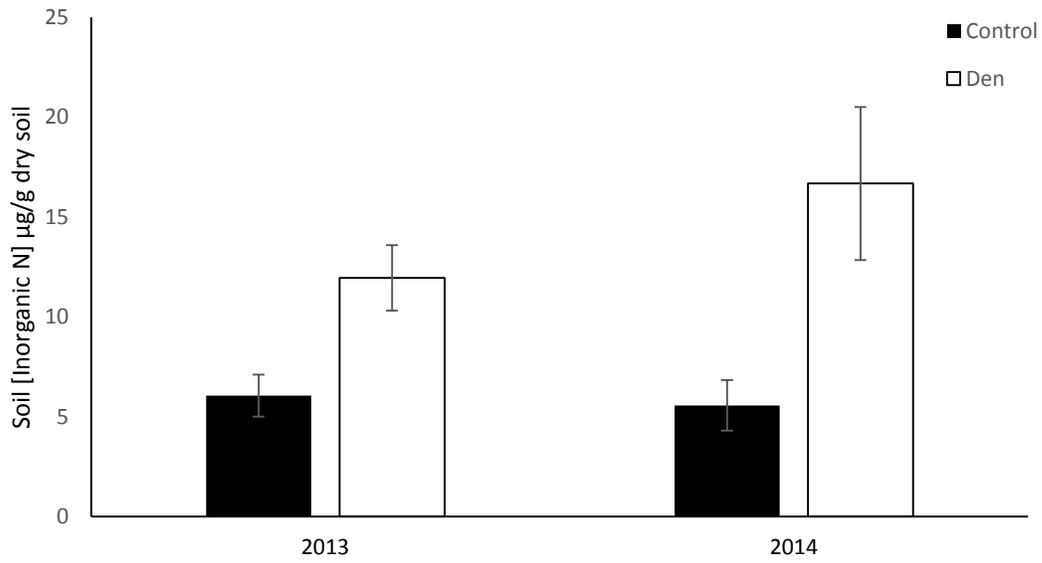


Figure A.1: Inorganic N concentration (mean \pm SE) of soil samples collected from fox dens and control sites in Wapusk National Park, Canada, in August 2013 and 2014.