Investigating the mechanism of Arctic fox (*Vulpes lagopus*) ecosystem engineering on dry heath communities in subarctic tundra

by

Liam Alexander Baron-Preston

A Thesis for submission to the Faculty of Graduate Studies of

The University of Manitoba

in partial fulfillment of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg, MB

Abstract

Arctic terrestrial ecosystems are some of the most extreme environments on earth, with a polar climate and landscapes recently carved by glacial retreat. Soil nutrient availability is a limiting factor for tundra productivity and under these conditions, the impacts of consumer-driven nutrient cycling can be magnified. Arctic foxes (*Vulpes lagopus*) are predators that act as ecosystem engineers in arctic and alpine tundra heath by altering the environment of their den sites, which exhibit increased soil nutrients, verdant atypical vegetation, and deeper snow. These fox dens are biogeochemical hotspots in otherwise nutrient-limited ecosystems and sources of cascading effects across trophic levels. It has been long hypothesized that these dens are so biotically productive because Arctic foxes increase the deposition rate of limiting nutrients by concentrating prey-derived nitrogen (N) and phosphorus (P) in the soil and this hypothesis has been descriptively supported but, the mechanism had not been confirmed with experimentation. To test the ability of the nutrients concentrated by Arctic foxes to cause the ecosystem effects observed on fox dens, I examined a long-term field experiment in Wapusk National Park. Vegetation plots received N and P additions (estimated from fox activity) and/or snow fencing on the windward side to increase snow depth. I investigated how the species composition of plot plant communities changed over 5 years, the treatment effects on plant productivity, intraspecific changes in prostrate shrub leaf metabolism, the response of resident insect communities, and the space use by collared lemmings. I found that nutrient addition facilitates the invasion of tall grass that can accumulate deep snow cover in the winter, deep snow can magnify some effects of increased nutrients, and the nutrient/snow combination can shape plant communities and create preferred lemming habitat. My thesis demonstrates how N and P deposition, increased to a rate within the ability of Arctic foxes, can drive the development of the atypical vegetation and cause

the cascading ecosystem effects described at Arctic fox dens. Thus, I support the ability of Arctic foxes to engineer unique den habitat in tundra ecosystems.

Contributions of Authors

Manuscript Authors: Liam Baron-Preston, John Markham, James D. Roth

Both manuscript chapters (2 and 3) use a long-term vegetation plot experiment, designed and established by John Markham and James D. Roth. Liam Baron-Preston designed and led the analyses with the advice of John Markham and James D. Roth. Liam Baron-Preston has written these manuscripts with revisions from John Markham.

Table of Contents

List of Tables

List of Figures

Acknowledgements

First, I would like to thank John Markham for his all his help and support over the last three years. It is difficult to put into words how much I have learned and grown from his mentorship and encouragement. His guidance throughout this research made this thesis possible, plain and simple. I would also like to thank my committee members Jim Roth and Colin Garroway for their support and advice throughout this process. Jim was particularly supportive during the pandemic and afforded me my first opportunity for tundra fieldwork in June of 2022.

My thanks to the whole Renault Lab for their good company and for answering innumerable laboratory questions. I would like to thank all the friends, students, and assistants who accompanied me in the field for making my time in Churchill truly unforgettable. Special thanks to Caitlin Moran for her friendship and support throughout my program. Thank you to Sean Johnson-Bice, Chloe Warret Rodrigues, and the rest of the Churchill Fox Project for your advice and camaraderie out in Wapusk. Thanks to the Parks Canada staff and the Province of Manitoba biologists for their help and cooperation at Nester 1.

I would like to thank the Natural Sciences and Engineering Research Council of Canada, Polar Continental Shelf, Polar Knowledge Canada, Parks Canada, the Province of Manitoba, the University of Manitoba, and the Manitoba Association of Plant Biologists for use of their facilities and their generous funding that made this research happen.

Finally, thanks you to my family and friends whose counsel, encouragement, and humor kept me going these last few years.

Chapter 1: Introduction

Arctic terrestrial ecosystems have long been characterized by extreme seasonality and low nutrient availability, which limit primary production and plant diversity. These limiting environmental conditions are now rapidly changing (Serreze et al., 2000), and large amounts of soil carbon and plant nutrients will be made available to these ecosystems (Keuper et al., 2012). Climate modelling of Canada's national parks projects a complete loss of tundra in Wapusk National Park and a rapid biome shift in the subarctic (Environment and Climate Change Canada, 2019; Kushner et al., 2018; Scott et al., 2002). Understanding the ecosystem processes and nutrient cycles in these systems is critical for informed conservation planning and future sustainable land management in Canada's North. Arctic foxes (*Vulpes lagopus*) act as ecosystem engineers in arctic tundra ecosystems, altering these processes, and in doing so, demonstrate a unique intersection of ecological theories in the field.

Tundra ecosystem functioning

The arctic tundra is a global region of vegetated lowland found north of the treeline: the climatic limit for tree growth (Bliss et al., 1973; Heijmans et al., 2022; Marschner & Rengel, 2007; Meltofte et al., 2013). It is a land of extremes. Seasonality at higher latitudes creates a short annual season of rapid growth, featuring up to 24 hours of sunlight per day to drive photosynthesis, contrasted with long, dark, and freezing winters (Meltofte et al., 2013). Summer temperatures remain low, with July averages ranging from 1-12°C, and annual precipitation is below 250mm most years (Heijmans et al., 2022; D. A. Walker et al., 2005). Tundra ecosystems exhibit a form of bottom-up control where environmental stressors have so limited primary production that soils remain underdeveloped, leading some to argue that these ecosystems have

not reached an ecological climax since the region deglaciated (Bliss et al., 1973; Dunbar, 1970). Ecological processes here are limited by decomposition, where plants develop tough tissues to withstand the extreme climate that take longer to break down in the soil than to produce. The inequality between the time required to produce biomass and that required for its decomposition results in long-term accumulation of organic matter in the soil, locking away not only fixed atmospheric carbon but also nutrients required for plant functioning (Marschner & Rengel, 2007). The availability of soil nutrients likely mediates production during the short growing season (Sullivan et al., 2015), further limiting growth to the rate at which nutrients can be made available (Zou et al., 2016).

Tundra heath communities, in particular, have been found to exhibit very low invasibility compared to other comparable communities (Milbau et al., 2013a). While due in part to the extreme environment, this resistance to invasion may also come from the dominance of species with certain types of mycorrhizal associations. Some ericoid (ErM) and ectomycorrhizal (EcM) fungi have the ability to mineralize or directly uptake organic compounds in the soil and access the constituent nutrients (Read & Perez-Moreno, 2003). In ecosystems where phytoavailable nutrients are limited, like those found in the tundra, there would be selective pressure for plants that could form symbiotic relationships with such fungi. As more soil nutrients are immobilized in organic matter, such selection pressure for plants with mycorrhizal associations would build, and in soils low enough in phytoavailable nutrients, plants without these associations could be excluded altogether. Tundra heaths are dominated by hardy prostrate shrubs, many of which are members of the Ericaceae, or heather family (hence the use of ‘heath’ or ‘heathland’ to describe such ecosystems), and form mycorrhizal relationships with ErM fungi that are well known for their ability to break down organic matter (Marschner & Rengel, 2007; Pandey et al., 2019; Read

et al., 2004; Read & Perez-Moreno, 2003). EcM fungi have also been found to facilitate the extraction of vital nutrients from organic matter (Cairney, 2011; Chalot & Brun, 1998; Pandey et al., 2019; Read & Perez-Moreno, 2003) and to form symbioses with tundra plants (Andresen et al., 2022; Hewitt et al., 2020, 2022). *Dryas* plants are particularly notable for EcM associations and dominate much of the dry upland heaths where Arctic foxes den (Billault-Penneteau et al., 2019; Bjorbækmo et al., 2010; Chesemore, 1969; Gharajehdaghipour et al., 2016; Prestrud, 1992). Isotope experiments have demonstrated the dependence of tundra plants on mycorrhizas for limiting nitrogen (Hobbie & Hobbie, 2006; Michelsen et al., 1998), which further supports this idea that mycorrhizal network access could be a determining factor in the composition of these plant communities. Such selective pressure would break down with increasing availability of alternative nutrient sources like consumer deposition (Gharajehdaghipour et al., 2016; Roy et al., 2022), lateral movement of waterborne nutrients (Rasmussen et al., 2022), leaching reduction (Van Cleve & Alexander, 1981), or increased activity in other biotic soil nutrient pathways (Keuper et al., 2012; Schimel et al., 2004; Standen et al., 2024). Theoretically, the exclusionary nature of a developed mycorrhizal 'monopoly' on limiting nutrients could stabilize the plant community but burden associated plants with a higher carbon cost, resulting in rapid community shift should nutrient limits change (Chapin et al., 1986; Hooper et al., 2005; Johnson et al., 1997).

Anthropogenic climate change is progressing more rapidly in the Arctic and vegetation ecologies are shifting in response (Bjorkman et al., 2018; Epstein et al., 2013; Heijmans et al., 2022; Serreze et al., 2000; M. D. Walker et al., 2006). Both greening (vegetation index increase) trends and browning (vegetation index decrease) events have been observed across Arctic landscapes, but in complex spatial patterns that indicate it is the interaction of numerous small-

scale factors facilitating change (Epstein et al., 2013; Heijmans et al., 2022; Myers-Smith et al., 2020). A large body of research on these small-scale factors and their interactions is required to adequately model how the terrestrial Arctic will change in the future, a critical scientific question with great social, environmental, and political import. Soil nutrient content and winter snow cover are two physical factors that shape the functional ecology of tundra vegetation (Bjorkman et al., 2018; Grünberg et al., 2020; Heijmans et al., 2022), and so influence the indices we use to measure arctic greening. The study of ecosystem engineering by Arctic foxes not only allows an examination of how these physical factors affect vegetation, but how consumers can shape tundra ecosystems at small scales, which I believe contributes to the spatial complexity observed at a circumpolar level (Myers-Smith et al., 2020).

Ecosystem engineering

In the description of Arctic fox den community dynamics, it is necessary to discuss three broad ecological concepts: mutualism, facilitation, and ecosystem engineering.

Mutualisms, reciprocally beneficial species interactions, have been recognized as a factor of evolution since Darwin (1859), yet they remained relatively unstudied by natural science for over a century when compared to processes like competition and predation (Bruno et al., 2003; Gould, 1988). While this discrepancy is likely due to the paradigm experienced by Darwin's western European contemporaries (and their successors), there is evidence of an early school of evolutionary thought in Russia that saw mutualism as a more important driver of evolution than competition (Gould, 1988; Kropotkin, 1902). It is not surprising that ecologists primarily studying arctic and subarctic systems would come to this conclusion. Kropotkin (1902) posited that mutualisms become more important in harsher environments, and there are few environments more challenging than the Arctic. As interspecific interactions, mutualisms are

more context dependant (i.e. the cost-benefit ratio more greatly varies with changes in biotic or abiotic context) and are more likely to involve sessile species than antagonistic interactions (Chamberlain et al., 2014). This makes intuitive sense; cooperation requires benefit to outweigh cost for both participating species where antagonism only requires net benefit for one, and sessile species will always share an environment, allowing more opportunities for reciprocally beneficial interactions to repeat. If conditions change, an interaction that was previously positive for both parties may lose benefit for or become detrimental to one side, at which point it ceases to be a mutualism (Johnson et al., 1997). While Kropotkin's hypothesis of environmental selection for mutualistic relationships is nigh untestable at a global scale, the basic idea of banding together in adverse conditions is congruent with this mutualism-parasitism spectrum and, at least among plants, positive interactions between species do increase with stress (Bertness & Callaway, 1994; Callaway et al., 2002; He et al., 2013)

Mutual benefits can also become harder to define when considering the indirect effects of one species on another or the effects of one species on a community. The concept of facilitation has its roots in plant community ecology, where it was used to discuss the benefits provided by some plants to other plants, to plant communities, and to community structure (Brooker et al., 2008; Callaway, 1995). The definition of facilitation was not always clear, but now Bronstein's definition is commonly accepted:

> *Facilitation […] an interaction in which the presence of one species alters the environment in a way that enhances growth, survival or reproduction of a second, neighbouring species.* (Bronstein, 2009)

Facilitation is open-ended, only requiring benefit to the neighboring species, and it is through the mechanism of altering the environment that these benefits are conferred. Species can facilitate

entire communities of other species by altering the environment, consider trees, but the interaction itself is still only between two species. When discussing communities and ecosystems, the effects of one species on the complexity, feedbacks, and equilibria of biotic and abiotic processes can sometimes be better described with the functional approach of species-community or species-ecosystem interactions.

Ecosystem engineering is the most recent of these three concepts and extends the effects of environment alteration across organizational levels to a functional framework (Jones et al., 2010). Ecosystem engineers are organisms that change the availability of resources by altering the physical state of the ecosystem, creating/modifying/maintaining habitat for other species (Jones et al., 1996). Engineering effects differ from the purely consumptive effects organisms have on the physical environment. Consumptive effects are independent of the environment, all organisms cycle resources to live, where engineering effects are environment dependant and the resulting physical change alters the flow of resources (Jones et al., 1996, 1997). A beaver consuming the tissues of a tree for sustenance would not itself be considered engineering. Even if it results in the death of the tree and more light for other plants, those would be considered consumptive effects and another tree could also grow to take its place. A beaver felling trees on a streambank and using the logs to dam that stream over time, however, is engineering; the heightened water table changes which plants can succeed the disturbance and the bank becomes a beaver meadow, thus habitat is created. Feedback effects can develop with the physical state of an ecosystem changes (Jones et al., 1997). In this example, the engineer directly benefits from feedback effects (forage from wetland plants, shelter from predators, etc…), but that may not always be the case and is not a criterion for ecosystem engineering (Jones et al., 1996). Ecosystem engineering provides a wholistic lens that connects species interactions with higher

organizational levels. The relationships defined by this concept could instead be mapped out with a complex web of mutualistic and facilitative interactions between species, but such a method would be inefficient for the study of functional ecology and obscure the forest with the trees. The ecosystem engineering framework uses functional process to inform the description of key connections and relationships, guiding investigators to the most relevant mutualisms and facilitations and connecting species interactions with larger community and ecosystem effects. Despite the local nature of physical engineering, which simply alters ecosystem processes, engineers provide net positive effects on species richness, biodiversity, and ecosystem function across wider spatial, temporal, and organizational scales (Hastings et al., 2007; Jones et al., 1997). Consider the mosaic of wetlands maintained by a beaver population across a landscape. These net effects are of particular interest in the context of complex vegetation patterns and limited biodiversity in Arctic tundra ecosystems.

Predators have been well studied for their role in controlling prey species (Rosenzweig & MacArthur, 1963; Stephens & Krebs, 1986; Werner & Peacor, 2003) and the non-consumptive effects they can have on the environment through ecologies of fear (Bleicher, 2017; Brown et al., 1999). Still, predators have been shown to affect the movement of resources in ecosystems through many pathways (Johnson-Bice, Gable, et al., 2023; Schmitz et al., 2010) on an apparent spectrum from direct consumptive effects to indirect non-consumptive effects. Sea otters drive a large productivity shift in coastal ecosystems through the direct consumption of sea urchins (Wilmers et al., 2012). These consumptive mechanisms employed by both otters and urchins underpin this ecosystem shift as a trophic cascade alone and not a result of ecosystem engineering. Wolves can change ecosystems by mediating the ecosystem engineering of beavers, either indirectly, by hunting larger herbivores that would otherwise over-browse beaver forage

(Ripple & Beschta, 2012), or directly, by killing them (Gable et al., 2020), but the engineering at play remains that of beavers.

Predators can act as ecosystem engineers through the long term deposition of prey-derived nutrients in discrete areas (Johnson-Bice, Gable, et al., 2023). American Black bears move salmon carcasses from riparian to adjacent forest habitats, driving scavenger activity, insect biomass, N enrichment of vegetation, and primary productivity on the west coast of British Columbia (Reimchen, 2017; Reimchen & Fox, 2013), engineering uniquely productive forests. Despite the recency of ecosystem engineering as a lens (Jones et al., 1996, 2010), how predators indirectly affect ecosystems through the control of mid-trophic engineers and how they can act as ecosystem engineers themselves still appear underrepresented in the literature (Gharajehdaghipour & Roth, 2018; Johnson-Bice, Gable, et al., 2023). The ecology of ecosystem engineering by mesopredators, like Arctic foxes, can be used to study the overlap of these two questions. Previous work by the Churchill Fox Project has described how Arctic foxes increase primary production and create atypical plant assemblages via nutrient deposition in Wapusk National Park (Fafard et al., 2020; Gharajehdaghipour et al., 2016). The resultant increase in physical complexity positively affects snow accumulation, creating shelter for less cold-tolerant species (Gharajehdaghipour & Roth, 2018). Evidence suggests that these effects create a positive feedback loop as the ecosystem moves to a new equilibrium state, but the constituent processes of this mechanism have not been tested in the field.

Arctic fox dens

The Arctic fox is a generalist mesopredator highly adapted to extreme tundra environments in the northern hemisphere (Tannerfeldt et al., 2003). They have a circumpolar range, where they can be found in both arctic and alpine tundra (Bruun et al., 2005; Gharajehdaghipour et al., 2016;

Prestrud, 1992). Coastal populations traverse great distances over sea ice in the winter where they are known to scavenge seal carcasses left by polar bears (*Ursus maritimus*), linking marine and terrestrial food webs (Johnson-Bice et al., 2024; Roth, 2003). As mobile opportunists, Arctic foxes access a variety of food sources across their range but depend greatly on Arctic rodent populations (Angerbjorn et al., 1999; Angerbjörn et al., 2004; Dudenhoeffer et al., 2021; Elmhagen et al., 2000; Graae et al., 2004; Roth, 2002). Coastal fox populations are thought to be less reliant on lemmings and have greater food resource stability than inland populations from a higher diversity of prey options (Angerbjörn et al., 2004) but even coastal populations are still affected by lemming abundance (Dudenhoeffer et al., 2021; Schmidt et al., 2012; Wrigley & Hatch, 1976). Arctic foxes form monogamous pairs and breed in summer natal dens (Angerbjörn et al., 2004; Tannerfeldt & Angerbjörn, 1996). Natal den sites are united by certain landscape attributes that indicate a strong preference for den quality: elevated earth forms, dry soils, warm microclimates, and permafrost depth (Chesemore, 1969; Gharajehdaghipour et al., 2016; Johnson-Bice, Roth, et al., 2023; Nielsen et al., 1994; Prestrud, 1992; Smith et al., 1992; Tannerfeldt et al., 2003), suggesting site selection may have a strong effect on reproduction. With a limited number of 'good' den sites in tundra landscapes and a significant energy cost for den construction (relative to fox size and ecosystem productivity), dens are re-used and expanded year after year (Gharajehdaghipour et al., 2016; Tannerfeldt et al., 2003). Arctic fox behaviour at a den appears to drive two long term processes: deposition of inorganic nutrients from prey remains and excreta, and soil bioturbation from digging activity (Chesemore, 1969; Gharajehdaghipour et al., 2016; Smith et al., 1992; Smits et al., 1988; Tannerfeldt et al., 2003). Tunnels can be extensive and littered with prey remains (Tannerfeldt et al., 2003) and soils become more organic and acidic over time (Smith et al., 1992), so this bioturbation may better

disperse nutrients throughout the soil column (Smits et al., 1988) and benefit decomposers by aerating increasingly organic soils. Bioturbation could also be lowering the permafrost horizon under these dens over time because den soils exhibit increased temperatures when compared to reference sites (Chesemore, 1969; Smits et al., 1988; Tannerfeldt et al., 2003). The subsidy of prey-derived nutrients is thought to drive a cascade of effects in the local area that result in distinct vegetation (Chesemore, 1969; Fafard et al., 2020). This process appears to straddle den vacancy periods; these den sites can be very old (~330 years on average in Canada) (Macpherson, 1969; Tannerfeldt et al., 2003) and both occupied and vacant fox dens exhibit increased nutrients and vegetation biomass relative to reference sites (Gharajehdaghipour et al., 2016). Increased nutrients can change the species composition, structure, and function of plants, leading to greater habitat complexity and, ultimately, further nutrient deposition by consumers and microbiota (An et al., 2022; Chapin et al., 1986; Freschet et al., 2015; Gough et al., 2002; Roy et al., 2022; Schimel et al., 2004; Schmitz et al., 2010; Wielgolaski et al., 1997).

Vegetation biomass is much greater on Arctic fox dens than the surrounding tundra (Gharajehdaghipour et al., 2016) and such increased primary production has resulted in significant greening (Johnson-Bice, Roth, et al., 2023). Reflected light is used by ecologists to remotely monitor changes in terrestrial ecosystems at large scales and the normalized difference vegetation index (NDVI) is a common index used for assessing primary production (Beck & Goetz, 2011; Epstein et al., 2013; D. A. Walker et al., 2012). Greening of the tundra has a large impact on ecosystem dynamics (Pearson et al., 2013), often resulting in shrubification: the combined range expansion and shift from prostrate to erect growth forms in shrub species (Epstein et al., 2013; Mekonnen et al., 2021). Greening is also associated with a decrease of plant defence compounds in tundra heath vegetation (De Long et al., 2016), possibly leading to

increased herbivory while vegetation quality increases from improved soil nutrient cycling (Hicks et al., 2020; Mekonnen et al., 2021). The decrease in plant defences could elevate arctic and subarctic populations of insect herbivores, and more flowers could lead to an increase in pollinators. Insect herbivores and pollinators likely play a large role in tundra ecology but remain poorly studied (Høye & Sikes, 2013). Once erect deciduous shrubs are established (Fafard et al., 2020), the long-term nutrient addition from foxes could be driving a dramatic increase in seed rain (Gough et al., 2015) that would open niche space for seed predator species.

Greater vegetation biomass also expands the physical structure of the environment. The increase in physical complexity appears to catch blowing snow, resulting in increased snow cover thickness on Arctic fox dens (Gharajehdaghipour & Roth, 2018). Deeper snow insulates the ground from the colder air above and provides more water when it melts (Grünberg et al., 2020). Due to its effect on soil temperature, deeper snow allows for greater microbial activity during the winter, causing increased N mineralization and nitrification in the soil (Schimel et al., 2004). Deeper snow also provides more insulation for the subnivean space, increasing habitat quality for small mammals (Gharajehdaghipour & Roth, 2018) and facilitating the establishment and survival of less cold tolerant plants, benefiting diversity (Hooper et al., 2005). The combined effects of increased vegetation biomass, reduced plant defence compounds, and better insulation from snow cover attract small mammals to these fox dens; Gharajedaghipur and Roth (2018) found evidence that collared lemmings (*Dicrostonyx sp.*) use Arctic fox dens in Wapusk National Park as winter nest sites. Not only would lemming excreta further increase nutrient deposition (von Beckerath et al., 2022), but if the lemmings stayed to take advantage of higher quality forage in the spring they could be an important food source for the foxes upon arrival.

These cascading effects likely lead to the development of the atypical plant assemblages documented by Fafard *et al.* in 2020. Biotic resistance appears to be more important than abiotic factors as an inhibitor of invasion in subarctic plant communities (Milbau et al., 2013b) but greater nutrient availability could decrease biotic resistance while reducing abiotic limits. With more nutrients available to plants, competition between plant species would shift from below-ground nutrient acquisition from fungal partners to above-ground light exposure. Any selective pressure for plants with highly specialized mycorrhizal associations would cease, and previously bare ground may be more suitable for colonization. Before the invasion of more productive species, there should be a metabolic response of extant prostrate shrubs as improving nutrient conditions enable greater production, resulting in intraspecific differences in leaf economic traits (Chapin et al., 1986; Reich, 2014; Siefert et al., 2015). Such a metabolic response could be characterized by changes to specific leaf area (SLA), leaf area per dry mass, and a greening effect because of the relationship between SLA and photosynthesis (Reich et al., 1998). Reports that *Dryas* species thrive on fox den sites (Tannerfeldt et al., 2003) suggest that this genus may respond better than most dry heath prostrate shrubs; a point of interest given the wide range and dry heath dominance of *Dryas* in the Arctic (Billault-Penneteau et al., 2019). A productive response in *Dryas* plants would be obscured from community weighted metrics by the interspecific variation of community turnover (Bjorkman et al., 2018; Bruun et al., 2005; Johnson-Bice, Roth, et al., 2023; Reich et al., 1998). Increases in resource availability and niche breadth positively affect invasion success (Byers & Noonburg, 2003) and plants adapted to poor nutrient availability generally exhibit lesser responses to nutrient subsidy than plants adapted to more fertile soil conditions (Chapin et al., 1986), so the species composition of these plant

communities may reflect distinct succession stages as nutrient and microclimatic conditions continue to improve.

Wapusk National Park

Nutrients deposited by Arctic foxes appear to drive positive feedback of greening and further nutrient deposition of *Dryas* heath communities in Wapusk National Park (Fafard et al., 2020; Gharajehdaghipour et al., 2016), changing the ecosystem processing from decomposition-limited dynamics to production-limited dynamics (Zou et al., 2016). As this is long-term process, adequate study requires a long-term experiment. If, as the evidence suggests, Arctic foxes are driving these dynamics by nutrient deposition, then limiting nutrients added to *Dryas* heath communities would drive a similar shift in ecosystem dynamics, resulting in communities like those found on Arctic fox dens. To study the community effects of increased nutrient deposition and increased snow deposition, Dr. John Markham and Dr. Jim Roth set up a field experiment in *Dryas* heath vegetation on a wide ridge in Wapusk National Park.

The area around and including Wapusk National Park straddles the border of a low arctic ecoregion and a subarctic ecoregion (D. A. Walker et al., 2005), and I use these both these terms in the coming chapters. Different ecological traditions have grouped the Subarctic with either the Arctic or the Boreal (Wielgolaski et al., 1997) but the resulting argument seems arbitrary; subarctic or forest-tundra regions simply represent the ecotone between these two biomes (Timoney et al., 1993). The low arctic classification of this park by the Circumpolar Arctic Vegetation Map (D. A. Walker et al., 2005) and the Arctic Biodiversity Assessment (Meltofte et al., 2013) is based on vegetation surveys from the late 1990s and early 2000s (D. A. Walker et al., 2005). As the landscape vegetation has continued to change over the intervening twenty years, ‘subarctic’ is a more appropriate regional term based on current vegetation characteristics

(Markham, *personal communication*) but the functional ecology of Arctic fox dens and the dry heath tundra communities studied in this thesis are more characteristic of the Low Arctic. Chapter 2 focuses more on ecosystem ecology and Chapter 3, on plant physiology, so I am more emphatic in my use of 'subarctic' in the second chapter. I also use '*Dryas* heath' to refer to specific dry heath communities associated with *Dryas* plants (Brook & Kenkel, 2002).

Wapusk National Park has a long history of scientific monitoring and has been an important focus of the Churchill Fox Project. We can be confident that data gathered here are representative and comparable to much of the existing literature on Arctic fox ecosystem engineering (Fafard et al., 2020; Gharajehdaghipour et al., 2016; Gharajehdaghipour & Roth, 2018; Johnson-Bice, Roth, et al., 2023; Zhao et al., 2022) and further tundra research serves the national park's conservation interests. The last assessment of the biome shift caused by increasing global temperatures in Canada's national parks (Scott et al., 2002) found that tundra ecosystems would be eventually excluded from Wapusk National Park in even the most conservative climate scenario they used. The model used by Scott et al. to generate that scenario (HadCM2 ghg) has an equilibrium climate sensitivity (ECS) of 2.5 and with recent estimates for ECS as high as 4.8 ±1.2 (Hansen et al., 2023), arctic warming from the carbon we have already released could be enough to affect the exclusion of tundra from Wapusk.

Dryas heath in Wapusk is a vegetation class used to map ecologically distinct heath communities that occur on ancient beach ridges near the coast of Hudson Bay (Brook & Kenkel, 2002). These beach ridges feature xeric, sandy soils and their relative elevation adds distance from underground permafrost and are preferred denning habitat for Arctic foxes (Johnson-Bice, Roth, et al., 2023). In our study area, *Dryas* heath communities are characterized by *Dryas integrifolia* Vahl.. *Dryas* species are found in both alpine and arctic tundra heaths and are known

for their root symbioses (Billault-Penneteau et al., 2019). *Dryas drummondii* Richardson ex. Hook. forms nitrogen fixing root nodules with *Frankia* actinobacteria (Kohls et al., 1994) and *Dryas octopetala* L. can support ectomycorrhizal relationships with a wide array of fungal partners (Bjorbækmo et al., 2010). Despite the ability of *D. integrifolia* to hybridize with both *D. drummondii* and *D. octopetala* in the wild (Billault-Penneteau et al., 2019), it appears to be the least studied of the three *Dryas* species, and the accepted literature even affirmed that *D. integrifolia* was actinorhizal for decades without sufficient evidence (Markham, 2009). *D. integrifolia* does form ectomycorrhizal associations (Bledsoe et al., 1990), and these symbiotic relationships likely facilitate the relative dominance of *D. integrifolia* over ericaceous plants on these ancient beach ridges. *Dryas* heath communities in Wapusk National Park are dominated by plants that have associations with ericoid, arbutoid, and ectomycorrhizal fungi, chiefly *Arctostaphylos rubra, Dryas integrifolia, Rhododendron lapponicum, Shepherdia canadensis,* and *Vaccinium uliginosum* (Billault-Penneteau et al., 2019; Brook, 2001; Pandey et al., 2019; Read et al., 2004; Yang et al., 2018). These local communities appear to be nutrient limited, as the increased deposition of nutrients by Arctic foxes is associated with increased productivity and atypical plant assemblages (Fafard et al., 2020; Gharajehdaghipour et al., 2016) and fit the description of tundra heath ecosystems limited by N (Chapin et al., 1995; Hewitt et al., 2020; Wielgolaski et al., 1997).

In this thesis, I examine the communities and ecosystem functions of Arctic fox dens in Wapusk National Park and, through the *Dryas* heath vegetation experiment, demonstrate a causal relationship between inorganic nutrients and den communities. The objective of this work is to experimentally test our hypothesis that Arctic foxes are capable of ecosystem engineering by nutrient deposition and finally resolve any remaining debate over this gap in the literature.

Chapter 2 describes the ecosystem processes that create den communities and the response of producer and consumer communities to increased deposition of inorganic N and P and deepened snow, showing how a subsidy of limiting nutrients that Arctic foxes can provide generates the functional dynamics and community characteristics observed at den sites. Chapter 3 takes a closer look at the ecophysiological response of dominant prostrate shrubs to these same treatments, confirming the contribution of intraspecific plant responses to the productivity metric used to study fox dens in *Dryas* heath and describing the plastic leaf response of *D. integrifolia* along a fast-slow productivity spectrum. Finally, I detail the combined implications of these analyses and how they answer our research questions in the concluding chapter.

1.1 References

An, T., Wang, F., Ren, L., Ma, S., Li, S., Liu, L., & Wang, J. (2022). Ratio of nitrate to ammonium mainly drives soil bacterial dynamics involved in nitrate reduction processes. *Applied Soil Ecology*, *169*, 104164. https://doi.org/10.1016/j.apsoil.2021.104164

Andresen, L. C., Bodé, S., Björk, R. G., Michelsen, A., Aerts, R., Boeckx, P., Cornelissen, J. H. C., Klanderud, K., van Logtestijn, R. S. P., & Rütting, T. (2022). Patterns of free amino acids in tundra soils reflect mycorrhizal type, shrubification, and warming. *Mycorrhiza*, *32*(3), 305–313. https://doi.org/10.1007/s00572-022-01075-4

Angerbjörn, A., Hersteinsson, P., & Tannerfeldt, M. (2004). Arctic foxes: Consequences of resource predictability in the Arctic fox—Two life history strategies. In D. W. MacDonald & C. Sillero-Zubiri (Eds.), *The Biology and Conservation of Wild Canids* (pp. 163–172). Oxford University Press.

Angerbjorn, A., Tannerfeldt, M., & Erlinge, S. (1999). Predator–prey relationships: Arctic foxes and lemmings. *Journal of Animal Ecology*, *68*(1), 34–49. https://doi.org/10.1046/j.1365-2656.1999.00258.x

Beck, P. S. A., & Goetz, S. J. (2011). Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: Ecological variability and regional differences. *Environmental Research Letters*, *6*(4), 045501. https://doi.org/10.1088/1748-9326/6/4/045501

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Billault-Penneteau, B., Sandré, A., Folgmann, J., Parniske, M., & Pawlowski, K. (2019). Dryas as a Model for Studying the Root Symbioses of the Rosaceae. *Frontiers in Plant Science*, *10*. https://www.frontiersin.org/article/10.3389/fpls.2019.00661

Bjorbækmo, M. F. M., Carlsen, T., Brysting, A., Vrålstad, T., Høiland, K., Ugland, K. I., Geml, J., Schumacher, T., & Kauserud, H. (2010). High diversity of root associated fungi in both alpine and arctic Dryas octopetala. *BMC Plant Biology*, *10*(1), 244. https://doi.org/10.1186/1471-2229-10-244

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57–62. https://doi.org/10.1038/s41586-018-0563-7

Bledsoe, C., Klein, P., & Bliss, L. C. (1990). A survey of mycorrhizal plants on Truelove Lowland, Devon Island, N.W.T., Canada. *Canadian Journal of Botany*, *68*(9), 1848–1856. https://doi.org/10.1139/b90-242

Bleicher, S. S. (2017). The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ*, *5*, e3772. https://doi.org/10.7717/peerj.3772

Bliss, L. C., Courtin, G. M., Pattie, D. L., Riewe, R. R., Whitfield, D. W. A., & Widden, P. (1973). Arctic Tundra Ecosystems. *Annual Review of Ecology and Systematics*, *4*(1), 359–399. https://doi.org/10.1146/annurev.es.04.110173.002043

Bronstein, J. L. (2009). The evolution of facilitation and mutualism. *Journal of Ecology*, *97*(6), 1160–1170. https://doi.org/10.1111/j.1365-2745.2009.01566.x

Brook, R. K. (2001). *Structure and dynamics of the vegetation in Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba, community and landscape scales* [Thesis, University of Manitoba]. http://hdl.handle.net/1993/2724

Brook, R. K., & Kenkel, N. C. (2002). A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing*, *23*(21), 4761–4776. https://doi.org/10.1080/01431160110113917

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., … Michalet, R. (2008). Facilitation in Plant Communities: The Past, the Present, and the Future. *Journal of Ecology*, *96*(1), 18–34.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, *18*(3), 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

Bruun, H. H., Österdahl, S., Moen, J., & Angerbjörn, A. (2005). Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography*, *28*(1), 81–87. https://doi.org/10.1111/j.0906-7590.2005.04033.x

Byers, J. E., & Noonburg, E. G. (2003). Scale Dependent Effects of Biotic Resistance to Biological Invasion. *Ecology*, *84*(6), 1428–1433. https://doi.org/10.1890/02-3131

Cairney, J. W. G. (2011). Ectomycorrhizal fungi: The symbiotic route to the root for phosphorus in forest soils. *Plant and Soil*, *344*(1), 51–71. https://doi.org/10.1007/s11104-011-0731-0

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, *61*(4), 306–349. https://doi.org/10.1007/BF02912621

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*(6891), Article 6891. https://doi.org/10.1038/nature00812

Chalot, M., & Brun, A. (1998). Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiology Reviews*, *22*(1), 21–44. https://doi.org/10.1111/j.1574-6976.1998.tb00359.x

Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, *17*(7), 881–890. https://doi.org/10.1111/ele.12279

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., & Laundre, J. A. (1995). Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology*, *76*(3), 694–711. https://doi.org/10.2307/1939337

Chapin, F. S., Vitousek, P. M., & Van Cleve, K. (1986). The Nature of Nutrient Limitation in Plant Communities. *The American Naturalist*, *127*(1), 48–58.

Chesemore, D. L. (1969). Den ecology of the Arctic fox in northern Alaska. *Canadian Journal of Zoology*, *47*(1), 121–129. https://doi.org/10.1139/z69-021

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. Murray.

De Long, J. R., Sundqvist, M. K., Gundale, M. J., Giesler, R., & Wardle, D. A. (2016). Effects of elevation and nitrogen and phosphorus fertilization on plant defence compounds in subarctic tundra heath vegetation. *Functional Ecology*, *30*(2), 314–325. https://doi.org/10.1111/1365-2435.12493

Dudenhoeffer, M., Roth, J. D., Johnson, L. K., & Petersen, S. D. (2021). Arctic fox winter dietary response to damped lemming cycles estimated from fecal DNA. *Journal of Mammalogy*, *102*(6), 1455–1465. https://doi.org/10.1093/jmammal/gyab115

Dunbar, M. J. (1970). The scientific importance of the circumpolar region, and its flora and fauna. *Productivity and Conservation in Northern Circumpolar Lands*, 71.

Elmhagen, B., Tannerfeldt, M., Verucci, P., & Angerbjörn, A. (2000). The arctic fox (Alopex lagopus): An opportunistic specialist. *Journal of Zoology*, *251*(2), 139–149. https://doi.org/10.1111/j.1469-7998.2000.tb00599.x

Environment and Climate Change Canada. (2019). *Canada's changing climate report.* (E. Bush & D. S. Lemmen, Eds.). http://publications.gc.ca/collections/collection_2019/eccc/En4-368-2019-eng.pdf

Epstein, H. E., Myers-Smith, I., & Walker, D. A. (2013). Recent dynamics of arctic and sub-arctic vegetation. *Environmental Research Letters*, *8*(1), 015040. https://doi.org/10.1088/1748-9326/8/1/015040

Fafard, P. M., Roth, J. D., & Markham, J. H. (2020). Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. *Journal of Vegetation Science*, *31*(1), 173–179. https://doi.org/10.1111/jvs.12828

Freschet, G. T., Swart, E. M., & Cornelissen, J. H. C. (2015). Integrated plant phenotypic responses to contrasting above- and below-ground resources: Key roles of specific leaf

area and root mass fraction. *New Phytologist*, *206*(4), 1247–1260. https://doi.org/10.1111/nph.13352

Gable, T. D., Johnson-Bice, S. M., Homkes, A. T., Windels, S. K., & Bump, J. K. (2020). Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. *Science Advances*, *6*(46), eabc5439. https://doi.org/10.1126/sciadv.abc5439

Gharajehdaghipour, T., & Roth, J. D. (2018). Predators attract prey through ecosystem engineering in the Arctic. *Ecosphere*, *9*(1), e02077. https://doi.org/10.1002/ecs2.2077

Gharajehdaghipour, 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., Bass, H., & McLaren, J. R. (2015). Effects of Increased Soil Nutrients on Seed Rain: A Role for Seed Dispersal in the Greening of the Arctic? *Arctic, Antarctic, and Alpine Research*, *47*(1), 27–34. https://doi.org/10.1657/AAAR0014-055

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*(2), 211–218. https://doi.org/10.2307/1552473

Gould, S. J. (1988). Kropotkin was no crackpot. *Natural History*, *97*(7), 12–21.

Graae, B. J., Pagh, S., & Bruun, H. H. (2004). An Experimental Evaluation of the Arctic Fox (Alopex lagopus) as a Seed Disperser. *Arctic, Antarctic, and Alpine Research*, *36*(4), 468–473. https://doi.org/10.1657/1523-0430(2004)036[0468:AEEOTA]2.0.CO;2

Grünberg, I., Wilcox, E. J., Zwieback, S., Marsh, P., & Boike, J. (2020). Linking tundra vegetation, snow, soil temperature, and permafrost. *Biogeosciences*, *17*(16), 4261–4279. https://doi.org/10.5194/bg-17-4261-2020

Hansen, J. E., Sato, M., Simons, L., Nazarenko, L. S., Sangha, I., Kharecha, P., Zachos, J. C., von Schuckmann, K., Loeb, N. G., Osman, M. B., Jin, Q., Tselioudis, G., Jeong, E., Lacis, A., Ruedy, R., Russell, G., Cao, J., & Li, J. (2023). Global warming in the pipeline. *Oxford Open Climate Change*, *3*(1), kgad008. https://doi.org/10.1093/oxfclm/kgad008

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S., & Wilson, W. G. (2007). Ecosystem engineering in space and time. *Ecology Letters*, *10*(2), 153–164. https://doi.org/10.1111/j.1461-0248.2006.00997.x

He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *ECOLOGY LETTERS*, *16*(5), 695–706. https://doi.org/10.1111/ele.12080

Heijmans, M. M. P. D., Magnússon, R. Í., Lara, M. J., Frost, G. V., Myers-Smith, I. H., van Huissteden, J., Jorgenson, M. T., Fedorov, A. N., Epstein, H. E., Lawrence, D. M., & Limpens, J. (2022). Tundra vegetation change and impacts on permafrost. *Nature Reviews Earth & Environment*, *3*(1), Article 1. https://doi.org/10.1038/s43017-021-00233-0

Hewitt, R. E., Alexander, H. D., Miller, S. N., & Mack, M. C. (2022). Root-associated fungi not tree density influences stand nitrogen dynamics at the larch forest–tundra ecotone. *Journal of Ecology*, *110*(6), 1419–1431. https://doi.org/10.1111/1365-2745.13882

Hewitt, R. E., DeVan, M. R., Lagutina, I. V., Genet, H., McGuire, A. D., Taylor, D. L., & Mack, M. C. (2020). Mycobiont contribution to tundra plant acquisition of permafrost-derived nitrogen. *New Phytologist*, *226*(1), 126–141. https://doi.org/10.1111/nph.16235

Hicks, L. C., Leizeaga, A., Rousk, K., Michelsen, A., & Rousk, J. (2020). Simulated rhizosphere deposits induce microbial N-mining that may accelerate shrubification in the subarctic. *Ecology*, *101*(9), e03094. https://doi.org/10.1002/ecy.3094

Hobbie, J. E., & Hobbie, E. A. (2006). 15n in Symbiotic Fungi and Plants Estimates Nitrogen and Carbon Flux Rates in Arctic Tundra. *Ecology*, *87*(4), 816–822. https://doi.org/10.1890/0012-9658(2006)87[816:NISFAP]2.0.CO;2

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *ECOLOGICAL MONOGRAPHS*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Høye, T. T., & Sikes, D. S. (2013). Arctic entomology in the 21st century. *The Canadian Entomologist*, *145*(2), 125–130. https://doi.org/10.4039/tce.2013.14

Johnson, N. C., Graham, J. H., & Smith, F. A. (1997). Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *The New Phytologist*, *135*(4), 575–585. https://doi.org/10.1046/j.1469-8137.1997.00729.x

Johnson-Bice, S. M., Baldwin, F. B., Richardson, E., & Roth, J. D. (2024). *Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice*. https://ecoevorxiv.org/repository/view/7384/

Johnson-Bice, S. M., Gable, T. D., Roth, J. D., & Bump, J. K. (2023). Patchy indirect effects of predation: Predators contribute to landscape heterogeneity and ecosystem function via localized pathways. *Oikos*, *2023*(10), e10065. https://doi.org/10.1111/oik.10065

Johnson-Bice, S. M., Roth, J. D., & Markham, J. H. (2023). A Cosmic View of "Tundra Gardens": Satellite Imagery Provides a Landscape-Scale Perspective of Arctic Fox Ecosystem Engineering. *ECOSYSTEMS*, *26*(8), 1670–1684. https://doi.org/10.1007/s10021-023-00857-x

Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., & Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*(12), 1862–1869.

Jones, C. G., Lawton, J. H., & Shachak, M. (1996). Organisms as Ecosystem Engineers. In F. B. Samson & F. L. Knopf (Eds.), *Ecosystem Management: Selected Readings* (pp. 130–147). Springer. https://doi.org/10.1007/978-1-4612-4018-1_14

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Keuper, F., van Bodegom, P. M., Dorrepaal, E., Weedon, J. T., van Hal, J., van Logtestijn, R. S. P., & Aerts, R. (2012). A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, *18*(6), 1998–2007. https://doi.org/10.1111/j.1365-2486.2012.02663.x

Kohls, S. J., Thimmapuram, J., Buschena, C. A., Paschke, M. W., & Dawson, J. O. (1994). Nodulation patterns of actinorhizal plants in the family rosaceae. *Plant and Soil*, *162*(2), 229–239. https://doi.org/10.1007/BF01347710

Kropotkin, P. (1902). *Mutual Aid: A Factor of Evolution*. McClure Phillips & Co.

Kushner, P. J., Mudryk, L. R., Merryfield, W., Ambadan, J. T., Berg, A., Bichet, A., Brown, R., Derksen, C., Déry, S. J., Dirkson, A., Flato, G., Fletcher, C. G., Fyfe, J. C., Gillett, N., Haas, C., Howell, S., Laliberté, F., McCusker, K., Sigmond, M., … Zwiers, F. W. (2018). Canadian snow and sea ice: Assessment of snow, sea ice, and related climate processes in Canada's Earth system model and climate-prediction system. *The Cryosphere*, *12*(4), 1137–1156. https://doi.org/10.5194/tc-12-1137-2018

Macpherson, A. H. (1969). *The dynamics of Canadian arctic fox populations* (Vol. 8). Department of Indian Affairs and Northern Development Ottawa. http://www.parkscanadahistory.com/wildlife/report-8.pdf

Markham, J. H. (2009). Does Dryas integrifolia fix nitrogen? *Botany*, *87*(11), 1106–1109. https://doi.org/10.1139/B09-071

Marschner, P., & Rengel, Z. (Eds.) (with Stark, S.). (2007). *Nutrient Cycling in Terrestrial Ecosystems* (Vol. 10). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-68027-7

Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C., & Grant, R. F. (2021). Arctic tundra shrubification: A review of mechanisms and impacts on ecosystem carbon balance. *Environmental Research Letters*, *16*(5), 053001. https://doi.org/10.1088/1748-9326/abf28b

Meltofte, H., Barry, T., Berteaux, D., Bültmann, H., Christiansen, J. S., Cook, J. A., Dahlberg, A., Daniëls, F. J. A., Ehrich, D., Fjeldså, J., Friðriksson, F., Ganter, B., Gaston, A. J., Gillespie, L. J., Grenoble, L., Hoberg, E. P., Hodkinson, I. D., Huntington, H. P., Ims, R.

A., … Wrona, F. J. (2013). *Arctic Biodiversity Assessment: Status and trends in Arctic biodiversity*. Conservation of Arctic Flora and Fauna (CAFF). https://oaarchive.arctic-council.org/handle/11374/232

Michelsen, A., Quarmby, C., Sleep, D., & Jonasson, S. (1998). Vascular plant 15N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia*, *115*(3), 406–418. https://doi.org/10.1007/s004420050535

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013a). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013b). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A., Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., … Wipf, S. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, *10*(2), Article 2. https://doi.org/10.1038/s41558-019-0688-1

Nielsen, S. M., Pedersen, V., & Klitgaard, B. B. (1994). Arctic Fox (Alopex lagopus) Dens in the Disko Bay Area, West Greenland. *Arctic*, *47*(4), 327–333.

Pandey, D., Kehri, H. K., Zoomi, I., Akhtar, O., & Singh, A. K. (2019). Mycorrhizal Fungi: Biodiversity, Ecological Significance, and Industrial Applications. In A. N. Yadav, S. Mishra, S. Singh, & A. Gupta (Eds.), *Recent Advancement in White Biotechnology Through Fungi: Volume 1: Diversity and Enzymes Perspectives* (pp. 181–199). Springer International Publishing. https://doi.org/10.1007/978-3-030-10480-1_5

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*(7), Article 7. https://doi.org/10.1038/nclimate1858

Prestrud, P. (1992). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Svalbard. *Arctic*, *45*(2), 154–158.

Rasmussen, L. H., Zhang, W., Ambus, P., Michelsen, A., Jansson, P.-E., Kitzler, B., & Elberling, B. (2022). Nitrogen transport in a tundra landscape: The effects of early and late growing season lateral N inputs on arctic soil and plant N pools and N2O fluxes. *Biogeochemistry*, *157*(1), 69–84. https://doi.org/10.1007/s10533-021-00855-y

Read, D. J., Leake, J. R., & Perez-Moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany*, *82*(8), 1243–1263. https://doi.org/10.1139/b04-123

Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, *157*(3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P. B., Ellsworth, D. S., & Walters, M. B. (1998). Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: Evidence from within and across species and functional groups. *Functional Ecology*, *12*(6), 948–958. https://doi.org/10.1046/j.1365-2435.1998.00274.x

Reimchen, T. E. (2017). Diverse Ecological Pathways of Salmon Nutrients Through an Intact Marine-terrestrial Interface. *The Canadian Field-Naturalist*, *131*(4), Article 4. https://doi.org/10.22621/cfn.v131i4.1965

Reimchen, T. E., & Fox, C. H. (2013). Fine-scale spatiotemporal influences of salmon on growth and nitrogen signatures of Sitka spruce tree rings. *BMC Ecology*, *13*(1), 38. https://doi.org/10.1186/1472-6785-13-38

Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, *145*(1), 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Rosenzweig, M. L., & MacArthur, R. H. (1963). Graphical Representation and Stability Conditions of Predator-Prey Interactions. *The American Naturalist*, *97*(895), 209–223. https://doi.org/10.1086/282272

Roth, J. D. (2002). Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*, *133*(1), 70–77. https://doi.org/10.1007/s00442-002-1004-7

Roth, J. D. (2003). Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology*, *72*(4), 668–676. https://doi.org/10.1046/j.1365-2656.2003.00739.x

Roy, A., Gough, L., Boelman, N. T., Rowe, R. J., Griffin, K. L., & McLaren, J. R. (2022). Small but mighty: Impacts of rodent-herbivore structures on carbon and nutrient cycling in arctic tundra. *Functional Ecology*, *36*(9), 2331–2343. https://doi.org/10.1111/1365-2435.14127

Schimel, J. P., Bilbrough, C., & Welker, J. M. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, *36*(2), 217–227. https://doi.org/10.1016/j.soilbio.2003.09.008

Schmidt, N. M., Ims, R. A., Høye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhamme, M. C., & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proceedings: Biological Sciences*, *279*(1746), 4417–4422.

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. https://doi.org/10.1111/j.1461-0248.2010.01511.x

Scott, D., Malcolm, J. R., & Lemieux, C. (2002). Climate change and modelled biome representation in Canada's national park system: Implications for system planning and park mandates. *Global Ecology and Biogeography*, *11*(6), 475–484. https://doi.org/10.1046/j.1466-822X.2002.00308.x

Serreze, M. C., Walsh, J. E., Chapin, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., & Barry, R. G. (2000). Observational Evidence of Recent Change in the Northern High-Latitude Environment. *Climatic Change*, *46*(1), 159–207. https://doi.org/10.1023/A:1005504031923

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de L. Dantas, V., de Bello, F., Duarte,

L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

Smith, C. A. S., Smits, C. M. M., & Slough, B. G. (1992). Landform Selection and Soil Modifications Associated with Arctic Fox (Alopex lagopus) Den Sites in Yukon Territory, Canada. *Arctic and Alpine Research*, *24*(4), 324–328. https://doi.org/10.1080/00040851.1992.12002964

Smits, C. M. M., Smith, C. A. S., & Slough, B. G. (1988). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Northern Yukon Territory, Canada. *Arctic*, *41*(1), 12–16.

Standen, K. M., Sniderhan, A. E., Sonnentag, O., Voigt, C., & Baltzer, J. L. (2024). Response of Boreal Plant Communities and Forest Floor Carbon Fluxes to Experimental Nutrient Additions. *Ecosystems*. https://doi.org/10.1007/s10021-023-00899-1

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press.

Sullivan, P. F., Ellison, S. B. Z., McNown, R. W., Brownlee, A. H., & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, *96*(3), 716–727. https://doi.org/10.1890/14-0626.1

Tannerfeldt, M., & Angerbjörn, A. (1996). Life history strategies in a fluctuating environment: Establishment and reproductive success in the arctic fox. *Ecography*, *19*(3), 209–220. https://doi.org/10.1111/j.1600-0587.1996.tb01247.x

Tannerfeldt, M., Moehrenschlager, A., & Angerbjörn, A. (2003). Den ecology of swift, kit and arctic foxes: A review. *The Swift Fox: Ecology and Conservation of Swift Foxes in a Changing World*, 167–181.

Timoney, K., Laroi, G., & Dale, M. (1993). Sub-Arctic Forest-Tundra Vegetation Gradients—The Sigmoid Wave Hypothesis. *Journal of Vegetation Science*, *4*(3), 387–394. https://doi.org/10.2307/3235597

Van Cleve, K., & Alexander, V. (1981). Nitrogen Cycling in Tundra and Boreal Ecosystems. *Ecological Bulletins*, *33*, 375–404.

von Beckerath, X., Benadi, G., Gilg, O., Sittler, B., Yannic, G., Klein, A.-M., & Eitzinger, B. (2022). Long-term monitoring reveals topographical features and vegetation that explain winter habitat use of an Arctic rodent. *Arctic Science*, *8*(2), 349–361. https://doi.org/10.1139/as-2021-0010

Walker, D. A., Epstein, H. E., Raynolds, M. K., Kuss, P., Kopecky, M. A., Frost, G. V., Daniëls, F. J. A., Leibman, M. O., Moskalenko, N. G., Matyshak, G. V., Khitun, O. V., Khomutov, A. V., Forbes, B. C., Bhatt, U. S., Kade, A. N., Vonlanthen, C. M., & Tichý, L. (2012). Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. *Environmental Research Letters*, *7*(1), 015504. https://doi.org/10.1088/1748-9326/7/1/015504

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & Team, C. (2005). The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science*, *16*(3), 267–282.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnússon, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., … Wookey, P. A. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, *103*(5), 1342–1346. https://doi.org/10.1073/pnas.0503198103

Werner, E. E., & Peacor, S. D. (2003). A Review of Trait-Mediated Indirect Interactions in Ecological Communities. *Ecology*, *84*(5), 1083–1100. https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Wielgolaski, F. E., Sømme, L., Thórhallsdóttir, T. E., Grabherr, G., Malinovsky, K. A., Zlotin, R. I., Miehe, G., Hedberg, O., Killick, D. J. B., & Campbell, J. S. (1997). *Polar and alpine tundra*. Elsevier Science Publishing Company, Inc. https://elibrary.ru/item.asp?id=26450837

Wilmers, C. C., Estes, J. A., Edwards, M., Laidre, K. L., & Konar, B. (2012). Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment*, *10*(8), 409–415. https://doi.org/10.1890/110176

Wrigley, R. E., & Hatch, D. R. M. (1976). Arctic Fox Migrations in Manitoba. *Arctic*, *29*(3), 147–158.

Yang, H., Zhao, X., Liu, C., Bai, L., Zhao, M., & Li, L. (2018). Diversity and characteristics of colonization of root-associated fungi of Vaccinium uliginosum. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-33634-1

Zhao, S.-T., Johnson-Bice, S. M., & Roth, J. D. (2022). Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. *Global Ecology and Conservation, 40*, e02310. https://doi.org/10.1016/j.gecco.2022.e02310

Zou, K., Thébault, E., Lacroix, G., & Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*, *30*(8), 1454–1465.

Chapter 2. Investigating the mechanistic effects of Arctic fox (*Vulpes lagopus*) driven nutrient cycling on tundra heath communities

Abstract

Arctic terrestrial ecosystems are characterized by extreme seasonality and low nutrient availability, which limit primary production and plant diversity. On the tundra, Arctic foxes (*Vulpes lagopus*) act as ecosystem engineers, increasing the concentration of plant available nutrients in the soils on and around denning sites, releasing previously limited primary production. In addition to the trophic effects of higher production, the physical complexity provided by vegetation acts as a wind break, altering microclimate and increasing snow accumulation. Deeper snow creates quality winter habitat for lemmings, which further cycle nutrients and serve as an important prey species for foxes. The atypical plant assemblages found on Arctic fox dens suggest that these effects create a positive feedback loop as the community moves to a new stable state, but this described mechanism remains untested. We established a controlled field experiment in 2017 to investigate the mechanisms of fox den activity on tundra heath in Wapusk National Park. Plots received added nutrients (N as urea and P as superphosphate) and/or snow fencing on the windward edge to increase snow depth. Plant species cover was recorded annually from permanent quadrats in each plot. Cover data were averaged per plot. Plot plant communities were compared across 5 treatment years and contrasted by established Arctic fox den plant communities using non-metric multidimensional scaling ordination and diversity metrics. In 2022, we examined second level trophic differences in insect communities and lemming activity across plot treatments. We found that inorganic N and P, deposited at a rate achievable by Arctic fox activity, are sufficient to release *Dryas* heath plant communities from nutrient limits and begin succession toward the atypical communities observed on Arctic fox dens. This succession does lead to taller vegetation that can increase winter snow cover and the combined effects of nutrient deposition and snow depth enable greater vegetation change. Our results support the creation of lemming habitat by such effects and demonstrate the ability of Arctic foxes to act as ecosystem engineers. Our findings highlight consumer activity as an important driver of small-scale ecosystem processes and a likely contributor to the complexity of vegetation change in Arctic tundra.

2.1 Introduction

Ecosystem engineers can be defined as organisms that change the availability of resources by altering the physical state of an ecosystem with non-consumptive effects, and in doing so, make space for new or expanded habitats (Jones et al., 1996). These structural alterations of the environment necessarily advantage and disadvantage different species, but have net effects that can increase species richness, biodiversity, and ecosystem functioning at larger spatial and temporal scales (Hastings et al., 2007; Jones et al., 1997, 2010). Despite the common occurrence of this ecological role, literature recognizing predators as engineers remains sparse as the consumption of other organisms as food does not constitute engineering. Trophic and competitive behaviours of predators can affect physical engineering of habitats (Monk & Schmitz, 2022) but remain independent of it (Jones et al., 1997).

In tundra ecosystems, Arctic foxes (*Vulpes lagopus*) are predators and ecosystem engineers (Gharajehdaghipour et al., 2016; Zhao et al., 2022). Arctic foxes are generalist predators adapted to life in the far north. Their diets and feeding strategies change across seasons and ranges (Graae et al., 2004; Roth, 2002; Tannerfeldt et al., 2003) but their summer denning behaviour remains consistent. Arctic foxes build summer natal dens in coarse, dry soils often elevated well above the permafrost layer on ridges or mounds, preferring well drained sites in alpine or arctic tundra heath (Bruun et al., 2005; Johnson-Bice, Roth, et al., 2023; Smits et al., 1988; Tannerfeldt et al., 2003). Microclimate also appears to play a role in site selection, with solar aspect and wind protection likely determining factors (Chesemore, 1969; Smits et al., 1988). Good den sites are limited in the lowlands of the Arctic and den construction is both energetically costly and dependant on the spatial distribution of fox territories, so established dens are re-used and expanded year after year (Tannerfeldt et al., 2003). Foxes concentrate nutrients (from both prey

remains and fox excreta) in the soils at their dens during summer occupation and the repeated use of established dens leads to a long-term increase in nitrogen and phosphorus deposition, altering the local environment (Gharajehdaghipour et al., 2016).

Arctic tundra ecosystems are often limited by soil nutrients; low temperatures inhibit mineralization of essential nutrients required for primary production such that plants quickly exhaust soil resource pools in the growing season (Bliss et al., 1973; Keuper et al., 2012; Marschner & Rengel, 2007). Wet tundra ecosystems can benefit from lateral nutrient inputs from the flow of water (Rasmussen et al., 2022), but the dry den sites preferred by Arctic foxes cannot, and those dry conditions further inhibit growth and slow soil development (Marschner & Rengel, 2007; Wielgolaski et al., 1997). This combination of drought and cold excludes most plants and leads to barrens and heaths occupied by cryptogams, cushion-forming plants, herbs, and prostrate shrubs at these elevated sites (Bliss et al., 1973; Wielgolaski et al., 1997). When Arctic foxes build and occupy dens in these communities, they alleviate some of that environmental stress, prompting increased production, increased soil development, establishment of previously excluded plant forms, and deeper winter snow cover (and spring snowmelt) in an otherwise stalled succession regime (Bruun et al., 2005; Fafard et al., 2020; Gharajehdaghipour et al., 2016; Gharajehdaghipour & Roth, 2018; Johnson-Bice, Roth, et al., 2023; Zhao et al., 2022). According to nutrient limitation theory, decomposition and production processes would speed up with the addition of fox derived nutrient subsidy and soil mixing, and continue past previous nutrient limits for as long as temperatures allow (Chapin et al., 1986; De Long et al., 2016). Soil development would improve over time if a new nutrient limit was not met, past the ability of the extant flora to productively respond, allowing the growth of more productive and fertility adapted plants that would continue this productive feedback (Bliss et al., 1973; Chapin et

al., 1986; Milbau et al., 2013b). More complex growth forms would develop, further expanding ecosystem structure, facilitating the establishment of new species and better retention of cycled nutrients within the ecosystem (Andresen et al., 2022; Fisher et al., 2016; Hicks et al., 2020). The shift in growth forms and productive species would attract summer herbivores, increasing insect abundance and visitations by transient macrofauna (Richardson et al., 2002; Zhao et al., 2022). The expanded physical structure of vegetation would slow passing air, increasing wind-deposited seeds in summer and snow accumulation in winter (Gough et al., 2015; Liu et al., 2022; Paradis et al., 2016). Thicker snow better insulates the ground from freezing winter temperatures, thus protecting plants, increasing soil processes, and creating ideal subnivean habitat for lemmings (*Dicrostonyx sp.*) to colonize (Gharajehdaghipour & Roth, 2018; Schimel et al., 2004; Sturm et al., 2005). Winter lemming activity may contribute to soil nutrient availability when their latrine chambers melt in the spring, further increasing the rate of nutrient deposition (Roy et al., 2022). Such community shift may benefit the Arctic foxes and their kits by stabilizing tunnels, improving insulation, providing visual cover from predators, and attracting prey (Gharajehdaghipour et al., 2016; Gharajehdaghipour & Roth, 2018; Zhao et al., 2022). Together these changes at fox den sites meet all four components of the ecosystem engineering framework (Jones et al., 2010), but this mechanism has yet to be experimentally supported in the field. Towards that end, we established a manipulative experiment in Wapusk National Park, Canada to test the effects of nutrient deposition and snow depth on tundra heath communities in 2017.

Wapusk National Park contains tundra ecosystems with well documented Arctic fox dens (Fafard et al., 2020; Gharajehdaghipour et al., 2016; Gharajehdaghipour & Roth, 2018; Johnson-Bice, Roth, et al., 2023; Zhao et al., 2022), and a protected conservation status. Park protections further support the representative nature of these ecosystems, and the threat posed by climate change

(Scott et al., 2002) provides greater incentive to expand our baseline understanding of Wapusk's ecology. The park itself crosses both Low Arctic and Boreal ecoregions, containing a complete Forest-Tundra or 'Subarctic' ecotone (Brook & Kenkel, 2002; D. A. Walker et al., 2005). Anthropogenic climate change is rapidly affecting arctic and subarctic vegetation (Bjorkman et al., 2018; Epstein et al., 2013; Heijmans et al., 2022; Myers-Smith et al., 2020; Serreze et al., 2000; D. A. Walker et al., 2012) and the part of Wapusk classified as Low Arctic where we established our experiment now contains taller erect shrubs at lake edges and sparse tree islands that characterize subarctic vegetation (D. A. Walker et al., 2005; Wielgolaski et al., 1997). The dry heath communities favoured by arctic foxes in the park are situated on elevated ancient beach ridges with sandy soils (Martini, 1989). These communities are limited to the coastal, more arctic areas and together classed as *Dryas* heath upland (Brook, 2001; Brook & Kenkel, 2002). This *Dryas* heath is characterized by *Dryas integrifolia* and exhibits a thin melanized topsoil above silicate-rich soil typical of *Dryas*-dominated dry heath across the North American Low Arctic (Wielgolaski et al., 1997). This heath class is also similar to other Low Arctic *Dryas* heaths in the degree to which it shares nutrient responses, shrub genera, and growth form patterns with High Arctic *Dryas* heaths (Eriksen et al., 2006; Fafard et al., 2020; Gough et al., 2002; Hudson & Henry, 2009) and we consider the ecology examined here to be comparable to such systems.

We aimed to investigate the community shift caused by Arctic fox ecosystem engineering by testing the effects of added limiting nutrients (inorganic N and P) and artificially deepened snow on *Dryas* heath communities in Wapusk National Park. We examined the richness, diversity, and composition of plant species and growth forms for effects on producers as well as resident

summer insect communities and winter lemming occupancy to estimate primary consumer responses. Here, we present the results of this experiment 5 years on.

2.2 Methods

Experimental Design and Site Description

In 2017, we set up a controlled experiment in Wapusk National Park tracking the effects of increased nutrient deposition and deeper snow on tundra communities to investigate how the unique communities found on fox dens are formed. The annual deposition of N and P on fox dens was calculated using an estimate of the number of prey items brought to dens (from prey remains) and the average mass of prey species. This deposition rate was used to formulate a nutrient addition treatment.

Plots were established on a wide ridge in *Dryas* tundra heath in two parallel lines, each with 8 plots. These lines were oriented north-south with a minimum of 100m between plots. Plots measure 10m x 10m and each plot contains 5 permanent 1m x 1m quadrats used to track species cover over time (**Figure 1**). Plots were fertilized annually with 100 kg ha^{-1} N using urea, and 28 kg ha^{-1} P using triple super phosphate, and/or snow fences established on the windward (northwest) side of the plot such that 4 plots received nutrients, 4 plots received fences, 4 plots received both treatments, and 4 plots received no treatments (controls). Treatments were arranged into two halves of a modified Latin square to control for spatial gradients (**Figure 2**). The percent cover of plant species in each quadrat was measured and averaged to estimate cover for each plot every year from 2017 - 2022. In 2022, additional metrics were used to compare the experimental communities after five years of treatment and contrast them with those of Arctic fox dens.

In 2022, eight local Arctic fox dens were selected for comparison. Dens were selected based on three criteria: 1. Dens must be situated in *Dryas* tundra heath. 2. Dens must have been occupied since 2017. 3. Dens cannot have been recently established (youngest den was 15 years old). Additionally, the dens had to be within a half day walk from the Nester 1 research station. At each den site, five quadrats were set up like in the experimental plots.

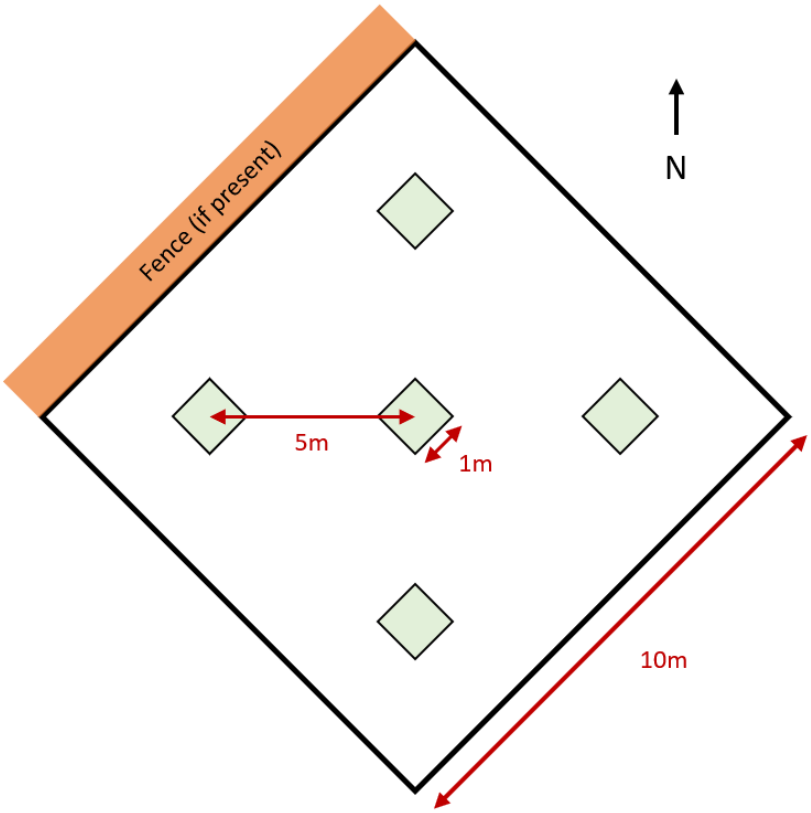

Figure 1. Configuration of tundra vegetation plots established in Wapusk National Park, MB. Permanent $1m^2$ quadrats (in green) were used to measure plant species cover in July from 2017 to 2022. On half the plots fencing was set up on the windward NW edge.

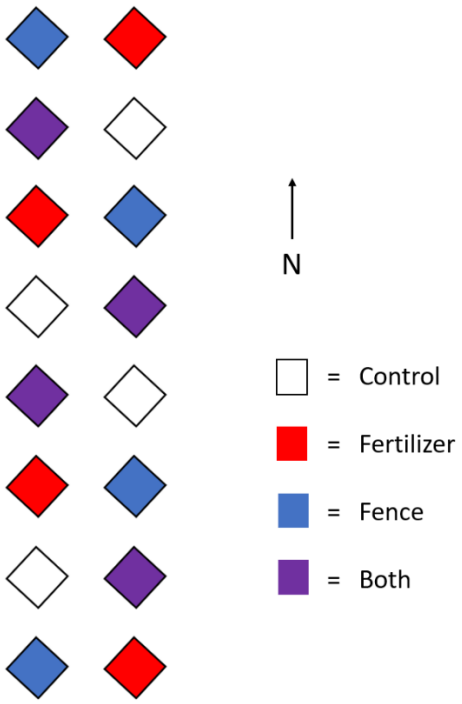

Figure 2. Spatial orientation of tundra vegetation plots along a north-south ridge in Wapusk National Park, MB. Plots measure 10m by 10m and were established a minimum of 100m between plots. Plots receiving the fertilizer treatment (red) received an annual application of 100 kg ha^{-1} N and 28 kg ha^{-1} P. Plots receiving the fence treatment (blue) had snow fences established on the NW edge of the plot. Plots receiving the fertilizer and fence treatment (purple) got both treatments as described.

Soil and Snow

Soil samples were collected at each site in July 2022 with a graduated hori-hori 3.5 m from the centre of each plot and fox den in each of four directions (NW, NE, SE, SW). Each sampling took the top 10 cm of soil in a 5 cm equilateral triangle. The 4 samples from each site were combined in one container.

At experimental plots with more than 3 lemming latrines, soil samples were taken from beneath 4 latrines and combined for a latrine soil sample that was used to determine what additional nutrient cycling lemmings may be providing over the winter. These latrine samples were processed separately from other samples at the same plot. This process resulted in 30 soil

samples overall: 16 standard and 6 latrine samples from experimental plots and 8 fox den samples. Samples were dried at 35˚C for a month (one week in Churchill and three at the university) and sieved to 2mm.

Soil inorganic N content was determined by microdiffusion (Khan et al., 2000) and duplicated such that each sample was run with and without Devarda's alloy to determine both N from ammonia and from nitrate.

Phosphorus can be found in many different forms in bioactive soils and each form occurs in varying quantities depending on soil type and texture (Bieleski, 1973). As such, functional soil P is difficult to estimate and single assay methods only measure fractions (Bray & Kurtz, 1945; Olsen, 1954). Here, phytoavailable inorganic soil P was measured using the Murphy-Riley molybdate assay (Kalra & Maynard, 1991), modified by using four different extractants to assess phosphates available by different uptake strategies used by plants. These strategies include root interception (mimicked by $CaCl_2$ solution), organic acid secretion (mimicked by citric acid), enzyme secretion (mimicked by phosphatase solution), and proton extrusion (mimicked by hydrochloric acid)(DeLuca et al., 2015).

Snow depths at each plot were measured in April of 2019, 2021, and 2022. Measurements were taken every 2.5 m from the centre of the NW edge of the plot (0m), across to the other side (10m), then averaged. Soil moisture was measured using a theta probe on all plots on July 25, 2022. In each plot, 9 measurements were taken in 3 lines of 3 readings and averaged for a whole plot estimate. Snow depth and soil moisture data were not collected at den sites.

Plant Cover

Abundances of plant species were recorded for each of the experimental plots annually from 2017 to 2022 and for the 8 fox dens in 2022. Percent cover of each plant species was measured in each of the permanent quadrats located in the experimental plots and their analogous locations at each fox den. Quadrat cover values for each species form were averaged per plot. Plants were classified into the following growth forms: prostrate shrubs, erect shrubs (> 25cm in height), sedges and rushes, grasses, forbs, mosses, and pteridophytes. This grouping was modified from Fafard et al. (2020) to reflect the new data collected. Beta diversity across time was calculated for each quadrat, then averaged per plot, using the species cover from 2017 and from 2022 to show change in species presence over the study period. **Equation 1** shows the beta diversity formula used (Koleff et al., 2003; Oksanen et al., 2007; Whittaker, 1960), where *a* is the number of species observed in both years, *b* is the number of species unique to 2017, and *c* is the number of species unique to 2022.

Equation 1. $$\beta_w = \frac{b + c}{2a + b + c}$$

Gini-Simpson Diversity Index (Jost, 2006; Simpson, 1949) was calculated for both species diversity and diversity of growth forms for the plant communities measured in 2022 to examine differences in diversity across treatments.

Lemming abundance

Lemming sign on the experimental plots was collected in June 2022 when it is most visible after snowmelt. In each plot we recorded the number of new lemming nests, old nests, and latrines as measure of winter site use, and fresh burrows as indicators of spring/summer site use. These data

had to be reduced to presence/absence for analysis (i.e. too many zeros) by binomial logistic regression.

Insect sampling

Insect community samples were taken on all the experimental plots and fox dens. Insects were collected by net sweeping and an aspirator was used to move insects to a kill jar containing plaster of Paris soaked with 96% ethyl acetate. Three $1m^2$ areas were swept per plot spread over the north, east, and south permanent quadrants. Samples were stored in a solution of 22% ethanol and 3% propylene glycol (RV antifreeze), as in Thomas (2008), initially in a freezer, then at 4°C. Once back at the university, these samples were transferred to 75% ethanol for longer term storage and identification. Insect orders were identified, and communities were further organized into sub-order operational taxonomic units (OTUs) for better community resolution. Non-insect arthropods collected in the sweeps were included to better estimate the community composition.

Statistical analyses

ANOVA and *post hoc* Tukey's HSD were used to determine the effect of the different treatments on individual metrics and compare differences between groups. When comparing Arctic fox dens to the experimental plots, den was included as an additional factor in the treatment effect. The number of total arthropods collected per site was log transformed to meet ANOVA assumptions and insect OTU richness data were modelled by Poisson GLM with generalized linear tests run using the multcomp package in R (Hothorn et al., 2008). Multivariate methods from the vegan package (Oksanen, 2022) included NMDS ordination of Bray-Curtis dissimilarities and PERMANOVA for the analysis of plant and insect communities in multivariate space. Mean relative abundances for each OTU (per site/year) were used to calculate a multidimensional

matrix of dissimilarities (function: vegdist) that was rank scaled to a 2D ordination (function: metaMDS). PERMANOVA (function: adonis2) and pairwise multiple comparisons (function: pairwise.adonis from Martinez Arbizu, 2020) used this matrix as input and multivariate dispersion was checked with the betadisper function.

2.3 Results

Abiotic Factors

Snow Depth and Soil Moisture

Plots with snow fencing exhibited snow 5.2 times deeper on average than plots without fencing in 2022 (see **Figure 3**). Snow depths did not vary significantly across recorded years (F = 0.029, df = 2, p = 0.97). See **Table 1** for 2022 one-way ANOVA results. Plot soil moisture measured in July averaged 21.3% (± 2.8%) and did not significantly respond to any of the treatments. No significant blocking effects were found between lines A and B (F = 1.461, df = 1, p = 0.25) or the treatment blocks (F = 2.342, df = 3, p = 0.12).

Table 1. One-way ANOVA results for the response of abiotic conditions to treatment in the experimental plots. Linear models are grouped by abiotic factor (summer soil moisture, spring snow depth, soil inorganic N content, and soil content of plant available P). Explanatory variables are categorical; Treatment (4 levels: control, fertilizer, fence, both).

Variable	Model	Df	F value	*Pr(>F)*
Soil Moisture (%)				
	Average Soil Moisture ~ Treatment	3	0.250	0.8601
Snow Depth (cm)				
	Average Snow Depth ~ Treatment	3	67.624	< 0.001**
Inorganic Nitrogen (µg N/g of soil)				
	Soil Ammonia ~ Treatment	3	0.844	0.4956
	Soil Nitrate ~ Treatment	3	0.162	0.9196
Phosphorus (µg P/g of soil)				
	$CaCl_2$ extracted P	*NA*	*NA*	*NA*
	Citric Acid extracted P ~ Treatment	3	8.052	0.0033*
	Phosphatase extracted P ~ Treatment	3	1.205	0.3499
	HCl extracted P ~ Treatment	3	7.828	0.0037*

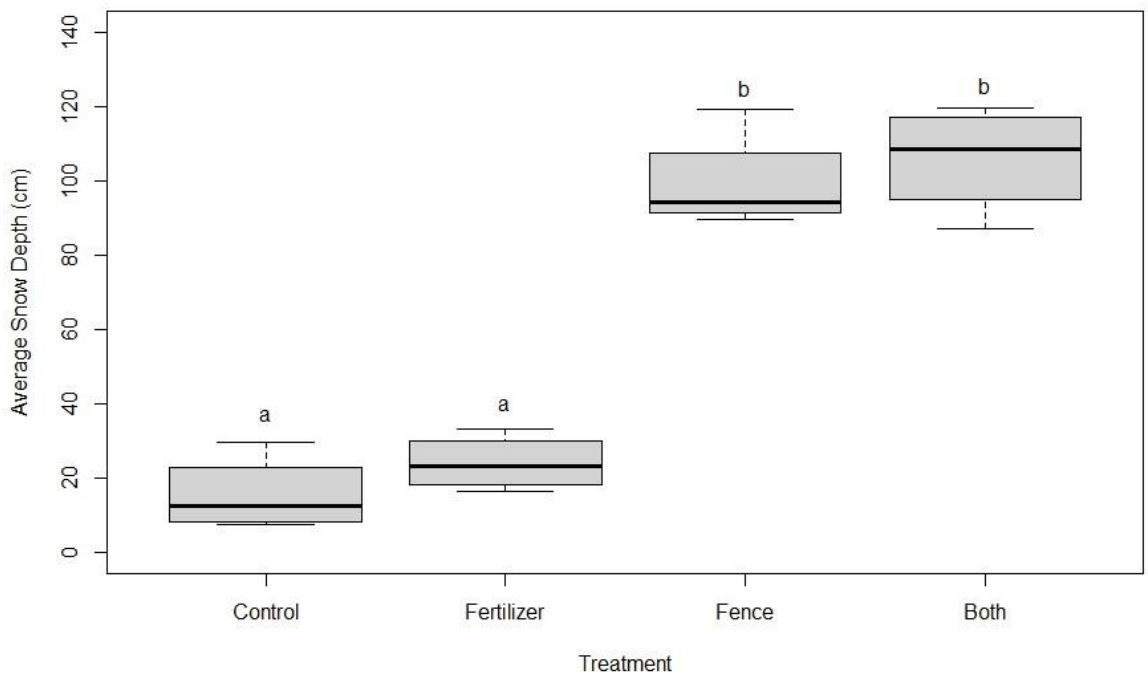

Figure 3. Mean snow depth of vegetation plots in April of 2022. Depths was measured every 2m across the center of each plot from the NW edge and averaged. Letters indicate significant differences found with a Tukey's test.

Soil Nitrogen

We found no difference in N content between treatment groups at the time of sampling (see Table 1). When comparing treatment groups with Arctic fox dens (**Figure 4**), we found no difference between soil N from nitrate ($F = 0.109$, df = 4, $p = 0.98$), which averaged 1.32 ±0.17 μg/g of soil, or from ammonia ($F = 0.843$, df = 4, $p = 0.52$), which averaged 2.9 ±0.35 μg/g.

Soil Phosphorous

Only two of the 4 estimated inorganic soil P pools showed significant effects of nutrient addition (Table 1, means in **Table 2**). P accessible by root interception i.e., extracted by $CaCl_2$ solution, was too rarely found for analysis (mean soil content = 9.27 ± 5.14 μg/g, only detectable at 7 of 24 sites) and P accessible by phosphatase enzyme hydrolysis i.e., extracted with an enzyme solution, did not statistically differ between groups (mean soil content = 11.63 ± 4.26 μg/g).

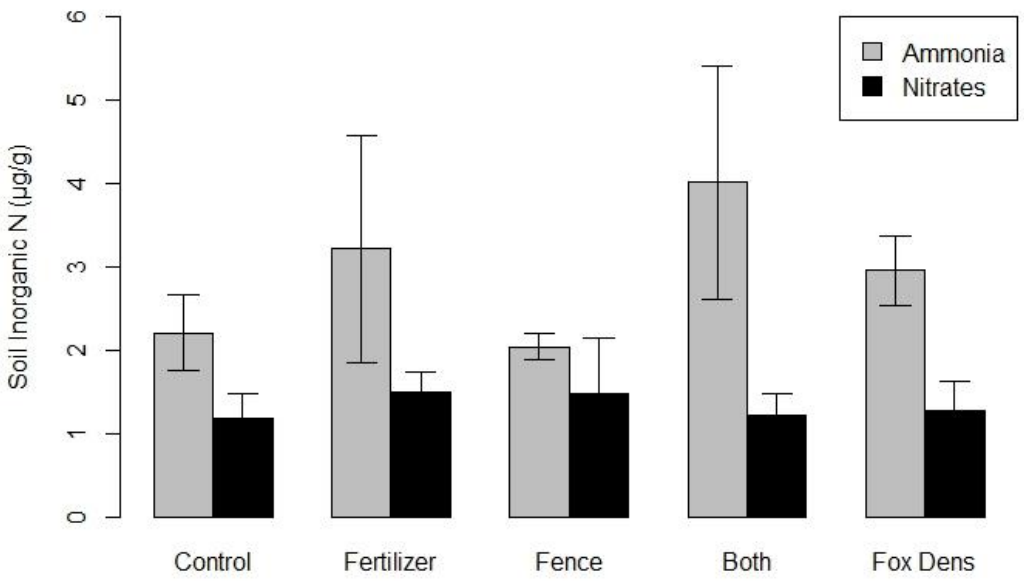

Figure 4. Inorganic N content of experimental plot and fox den soil samples collected in July 2022 from Wapusk National Park. Experimental plot treatment groups (Control, Fertilizer, Fence, Both) show means of 4 sites each and the fox den group shows means of 8 sites. Error bars represent standard error.

Differences were found in P accessible via organic acid release i.e., extracted by citric acid, and P accessible by proton extrusion i.e., extracted with HCl (see **Figure 5 a, b**). **Table 3** shows how treatment groups compare with Arctic fox dens in these two soil P pools. While we found significant differences between groups in both pools when fox dens were included (F = 2.996, df = 4, p = 0.0449 for citric acid extracted P, and F = 2.979, df = 4, p = 0.0457 for HCl extracted P), there was not sufficient power for *post hoc* tests. To preserve power, the experimental plot samples were analyzed comparing plots just by the addition of fertilizer treatment or not with 8 plots receiving nutrient fertilizer and 8 plots serving as controls. When these groups were compared with fox den soil samples significant differences were found for both citric acid extracted (F = 6.180, df = 2, p = 0.0078) and HCl extracted (F = 6.016, df = 2, p = 0.0086) P pools. The differences found with *post hoc* Tukey's tests can be seen in **Figure 5c** for citric acid extracted P and **5d** for HCl extracted P.

Table 2. Plant accessible soil P content of experimental plot and fox den soil samples collected in July 2022 from Wapusk National Park. Extractants were used to mimic four P uptake mechanisms employed by plants to estimate available P across sites. Means (with standard error) for each treatment group are shown for comparison to fox den soils.

Pool of plant accessible soil P	Extractants used	Control	Fertilizer	Fence	Both	Fox dens
P accessible by root interception	0.01 M $CaCl_2$	0	11.70 (± 11.70)	0.77 (± 0.77)	11.99 (± 7.40)	15.60 (± 14.19)
P accessible by organic acid excretion	10 mM Citric Acid	6.85 (± 3.09)	21.64 (± 3.87)	5.61 (±0.86)	16.19 (± 1.99)	24.65 (± 5.98)
P accessible by phosphatase hydrolysis	0.2 U Phosphatase	4.78 (± 0.93)	33.07 (±24.19)	3.45 (±1.39)	13.67 (± 5.60)	7.40 (± 1.64)
P accessible by proton excretion	1.0M HCl	24.65 (± 3.48)	107.04 (± 24.77)	43.39 (± 6.86)	89.38 (± 9.25)	100.46 (± 22.88)

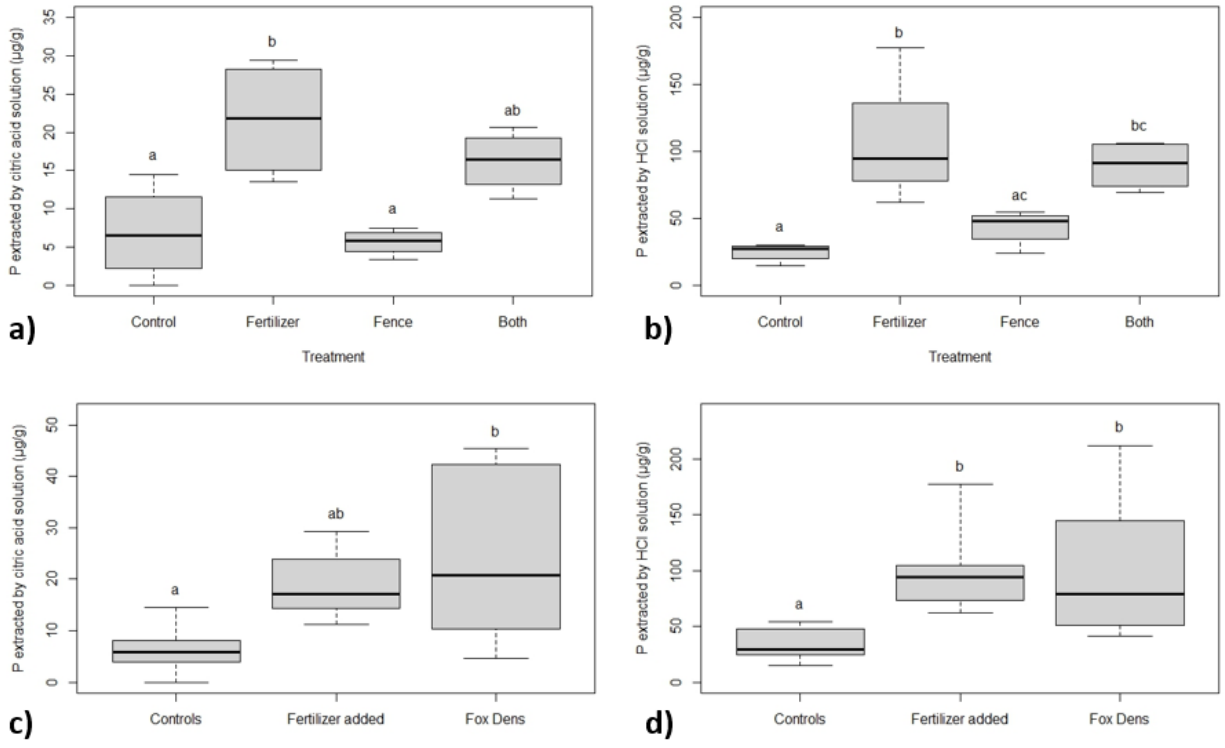

Figure 5. Soil P extracted by citric acid and hydrochloric acid solutions from experimental plot and fox den soil samples collected in July 2022 from Wapusk National Park. **a)** Experimental plot soil P extractable by citric acid, estimating P available by organic acid secretion by plants, across treatment groups. **b)** Experimental plot soil P extractable by hydrochloric acid, estimating P available by proton extrusion by plants, across treatment groups. **c)** Soil P extracted by citric acid comparing soils from plots that received fertilizer and fox den soils with controls. **d)** Soil P extracted by hydrochloric acid comparing soils from plots that received fertilizer and fox den soils with controls.

Plant Communities

Diversity and Growth Forms

Temporal beta diversity reveals a strong effect of treatment on how experimental plot communities have changed between 2017 and 2022 (F = 3.914, df = 3, p = 0.037). All plots, including controls, show a change in species composition over the study period, with a significantly greater change seen in plots receiving fertilizer and fencing (**Figure 6).**

Gini-Simpson diversity was calculated for both species diversity and diversity of growth forms for the plant communities measured in 2022. The diversity of growth forms was significantly higher in fox den communities when compared to controls and plots that received only nutrient

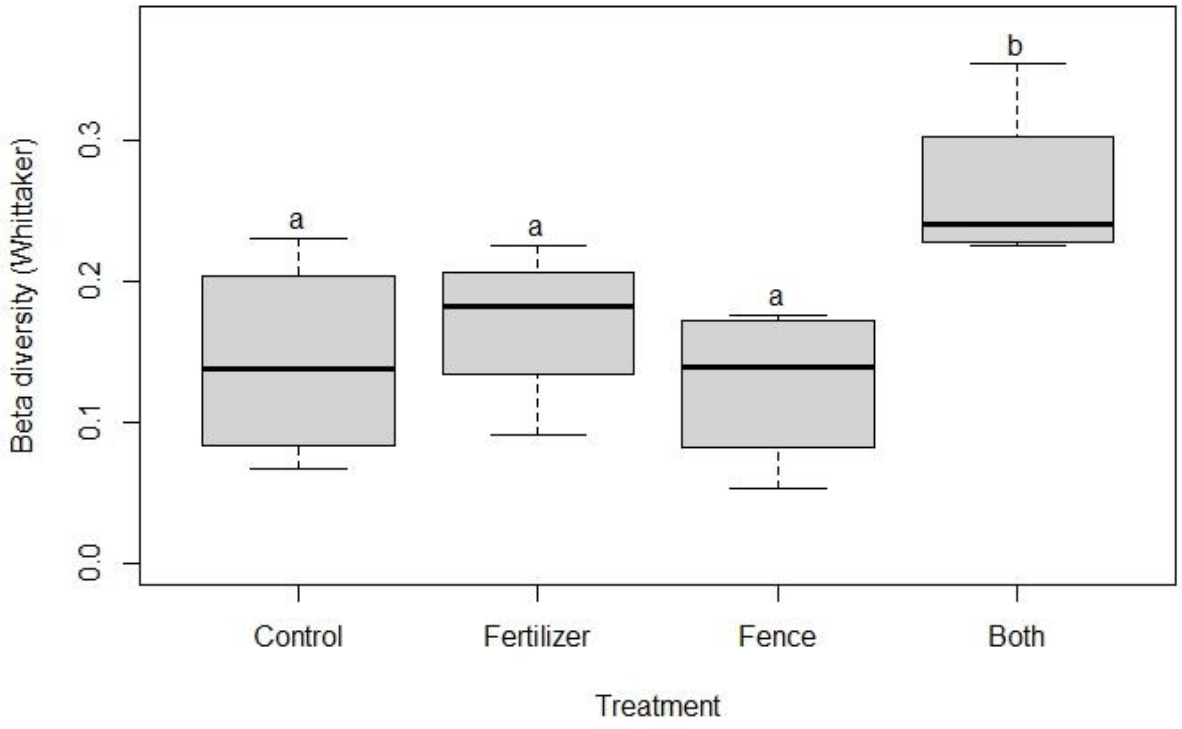

Figure 6. Temporal beta diversity of experimental vegetation plots between 2017 and 2022. Beta diversities between the plant communities in 2017 and 2022 were calculated for each internal quadrat and averaged per plot. Boxes show the distribution of plot means per treatment. Letters indicate significant differences.

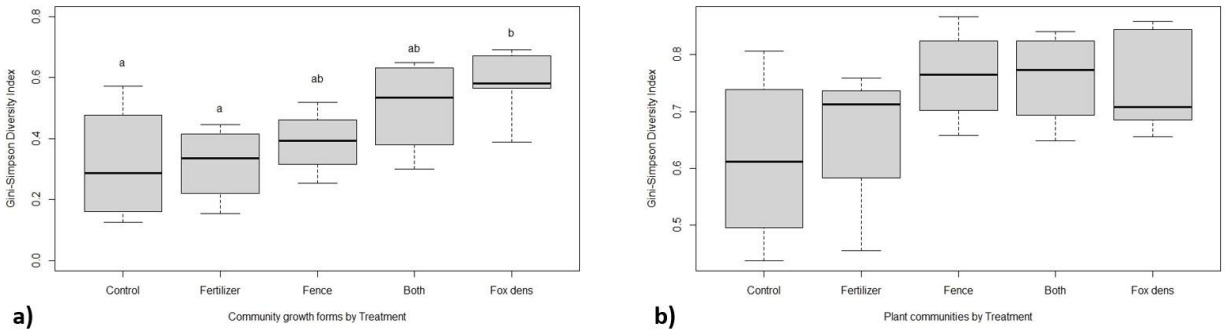

Figure 7. Biodiversity of vegetation plot communities in 2022. Higher Gini-Simpson index (1-D) indicates higher diversity. **a)** Diversity of growth forms (prostrate shrub, sedge and rush, moss, forb, grass, erect shrub, and pteridophyte) across experimental treatment group and fox den communities. Letters indicate significant differences. **b)** Diversity of plant species (44 species total) across experimental treatment group and fox den communities.

subsidies (**Figure 7a**, $F = 4.407$, df = 4, $p = 0.011$). Plots that received snow fencing were not significantly different from fox dens or plots that did not receive fencing. Species diversity was not statistically different across treatment groups (**Figure 7b**, $F = 1.601$, df = 4, $p = 0.215$). A breakdown of growth form cover by treatment groups can be seen in **Figure 8**. Fox dens exhibited the lowest mean prostrate shrub cover and the highest erect shrub cover, with erect shrubs found rarely in treated plots and not found in control plots. Fox dens were also found to have the highest mean cover of forbs and grasses. Sedges and rushes (cyperid graminoids) were

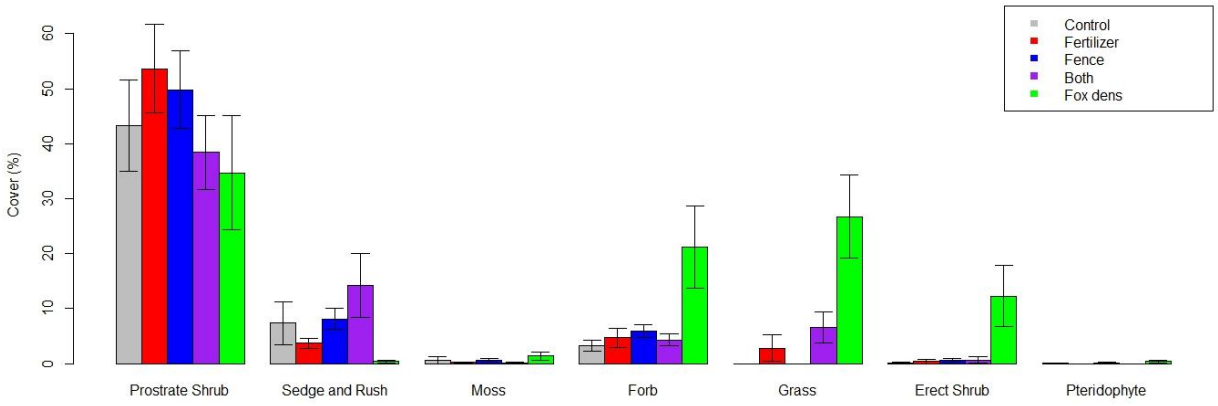

Figure 8. Mean precent cover of growth forms (prostrate shrub, sedge and rush, moss, forb, grass, erect shrub, and pteridophyte) found in experimental plot treatment groups and fox den communities in 2022. Error bars indicate standard error.

more commonly found in the experimental plots and only occasionally at fox dens. Despite lower power, differences were found within individual growth forms once the data were log transformed for normality. Treatment groups affected grass cover ($F = 15.813$, df = 4, $p < 0.001$), forb cover ($F = 6.096$, df = 4, $p = 0.002$), and sedge and rush cover ($F = 19.562$, df = 4, $p < 0.001$). **Figure 9** shows the differences found within these three growth forms. Grasses were only recorded in experimental plots receiving fertilizer and fox den grass cover was significantly greater than that of plots receiving only fertilizer, but not so with plots receiving both fertilizer and fence treatments. Forb cover on fox dens was significantly higher than that of all treatments except plots receiving only fences. Sedges and rushes were almost completely excluded on fox dens. No significant effect of treatment groups was found in prostrate shrubs ($F = 1.252$, df = 4, $p = 0.32$), erect shrubs ($F = 1.657$, df = 4, $p = 0.20$), and mosses ($F = 1.627$, df = 4, $p = 0.21$). Pteridophytes were not common enough for individual analysis (found at 5 of 24 sites) but were not found in any plots receiving fertilizer.

Multivariate Community Analysis

A comparison of the experimental plot communities from 2017 to 2022 using NMDS ordination of Bray-Curtis dissimilarities (stress = 0.12) shows of differentiation of the experimental plots over time (**Figure 10)**. These communities appear to be differentiating, with the plots that received both fertilizer and fencing being highest in similarity to fox den communities and the controls the lowest. All plots are moving away from pre-treatment conditions and in the direction of the Arctic fox den communities surveyed in 2022. These communities are significantly different, with a PERMANOVA finding a significant effect of community groups (2017 pre-treatment communities, control plot communities in all treatment years, fertilizer plot communities in all treatment years, fence plot communities in all treatment years, fence and fertilizer plot communities in all treatment years, and fox den communities), on community composition ($F = 9.225$, df = 5, $p < 0.001$). It is important to note that the fox den communities

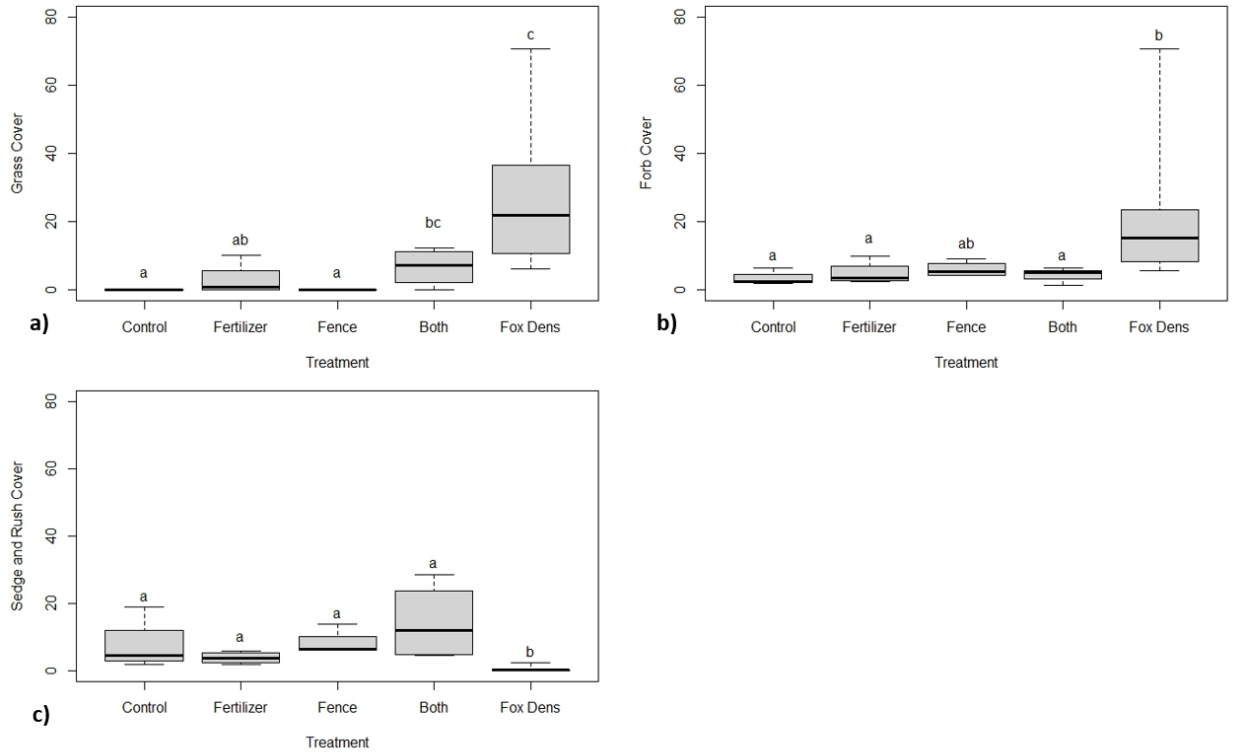

Figure 9. Relative abundance (cover) of growth forms with significant differences across experimental plot treatment groups and fox den communities. Letters indicate Tukey's honest significance. **a)** Mean percent cover of grasses (graminid graminoids). **b)** Mean percent cover of forbs. **c)** Mean percent cover of sedges and rushes (cyperid graminoids).

are more widely dispersed in multivariate space than the experimental plots (F = 12.403, df = 5, $p < 0.001$, den betadispersion = 0.45, all other groups ~ 0.2) and may affect the PERMANOVA result. Given that another PERMANOVA excluding the fox dens also found a significant effect (F = 4.720, df = 4, $p < 0.001$), the fox den group has twice the sample size of the plot groups, and the adonis2 function is more robust to dispersion differences than previous versions and similar tests (Oksanen, 2022), we determined that a *post-hoc* test of pairwise multiple comparisons was appropriate. These results can be seen in **Table 3** and show that all the experimental plot communities have changed since 2017 (including controls), with communities receiving both fertilizer and fencing differing significantly from controls. Communities on plots that received fertilizer are also significantly different from those which received fencing (deeper snow).

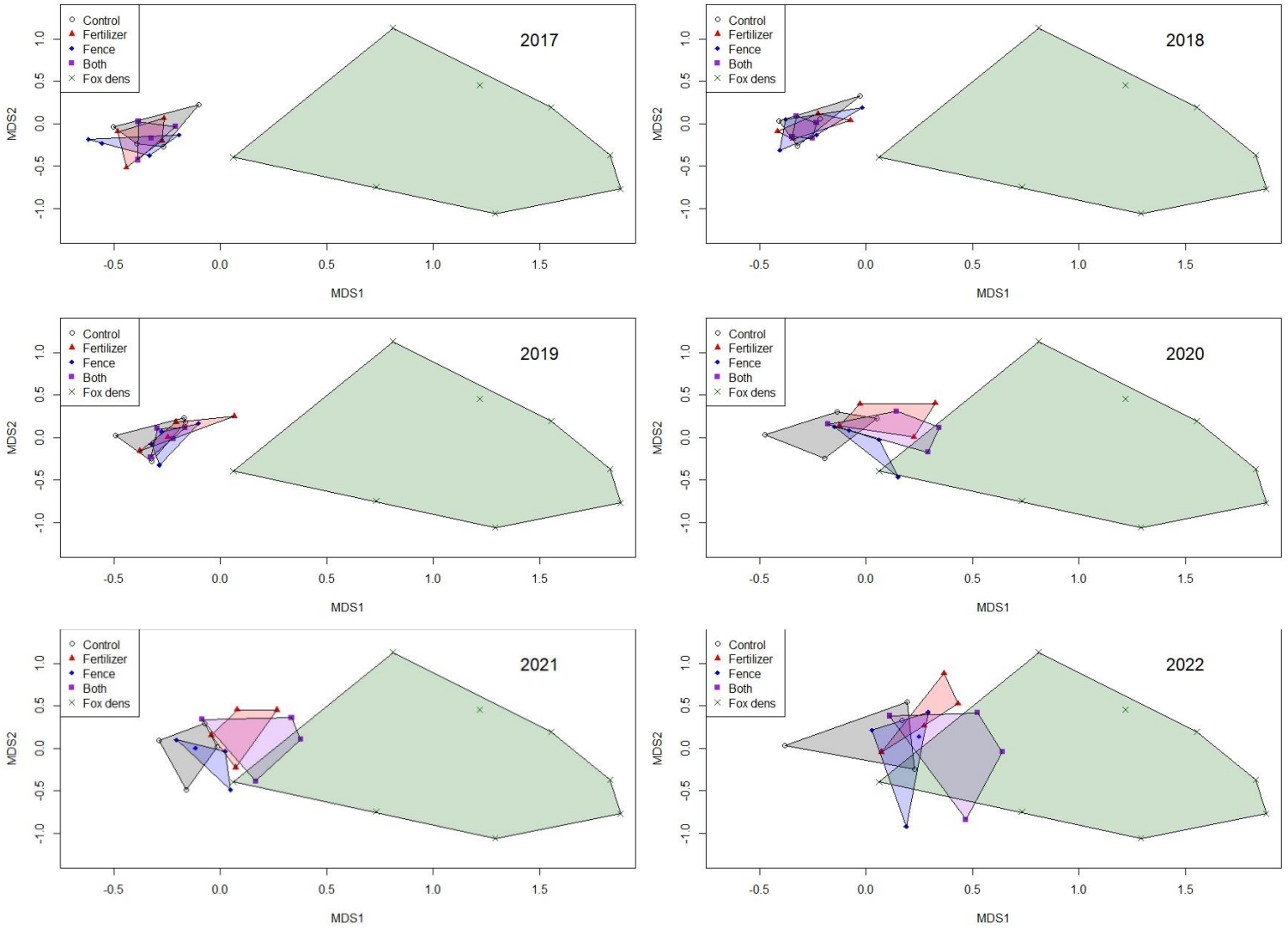

Figure 10. NMDS ordination of plant cover data from experimental plots and Arctic fox dens in Wapusk National Park, MB. Data from experimental plots were collected each summer from 2017 to 2022 and cover data from established fox dens were collected in 2022. These 2022 dens are shown in all years to represent fox dens communities. Points are plot communities repeated per year. Hulls are coloured for each treatment, grey for controls, red for fertilizer, blue for snow fencing, and purple for both fence and fertilizer treatments, and the fox den communities are hulled in green.

Table 3. *Post-hoc* pairwise multiple comparison of the composition of plant communities from experimental plots and Arctic fox dens in Wapusk National Park, MB. Treatment groups were compared using the pairwiseAdonis package. Comparisons were performed on a matrix of Bray-Curtis dissimilarities computed from our experimental plot community data from 2017 to 2022. The 2017 communities from before any treatments were applied are grouped under pre-treatment. P-values were adjusted by the Benjamini-Hochberg method. Differences with fox dens may be influenced by dispersion effects.

pairs	adjusted p-value
Pre-treatment vs Control	0.0006*
Pre-treatment vs Fertilizer	0.0006*
Pre-treatment vs Fence	0.0006*
Pre-treatment vs Both	0.0006*
Control vs Fertilizer	0.0679’
Control vs Fence	0.0693’
Control vs Both	0.0420*
Fertilizer vs Fence	0.0473*
Fertilizer vs Both	0.3116
Fence vs Both	0.0693’
Fox Dens vs Pre-treatment	0.0006***
Fox Dens vs Control	0.0006***
Fox Dens vs Fertilizer	0.0006***
Fox Dens vs Fence	0.0006***
Fox Dens vs Both	0.0006***

Table 4 shows the differences in the mean percent cover and mean frequency of occurrence of each plant species between 2022 and 2017, separated by treatment. There were few significant differences found within taxa, with only bare ground and *D. integrifolia* cover both responding to time. An ANOVA found no statistical difference in the change in bare ground cover over the study period by treatment ($F = 2.014$, df = 3, $p = 0.17$), but a paired t-test found the bare ground cover across all plots in 2022 is lower than that of 2017 ($t = 11.463$, df = 15, $p < 0.001$) by 34 percent cover. Another t-test found *D. integrifolia* cover is ~3.4 times higher in 2022 than 2017 on average ($t = 6.192$, df = 15, $p < 0.001$). No effect of treatment was found on *D. integrifolia* cover between 2017 and 2022 ($F = 0.927$, df = 3, $p = 0.46$).

Table 4. Mean differences in plant cover and frequency of occurrence in each experimental plot treatment group between 2017 and 2022 for all species recorded. Differences were calculated in each quadrat, averaged per plot, then averaged per treatment. Positive differences indicate an increase in cover/frequency over time. Bold values indicate difference from zero.

	Mean Cover Change (% ± error)				**Mean Frequency Change ((% ± error)**			
Species	Control	Fence	Fertilizer	Both	Control	Fence	Fertilizer	Both
Andronmeda polifolia	0.3 ± 0.3	**1.4 ± 0.9**	-0.2 ± 0.2	**0.6 ± 0.5**	10.0 ± 10.0	10.0 ± 5.8	5.0 ± 5.0	**15.0 ± 9.6**
Arctostaphylos rubra	0 ± 0.5	**1.5 ± 0.7**	**0.4 ± 0.2**	0.3 ± 0.6	**20.0 ± 8.2**	10.0 ± 5.8	5.0 ± 5.0	10.0 ± 10.0
Bartsia alpina	0.2 ± 0.2	0	-0.1 ± 0.1	0.1 ± 0.1	-5.0 ± 5.0	0	-5.0 ± 5.0	5.0 ± 5.0
Betula glandulosa	0	0	0	0	0	0	0	0
Carex sp.	0.8 ± 2.9	-0.1 ± 1.1	0.4 ± 0.9	**8.6 ± 4.1**	0	**10.0 ± 5.8**	5.0 ± 9.6	0 ± 8.2
Juncus albescens	0	0	0	0.3 ± 0.3	0	0	0	5.0 ± 5.0
Cerastium alpinum	0	0	0.1 ± 0.1	0.1 ± 0.1	0	0	5.0 ± 5.0	5.0 ± 5.0
Chamaenerion angustifolium	0	0	0.1 ± 0.1	0.1 ± 0.1	0	0	5.0 ± 5.0	**10.0 ± 5.8**
Dryas integrifolia	**19.5 ± 9.0**	**23.1 ± 9.5**	**31.6 ± 6.9**	**16.6 ± 4.7**	5.0 ± 5.0	-15.0 ± 15.0	0	0
Empetrum nigrum	-0.1 ± 0.1	-0.1 ± 0.1	**-0.7 ± 0.6**	0	-5.0 ± 5.0	-5.0 ± 5.0	**-20.0 ± 14.1**	0
Lesquerella arctica	**0.4 ± 0.2**	**0.2 ± 0.1**	**0.2 ± 0.1**	**0.2 ± 0.1**	**35.0 ± 23.6**	**20.0 ± 11.5**	**15.0 ± 9.6**	**20.0 ± 11.5**
Leymus mollis	-0.1 ± 0.1	-0.1 ± 0.1	**2.8 ± 2.4**	**6.6 ± 2.8**	-5.0 ± 5.0	-10.0 ± 10.0	10.0 ± 10.0	**35.0 ± 17.1**
Minuartia	0	0.2 ± 0.2	**0.4 ± 0.2**	**0.4 ± 0.3**	0	15.0 ± 15.0	**35.0 ± 17.1**	**20.0 ± 8.2**
Oxytropis sp.	-0.4 ± 0.4	-0.2 ± 0.2	**-0.5 ± 0.3**	-0.9 ± 0.9	5.0 ± 5.0	0	**15.0 ± 9.6**	0 ± 8.2
Pedicularis sp.	0	0 ± 0.1	0	0	0	0 ± 8.2	0	0
Pinguicula vulgaris	0.1 ± 0.1	0.1 ± 0.1	0	-0.1 ± 0.1	10.0 ± 10.0	5.0 ± 12.6	0	-5.0 ± 5.0
Polygonum vivparaum	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	**0.5 ± 0.2**	10.0 ± 10.0	5.0 ± 5.0	**10.0 ± 5.8**	**45.0 ± 17.1**
Pyrola grandiflora	0	0.1 ± 0.1	0	-0.1 ± 0.1	0	5.0 ± 5.0	0	-5.0 ± 5.0
Rhododendron lapponicum	-3.8 ± 4.1	1.0 ± 1.7	**-5.6 ± 4.5**	**-4.1 ± 3.0**	5.0 ± 5.0	0 ± 8.2	**-15.0 ± 5.0**	**-15.0 ± 9.6**
Salix lanata	0	0.4 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0	0	0	**10.0 ± 5.8**
Salix planifolia	0	0	0	0.1 ± 0.1	0	0	0	5.0 ± 5.0
Salix reticulata	0	0.1 ± 0.1	0.1 ± 0.1	**0.7 ± 0.3**	5.0 ± 5.0	10.0 ± 10.0	5.0 ± 5.0	**25.0 ± 12.6**
Saxifraga aizoides	-0.4 ± 0.4	-0.4 ± 0.4	**-0.3 ± 0.2**	**-0.4 ± 0.2**	0	0 ± 8.2	**-25.0 ± 18.9**	**-15.0 ± 5.0**
Saxifraga oppositifolia	**0.4 ± 0.2**	**0.5 ± 0.3**	**0.7 ± 0.5**	**0.9 ± 0.3**	**15.0 ± 9.6**	10.0 ± 10.0	5.0 ± 17.1	**10.0 ± 5.8**
Saxifraga tricuspidata	-0.1 ± 0.1	0	0.2 ± 0.2	0.1 ± 0.1	-5.0 ± 5.0	0	15.0 ± 15.0	5.0 ± 5.0
Scirpus caepetosis	0	1.8 ± 1.8	0	0	0	15.0 ± 15.0	0	0
Shepherdia canadensis	0	0.8 ± 0.8	-0.1 ± 0.1	0	0	5.0 ± 5.0	-5.0 ± 5.0	0
Stellaria longipes	0.3 ± 0.3	0.1 ± 0.1	1.1 ± 1.1	**0.3 ± 0.2**	0	5.0 ± 5.0	25.0 ± 25.0	**10.0 ± 5.8**
Tofeldia pusilla	0.2 ± 0.2	**0.9 ± 0.6**	-0.1 ± 0.1	**-0.6 ± 0.3**	0	5.0 ± 12.6	-5.0 ± 5.0	**-15.0 ± 9.6**
Vaccinium uliginosum	**1.5 ± 1.4**	**1.3 ± 0.8**	-0.9 ± 1.1	0.3 ± 0.9	**10.0 ± 5.8**	**20.0 ± 8.2**	-5.0 ± 12.6	**10.0 ± 5.8**
Moss sp	**2.7 ± 0.9**	**4.0 ± 1.7**	**7.2 ± 1.3**	**12.0 ± 4.1**	**50.0 ± 12.9**	**65.0 ± 5.0**	**60.0 ± 24.5**	**50.0 ± 12.9**
Pleurozium	**0.7 ± 0.6**	**0.6 ± 0.3**	**0.2 ± 0.1**	0.1 ± 0.1	15.0 ± 15.0	**35.0 ± 15.0**	**20.0 ± 14.1**	10.0 ± 10.0
Equisetum	0.1 ± 0.1	0.1 ± 0.1	0	0	5.0 ± 5.0	10.0 ± 10.0	0	0
Bare Ground	**-25.2 ± 6.2**	**-38.1 ± 5.0**	**-38.2 ± 7.6**	**-43.0 ± 1.8**	0	0	0	0

Consumer Communities

Lemming Evidence

Fresh summer burrows were only found at 3 sites, 2 plots that had received fertilizer (3 burrows and 5 burrows) and 1 plot that received fertilizer and fencing (3 burrows)(**Table 5**). New winter nests and latrines were only found in plots with fencing to deepen winter snow. Few old winter nests were found, and only in plots that also had new nests. Latrines were found on all plots that received both fence and fertilizer and on half of the plots with only fences, but were not found in any unfenced plots. Binomial logistic regressions found significant effects of treatment on new

winter nest abundance (X^2 = 15.7, df = 3, p = 0.001) and latrine abundance (X^2 = 15.7, df = 3, p = 0.001), but lacked power for *post-hoc* comparisons.

Soil samples taken from beneath lemming latrines did not exhibit any statistical differences from the standard soil samples at the same sites in ammonia content (logtransformed; F = 0.020, df = 1, p = 0.89,), total inorganic N (F = 1.539, df = 1, p = 0.24), or any of the three comparable P pools assayed (citric acid extracted: F = 0.055, df = 1, p = 0.82, phosphatase extracted: F = 0.180, df = 1, p = 0.68, hydrochloric acid extracted: F = 1.922, df = 1, p = 0.20).

Table 5. Lemming sign collected visually from each of the experimental plots in June 2022. Each row contains means for that treatment (and standard error). Zeros without error indicate no sign found across that treatment.

Treatment	Fresh burrows	New nests	Old nests	Latrines
Control	0	0	0	0
Fence	0	0.75 (±0.48)	0	8 (±5.43)
Fertilizer	2 (±1.22)	0	0	0
Fence + Fertilizer	0.75 (±0.75)	3 (±0.71)	0.75 (±0.48)	20.75 (±7.19)

Insect Communities

Net sweeps conducted at each of the vegetation plots and the 8 fox dens in 2022 found arthropods from 6 insect orders (Diptera, Hemiptera, Hymenoptera, Orthoptera, Trichoptera) and 1 arachnid order (Araneae). Arthropods were organized into 40 OTUs (39 insect, 1 arachnid). No arthropods were found at one of the control plots. See **Table 6** for summary of OTU richness per order.

Table 6. Total number of operational taxonomic units (OTUs) assigned to each arthropod order. Order OTU totals for vegetation plot treatment groups and fox dens are included for cross comparison.

Order	Control	Fertilizer	Fence	Both	Fox dens	Total OTUs
Diptera	3	5	5	13	18	23
Hemiptera	3	5	5	4	6	7
Hymenoptera	0	0	0	1	4	5
Lepidoptera	0	1	0	0	1	2
Orthoptera	0	0	0	0	1	1
Trichoptera	0	0	0	0	1	1
Araneae	0	0	0	0	1	1

We found significantly higher arthropod abundance in communities that received nutrient subsidies (including fox dens) than in controls (**Figure 11**, $F = 9.915$, df = 4, $p < 0.001$). A *post hoc* Tukey's revealed that plots with only fencing were statistically similar to controls and had a lower arthropod abundance than plots with fencing and fertilizer treatments and fox den communities. Comparing OTU richness revealed a similar pattern, only with no significant differences found between plots receiving both experimental treatments and plots receiving

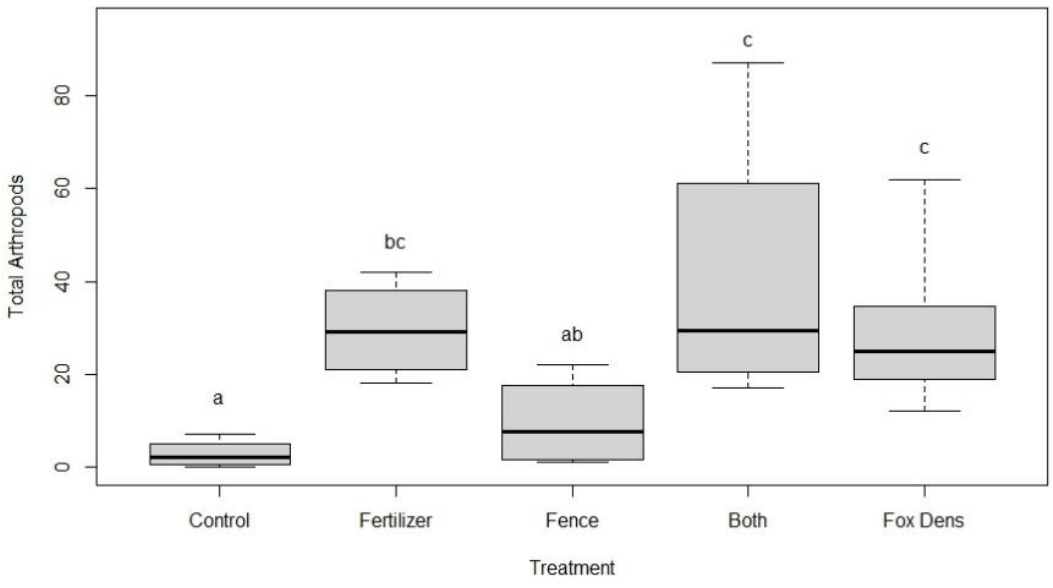

Figure 11. Total arthropods collected by net sweeps at experimental plots and fox dens in Wapusk National Park in July 2022. Plots are grouped by treatment (control, fertilizer, fence, both fertilizer and fence), with fox dens included for comparison. Letters indicate Tukey's honest significance.

either treatment independently (**Figure 12**, $X^2 = 29.7$, df = 4, $p < 0.001$). No statistical difference was found in the Gini-Simpson diversity indices of these communities when grouping by OTUs ($F = 1.354$, df = 4, $p = 0.29$) or taxonomic orders ($F = 1.753$, df = 4, $p = 0.18$). There is less variability among OTU diversities where fertilizer was added than in control or fence-only plots (**Figure 13a**). The same trend may be seen in order diversities (**Figure 13b**), but only controls exhibited broad variability. Only control and fence-only groups contained plots with zero diversity.

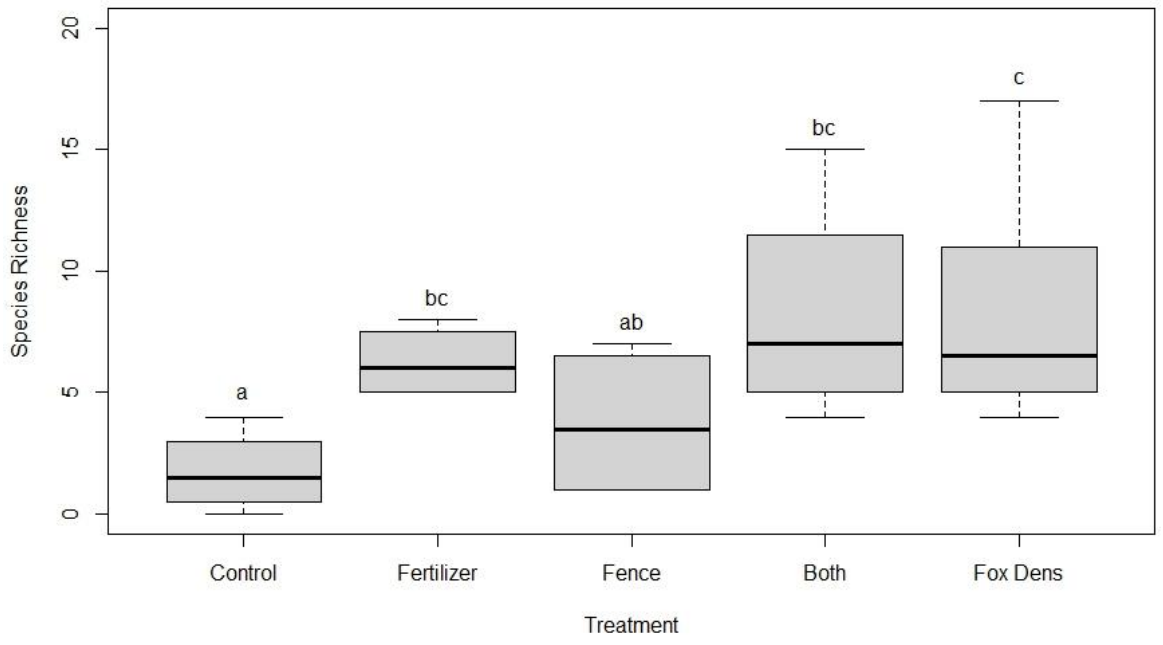

Figure 12. Richness of operational taxonomic units (OTUs) in net sweep collections at experimental plots and fox dens in Wapusk National Park in July 2022. Plots are grouped by treatment (control, fertilizer, fence, both fertilizer and fence), with fox dens included for comparison. Letters indicate Tukey's honest significance.

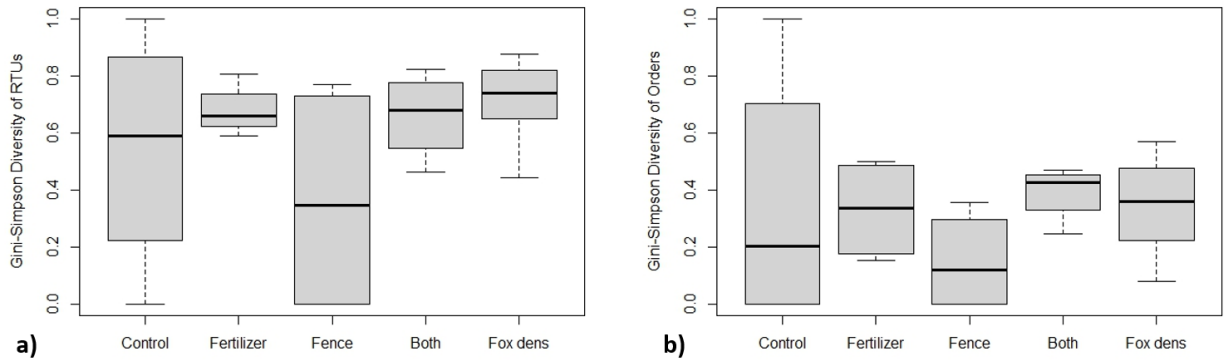

Figure 13. Diversity of insect communities sampled by net sweep in experimental plots and fox dens in July 2022 from Wapusk National Park. Plots are grouped by treatment (control, fertilizer, fence, both fertilizer and fence) and compared alongside fox den insect communities. **a)** Diversity of communities calculated from relative abundances of OTUs. **b)** Diversity of communities calculated from relative abundances of taxonomic orders.

An ordination of the experimental plot and fox den insect communities using Bray-Curtis dissimilarities of taxonomic orders shows that the fertilizer treatment, fertilizer and fence treatment, and fox den community groups overlap (stress = 0.113). MDS1 appears to align with nutrient subsidy effects in this ordination (**Figure 14a)**. A similar ordination of communities, this time using insect OTUs instead of orders, groups those same treatments closely, but also overlaps with control and fence communities (stress = 0.146, **Figure 14b**). These ordinations required the exclusion of one control plot, at which no insects were found. A PERMANOVA run on each dissimilarity matrix found a significant difference between the community composition of treatment groups in both community models (F = 3.903, df = 1, p = 0.006 for the taxonomic order community matrix; F = 1.862, df = 1, p = 0.041 for the OTU community matrix), but pairwise multiple comparisons were not powerful enough to detect this effect in either case after adjusting for false discovery rate (**Table 7** and **Table 8** respectively).

Table 7. *Post-hoc* pairwise multiple comparison of the composition of insect communities from experimental plots and Arctic fox dens in Wapusk National Park, MB. Treatment groups were compared using the pairwiseAdonis package. Comparisons were performed on a matrix of Bray-Curtis dissimilarities calculated from the relative abundances of 6 insect orders. P-values were adjusted by the Benjamini-Hochberg method for false discovery rate.

Insect Community Resolution:	**Orders**	
pairs	p-value	adjusted p-value
Control vs Fertilizer	0.0286*	0.0576’
Control vs Fence	0.1716	0.2060
Control vs Both	0.0288*	0.0576’
Control vs Dens	0.0120*	0.0576’
Fertilizer vs Fence	0.1103	0.1577
Fertilizer vs Both	0.3595	0.3595
Fertilizer vs Dens	0.0289*	0.0576’
Fence vs Both	0.1102	0.1577
Fence vs Dens	0.0256*	0.0576’
Both vs Dens	0.1854	0.2060

Table 8. *Post-hoc* pairwise multiple comparison of the composition of insect communities from experimental plots and Arctic fox dens in Wapusk National Park, MB. Treatment groups were compared using the pairwiseAdonis package. Comparisons were performed on a matrix of Bray-Curtis dissimilarities calculated from the relative abundances of 39 insect OTUs. P-values were adjusted by the Benjamini-Hochberg method for false discovery rate.

Insect Community Resolution:	**Operational Taxonomic Units**	
pairs	p-value	adjusted p-value
Control vs Fertilizer	0.2288	0.4472
Control vs Fence	0.8286	0.9207
Control vs Both	0.2002	0.4575
Control vs Dens	0.0320*	0.2100
Fertilizer vs Fence	0.2903	0.4839
Fertilizer vs Both	0.9742	0.9742
Fertilizer vs Dens	0.1342	0.4472
Fence vs Both	0.6605	0.8256
Fence vs Dens	0.0420*	0.2100
Both vs Dens	0.3403	0.4862

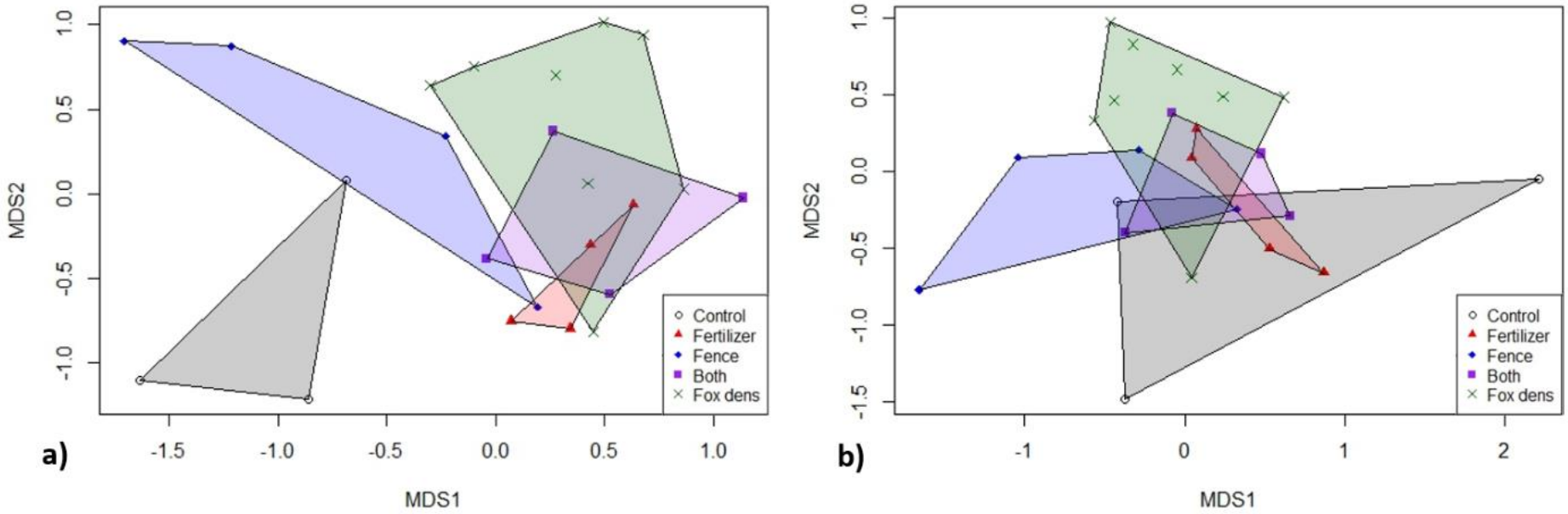

Figure 14. NMDS ordinations of the same insect communities sampled in experimental plots and fox dens using **a)** taxonomic orders and **b)** OTUs for the dissimilarity calculations. One control site was excluded because no insects were found. Hull colour indicates group.

2.4 Discussion

Overall, these results provide evidence that supports the hypothesis that Arctic foxes engineer den communities through nutrient deposition. The composition of plant communities is shifting, and our treatments are diverging from controls. Our nutrient treatment is attracting tall productive plants that can trap wind-blown snow in winter and our snow treatment is ameliorating environmental stress and creating habitat. Together these effects feed back to each other, more rapidly driving change. Insect communities are primarily responding to fertilized plots, lemmings are selecting for deep snow, and both consumer groups respond more greatly in the combined fertilizer/fence treatment plots.

Abiotic Factors

Our treatments appear to be functioning as intended. The snow fences are deepening snow at a magnitude similar to the deepening effect of den vegetation found by Gharajehdaghipour and Roth (2018) and the lack of difference in soil moisture between fenced and unfenced plots demonstrates soil drainage. We would also expect the extended build-up of organic soils from released production to increase retention of soil moisture in fertilized plots relative to controls, but it is either too early in the experiment for such an effect to develop or conditions at the time of sampling may have reduced detection. It is also unknown if fox dens in this region exhibit a detectable difference in soil moisture from surrounding tundra. While we did not find a difference in soil inorganic N content between plot treatments, we also did not find a difference between fox dens and controls and assessed N content was low when compared to previous measurements (Gharajehdaghipour et al., 2016). These ubiquitous low inorganic N levels are consistent with the depletion of limiting soil nutrients after tundra green-up (Chapin et al., 1986; Rasmussen et al., 2022) and similar to those found in tundra controls by Gharajehdaghipour et al.

(2016) in June and August, suggesting that our sample time in July was too close to green-up to measure long term differences. This result does show that the N we added as urea has left the surface soil pool, either by plant uptake or leaching to deeper soils. Plant uptake during green-up is more likely as fox den inorganic N pools were also depleted and those pools have shown elevated levels in August, when annual precipitation peaks (Environment and Climate Change Canada, 2024a).

The differences found in phytoavailable P are also consistent with recent plant uptake. No P accessible by root interception, the easiest and most direct method of uptake (Bucher, 2007), was detected in most samples and levels were low at the sites where it was present. Our addition of sodium triphosphate in the fertilized plots should initially dissolve into this soil pool, but can be readily accessed by organisms or chemically bound to other soil constituents (Bucher, 2007; Prabhu et al., 2019) and we cannot rule out leaching in these sandy soils. Soil P accessible by phosphatase enzyme release are organic forms of P that would not be affected by our treatments and the similar quantities found across our treatments and at fox dens suggests that the organic forms of P from prey remains are being adequately decomposed in den soils. The triphosphate added in the fertilizer treatment explains the different extractable soil P content between treatments when using citric and hydrochloric acid extractants; both methods detect weakly bound phosphates. The similar extractable soil P content of fertilized plots and fox dens relative to controls found using these two extractants and the null finding of the phosphatase extraction both experimentally support long term inorganic phosphate deposition by foxes as the mechanism behind the elevated extractable P levels found on fox dens by Gharajhedaghipour et al. (2016).

The combined results of our soil N and P assays in the context of previous measurements (Gharajehdaghipour et al., 2016) suggests that inorganic N availability is limiting for plant production in these *Dryas* heath communities and it is weakly bound phosphates that accumulate in fox den soils over time. Soluble inorganic P accessible by root interception is possibly also limiting and should be studied further in these soils. Our results also support the intensive uptake of limiting soil nutrients at the beginning of the growing season in upland tundra, suggesting that nutrient pool analyses should use soil samples taken between melt and green up. Physical soil characteristics (profile, fraction, texture) of the plots and dens should be evaluated along with inorganic N and phytoavailable P chemistry for a better understanding of the effect(s) of our treatments on these soils. Such a comparison would also begin to show some of the possible effects from bioturbation on Arctic fox dens, which we have not replicated in our plots.

Plant communities and fox den vegetation

The vegetation plots have increased in similarity to fox den plant communities over time in response to our treatments. Both limiting nutrients and snow depth affect *Dryas* heath plant community composition but do so at different magnitudes. Increased snow depth alone produces minimal interspecific changes in composition, but it can combine with the effects of limiting nutrient subsidy to accelerate succession; plot plant communities that received both fertilizer and snow fence treatments are more quickly increasing in similarity to fox dens than those of plots receiving either treatment.

The N and P added in the fertilizer treatment improved soil conditions enough for a more productive and fertility-adapted species, sea lyme grass (*Leymus mollis*), to begin invading *Dryas* heath communities within just 5 years. *L. mollis* first achieved 1% cover in one of the fertilized plots in 2019, and 10% in 2021. This invasion demonstrates succession from species adapted to

low nutrient conditions to species better able to exploit fertile soils and the first change in community composition predicted by our hypothesized mechanism. *L. mollis* is a tall, hardy grass capable of trapping airborne snow and increasing snow cover thickness (Gharajehdaghipour & Roth, 2018) so we expect snow depth effects to develop in the next few years in these fertilizer plots. The fertilizer treatment is likely responsible for many more changes in individual species cover, as suggested by cover shifts in Table 5, but these cover changes are not yet statistically supported. As these communities continue to grow, more individual species effects will likely become detectable.

The deep snow from our fence treatment appears to have had an intermediate effect on plant diversity. Thicker snow cover was predicted to protect plants from freezing air temperatures and fenced plots were the only plot communities with statistically similar forb cover to fox dens. Forb cover variation may partially explain the intermediate growth form diversity found on fenced plots (Figure 9), but the plant species diversity results suggest a broader thresholding effect of snow depth on diversity (Figure 7b), so it is likely that the insulation and melt water provided by deeper snow are advantaging less cold and drought tolerant species in such a way that they can better compete with the more tolerant species in the community.

When combined, the fence and fertilizer treatments enabled more rapid vegetation shifts. Plot communities that received both treatments significantly differed from controls in species composition after only 5 years and are increasing in similarity with fox den communities while diverging from controls in species space. While these communities had a response in growth from and species diversity similar to fenced communities that did not receive fertilizer, that response led to greater change in the same period, shown by the difference in temporal beta

diversity. The combined treatment also caused an invasion of *L. mollis* like in the fertilized, unfenced plots, but with a greater response statistically similar to the grass cover found at fox dens. Where this pattern of greater responses and increased similarity to fox dens in these plots repeats in most of our findings, sedge and rush cover is a notable outlier. These graminoids were found across the vegetation plots, with the greatest relative abundance in plots receiving the combined treatment, but almost excluded from fox den communities. This discrepancy suggests that sedges and rushes may be able to take advantage of our experimental conditions but are either outcompeted by other plants before the communities reach equilibrium on fox dens or are excluded from succession altogether. Together, our results demonstrate the ability of vegetation to respond to the amount of N and P arctic foxes are capable of depositing on their dens and support this response as the primary reason for the unique assemblages of vegetation described by Fafard et al. (2020). The succession regime from prostrate shrub heath to fox den vegetation begins with heath enrichment, followed by *L. mollis* invasion. We suggest that snow trapping vegetation like *L. mollis* and erect shrubs drive the accumulation of thick snow cover and facilitate promotion of less stress-tolerant species by altering microclimates.

The increases of *D. integrifolia* cover and the reductions of bare ground that were observed in all vegetation plots were likely due to the rapid climate change affecting this region. The annual period of sea ice conditions that drive the arctic terrestrial dynamics in Western Hudson Bay is decreasing (Florko et al., 2018; Gupta et al., 2022) allowing decomposition processes to begin earlier and end later in the year, mineralizing more soil nutrients per annum (Keuper et al., 2012), and no other climatic abnormalities were observed in the study period (Environment and Climate Change Canada, 2024b). While our treatments likely also affected bare ground cover in a similar way to varying magnitudes, this study lacks the statistical power

to discern causal differences at this scale. Critically, the significant change in the species composition of our control communities over the study period shows that climate effects are driving vegetation change in this *Dryas* heath and that change is slightly increasing the similarity of our controls to fox dens. Expansion of *D. integrifolia* cover and enrichment of *Dryas* heath from climate change in this region may benefit collared lemmings (*Dicrostonyx richardsoni*), which rely on these communities for winter forage and habitat (Bergman & Krebs, 1993; von Beckerath et al., 2022). Should this effect extend across the Low Arctic, it could support decreasing lemming populations (Ehrich et al., 2020) and so indirectly benefit Arctic foxes and affect their alternative prey species (Dudenhoeffer et al., 2021; Roth, 2002). Such a benefit would be limited to an upper climate change threshold, as these communities will be succeeded by boreal vegetation with enough warming (Scott et al., 2002). It is likely that the effects of climate change are increasing the responsiveness of tundra vegetation to our treatments more broadly, which may cause an underestimate of community response time. This latitude is the lowest at which arctic tundra occurs (D. A. Walker et al., 2005) and plants will benefit from extended photoperiods as the growing season gets longer.

Consumer activity

Lemming sign collected in 2022 at our vegetation plots shows a clear winter space-use response by lemmings to the thicker snow on fenced plots and a preference for fertilized plots. These results support the hypothesis that lemmings are attracted to the thicker snow and higher-quality vegetation on Arctic fox dens posited by Gharajehdaghipour and Roth (2018). Lemmings occupying fox dens in the winter could still further aid nutrient cycling despite our latrine soil results; soils could be exhausted from green up or soil microbiota could have limited leaching by directly colonizing latrine feces, which were removed before soil sampling. Monitoring of the

number of new burrows and winter nests should continue, for lemming carrying capacity may increase as vegetation becomes increasingly productive on these plots.

Insect communities not only responded to our treatments, but also support the interaction of nutrient and snow effects. Insect abundance and OTU richness were increased in plots treated with fertilizer to levels already comparable with fox dens after only 5 years, suggesting that these communities are primarily limited by the availability of food from net aboveground primary productivity (McNaughton et al., 1991; Richardson et al., 2002). There also appears to be a thresholding effect of fertilizer on the lower limit of insect OTU diversity consistent with this conclusion. The greater abundances found in fertilized plots with fences suggest an effect of thicker snow when production is not limiting, but this could be a direct effect (e.g. better winter insulation improving egg survival), indirect effect (e.g. carrying capacity improved by plant diversity), or combination thereof. Despite the lack of power for pairwise comparisons, the ordination of insect communities by order composition clearly shows the difference found by our PERMANOVA test. Fox dens, plots receiving both treatments, and fertilizer plots are the most similar groups and cluster on the higher end of MDS1 where the control group is most dissimilar to other treatments and occupies lower MDS1 values. The contrast with the OTU-based ordination, where there is no such clear division, highlights the low capture rate of our net sweep method of insect collection. While captures were high enough to reflect differences in 7 orders, we did not collect enough insects for the same differences to show up across 40 OTUs. Yellow pan-pitfall traps have been used more effectively to estimate tundra arthropod communities in this region (Ernst et al., 2016) and should better reflect habitat specificity and Dipteran diversity than our net sweeps (Disney et al., 1982; Høye & Sikes, 2013; Wyant et al., 2011). While our results are enough to demonstrate the trophic effects of nutrient-based ecosystem engineering on

insect communities, a more effective collection method would allow for closer analysis of the functional ecology at play.

Conclusion

This study experimentally supports the role of arctic foxes as ecosystem engineers by demonstrating that quantities of phytoavailable N and P arctic foxes are capable of depositing at den sites are sufficient to overcome limiting nutrient dynamics at a local scale and begin succession to more productive vegetative communities with tall species capable of trapping snow in winter. Our findings show that increased snow thickness and these limiting nutrients can interact to reenforce the creation of new habitat and that this habitat can support secondary trophic responses. We provide additional evidence that arctic fox ecosystem engineering can attract and benefit collared lemmings (Gharajehdaghipour et al., 2016) that select for habitat created by this mechanism. We accept that arctic foxes can drive the development of distinct communities in upland *Dryas* heaths by concentrating nutrient deposition and reject the hypothesis that arctic foxes lack this ability and simply select verdant den sites.

2.5 References

Aleksandrova, V. D. (1970). The Vegetation of the Tundra Zones in the USSR and Data about its Productivity. *Productivity and Conservation in Northern Circumpolar Lands*.

An, T., Wang, F., Ren, L., Ma, S., Li, S., Liu, L., & Wang, J. (2022). Ratio of nitrate to ammonium mainly drives soil bacterial dynamics involved in nitrate reduction processes. *Applied Soil Ecology*, *169*, 104164. https://doi.org/10.1016/j.apsoil.2021.104164

Andresen, L. C., Bodé, S., Björk, R. G., Michelsen, A., Aerts, R., Boeckx, P., Cornelissen, J. H. C., Klanderud, K., van Logtestijn, R. S. P., & Rütting, T. (2022). Patterns of free amino

acids in tundra soils reflect mycorrhizal type, shrubification, and warming. *Mycorrhiza*, *32*(3), 305–313. https://doi.org/10.1007/s00572-022-01075-4

Angerbjörn, A., Hersteinsson, P., & Tannerfeldt, M. (2004). Arctic foxes: Consequences of resource predictability in the Arctic fox—Two life history strategies. In D. W. MacDonald & C. Sillero-Zubiri (Eds.), *The Biology and Conservation of Wild Canids* (pp. 163–172). Oxford University Press.

Angerbjorn, A., Tannerfeldt, M., & Erlinge, S. (1999). Predator–prey relationships: Arctic foxes and lemmings. *Journal of Animal Ecology*, *68*(1), 34–49. https://doi.org/10.1046/j.1365-2656.1999.00258.x

Armstrong McKay, D. I., Staal, A., Abrams, J. F., Winkelmann, R., Sakschewski, B., Loriani, S., Fetzer, I., Cornell, S. E., Rockström, J., & Lenton, T. M. (2022). Exceeding 1.5°C global warming could trigger multiple climate tipping points. *Science*, *377*(6611), eabn7950. https://doi.org/10.1126/science.abn7950

Beck, P. S. A., & Goetz, S. J. (2011). Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: Ecological variability and regional differences. *Environmental Research Letters*, *6*(4), 045501. https://doi.org/10.1088/1748-9326/6/4/045501

Bergman, C. M., & Krebs, C. J. (1993). Diet overlap of collared lemmings and tundra voles at Pearce Point, Northwest Territories. *Canadian Journal of Zoology*, *71*(9), 1703–1709. https://doi.org/10.1139/z93-241

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bieleski, R. L. (1973). Phosphate Pools, Phosphate Transport, and Phosphate Availability. *Annual Review of Plant Biology*, *24*(Volume 24, 1973), 225–252. https://doi.org/10.1146/annurev.pp.24.060173.001301

Billault-Penneteau, B., Sandré, A., Folgmann, J., Parniske, M., & Pawlowski, K. (2019). Dryas as a Model for Studying the Root Symbioses of the Rosaceae. *Frontiers in Plant Science*, *10*. https://www.frontiersin.org/article/10.3389/fpls.2019.00661

Bjorbækmo, M. F. M., Carlsen, T., Brysting, A., Vrålstad, T., Høiland, K., Ugland, K. I., Geml, J., Schumacher, T., & Kauserud, H. (2010). High diversity of root associated fungi in both alpine and arctic Dryas octopetala. *BMC Plant Biology*, *10*(1), 244. https://doi.org/10.1186/1471-2229-10-244

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57–62. https://doi.org/10.1038/s41586-018-0563-7

Bledsoe, C., Klein, P., & Bliss, L. C. (1990). A survey of mycorrhizal plants on Truelove Lowland, Devon Island, N.W.T., Canada. *Canadian Journal of Botany*, *68*(9), 1848–1856. https://doi.org/10.1139/b90-242

Bleicher, S. S. (2017). The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ*, *5*, e3772. https://doi.org/10.7717/peerj.3772

Bliss, L. C. (1962). Adaptations of Arctic and Alpine Plants to Environmental Conditions. *Arctic*, *15*(2), 117–144.

Bliss, L. C., Courtin, G. M., Pattie, D. L., Riewe, R. R., Whitfield, D. W. A., & Widden, P. (1973). Arctic Tundra Ecosystems. *Annual Review of Ecology and Systematics*, *4*(1), 359–399. https://doi.org/10.1146/annurev.es.04.110173.002043

Bray, R. H., & Kurtz, L. T. (1945). DETERMINATION OF TOTAL, ORGANIC, AND AVAILABLE FORMS OF PHOSPHORUS IN SOILS. *Soil Science*, *59*(1), 39.

Bronstein, J. L. (2009). The evolution of facilitation and mutualism. *Journal of Ecology*, *97*(6), 1160–1170. https://doi.org/10.1111/j.1365-2745.2009.01566.x

Brook, R. K. (2001). *Structure and dynamics of the vegetation in Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba, community and landscape scales* [Thesis, University of Manitoba]. http://hdl.handle.net/1993/2724

Brook, R. K., & Kenkel, N. C. (2002). A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing*, *23*(21), 4761–4776. https://doi.org/10.1080/01431160110113917

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., … Michalet, R. (2008). Facilitation in Plant Communities: The Past, the Present, and the Future. *Journal of Ecology*, *96*(1), 18–34.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, *18*(3), 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

Bruun, H. H., Österdahl, S., Moen, J., & Angerbjörn, A. (2005). Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography*, *28*(1), 81–87. https://doi.org/10.1111/j.0906-7590.2005.04033.x

Bucher, M. (2007). Functional Biology of Plant Phosphate Uptake at Root and Mycorrhiza Interfaces. *The New Phytologist*, *173*(1), 11–26.

Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, *30*(1), 70–78. https://doi.org/10.1111/1365-2435.12528

Büntgen, U., Hellmann, L., Tegel, W., Normand, S., Myers-Smith, I., Kirdyanov, A. V., Nievergelt, D., & Schweingruber, F. H. (2015). Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *Journal of Ecology*, *103*(2), 489–501.

Byers, J. E., & Noonburg, E. G. (2003). Scale Dependent Effects of Biotic Resistance to Biological Invasion. *Ecology*, *84*(6), 1428–1433. https://doi.org/10.1890/02-3131

Cairney, J. W. G. (2011). Ectomycorrhizal fungi: The symbiotic route to the root for phosphorus in forest soils. *Plant and Soil*, *344*(1), 51–71. https://doi.org/10.1007/s11104-011-0731-0

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, *61*(4), 306–349. https://doi.org/10.1007/BF02912621

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J.

(2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*(6891), Article 6891. https://doi.org/10.1038/nature00812

Chalot, M., & Brun, A. (1998). Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiology Reviews*, *22*(1), 21–44. https://doi.org/10.1111/j.1574-6976.1998.tb00359.x

Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, *17*(7), 881–890. https://doi.org/10.1111/ele.12279

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., & Laundre, J. A. (1995). Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology*, *76*(3), 694–711. https://doi.org/10.2307/1939337

Chapin, F. S., Vitousek, P. M., & Van Cleve, K. (1986). The Nature of Nutrient Limitation in Plant Communities. *The American Naturalist*, *127*(1), 48–58.

Chesemore, D. L. (1969). Den ecology of the Arctic fox in northern Alaska. *Canadian Journal of Zoology*, *47*(1), 121–129. https://doi.org/10.1139/z69-021

Cornelissen, J. H. C., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S. P., Alatalo, J., Stuart Chapin, F., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A. E., Hik, D. S., Hofgaard, A., Jónsdóttir, I. S., Karlsson, S., Klein, J. A., Laundre, J., Magnusson, B., Michelsen, A., … Team, M. O. L. (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, *10*(7), 619–627. https://doi.org/10.1111/j.1461-0248.2007.01051.x

Craine, J. M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M., & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology*, *16*(5), 563–574. https://doi.org/10.1046/j.1365-2435.2002.00660.x

Dakos, V., Matthews, B., Hendry, A. P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M., & De Meester, L. (2019). Ecosystem tipping points in an evolving world. *Nature Ecology & Evolution*, *3*(3), 355–362. https://doi.org/10.1038/s41559-019-0797-2

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. Murray.

Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *Proceedings of the Colloquium on Conservation Problems in Antarctica*, 81–96.

De Long, J. R., Sundqvist, M. K., Gundale, M. J., Giesler, R., & Wardle, D. A. (2016). Effects of elevation and nitrogen and phosphorus fertilization on plant defence compounds in subarctic tundra heath vegetation. *Functional Ecology*, *30*(2), 314–325. https://doi.org/10.1111/1365-2435.12493

Deans, C. A., Sword, G. A., Lenhart, P. A., Burkness, E., Hutchison, W. D., & Behmer, S. T. (2018). Quantifying Plant Soluble Protein and Digestible Carbohydrate Content, Using Corn (Zea mays) As an Exemplar. *JoVE (Journal of Visualized Experiments)*, *138*, e58164. https://doi.org/10.3791/58164

DeLuca, T. H., Glanville, H. C., Harris, M., Emmett, B. A., Pingree, M. R. A., de Sosa, L. L., Cerdá-Moreno, C., & Jones, D. L. (2015). A novel biologically-based approach to evaluating soil phosphorus availability across complex landscapes. *Soil Biology and Biochemistry*, *88*, 110–119. https://doi.org/10.1016/j.soilbio.2015.05.016

Disney, R. H. L., Erzinclioglu, Y. Z., Henshaw, D. J. D. C., Howse, D., Unwin, D. M., Withers, P., & Woods, A. (1982). Collecting methods and the adequacy of attempted fauna surveys with reference to the Diptera. *Field Studies*, *5*(4), 607–622.

Dudenhoeffer, M., Roth, J. D., Johnson, L. K., & Petersen, S. D. (2021). Arctic fox winter dietary response to damped lemming cycles estimated from fecal DNA. *Journal of Mammalogy*, *102*(6), 1455–1465. https://doi.org/10.1093/jmammal/gyab115

Dunbar, M. J. (1970). The scientific importance of the circumpolar region, and its flora and fauna. *Productivity and Conservation in Northern Circumpolar Lands*, 71.

Ehrich, D., Schmidt, N. M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., Ecke, F., Eide, N. E., Framstad, E., Frandsen, J., Franke, A., Gilg, O., Giroux, M.-A., Henttonen, H., Hörnfeldt, B., Ims, R. A., Kataev, G. D., Kharitonov, S. P., Killengreen, S. T., … Solovyeva, D. V. (2020). Documenting lemming population change in the Arctic: Can we detect trends? *Ambio*, *49*(3), 786–800. https://doi.org/10.1007/s13280-019-01198-7

Elmhagen, B., Tannerfeldt, M., Verucci, P., & Angerbjörn, A. (2000). The arctic fox (Alopex lagopus): An opportunistic specialist. *Journal of Zoology*, *251*(2), 139–149. https://doi.org/10.1111/j.1469-7998.2000.tb00599.x

Environment and Climate Change Canada. (2019). *Canada's changing climate report.* (E. Bush & D. S. Lemmen, Eds.). http://publications.gc.ca/collections/collection_2019/eccc/En4-368-2019-eng.pdf

Environment and Climate Change Canada. (2024a). *Canadian Climate Normals 1991-2020 Data—Climate—Environment and Climate Change Canada*. Government of Canada. https://climate.weather.gc.ca/climate_normals/results_1991_2020_e.html?searchType=stnName_1991&txtStationName_1991=Churchill&searchMethod=contains&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=2200000000&dispBack=1

Environment and Climate Change Canada. (2024b). *Historical Data—Climate—Environment and Climate Change Canada*. Government of Canada. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Epstein, H. E., Myers-Smith, I., & Walker, D. A. (2013). Recent dynamics of arctic and sub-arctic vegetation. *Environmental Research Letters*, *8*(1), 015040. https://doi.org/10.1088/1748-9326/8/1/015040

Eriksen, B., Bölter, M., Breen, K., Henry, G., Lévesque, E., Mattson, J.-E., Parker, C. L., & Rayback, S. (2006). Environment and site descriptions of an ecological baseline study in the Canadian Arctic: The Tundra Northwest Expedition 1999 (Nunavut and Northwest Territories, Canada). *Polarforschung*, *73*(2/3), 77–88.

Ernst, C. M., Loboda, S., & Buddle, C. M. (2016). Capturing northern biodiversity: Diversity of arctic, subarctic and north boreal beetles and spiders are affected by trap type and habitat. *Insect Conservation and Diversity*, *9*(1), 63–73. https://doi.org/10.1111/icad.12143

Euskirchen, E. S., Bennett, A. P., Breen, A. L., Genet, H., Lindgren, M. A., Kurkowski, T. A., McGuire, A. D., & Rupp, T. S. (2016). Consequences of changes in vegetation and snow cover for climate feedbacks in Alaska and northwest Canada. *Environmental Research Letters*, *11*(10), 105003. https://doi.org/10.1088/1748-9326/11/10/105003

Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, *78*(1), 9–19. https://doi.org/10.1007/BF00377192

Evans, J. R., & Poorter, H. (2001). Photosynthetic acclimation of plants to growth irradiance: The relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell & Environment*, *24*(8), 755–767. https://doi.org/10.1046/j.1365-3040.2001.00724.x

Fafard, P. M., Roth, J. D., & Markham, J. H. (2020). Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. *Journal of Vegetation Science*, *31*(1), 173–179. https://doi.org/10.1111/jvs.12828

Fisher, J. P., Estop-Aragonés, C., Thierry, A., Charman, D. J., Wolfe, S. A., Hartley, I. P., Murton, J. B., Williams, M., & Phoenix, G. K. (2016). The influence of vegetation and soil characteristics on active-layer thickness of permafrost soils in boreal forest. *Global Change Biology*, *22*, 3127–3140.

Florko, K. R. N., Bernhardt, W., Breiter, C.-J. C., Ferguson, S. H., Hainstock, M., Young, B. G., & Petersen, S. D. (2018). Decreasing sea ice conditions in western Hudson Bay and an increase in abundance of harbour seals (Phoca vitulina) in the Churchill River. *Polar Biology*, *41*(6), 1187–1195. https://doi.org/10.1007/s00300-018-2277-6

Forkel, M., Carvalhais, N., Rödenbeck, C., Keeling, R., Heimann, M., Thonicke, K., Zaehle, S., & Reichstein, M. (2016). Enhanced seasonal CO2 exchange caused by amplified plant productivity in northern ecosystems. *Science*, *351*(6274), 696–699. https://doi.org/10.1126/science.aac4971

Freschet, G. T., Swart, E. M., & Cornelissen, J. H. C. (2015). Integrated plant phenotypic responses to contrasting above- and below-ground resources: Key roles of specific leaf area and root mass fraction. *New Phytologist*, *206*(4), 1247–1260. https://doi.org/10.1111/nph.13352

Gable, T. D., Johnson-Bice, S. M., Homkes, A. T., Windels, S. K., & Bump, J. K. (2020). Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. *Science Advances*, *6*(46), eabc5439. https://doi.org/10.1126/sciadv.abc5439

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. (2004). Plant Functional Markers Capture Ecosystem Properties During Secondary Succession. *Ecology*, *85*(9), 2630–2637. https://doi.org/10.1890/03-0799

Gharajehdaghipour, T., & Roth, J. D. (2018). Predators attract prey through ecosystem engineering in the Arctic. *Ecosphere*, *9*(1), e02077. https://doi.org/10.1002/ecs2.2077

Gharajehdaghipour, 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

Ghirardo, A., Lindstein, F., Koch, K., Buegger, F., Schloter, M., Albert, A., Michelsen, A., Winkler, J. B., Schnitzler, J.-P., & Rinnan, R. (2020). Origin of volatile organic compound emissions from subarctic tundra under global warming. *Global Change Biology*, *26*(3), 1908–1925. https://doi.org/10.1111/gcb.14935

Gough, L., Bass, H., & McLaren, J. R. (2015). Effects of Increased Soil Nutrients on Seed Rain: A Role for Seed Dispersal in the Greening of the Arctic? *Arctic, Antarctic, and Alpine Research*, *47*(1), 27–34. https://doi.org/10.1657/AAAR0014-055

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*(2), 211–218. https://doi.org/10.2307/1552473

Gould, S. J. (1988). Kropotkin was no crackpot. *Natural History*, *97*(7), 12–21.

Graae, B. J., Pagh, S., & Bruun, H. H. (2004). An Experimental Evaluation of the Arctic Fox (Alopex lagopus) as a Seed Disperser. *Arctic, Antarctic, and Alpine Research*, *36*(4), 468–473. https://doi.org/10.1657/1523-0430(2004)036[0468:AEEOTA]2.0.CO;2

Grünberg, I., Wilcox, E. J., Zwieback, S., Marsh, P., & Boike, J. (2020). Linking tundra vegetation, snow, soil temperature, and permafrost. *Biogeosciences*, *17*(16), 4261–4279. https://doi.org/10.5194/bg-17-4261-2020

Gupta, K., Mukhopadhyay, A., Babb, D. G., Barber, D. G., & Ehn, J. K. (2022). Landfast sea ice in Hudson Bay and James Bay: Annual cycle, variability and trends, 2000–2019. *Elementa: Science of the Anthropocene*, *10*(1), 00073. https://doi.org/10.1525/elementa.2021.00073

Hansen, J. E., Sato, M., Simons, L., Nazarenko, L. S., Sangha, I., Kharecha, P., Zachos, J. C., von Schuckmann, K., Loeb, N. G., Osman, M. B., Jin, Q., Tselioudis, G., Jeong, E., Lacis, A., Ruedy, R., Russell, G., Cao, J., & Li, J. (2023). Global warming in the pipeline. *Oxford Open Climate Change*, *3*(1), kgad008. https://doi.org/10.1093/oxfclm/kgad008

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S., & Wilson, W. G. (2007). Ecosystem engineering in space and time. *Ecology Letters*, *10*(2), 153–164. https://doi.org/10.1111/j.1461-0248.2006.00997.x

He, Q., & Bertness, M. D. (2014). Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, *95*(6), 1437–1443. https://doi.org/10.1890/13-2226.1

He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *ECOLOGY LETTERS*, *16*(5), 695–706. https://doi.org/10.1111/ele.12080

Heijmans, M. M. P. D., Magnússon, R. Í., Lara, M. J., Frost, G. V., Myers-Smith, I. H., van Huissteden, J., Jorgenson, M. T., Fedorov, A. N., Epstein, H. E., Lawrence, D. M., & Limpens, J. (2022). Tundra vegetation change and impacts on permafrost. *Nature*

Reviews Earth & Environment, *3*(1), Article 1. https://doi.org/10.1038/s43017-021-00233-0

Hewitt, R. E., Alexander, H. D., Miller, S. N., & Mack, M. C. (2022). Root-associated fungi not tree density influences stand nitrogen dynamics at the larch forest–tundra ecotone. *Journal of Ecology*, *110*(6), 1419–1431. https://doi.org/10.1111/1365-2745.13882

Hewitt, R. E., DeVan, M. R., Lagutina, I. V., Genet, H., McGuire, A. D., Taylor, D. L., & Mack, M. C. (2020). Mycobiont contribution to tundra plant acquisition of permafrost-derived nitrogen. *New Phytologist*, *226*(1), 126–141. https://doi.org/10.1111/nph.16235

Hicks, L. C., Leizeaga, A., Rousk, K., Michelsen, A., & Rousk, J. (2020). Simulated rhizosphere deposits induce microbial N-mining that may accelerate shrubification in the subarctic. *Ecology*, *101*(9), e03094. https://doi.org/10.1002/ecy.3094

Hobbie, J. E., & Hobbie, E. A. (2006). 15n in Symbiotic Fungi and Plants Estimates Nitrogen and Carbon Flux Rates in Arctic Tundra. *Ecology*, *87*(4), 816–822. https://doi.org/10.1890/0012-9658(2006)87[816:NISFAP]2.0.CO;2

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *ECOLOGICAL MONOGRAPHS*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346–363.

Høye, T. T., Mølgaard Ellebjerg, S., & Philipp, M. (2007). The Impact of Climate on Flowering in the High Arctic—The Case of Dryas in a Hybrid Zone. *Arctic, Antarctic, and Alpine Research*, *39*(3), 412–421. https://doi.org/10.1657/1523-0430(06-018)[HOYE]2.0.CO;2

Høye, T. T., & Sikes, D. S. (2013). Arctic entomology in the 21st century. *The Canadian Entomologist*, *145*(2), 125–130. https://doi.org/10.4039/tce.2013.14

Hudson, J. M. G., & Henry, G. H. R. (2009). Increased Plant Biomass in a High Arctic Heath Community from 1981 to 2008. *Ecology*, *90*(10), 2657–2663.

IPCC. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, Ö. Yelekçi, R. Yu, & B. Zhou, Eds.). Cambridge University Press.

Johnson, N. C., Graham, J. H., & Smith, F. A. (1997). Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *The New Phytologist*, *135*(4), 575–585. https://doi.org/10.1046/j.1469-8137.1997.00729.x

Johnson-Bice, S. M., Baldwin, F. B., Richardson, E., & Roth, J. D. (2024). *Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice*. https://ecoevorxiv.org/repository/view/7384/

Johnson-Bice, S. M., Gable, T. D., Roth, J. D., & Bump, J. K. (2023). Patchy indirect effects of predation: Predators contribute to landscape heterogeneity and ecosystem function via localized pathways. *Oikos*, *2023*(10), e10065. https://doi.org/10.1111/oik.10065

Johnson-Bice, S. M., Roth, J. D., & Markham, J. H. (2023). A Cosmic View of "Tundra Gardens": Satellite Imagery Provides a Landscape-Scale Perspective of Arctic Fox Ecosystem Engineering. *ECOSYSTEMS*, *26*(8), 1670–1684. https://doi.org/10.1007/s10021-023-00857-x

Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., & Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*(12), 1862–1869.

Jones, C. G., Lawton, J. H., & Shachak, M. (1996). Organisms as Ecosystem Engineers. In F. B. Samson & F. L. Knopf (Eds.), *Ecosystem Management: Selected Readings* (pp. 130–147). Springer. https://doi.org/10.1007/978-1-4612-4018-1_14

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kalra, Y. P., & Maynard, D. G. (1991). *Methods manual for forest soil and plant analysis* (Vol. 319E). http://scf.rncan.gc.ca/publications?id=11845

Keuper, F., van Bodegom, P. M., Dorrepaal, E., Weedon, J. T., van Hal, J., van Logtestijn, R. S. P., & Aerts, R. (2012). A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, *18*(6), 1998–2007. https://doi.org/10.1111/j.1365-2486.2012.02663.x

Khan, S. A., Mulvaney, R. L., & Hoeft, R. G. (2000). Direct-Diffusion Methods for Inorganic-Nitrogen Analysis of Soil. *Soil Science Society of America Journal*, *64*(3), 1083–1089. https://doi.org/10.2136/sssaj2000.6431083x

Knops, J. M., & Reinhart, K. (2000). Specific Leaf Area Along a Nitrogen Fertilization Gradient. *The American Midland Naturalist*, *144*(2), 265–272. https://doi.org/10.1674/0003-0031(2000)144[0265:SLAAAN]2.0.CO;2

Kohls, S. J., Thimmapuram, J., Buschena, C. A., Paschke, M. W., & Dawson, J. O. (1994). Nodulation patterns of actinorhizal plants in the family rosaceae. *Plant and Soil*, *162*(2), 229–239. https://doi.org/10.1007/BF01347710

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring Beta Diversity for Presence-Absence Data. *Journal of Animal Ecology*, *72*(3), 367–382.

Kropotkin, P. (1902). *Mutual Aid: A Factor of Evolution*. McClure Phillips & Co.

Kudo, G., Molau, U., & Wada, N. (2001). Leaf-trait Variation of Tundra Plants along a Climatic Gradient: An Integration of Responses in Evergreen and Deciduous Species. *Arctic, Antarctic, and Alpine Research*, *33*(2), 181–190. https://doi.org/10.1080/15230430.2001.12003421

Kushner, P. J., Mudryk, L. R., Merryfield, W., Ambadan, J. T., Berg, A., Bichet, A., Brown, R., Derksen, C., Déry, S. J., Dirkson, A., Flato, G., Fletcher, C. G., Fyfe, J. C., Gillett, N., Haas, C., Howell, S., Laliberté, F., McCusker, K., Sigmond, M., … Zwiers, F. W. (2018). Canadian snow and sea ice: Assessment of snow, sea ice, and related climate processes in Canada's Earth system model and climate-prediction system. *The Cryosphere*, *12*(4), 1137–1156. https://doi.org/10.5194/tc-12-1137-2018

Landhäusser, S. M., Chow, P. S., Dickman, L. T., Furze, M. E., Kuhlman, I., Schmid, S., Wiesenbauer, J., Wild, B., Gleixner, G., & Hartmann, H. (2018). Standardized protocols and procedures can precisely and accurately quantify non-structural carbohydrates. *Tree Physiology*, *38*(12), 1764–1778.

Liu, Y., Riley, W. J., Keenan, T. F., Mekonnen, Z. A., Holm, J. A., Zhu, Q., & Torn, M. S. (2022). Dispersal and fire limit Arctic shrub expansion. *Nature Communications*, *13*(1), 3843. https://doi.org/10.1038/s41467-022-31597-6

Markham, J. H. (2009). Does Dryas integrifolia fix nitrogen? *Botany*, *87*(11), 1106–1109. https://doi.org/10.1139/B09-071

Marschner, P., & Rengel, Z. (Eds.) (with Stark, S.). (2007). *Nutrient Cycling in Terrestrial Ecosystems* (Vol. 10). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-68027-7

Martinez Arbizu, P. (2021). *pairwiseAdonis: Pairwise multilevel comparison using adonis* [R package version 0.4]. https://github.com/pmartinezarbizu/pairwiseAdonis

Martini, I. P. (1989). The Hudson Bay Lowland: Major geologic features and assets. In W. J. M. van der Linden, S. A. P. L. Cloetingh, J. P. K. Kaasschieter, W. J. E. van de Graaff, J. Vandenberghe, & J. A. M. van der Gun (Eds.), *Coastal Lowlands: Geology and Geotechnology* (pp. 25–34). Springer Netherlands. https://doi.org/10.1007/978-94-017-1064-0_2

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1991). Primary and Secondary Production in Terrestrial Ecosystems. In J. Cole, G. Lovett, & S. Findlay (Eds.), *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories* (pp. 120–139). Springer. https://doi.org/10.1007/978-1-4612-3122-6_7

Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C., & Grant, R. F. (2021). Arctic tundra shrubification: A review of mechanisms and impacts on ecosystem carbon balance. *Environmental Research Letters*, *16*(5), 053001. https://doi.org/10.1088/1748-9326/abf28b

Meltofte, H., Barry, T., Berteaux, D., Bültmann, H., Christiansen, J. S., Cook, J. A., Dahlberg, A., Daniëls, F. J. A., Ehrich, D., Fjeldså, J., Friðriksson, F., Ganter, B., Gaston, A. J., Gillespie, L. J., Grenoble, L., Hoberg, E. P., Hodkinson, I. D., Huntington, H. P., Ims, R. A., … Wrona, F. J. (2013). *Arctic Biodiversity Assessment: Status and trends in Arctic biodiversity*. Conservation of Arctic Flora and Fauna (CAFF). https://oaarchive.arctic-council.org/handle/11374/232

Michelsen, A., Quarmby, C., Sleep, D., & Jonasson, S. (1998). Vascular plant 15N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia*, *115*(3), 406–418. https://doi.org/10.1007/s004420050535

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013a). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013b). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Monk, J. D., & Schmitz, O. J. (2022). Landscapes shaped from the top down: Predicting cascading predator effects on spatial biogeochemistry. *Oikos*, *2022*(5), e08554. https://doi.org/10.1111/oik.08554

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20152434. https://doi.org/10.1098/rspb.2015.2434

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A., Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., … Wipf, S. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, *10*(2), Article 2. https://doi.org/10.1038/s41558-019-0688-1

Natali, S. M., Watts, J. D., Rogers, B. M., Potter, S., Ludwig, S. M., Selbmann, A.-K., Sullivan, P. F., Abbott, B. W., Arndt, K. A., Birch, L., Björkman, M. P., Bloom, A. A., Celis, G., Christensen, T. R., Christiansen, C. T., Commane, R., Cooper, E. J., Crill, P., Czimczik, C., … Zona, D. (2019). Large loss of CO2 in winter observed across the northern permafrost region. *Nature Climate Change*, *9*(11), 852–857. https://doi.org/10.1038/s41558-019-0592-8

Nielsen, S. M., Pedersen, V., & Klitgaard, B. B. (1994). Arctic Fox (Alopex lagopus) Dens in the Disko Bay Area, West Greenland. *Arctic*, *47*(4), 327–333.

Oksanen, J. (2022, October 11). *Package "vegan."* CRAN. https://github.com/vegandevs/vegan

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). The vegan package. *Community Ecology Package*, *10*(631–637), 719.

Olsen, S. R. (1954). *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*. U.S. Department of Agriculture.

Pandey, D., Kehri, H. K., Zoomi, I., Akhtar, O., & Singh, A. K. (2019). Mycorrhizal Fungi: Biodiversity, Ecological Significance, and Industrial Applications. In A. N. Yadav, S. Mishra, S. Singh, & A. Gupta (Eds.), *Recent Advancement in White Biotechnology Through Fungi: Volume 1: Diversity and Enzymes Perspectives* (pp. 181–199). Springer International Publishing. https://doi.org/10.1007/978-3-030-10480-1_5

Paradis, M., Lévesque, E., & Boudreau, S. (2016). Greater effect of increasing shrub height on winter versus summer soil temperature. *Environmental Research Letters*, *11*(8), 085005. https://doi.org/10.1088/1748-9326/11/8/085005

Parrot. (2021). *Parrot Sequoia+ multispectral drone camera*. Parrot. https://www.parrot.com/en/support/documentation/sequoia

Parsons, A. N., Welker, J. M., Wookey, P. A., Press, M. C., Callaghan, T. V., & Lee, J. A. (1994). Growth Responses of Four Sub-Arctic Dwarf Shrubs to Simulated Environmental Change. *Journal of Ecology*, *82*(2), 307–318. https://doi.org/10.2307/2261298

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*(7), Article 7. https://doi.org/10.1038/nclimate1858

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, *46*(1), 15–27. https://doi.org/10.3354/cr00936

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change.

Trends in Ecology & Evolution, *20*(9), 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Pix4D. (2023a). *Pix4Dcapture* [Windows]. Pix4D SA. https://www.pix4d.com/product/pix4dcapture/

Pix4D. (2023b). *Pix4Dfields* [Windows]. Pix4D SA. https://www.pix4d.com/product/pix4dfields/

Poorter, H., & Evans, J. R. (1998). Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia*, *116*(1), 26–37. https://doi.org/10.1007/s004420050560

Poorter, H., & Ryser, P. (2015). The limits to leaf and root plasticity: What is so special about specific root length? *The New Phytologist*, *206*(4), 1188–1190.

Prabhu, N., Borkar, S., & Garg, S. (2019). Chapter 11 - Phosphate solubilization by microorganisms: Overview, mechanisms, applications and advances. In S. N. Meena & M. M. Naik (Eds.), *Advances in Biological Science Research* (pp. 161–176). Academic Press. https://doi.org/10.1016/B978-0-12-817497-5.00011-2

Prestrud, P. (1992). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Svalbard. *Arctic*, *45*(2), 154–158.

QGIS Development team. (2023). *QGIS Geographic Information System* (3.30.3) [Windows]. QGIS Association. https://www.qgis.org/

Rasband, W. S. (1997). *ImageJ* [Computer software]. U. S. National Institutes of Health. https://imagej.nih.gov/ij/

Rasmussen, L. H., Zhang, W., Ambus, P., Michelsen, A., Jansson, P.-E., Kitzler, B., & Elberling, B. (2022). Nitrogen transport in a tundra landscape: The effects of early and late growing

season lateral N inputs on arctic soil and plant N pools and N2O fluxes. *Biogeochemistry*, *157*(1), 69–84. https://doi.org/10.1007/s10533-021-00855-y

Read, D. J., Leake, J. R., & Perez-Moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany*, *82*(8), 1243–1263. https://doi.org/10.1139/b04-123

Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, *157*(3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P. B., Ellsworth, D. S., & Walters, M. B. (1998). Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: Evidence from within and across species and functional groups. *Functional Ecology*, *12*(6), 948–958. https://doi.org/10.1046/j.1365-2435.1998.00274.x

Reimchen, T. E. (2017). Diverse Ecological Pathways of Salmon Nutrients Through an Intact Marine-terrestrial Interface. *The Canadian Field-Naturalist*, *131*(4), Article 4. https://doi.org/10.22621/cfn.v131i4.1965

Reimchen, T. E., & Fox, C. H. (2013). Fine-scale spatiotemporal influences of salmon on growth and nitrogen signatures of Sitka spruce tree rings. *BMC Ecology*, *13*(1), 38. https://doi.org/10.1186/1472-6785-13-38

Richardson, S. J., Press, M. C., Parsons, A. N., & Hartley, S. E. (2002). How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a

sub-Arctic heath. *Journal of Ecology*, *90*(3), 544–556. https://doi.org/10.1046/j.1365-2745.2002.00681.x

Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, *145*(1), 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Rosenzweig, M. L., & MacArthur, R. H. (1963). Graphical Representation and Stability Conditions of Predator-Prey Interactions. *The American Naturalist*, *97*(895), 209–223. https://doi.org/10.1086/282272

Roth, J. D. (2002). Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*, *133*(1), 70–77. https://doi.org/10.1007/s00442-002-1004-7

Roth, J. D. (2003). Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology*, *72*(4), 668–676. https://doi.org/10.1046/j.1365-2656.2003.00739.x

Roy, A., Gough, L., Boelman, N. T., Rowe, R. J., Griffin, K. L., & McLaren, J. R. (2022). Small but mighty: Impacts of rodent-herbivore structures on carbon and nutrient cycling in arctic tundra. *Functional Ecology*, *36*(9), 2331–2343. https://doi.org/10.1111/1365-2435.14127

Schimel, J. P., Bilbrough, C., & Welker, J. M. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, *36*(2), 217–227. https://doi.org/10.1016/j.soilbio.2003.09.008

Schmidt, N. M., Ims, R. A., Høye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhamme, M. C., & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proceedings: Biological Sciences*, *279*(1746), 4417–4422.

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. https://doi.org/10.1111/j.1461-0248.2010.01511.x

Scott, D., Malcolm, J. R., & Lemieux, C. (2002). Climate change and modelled biome representation in Canada's national park system: Implications for system planning and park mandates. *Global Ecology and Biogeography*, *11*(6), 475–484. https://doi.org/10.1046/j.1466-822X.2002.00308.x

Serreze, M. C., Walsh, J. E., Chapin, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., & Barry, R. G. (2000). Observational Evidence of Recent Change in the Northern High-Latitude Environment. *Climatic Change*, *46*(1), 159–207. https://doi.org/10.1023/A:1005504031923

Shaver, G. R., & Chapin, F. S. (1991). Production: Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs*, *61*(1), 1–31. https://doi.org/10.2307/1942997

Shevtsova, A., Ojala, A., Neuvonen, S., Vieno, M., & Haukioja, E. (1995). Growth and Reproduction of Dwarf Shrubs in a Subarctic Plant Community: Annual Variation and Above-Ground Interactions with Neighbours. *Journal of Ecology*, *83*(2), 263–275. https://doi.org/10.2307/2261565

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de L. Dantas, V., de Bello, F., Duarte,

L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

Simpson, E. H. (1949). Measurement of Diversity. *Nature*, *163*(4148), 688–688. https://doi.org/10.1038/163688a0

Skrede, I., Eidesen, P. B., PorTELa, R. P., & Brochmann, C. (2006). Refugia, differentiation and postglacial migration in arctic-alpine Eurasia, exemplified by the mountain avens (Dryas octopetala L.). *Molecular Ecology*, *15*(7), 1827–1840. https://doi.org/10.1111/j.1365-294X.2006.02908.x

Smith, C. A. S., Smits, C. M. M., & Slough, B. G. (1992). Landform Selection and Soil Modifications Associated with Arctic Fox (Alopex lagopus) Den Sites in Yukon Territory, Canada. *Arctic and Alpine Research*, *24*(4), 324–328. https://doi.org/10.1080/00040851.1992.12002964

Smits, C. M. M., Smith, C. A. S., & Slough, B. G. (1988). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Northern Yukon Territory, Canada. *Arctic*, *41*(1), 12–16.

Standen, K. M., Sniderhan, A. E., Sonnentag, O., Voigt, C., & Baltzer, J. L. (2024). Response of Boreal Plant Communities and Forest Floor Carbon Fluxes to Experimental Nutrient Additions. *Ecosystems*. https://doi.org/10.1007/s10021-023-00899-1

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press.

Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J., & Romanovsky, V. E. (2005). Winter Biological Processes Could Help

Convert Arctic Tundra to Shrubland. *BioScience*, *55*(1), 17–26. https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Sullivan, P. F., Ellison, S. B. Z., McNown, R. W., Brownlee, A. H., & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, *96*(3), 716–727. https://doi.org/10.1890/14-0626.1

Swann, A. L., Fung, I. Y., Levis, S., Bonan, G. B., & Doney, S. C. (2010). Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. *Proceedings of the National Academy of Sciences*, *107*(4), 1295–1300. https://doi.org/10.1073/pnas.0913846107

Tannerfeldt, M., & Angerbjörn, A. (1996). Life history strategies in a fluctuating environment: Establishment and reproductive success in the arctic fox. *Ecography*, *19*(3), 209–220. https://doi.org/10.1111/j.1600-0587.1996.tb01247.x

Tannerfeldt, M., Moehrenschlager, A., & Angerbjörn, A. (2003). Den ecology of swift, kit and arctic foxes: A review. *The Swift Fox: Ecology and Conservation of Swift Foxes in a Changing World*, 167–181.

Thomas, D. B. (2008). Nontoxic Antifreeze for Insect Traps. *Entomological News*, *119*(4), 361–365. https://doi.org/10.3157/0013-872X-119.4.361

Timoney, K., Laroi, G., & Dale, M. (1993). Sub-Arctic Forest-Tundra Vegetation Gradients—The Sigmoid Wave Hypothesis. *Journal of Vegetation Science*, *4*(3), 387–394. https://doi.org/10.2307/3235597

Van Cleve, K., & Alexander, V. (1981). Nitrogen Cycling in Tundra and Boreal Ecosystems. *Ecological Bulletins*, *33*, 375–404.

von Beckerath, X., Benadi, G., Gilg, O., Sittler, B., Yannic, G., Klein, A.-M., & Eitzinger, B. (2022). Long-term monitoring reveals topographical features and vegetation that explain winter habitat use of an Arctic rodent. *Arctic Science*, *8*(2), 349–361. https://doi.org/10.1139/as-2021-0010

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschleger, S. D., & Woodward, F. I. (2014). The relationship of leaf photosynthetic traits – Vcmax and Jmax – to leaf nitrogen, leaf phosphorus, and specific leaf area: A meta-analysis and modeling study. *Ecology and Evolution*, *4*(16), 3218–3235. https://doi.org/10.1002/ece3.1173

Walker, D. A., Epstein, H. E., Raynolds, M. K., Kuss, P., Kopecky, M. A., Frost, G. V., Daniëls, F. J. A., Leibman, M. O., Moskalenko, N. G., Matyshak, G. V., Khitun, O. V., Khomutov, A. V., Forbes, B. C., Bhatt, U. S., Kade, A. N., Vonlanthen, C. M., & Tichý, L. (2012). Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. *Environmental Research Letters*, *7*(1), 015504. https://doi.org/10.1088/1748-9326/7/1/015504

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & Team, C. (2005). The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science*, *16*(3), 267–282.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnússon, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., … Wookey, P. A. (2006). Plant community responses to

experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, *103*(5), 1342–1346. https://doi.org/10.1073/pnas.0503198103

Wang, W., Scali, M., Vignani, R., Spadafora, A., Sensi, E., Mazzuca, S., & Cresti, M. (2003). Protein extraction for two-dimensional electrophoresis from olive leaf, a plant tissue containing high levels of interfering compounds. *ELECTROPHORESIS*, *24*(14), 2369–2375. https://doi.org/10.1002/elps.200305500

Werner, E. E., & Peacor, S. D. (2003). A Review of Trait-Mediated Indirect Interactions in Ecological Communities. *Ecology*, *84*(5), 1083–1100. https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Wielgolaski, F. E., Sømme, L., Thórhallsdóttir, T. E., Grabherr, G., Malinovsky, K. A., Zlotin, R. I., Miehe, G., Hedberg, O., Killick, D. J. B., & Campbell, J. S. (1997). *Polar and alpine tundra*. Elsevier Science Publishing Company, Inc. https://elibrary.ru/item.asp?id=26450837

Wilmers, C. C., Estes, J. A., Edwards, M., Laidre, K. L., & Konar, B. (2012). Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment*, *10*(8), 409–415. https://doi.org/10.1890/110176

Wrigley, R. E., & Hatch, D. R. M. (1976). Arctic Fox Migrations in Manitoba. *Arctic*, *29*(3), 147–158.

Wyant, K. A., Draney, M. L., & Moore, J. C. (2011). Epigeal Spider (Araneae) Communities in Moist Acidic and Dry Heath Tundra at Toolik Lake, Alaska. *Arctic, Antarctic, and Alpine Research*, *43*(2), 301–312. https://doi.org/10.1657/1938-4246-43.2.301

Yang, H., Zhao, X., Liu, C., Bai, L., Zhao, M., & Li, L. (2018). Diversity and characteristics of colonization of root-associated fungi of Vaccinium uliginosum. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-33634-1

Zhao, S.-T., Johnson-Bice, S. M., & Roth, J. D. (2022). Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. *Global Ecology and Conservation*, *40*, e02310. https://doi.org/10.1016/j.gecco.2022.e02310

Zou, K., Thébault, E., Lacroix, G., & Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*, *30*(8), 1454–1465.

Chapter 3. Response of prostrate shrub functional traits and community NDVI to limiting nutrients and deep snow in Arctic tundra heath communities

Abstract

Arctic prostrate shrubs are some of the relatively few plants that can survive the extreme conditions of Canada's North, where they dominate tundra heath ecosystems. As arctic temperatures continue to increase, the response of prostrate shrubs to changing environmental conditions will lay the groundwork for new succession regimes in the tundra. Arctic foxes (*Vulpes lagopus*) act as ecosystem engineers in tundra heath, where their den sites exhibit increased soil nutrients, atypical plant communities, and deeper snow. We treated tundra heath vegetation plots with N and P fertilizers and/or increased snow depth to examine how these den communities develop, and here we present how these treatments affected the leaf traits of 5 dominant prostrate shrub species (*Arctostaphylos rubra, Dryas integrifolia, Rhododendron lapponicum, Shepherdia canadensis, Vaccinium uliginosum*) after 5 years. We used ANOVA tests and principal components analyses (PCA) of leaf soluble protein content, leaf carbohydrate content, and specific leaf area (SLA) to show responses in leaf phenotype and abundance-weighted site means to evaluate these dominant species as a group. We found that the SLA of prostrate shrubs in plots that received fertilizer was ~50% higher than those in controls and this effect was doubled in plots with both fertilizer and snow fence treatments. The PCAs show an inverse relationship between SLA and soluble leaf protein content and highlight the effect of snow depth on leaf phenotype when nutrients are not limiting. The increase in specific leaf area is correlated with differences in the normalized difference vegetation index (NDVI) of each treatment plot, which shows significantly higher NDVI in all plots that received fertilizer

compared to those that did not. Our results show that some arctic prostrate shrubs exhibit a productive phenotypic response to limiting nutrients independent from annual temperature and we add to the growing body of literature recognizing SLA and NDVI as key plant functional traits in a warming Arctic.

3.1 Introduction

Arctic tundra ecosystems are experiencing climatic warming at a greater rate than the rest of the world (Environment and Climate Change Canada, 2019; IPCC, 2021; Kushner et al., 2018). While modern arctic tundra ecosystems have been experiencing some degree of climatic warming since their establishment after the retreat of continental ice sheets (Bliss et al., 1973; Dunbar, 1970), warming in this northern region is driving dramatic changes to vegetation at every organizational scale and affecting a biome shift at the edge of the Arctic (Bjorkman et al., 2018; Epstein et al., 2013; Heijmans et al., 2022; Myers-Smith et al., 2020; M. D. Walker et al., 2006). Arctic vegetation has the capacity to affect climate change through various mechanisms (Euskirchen et al., 2016; Forkel et al., 2016; Ghirardo et al., 2020; Keuper et al., 2012; Natali et al., 2019; Pearson et al., 2013; Swann et al., 2010), and the potential development of climate feedbacks has extended the relevance of arctic vegetation change beyond its regional extent (Armstrong McKay et al., 2022; Cornelissen et al., 2007; Dakos et al., 2019; Keuper et al., 2012).

Monitoring of arctic tundra has revealed widespread increases in greening and shrubification (Bjorkman et al., 2018; Epstein et al., 2013; Heijmans et al., 2022; Mekonnen et al., 2021) and the complex spatial patterns observed emphasize the impact of small-scale vegetation dynamics on these broad-scale metrics (Myers-Smith et al., 2020). Tundra ecosystems are nutrient limited, with underdeveloped soils and low rates of organic decomposition (Bliss et al., 1973; Chapin et al., 1995; Marschner & Rengel, 2007; Wielgolaski et al., 1997), so nutrient cycling by consumers can result in community-level shifts in plant productivity (Gharajehdaghipour et al., 2016; Johnson-Bice, Gable, et al., 2023; Milbau et al., 2013b; Roy et al., 2022). The Arctic fox (*Vulpes lagopus*) is one such consumer; they act as ecosystem

engineers by concentrating nutrient deposition on their dens, resulting in small-scale greening at distinct locations across the landscape (Gharajehdaghipour et al., 2016; Johnson-Bice, Roth, et al., 2023). The increased productivity on these dens is largely attributed to interspecies variation in reflectance from the invasion of erect shrubs and grasses, which are also thought to accumulate more snow in the winter and so insulate the community from low air temperatures (Fafard et al., 2020; Gharajehdaghipour & Roth, 2018; Grünberg et al., 2020; Johnson-Bice, Roth, et al., 2023; Schimel et al., 2004). Arctic foxes build dens in dry tundra heaths atop elevated landscape features with coarse sandy soils (Chesemore, 1969; Gharajehdaghipour et al., 2016; Johnson-Bice, Roth, et al., 2023; Smith et al., 1992). Dry tundra heaths are physically limited by cold exposure and water scarcity in addition to poor soil nutrient content and are often dominated by prostrate shrubs (Aleksandrova, 1970; Bliss et al., 1973; Gough et al., 2002; Wielgolaski et al., 1997). A productive shift in such limited plant communities not only highlights the role consumers can have in Arctic greening but allows for a close examination of the effects of limiting nutrients and snow cover thickness on prostrate shrubs and their capacity to respond to ameliorated stress.

The stress-gradient hypothesis (SGH) describes how environmental stress affects niche space through species interactions in plant communities, in addition to the direct determination of niche limits (Bertness & Callaway, 1994; Bruno et al., 2003; He & Bertness, 2014). At environmental extremes, the pressure for facilitation may be great, but facilitation is instead limited by the ability of existing species to ameliorate the physical stress and the difference from the fundamental niches of other species (He & Bertness, 2014), so niche expansion may halt with sufficient stress (Bulleri et al., 2016). The species richness of tundra communities can be relatively insensitive to environmental changes, but in these communities, individual species do

respond, eliciting shifts in dominance and production as conditions vary (Bliss, 1962; Chapin et al., 1995; Milbau et al., 2013b; Parsons et al., 1994; Shaver & Chapin, 1991). Variable growth responses have been observed in co-occurring prostrate shrubs (Parsons et al., 1994) and arctic prostrate shrubs are both long-lived and can positively interact while growing together (Büntgen et al., 2015; Shevtsova et al., 1995), so temporal shifts in productive advantage could reinforce mutual facilitation with enough time. Prostrate shrub communities in dry tundra heaths likely exhibit the same stable-community and individual-response dynamic, just on longer timescales than other tundra communities (Büntgen et al., 2015; Chapin et al., 1995). While community shift displaces prostrate shrubs on Arctic fox dens (Fafard et al., 2020), the addition of nutrients may so disproportionally benefit one or two prostrate shrub species that facilitation feedbacks are overcome by competitive pressure before new species invade (Bruno et al., 2003; Bulleri et al., 2016; Chapin et al., 1986). Reports of thriving prostrate *Salix* and *Dryas* at den sites (Tannerfeldt et al., 2003) could suggest that these plants are so advantaged in this context.

Wild plants adapted to poor nutrient availability may lack the capacity to respond to increased nutrient subsidy as well as the fertility-adapted crops that represent the bulk of nutrient addition research (Chapin et al., 1986), but do still exhibit a response (Chapin et al., 1986, 1995; Craine et al., 2002; Knops & Reinhart, 2000). Fertilization of soil with a limiting nutrient triggers a productive metabolic response in plants and alters functional traits for “faster” ecophysiology (Chapin et al., 1986; Reich, 2014). Given the consistent intraspecific variation of leaf economic traits globally (Siefert et al., 2015), the plastic reallocation of mass to leaves in plants released from nutrient limits (Freschet et al., 2015), and the documented leaf trait responses of tundra prostrate shrubs to climate (Bjorkman et al., 2018; Chapin et al., 1995; Kudo et al., 2001), prostrate shrubs in dry tundra heath communities should exhibit a plastic response

in leaf phenology when limiting nutrients are subsidized by consumer activity. Should the nutrient subsidy be sufficient to affect plant community change, like at Arctic fox dens (Chapter 1), invasion of new species would only occur after the subsidy exceeds the ability of extant species to immediately utilize the increased nutrients and those nutrients accumulate in the soil (Chapin et al., 1986). Changes in prostrate shrub leaf phenology could develop in advance of succession.

The slow growth strategy of arctic prostrate shrubs and combination with water, wind, and temperature stresses in dry heaths could mean even this relative shift to "faster" traits on the fast-slow economic trait spectrum (Reich, 2014) may not be a rapid process (Bliss, 1962; Büntgen et al., 2015; He & Bertness, 2014) but in Wapusk National Park, dry tundra heath communities can be found at their lowest, subarctic extent (Brook, 2001). This *Dryas* heath (Brook & Kenkel, 2002) is the preferred denning habitat of Arctic foxes in the region (Johnson-Bice, Roth, et al., 2023) and the metabolic reaction time of prostrate shrubs should be reduced in this subarctic landscape, relative to that at higher latitudes (Büntgen et al., 2015; He & Bertness, 2014; Reich, 2014). Elevated levels of inorganic N and P have been found in the soils of fox dens here (Gharajehdaghipour et al., 2016) so I hypothesized that prostrate shrubs in these communities should exhibit a plastic response in leaf phenology with increased deposition of phytoavailable N and P (Craine et al., 2002; Freschet et al., 2015; Reich, 2014, 2014). Increased snow cover thickness may have a complementary but smaller effect on leaf metabolism from extended winter soil processes and water subsidy (Bliss, 1962; Schimel et al., 2004). I predicted that when N and P limits were released, dominant prostrate shrub leaf physiology would change: leaf photosynthetic protein content would increase as the plant could invest more N in these resources (Evans, 1989), leaf photosynthate content would decrease as vegetative growth should

accelerate and increase carbohydrate demand (Sullivan et al., 2015), and specific leaf area (SLA) would increase to better take advantage of available light (Bjorkman et al., 2018; Freschet et al., 2015).

3.2 Methods

Site Description and Experimental Design

Our vegetation experiment was initiated in 2017 to track the effects of increased annual nutrient deposition and deepened snow on these tundra heath communities and compare them to the unique communities found on fox dens. Wapusk National Park straddles the boundary of the Canadian Low Arctic and Boreal ecozones (D. A. Walker et al., 2005). The northern and coastal regions of the park exhibit subarctic vegetation communities, with *Dryas* heath dominating the wide elevated ridges preferred by Arctic foxes (Brook & Kenkel, 2002; Johnson-Bice, Roth, et al., 2023). Arctic fox dens are found on these ridges and are characterized by the unique vegetation assemblages indicative of ecosystem engineering (Fafard et al., 2020). The experiment was set up south of the Nester 1 research station in Wapusk National Park, with 16 vegetation plots arranged in two parallel lines running north-south along an elevated ridge in representative tundra heath. Plots are each 10m x 10m and spaced by a minimum of 100m. Plots were treated with annual fertilizer and/or snow fences such that 4 plots received fertilizer, 4 plots received fences, 4 plots received both treatments, and 4 plots received no treatments (controls). Treatments were arranged into two halves of a modified Latin square to control for spatial gradients (see Chapter 2, Figure 2). The fertilizer treatment consisted of 100 kg ha^{-1} N as urea, and 28 kg ha^{-1} P as triple super phosphate. These quantities were based on an estimate of annual N and P deposition on fox dens calculated from the number of prey items brought to dens

(estimated from prey remains) and the average mass of prey species. Snow fences were established along the NW edge of treated plots to face the prevailing winds.

For comparison in 2022, 8 Arctic fox dens were selected using the following criteria:

1. Dens must be situated in representative, *Dryas* tundra heath.
2. Dens must have been occupied in recent years (since 2017).
3. Dens were at least 15 years old.

Additionally, the dens had to be within a half day walk from the Nester 1 research station.

Plot NDVI

NDVI was calculated from multispectral images collected by drone in 2021, after 4 years of treatment (the drone was not functional in 2022). Images were collected during mid day (9 am to 2 pm). There were no images of the fox dens, so they were not compared. Multispectral images were collected in July using a Parrot Sequoia Multispectral camera with a sunshine sensor (Parrot, 2021) mounted on a drone running Pix4Dcapture (Pix4D, 2023a) for autonomous grid photography at each plot, with 80% overlap between images. These images were compiled into multispectral orthomosaics using Pix4Dfields (Pix4D, 2023b). QGIS v3.30.3 (QGIS Development team, 2023) was used to select plot areas from the othomosaics, calculate NDVI per pixel (pixel area ~ 1.25cm^2), and export the datasets for statistics. The NDVI was calculated from red and near-infrared reflectance such that NDVI = (NIR-RED)/(NIR+RED), where NIR is the near-infrared reflectance at 790nm and RED is red reflectance at 660nm (Parrot, 2021; Pettorelli et al., 2005). NDVI calculated for some completely bare areas could be greater than 0, so only values ≥0.3 were used in analysis to ensure a comparison of plant productivity.

Leaf Plasticity in Prostrate Shrubs

Leaf samples were taken from each experimental plot community in July 2022. Analyses were limited to prostrate shrubs because of the dominance of this growth form in these communities, to target plants that were present for the whole study period, and to reduce functional trait variance from plants with opposing survival strategies. Leaves from the most abundant prostrate shrubs: *Dryas integrifolia, Arctostaphylos rubra, Vaccinium uliginosum, Rhododendron lapponicum,* and *Shepherdia canadensis* were collected, if those plants were present.

D. integrifolia was the only plant to occur in all plots, and *D. integrifolia* leaf samples were collected from 6 of the 8 fox dens (it was not present at 2 dens) for comparison. Samples were dried at 60°C in Churchill before transport and were dried at 65°C in the laboratory for two hours prior to processing.

SLA was calculated for leaves from the experimental plots only. SLA was calculated as the fresh leaf area, determined from photos taken shortly after collection, divided by the dry mass of the tissue. Leaves were photographed on grid paper after harvest in the field and leaf area was measured by digital analysis in ImageJ (Rasband, 1997). Leaf protein content was determined using the standard Bradford assay with a pretreatment of cold acetone with 10% trichloroacetic acid (Wang et al., 2003) to remove waxes, followed by the solubilization of proteins in 0.1M NaOH with the addition of 100 mg ml^{-1} PVP 40 to prevent interactions from leaf polyphenols (Deans et al. (2018). Non-structural carbohydrate content was determined using phenol-sulfuric acid colorimetry (Landhäusser et al., 2018) with each sample run in triplicate and averaged.

One *Vaccinium uliginosum* sample collected from one plot could not be analysed for carbohydrate content due to insufficient tissue.

Percent plant species cover collected in 2022 was measured in 5 permanent quadrats in each of the experimental plots. Quadrats measured $1m^2$ and species cover values were averaged across quadrats for a site cover estimate. Abundance-weighted means (AWMs) for all experimental plots were calculated to measure how the dominant prostrate shrub traits responded to the experimental treatment AWMs were calculated for all three leaf traits according to **Equation 1**, where a_{ip} is the mean abundance (percent cover) of species i in plots p, t_i is the trait value for each species, and s is the total number of species examined.

$$AWM_{tp} = \frac{\sum_{i=1}^{s} a_{ip} \times t_i}{\sum_{i=1}^{s} a_{ip}} \quad \text{(Eq. 1)}$$

Equation 1 was modified from the community-weighted mean formula (Garnier et al., 2004; Muscarella & Uriarte, 2016; Standen et al., 2024) to account for variation in total prostrate shrub cover.

Statistics

Multivariate methods from the vegan package (Oksanen, 2022) were used to examine the effects of treatments on leaf traits. All prostrate shrub leaf samples were collectively analysed by PERMANOVA of Bray-Curtis dissimilarities and *post hoc* pairwise comparisons (Martinez Arbizu, 2021). Treatment effects on AWM leaf traits and *D. integrifolia* leaf traits were each analysed by principal components analysis (PCA), followed by examination of individual traits. *D. integriolia* specific analysis was possible because it was present in all plots. ANOVA was used to detect the effect of treatment groups on each functional trait, with Tukey's HSD used if significance was found.

3.3 Results

Plot NDVI

Mean plot NDVI was significantly different between treatments (F = 35.028, df = 3, $p < 0.001$). Plots that received the fertilizer treatment had higher mean plant NDVI than those that did not (**Figure 15**). The fertilizer treatment and the fertilizer with fencing treatment were statistically similar and both were different from controls and plots receiving only fencing remained similar to controls. **Figure 16** shows the percent cover of bare ground in each calculated on each plot from the NDVI image. There was no detectable effect of treatment on bare ground (F = 1.780, df = 3, p = 0.20). Bare ground cover from NDVI and mean bare ground cover from the 5 quadrats (visually assessed in 2021) were positively related with an R^2 value of 0.68 (**Figure 17**) suggesting that bare ground estimates from the quadrat reflected changes in the whole plot.

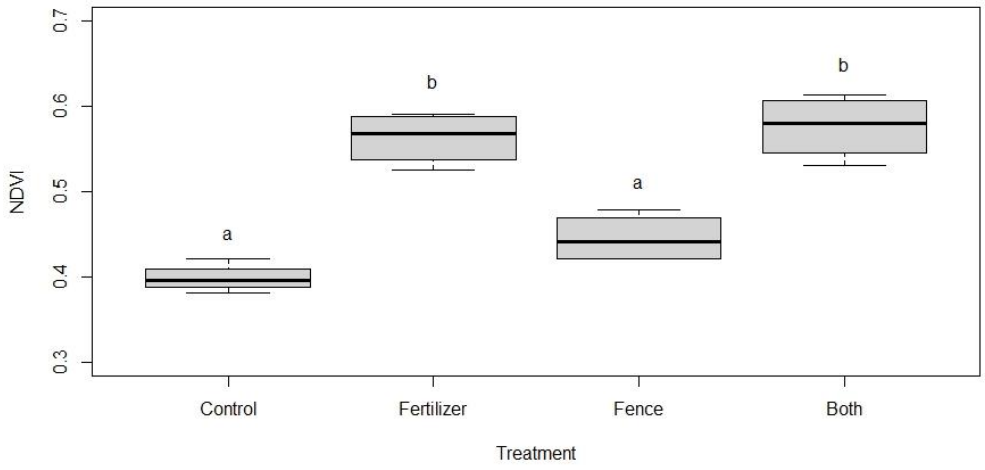

Figure 15. Mean NDVI of productive vegetation in experimental plots, organized by treatment. Only NDVI values greater that 0.3 were averaged per plot to exclude bare ground. Letters indicate Tukey's honest significance.

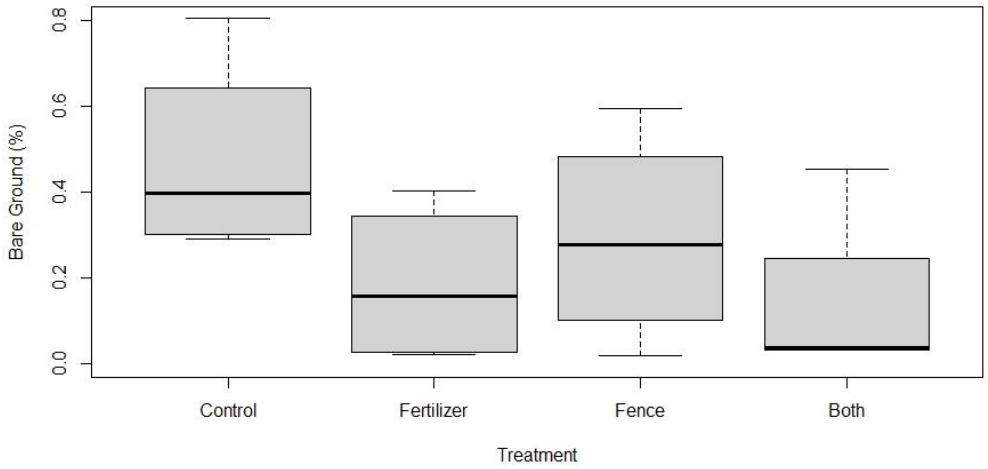

Figure 16. Percent bare ground in experimental plots calculated from NDVI, organized by treatment. Presented are means of NDVI values between 0.3 and -1, excluding productive vegetation.

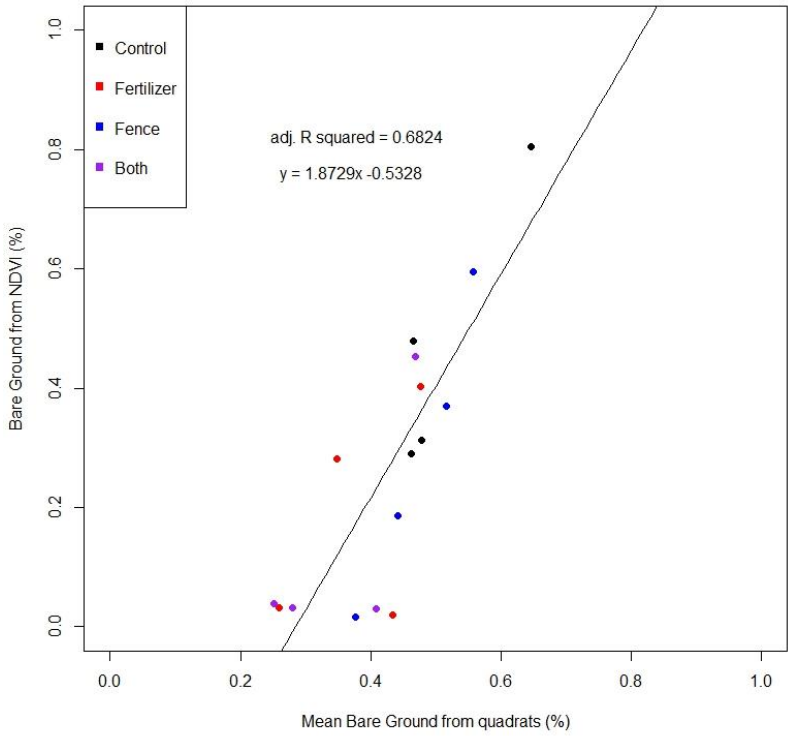

Figure 17. Comparison of ground-truthed and calculated bare ground area in each experimental plot. Ground truthed bare ground was estimated by averaging cover in 5 1m^2 quadrats per site. Calculated bare ground uses NDVI data from whole plot images.

Leaf Plasticity in Prostrate Shrubs

The leaves collected appeared to vary across prostrate shrub species and plot treatment in all measured traits (**Figure 18**). PERMANOVA conducted using Bray-Curtis dissimilarities calculated from the traits of all leaf samples found a significant effect of plot treatment on prostrate shrub leaves (F = 2.315, df = 3, p = 0.019), with *post hoc* pairwise comparisons

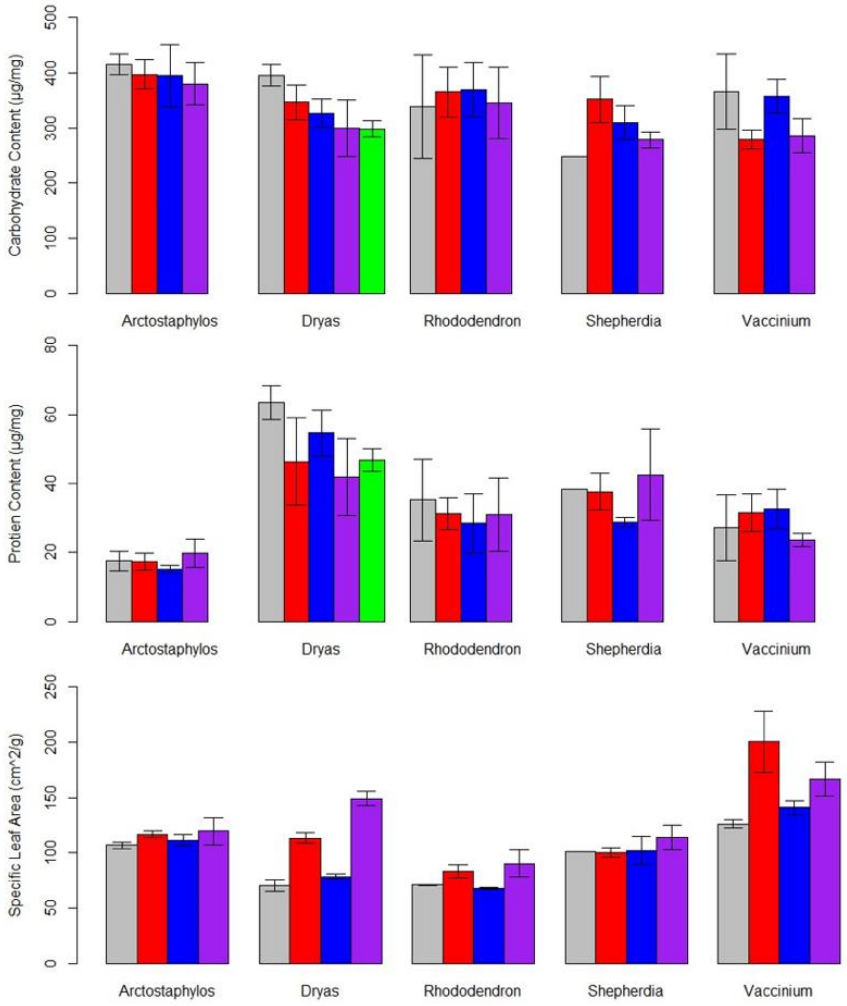

Figure 18. Leaf trait means for each prostrate shrub species sampled (*Arctostaphylos rubra, Dryas integrifolia, Rhododendron lapponicum, Shepherdia canadensis, Vaccinium uliginosum*) in each treatment group. Error bars show standard error. Columns without error bars have a sample size of 1 (the species was only found at a single site of that treatment). Columns are colour coded to the treatment group: grey for controls, red for fertilizer treatment, blue for fence treatment, purple for fence and fertilizer. Fox den sample means are shown in green.

Table 9. *Post hoc* pairwise comparisons of dissimilarities across plot treatment groups. Bray-Curtis dissimilarities were calculated from the traits of all prostrate shrub leaf samples. P-values were adjusted by the Benjamini-Hochberg method for false discovery rate among multiple comparisons.

pairs	adjusted p-value
Control vs Fertilizer	0.3120
Control vs Fence	0.4272
Control vs Both	0.0480*
Fertilizer vs Fence	0.6730
Fertilizer vs Both	0.3120
Fence vs Both	0.1680

revealing a difference between controls and leaves from plots receiving both experimental treatments (**Table 9**).

A PCA of AWM trait values shows leaf phenology differentiating between treatments (**Figure 19**). The axial components explain 84% (PC1) and 12% (PC2) of multivariate difference respectively, with site scores clearly diverging by treatment. Loading values show an inverse relationship between SLA (3.7, -5.4) and leaf protein content (-1.4, 1.5) and a large magnitude for leaf carbohydrate content (-15.2, -1.5) at a distinct angle from the main axis of treatment divergence. When separated into individual traits, AWM SLA is higher in plots receiving fertilizer ($F = 24.5$, df = 3, $p < 0.001$) while AWM protein content and AWM carbohydrate content both exhibit decreasing, but insignificant, trends in treated plots when compared to controls (**Figure 20**; protein: $F = 0.97$, df = 3, $p = 0.44$; carbohydrate: $F = 1.56$, df = 3, $p = 0.25$).

As *D. integrifolia* was the only one of the five sampled prostrate shrub species present at every site, the *D. integrifolia* data met assumptions for PCA in isolation, shown in **Figure 21**. The axial components represent 82% (PC1) and 14% (PC2) respectively, separating by treatment in a similar manner to the AWM trait PCA. Loading values show the same patterns between traits as the previous analysis, all exhibiting similar magnitudes and inverted signs, with SLA (-3.9, 6.1),

leaf protein content (1.6, -1.8), and leaf carbohydrate content (15.4, 1.7). *D. integrifolia* also exhibits clearer trends in individual leaf traits than the AWM site values (**Figure 20**).

The only statistically significant effect found was the response of *D. integrifolia* SLA to treatment ($F = 55.001$, df = 3, $p < 0.001$, **Figure 18f**), with higher SLA in plants receiving annual fertilizer than controls and higher SLA in plants receiving both fertilizer and fencing than plants receiving only fertilizer.

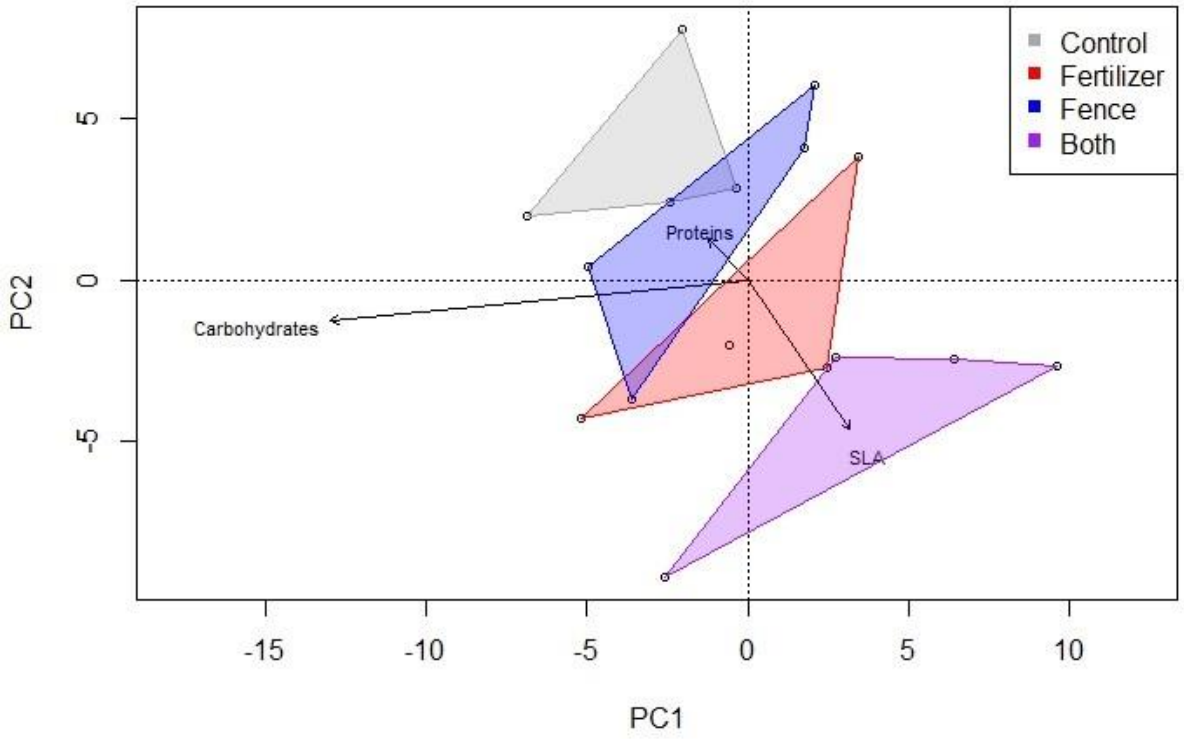

Figure 19. Principal components analysis **(**PCA) showing the influence of experimental treatments on abundance-weighted mean leaf traits (soluble protein content, carbohydrate content, and specific leaf area) for dominant prostrate shrub species in each of our vegetation plots. Plot points are hulled by treatment received. PC1 explains 84% of variation in the dataset and PC2 explains 12%.

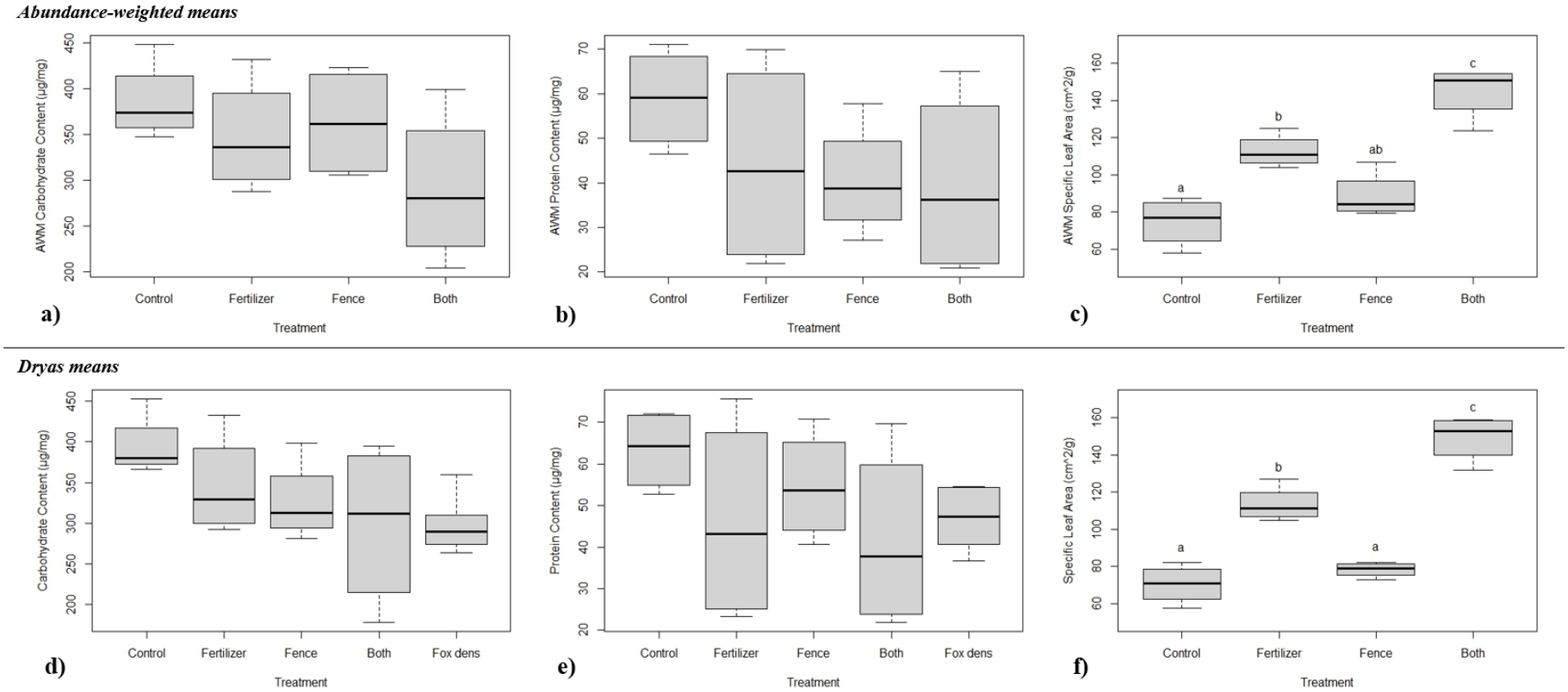

Figure 20. Leaf traits across treatment groups for both abundance-weighted dominant prostrate shrub means and *Dryas integrifolia* means. **a)** Abundance-weighted prostrate shrub leaf carbohydrate content. **b)** Abundance-weighted prostrate shrub leaf soluble protein content. **c)** Abundance-weighted prostrate shrub specific leaf area (SLA). Letters indicate Tukey's honest significance. **d)** *Dryas integrifolia* leaf carbohydrate content. Fox den samples are included for comparison. **e)** *Dryas integrifolia* leaf soluble protein content. Fox den samples are included for comparison. **f)** *Dryas integrifolia* SLA. Letters indicate Tukey's honest significance.

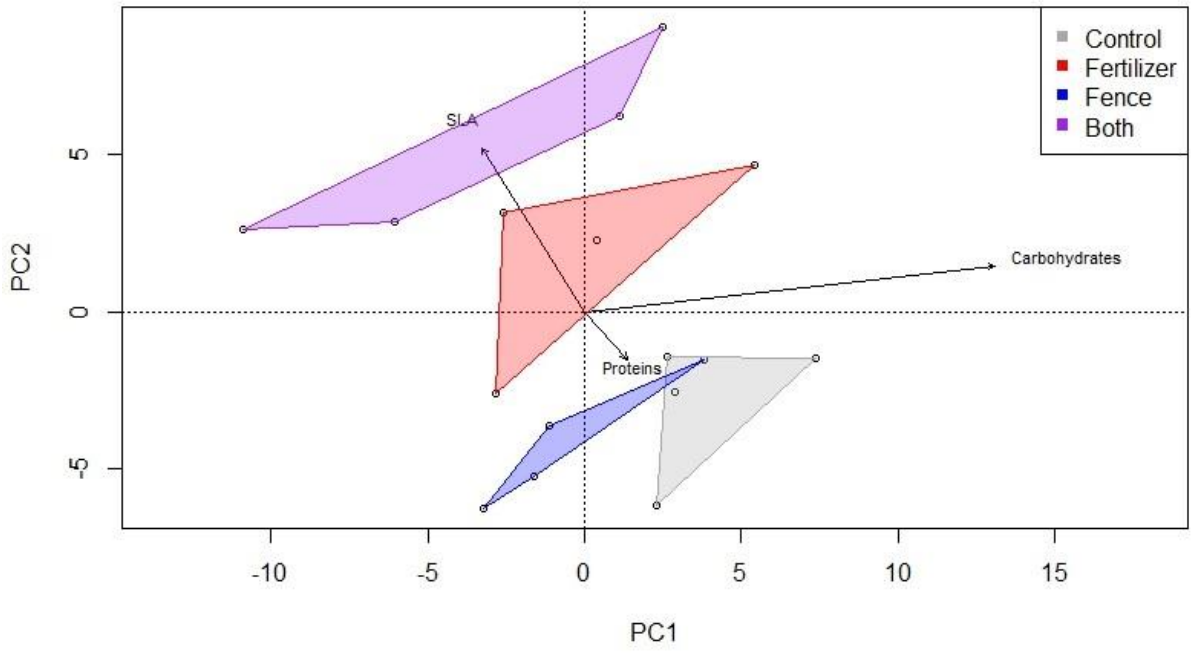

Figure 21. Principal components analysis **(**PCA) showing the influence of experimental treatments on mean *Dryas integrifolia* leaf traits (soluble protein content, carbohydrate content, and specific leaf area) for dominant prostrate shrub species in each of our vegetation plots. Plot points hulled by treatment received. PC1 explains 82% of variation in the dataset and PC2 explains 14%.

3.4 Discussion

Plot NDVI

Our results demonstrate a clear relationship between annual inorganic N and P deposition and NDVI in arctic tundra heath communities. This change is indicative of increased plant productivity consistent with the application of limiting nutrients, suggesting one or both of soil N and P are not consistently phytoavailable *Dryas* heath and limit plant growth. This increased productivity is likely still limited by N and/or P available at the start of the growing season, as the most extractable soil nutrient pools exhibit similar levels across treatment groups after green up (see Chapter 2, Table 1). This response experimentally confirms that soil N and P, increased

at levels Arctic foxes can deposit, is enough to significantly increase NDVI in tundra vegetation as described by Johnson-Bice et al. (2023).

Given the lack of significant difference in bare ground between treatments, the mean NDVI change appears to be a direct response to plant productivity and not an artifact of increased colonization of unmined soils. While colonization of bare ground is occurring over time in the vegetation plots (Chapter 1, Table 4), colonization does not appear to have significantly contributed to plant productivity after only 4 years of treatment. Unfortunately, the lack of drone data from year 5 prevents direct comparison of extant *D. integrifolia* leaf traits and NDVI, instead simply confirms a community level shift in response to fertilization (Johnson-Bice, Roth, et al., 2023; Pettorelli et al., 2011).

The fact that some bare ground patches had NDVI above 0 was likely due to instrument error. Our Parrot Sequoia camera uses a sunshine sensor for light calibration and there was thin cloud cover on the day the multispectral photos were taken. That cloud layer may have scattered more red light than near-infrared light and the sunshine sensor would not have been able to detect the difference. Other sources of error could include soil reflectance and differences in light detection from the slight distance between red and near-infrared sensor modules in the camera itself.

Leaf Plasticity in Prostrate Shrubs

The PCA results of leaf functional traits show that both soil nutrients and snow depth affect the phenology and metabolism of these prostrate shrubs and that these effects work in concert. The leaf response is largely plastic, with a strong positive effect on SLA and a weak negative effect on leaf soluble protein content both aligned in the direction of treatment response. Leaf

carbohydrate content is shown with a large loading value (arrow), but at such an angle that the leaf response can only be considered to have a weak negative effect on it. The AWM trait PCA shows that deepened snow effects and fertilized soil effects act along a similar axis of leaf response and compound to enhance the leaf response of these prostrate shrubs in plots receiving both fertilizer and snow fences. The linearity of this observed axis of change illustrates the fast-slow spectrum of economic traits (Reich, 2014) as both treatments ameliorate stresses that limit function.

The abundance-weighted response of all five examined species is being driven by the response of *D. integrifolia*. As the most dominant prostrate shrub, the *D. integrifolia* data were weighted more heavily in the community mean trait calculation, resulting in very similar PCA plots and individual trait data. However, the PCAs calculated nearly identical loading values for each leaf trait in both plots (albeit inverted by ordination), allowing for a very close comparison of *D. integrifolia* and abundance- weighted responses. The *Dryas* plot shows much less overlap between treatment groups than in the AWM plot, enough to suggest that responses to fertilizer are more variable in the other four species when *D. integrifolia* is present. Fence treatment plots are comparable to controls along the main axis of change in the *D. integrifolia* response and occupy an intermediate position between fertilizer and control groups in the abundance-weighted group response, suggesting that at least one of the other species can productively respond better to increased snow depth than *D. integrifolia*. When broken down into individual metrics, the only statistical evidence supporting this idea is the lack of statistical difference between fence treatment plots and fertilizer treatment plots in AWM SLA, when this difference is significant for *D. integrifolia* alone. This could be an effect of low power but the pattern shows up in the PCAs as well and should be considered for future investigation. The ability of *D. integrifolia* to

better respond to increased nutrient availability than other prostrate shrubs could explain its primary dominance among prostrate shrubs in these *Dryas* heath communities (Chapter 2, Table 4) and reports of thriving *Dryas* plants at Arctic fox den sites referenced by Tannerfeldt et al. (2003).

While our evidence supports that these prostrate shrubs exhibit plastic changes in leaf traits consistent with a release from nutrient limits (Chapin et al., 1986; Freschet et al., 2015; Reich, 2014) and that co-occurring subarctic prostrate shrubs vary in their ability to respond to limiting nutrient subsidy (Parsons et al., 1994), the possible trends in soluble leaf protein content and leaf photosynthate content (non-structural carbohydrates) presented here are not conclusive. The inverse relationship between leaf protein content and SLA was opposite to our hypothesis that both would increase. The interrelationship between both of these traits and photosynthesis is well accepted (Evans & Poorter, 2001; Poorter & Evans, 1998; Poorter & Ryser, 2015; Reich et al., 1998; A. P. Walker et al., 2014), but there appears to be a dearth of literature on the subject in wild subarctic prostrate shrubs, let alone *D. integrifolia*. Given the extreme environmental stress tolerated dry tundra heath communities and the high light conditions of summer in northern latitudes, it is possible that these plants are allocating N differently to maximize biomass increase (Evans, 1989; Evans & Poorter, 2001). The inclusion of P in our nutrient treatment could impact this allocation by increasing the sensitivity of carboxylation rates to invested leaf N (Evans, 1989; A. P. Walker et al., 2014) effectively requiring less N for similar RuBisCO activity. Another explanation could be that the adaptation to nutrient-poor high light conditions has somehow made SLA modification more photosynthetic nitrogen use-efficient than additional investment in photosynthetic proteins (Poorter & Evans, 1998; Reich et al., 1998) at the cost of the maximum productive rate (Chapin et al., 1986). What is evident is that the

increase in SLA is increasing photosynthetic capacity (Reich et al., 1998) and mediated by nutrient phytoavailability (Knops & Reinhart, 2000). The weak negative trend in non-structural leaf carbohydrates aligns with our hypothesis but cannot provide support without statistical evidence. Our experiment did suffer from the low statistical power of our sample size (16 plots, 4 treatments, 8 fox dens) but the existence of highly responsive prostrate shrub species on and off Arctic fox dens, *D. integrifolia* in this case, provides an excellent opportunity to study the interrelationship between plastic leaf phenology, productivity, and nutrient availability in arctic and subarctic prostrate shrubs across the fox's range.

The ecophysiology of prostrate shrubs undergoing this nutrient-induced metabolic shift has not been well studied. Such research would expand our understanding facilitation and plant adaptations in extreme terrestrial environments and could have broad implications for vegetation modelling in the Arctic. Predictive ecosystem models rely on the upscaling of biogeochemical process and community shift models (Heijmans et al., 2022; Myers-Smith et al., 2020) and more information on heath plant functioning above the shrub line could prove valuable. Any contribution to community-level greening or leaf trait metrics by prostrate shrubs would be lost to interspecific variation after shrubification, but before the invasion of erect shrubs, remote sensing might be capable of predicting shifts in function and even invasion probability with adequate understanding of processes like these (Bjorkman et al., 2018).

Conclusion

The effects of Arctic fox ecosystem engineering can drive intraspecific changes in the ecophysiology of local plants. We demonstrated that dominant, co-occurring prostrate shrubs in a subarctic dry tundra heath productively respond to the addition of limiting nutrients and increased snow cover thickness. This response is magnified when these effects combine and

characterized by increased SLA. These shrub species vary in their capacity to respond to different growth-limiting stresses, but exhibit changes in leaf traits consistent with the fast-slow economic trait spectrum (Reich, 2014). This study is the first to examine the response of prostrate shrub leaf economic traits to the environmental alterations from Arctic fox ecosystem engineering and the first to quantitatively describe the intraspecific variation of leaf economic traits in *D. integrifolia*. We have shown that the annual deposition of N and P, increased at rates achievable by Arctic foxes, can cause a significant increase in the NDVI of dry tundra heath vegetation with only 4 years of subsidy but we could not assess the contribution of extant prostrate shrubs to this early greening. Our results experimentally support the ability of Arctic foxes to increase the productivity of local vegetation via ecosystem engineering and the capacity of prostrate shrubs to respond to this stimulus. Understanding that plant productivity on Arctic fox dens is enhanced by increased long term nutrient deposition creates new applications for descriptive study design to contribute to the research of functional ecology in tundra ecosystems. Additionally, we contribute to a growing pool of research describing how small-scale environmental factors, like consumer activity, can govern plant productivity in tundra ecosystems and influence greening dynamics in subarctic vegetation.

3.5 References

Aleksandrova, V. D. (1970). The Vegetation of the Tundra Zones in the USSR and Data about its Productivity. *Productivity and Conservation in Northern Circumpolar Lands*.

An, T., Wang, F., Ren, L., Ma, S., Li, S., Liu, L., & Wang, J. (2022). Ratio of nitrate to ammonium mainly drives soil bacterial dynamics involved in nitrate reduction processes. *Applied Soil Ecology*, *169*, 104164. https://doi.org/10.1016/j.apsoil.2021.104164

Andresen, L. C., Bodé, S., Björk, R. G., Michelsen, A., Aerts, R., Boeckx, P., Cornelissen, J. H. C., Klanderud, K., van Logtestijn, R. S. P., & Rütting, T. (2022). Patterns of free amino acids in tundra soils reflect mycorrhizal type, shrubification, and warming. *Mycorrhiza*, *32*(3), 305–313. https://doi.org/10.1007/s00572-022-01075-4

Angerbjörn, A., Hersteinsson, P., & Tannerfeldt, M. (2004). Arctic foxes: Consequences of resource predictability in the Arctic fox—Two life history strategies. In D. W. MacDonald & C. Sillero-Zubiri (Eds.), *The Biology and Conservation of Wild Canids* (pp. 163–172). Oxford University Press.

Angerbjorn, A., Tannerfeldt, M., & Erlinge, S. (1999). Predator–prey relationships: Arctic foxes and lemmings. *Journal of Animal Ecology*, *68*(1), 34–49. https://doi.org/10.1046/j.1365-2656.1999.00258.x

Armstrong McKay, D. I., Staal, A., Abrams, J. F., Winkelmann, R., Sakschewski, B., Loriani, S., Fetzer, I., Cornell, S. E., Rockström, J., & Lenton, T. M. (2022). Exceeding 1.5°C global warming could trigger multiple climate tipping points. *Science*, *377*(6611), eabn7950. https://doi.org/10.1126/science.abn7950

Beck, P. S. A., & Goetz, S. J. (2011). Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: Ecological variability and regional differences. *Environmental Research Letters*, *6*(4), 045501. https://doi.org/10.1088/1748-9326/6/4/045501

Bergman, C. M., & Krebs, C. J. (1993). Diet overlap of collared lemmings and tundra voles at Pearce Point, Northwest Territories. *Canadian Journal of Zoology*, *71*(9), 1703–1709. https://doi.org/10.1139/z93-241

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bieleski, R. L. (1973). Phosphate Pools, Phosphate Transport, and Phosphate Availability. *Annual Review of Plant Biology*, *24*(Volume 24, 1973), 225–252. https://doi.org/10.1146/annurev.pp.24.060173.001301

Billault-Penneteau, B., Sandré, A., Folgmann, J., Parniske, M., & Pawlowski, K. (2019). Dryas as a Model for Studying the Root Symbioses of the Rosaceae. *Frontiers in Plant Science*, *10*. https://www.frontiersin.org/article/10.3389/fpls.2019.00661

Bjorbækmo, M. F. M., Carlsen, T., Brysting, A., Vrålstad, T., Høiland, K., Ugland, K. I., Geml, J., Schumacher, T., & Kauserud, H. (2010). High diversity of root associated fungi in both alpine and arctic Dryas octopetala. *BMC Plant Biology*, *10*(1), 244. https://doi.org/10.1186/1471-2229-10-244

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57–62. https://doi.org/10.1038/s41586-018-0563-7

Bledsoe, C., Klein, P., & Bliss, L. C. (1990). A survey of mycorrhizal plants on Truelove Lowland, Devon Island, N.W.T., Canada. *Canadian Journal of Botany*, *68*(9), 1848–1856. https://doi.org/10.1139/b90-242

Bleicher, S. S. (2017). The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ*, *5*, e3772. https://doi.org/10.7717/peerj.3772

Bliss, L. C. (1962). Adaptations of Arctic and Alpine Plants to Environmental Conditions. *Arctic*, *15*(2), 117–144.

Bliss, L. C., Courtin, G. M., Pattie, D. L., Riewe, R. R., Whitfield, D. W. A., & Widden, P. (1973). Arctic Tundra Ecosystems. *Annual Review of Ecology and Systematics*, *4*(1), 359–399. https://doi.org/10.1146/annurev.es.04.110173.002043

Bray, R. H., & Kurtz, L. T. (1945). DETERMINATION OF TOTAL, ORGANIC, AND AVAILABLE FORMS OF PHOSPHORUS IN SOILS. *Soil Science*, *59*(1), 39.

Bronstein, J. L. (2009). The evolution of facilitation and mutualism. *Journal of Ecology*, *97*(6), 1160–1170. https://doi.org/10.1111/j.1365-2745.2009.01566.x

Brook, R. K. (2001). *Structure and dynamics of the vegetation in Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba, community and landscape scales* [Thesis, University of Manitoba]. http://hdl.handle.net/1993/2724

Brook, R. K., & Kenkel, N. C. (2002). A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing*, *23*(21), 4761–4776. https://doi.org/10.1080/01431160110113917

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., … Michalet, R. (2008). Facilitation in Plant Communities: The Past, the Present, and the Future. *Journal of Ecology*, *96*(1), 18–34.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, *18*(3), 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

Bruun, H. H., Österdahl, S., Moen, J., & Angerbjörn, A. (2005). Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography*, *28*(1), 81–87. https://doi.org/10.1111/j.0906-7590.2005.04033.x

Bucher, M. (2007). Functional Biology of Plant Phosphate Uptake at Root and Mycorrhiza Interfaces. *The New Phytologist*, *173*(1), 11–26.

Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, *30*(1), 70–78. https://doi.org/10.1111/1365-2435.12528

Büntgen, U., Hellmann, L., Tegel, W., Normand, S., Myers-Smith, I., Kirdyanov, A. V., Nievergelt, D., & Schweingruber, F. H. (2015). Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *Journal of Ecology*, *103*(2), 489–501.

Byers, J. E., & Noonburg, E. G. (2003). Scale Dependent Effects of Biotic Resistance to Biological Invasion. *Ecology*, *84*(6), 1428–1433. https://doi.org/10.1890/02-3131

Cairney, J. W. G. (2011). Ectomycorrhizal fungi: The symbiotic route to the root for phosphorus in forest soils. *Plant and Soil*, *344*(1), 51–71. https://doi.org/10.1007/s11104-011-0731-0

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, *61*(4), 306–349. https://doi.org/10.1007/BF02912621

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J.

(2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*(6891), Article 6891. https://doi.org/10.1038/nature00812

Chalot, M., & Brun, A. (1998). Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiology Reviews*, *22*(1), 21–44. https://doi.org/10.1111/j.1574-6976.1998.tb00359.x

Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, *17*(7), 881–890. https://doi.org/10.1111/ele.12279

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., & Laundre, J. A. (1995). Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology*, *76*(3), 694–711. https://doi.org/10.2307/1939337

Chapin, F. S., Vitousek, P. M., & Van Cleve, K. (1986). The Nature of Nutrient Limitation in Plant Communities. *The American Naturalist*, *127*(1), 48–58.

Chesemore, D. L. (1969). Den ecology of the Arctic fox in northern Alaska. *Canadian Journal of Zoology*, *47*(1), 121–129. https://doi.org/10.1139/z69-021

Cornelissen, J. H. C., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S. P., Alatalo, J., Stuart Chapin, F., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A. E., Hik, D. S., Hofgaard, A., Jónsdóttir, I. S., Karlsson, S., Klein, J. A., Laundre, J., Magnusson, B., Michelsen, A., … Team, M. O. L. (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, *10*(7), 619–627. https://doi.org/10.1111/j.1461-0248.2007.01051.x

Craine, J. M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M., & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology*, *16*(5), 563–574. https://doi.org/10.1046/j.1365-2435.2002.00660.x

Dakos, V., Matthews, B., Hendry, A. P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M., & De Meester, L. (2019). Ecosystem tipping points in an evolving world. *Nature Ecology & Evolution*, *3*(3), 355–362. https://doi.org/10.1038/s41559-019-0797-2

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. Murray.

Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *Proceedings of the Colloquium on Conservation Problems in Antarctica*, 81–96.

De Long, J. R., Sundqvist, M. K., Gundale, M. J., Giesler, R., & Wardle, D. A. (2016). Effects of elevation and nitrogen and phosphorus fertilization on plant defence compounds in subarctic tundra heath vegetation. *Functional Ecology*, *30*(2), 314–325. https://doi.org/10.1111/1365-2435.12493

Deans, C. A., Sword, G. A., Lenhart, P. A., Burkness, E., Hutchison, W. D., & Behmer, S. T. (2018). Quantifying Plant Soluble Protein and Digestible Carbohydrate Content, Using Corn (Zea mays) As an Exemplar. *JoVE (Journal of Visualized Experiments)*, *138*, e58164. https://doi.org/10.3791/58164

DeLuca, T. H., Glanville, H. C., Harris, M., Emmett, B. A., Pingree, M. R. A., de Sosa, L. L., Cerdá-Moreno, C., & Jones, D. L. (2015). A novel biologically-based approach to evaluating soil phosphorus availability across complex landscapes. *Soil Biology and Biochemistry*, *88*, 110–119. https://doi.org/10.1016/j.soilbio.2015.05.016

Disney, R. H. L., Erzinclioglu, Y. Z., Henshaw, D. J. D. C., Howse, D., Unwin, D. M., Withers, P., & Woods, A. (1982). Collecting methods and the adequacy of attempted fauna surveys with reference to the Diptera. *Field Studies*, *5*(4), 607–622.

Dudenhoeffer, M., Roth, J. D., Johnson, L. K., & Petersen, S. D. (2021). Arctic fox winter dietary response to damped lemming cycles estimated from fecal DNA. *Journal of Mammalogy*, *102*(6), 1455–1465. https://doi.org/10.1093/jmammal/gyab115

Dunbar, M. J. (1970). The scientific importance of the circumpolar region, and its flora and fauna. *Productivity and Conservation in Northern Circumpolar Lands*, 71.

Ehrich, D., Schmidt, N. M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., Ecke, F., Eide, N. E., Framstad, E., Frandsen, J., Franke, A., Gilg, O., Giroux, M.-A., Henttonen, H., Hörnfeldt, B., Ims, R. A., Kataev, G. D., Kharitonov, S. P., Killengreen, S. T., … Solovyeva, D. V. (2020). Documenting lemming population change in the Arctic: Can we detect trends? *Ambio*, *49*(3), 786–800. https://doi.org/10.1007/s13280-019-01198-7

Elmhagen, B., Tannerfeldt, M., Verucci, P., & Angerbjörn, A. (2000). The arctic fox (Alopex lagopus): An opportunistic specialist. *Journal of Zoology*, *251*(2), 139–149. https://doi.org/10.1111/j.1469-7998.2000.tb00599.x

Environment and Climate Change Canada. (2019). *Canada's changing climate report.* (E. Bush & D. S. Lemmen, Eds.). http://publications.gc.ca/collections/collection_2019/eccc/En4-368-2019-eng.pdf

Environment and Climate Change Canada. (2024a). *Canadian Climate Normals 1991-2020 Data—Climate—Environment and Climate Change Canada*. Government of Canada. https://climate.weather.gc.ca/climate_normals/results_1991_2020_e.html?searchType=stnName_1991&txtStationName_1991=Churchill&searchMethod=contains&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=2200000000&dispBack=1

Environment and Climate Change Canada. (2024b). *Historical Data—Climate—Environment and Climate Change Canada*. Government of Canada. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Epstein, H. E., Myers-Smith, I., & Walker, D. A. (2013). Recent dynamics of arctic and sub-arctic vegetation. *Environmental Research Letters*, *8*(1), 015040. https://doi.org/10.1088/1748-9326/8/1/015040

Eriksen, B., Bölter, M., Breen, K., Henry, G., Lévesque, E., Mattson, J.-E., Parker, C. L., & Rayback, S. (2006). Environment and site descriptions of an ecological baseline study in the Canadian Arctic: The Tundra Northwest Expedition 1999 (Nunavut and Northwest Territories, Canada). *Polarforschung*, *73*(2/3), 77–88.

Ernst, C. M., Loboda, S., & Buddle, C. M. (2016). Capturing northern biodiversity: Diversity of arctic, subarctic and north boreal beetles and spiders are affected by trap type and habitat. *Insect Conservation and Diversity*, *9*(1), 63–73. https://doi.org/10.1111/icad.12143

Euskirchen, E. S., Bennett, A. P., Breen, A. L., Genet, H., Lindgren, M. A., Kurkowski, T. A., McGuire, A. D., & Rupp, T. S. (2016). Consequences of changes in vegetation and snow cover for climate feedbacks in Alaska and northwest Canada. *Environmental Research Letters*, *11*(10), 105003. https://doi.org/10.1088/1748-9326/11/10/105003

Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, *78*(1), 9–19. https://doi.org/10.1007/BF00377192

Evans, J. R., & Poorter, H. (2001). Photosynthetic acclimation of plants to growth irradiance: The relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell & Environment*, *24*(8), 755–767. https://doi.org/10.1046/j.1365-3040.2001.00724.x

Fafard, P. M., Roth, J. D., & Markham, J. H. (2020). Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. *Journal of Vegetation Science, 31*(1), 173–179. https://doi.org/10.1111/jvs.12828

Fisher, J. P., Estop-Aragonés, C., Thierry, A., Charman, D. J., Wolfe, S. A., Hartley, I. P., Murton, J. B., Williams, M., & Phoenix, G. K. (2016). The influence of vegetation and soil characteristics on active-layer thickness of permafrost soils in boreal forest. *Global Change Biology, 22*, 3127–3140.

Florko, K. R. N., Bernhardt, W., Breiter, C.-J. C., Ferguson, S. H., Hainstock, M., Young, B. G., & Petersen, S. D. (2018). Decreasing sea ice conditions in western Hudson Bay and an increase in abundance of harbour seals (Phoca vitulina) in the Churchill River. *Polar Biology, 41*(6), 1187–1195. https://doi.org/10.1007/s00300-018-2277-6

Forkel, M., Carvalhais, N., Rödenbeck, C., Keeling, R., Heimann, M., Thonicke, K., Zaehle, S., & Reichstein, M. (2016). Enhanced seasonal CO2 exchange caused by amplified plant productivity in northern ecosystems. *Science, 351*(6274), 696–699. https://doi.org/10.1126/science.aac4971

Freschet, G. T., Swart, E. M., & Cornelissen, J. H. C. (2015). Integrated plant phenotypic responses to contrasting above- and below-ground resources: Key roles of specific leaf area and root mass fraction. *New Phytologist, 206*(4), 1247–1260. https://doi.org/10.1111/nph.13352

Gable, T. D., Johnson-Bice, S. M., Homkes, A. T., Windels, S. K., & Bump, J. K. (2020). Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. *Science Advances, 6*(46), eabc5439. https://doi.org/10.1126/sciadv.abc5439

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. (2004). Plant Functional Markers Capture Ecosystem Properties During Secondary Succession. *Ecology*, *85*(9), 2630–2637. https://doi.org/10.1890/03-0799

Gharajehdaghipour, T., & Roth, J. D. (2018). Predators attract prey through ecosystem engineering in the Arctic. *Ecosphere*, *9*(1), e02077. https://doi.org/10.1002/ecs2.2077

Gharajehdaghipour, 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

Ghirardo, A., Lindstein, F., Koch, K., Buegger, F., Schloter, M., Albert, A., Michelsen, A., Winkler, J. B., Schnitzler, J.-P., & Rinnan, R. (2020). Origin of volatile organic compound emissions from subarctic tundra under global warming. *Global Change Biology*, *26*(3), 1908–1925. https://doi.org/10.1111/gcb.14935

Gough, L., Bass, H., & McLaren, J. R. (2015). Effects of Increased Soil Nutrients on Seed Rain: A Role for Seed Dispersal in the Greening of the Arctic? *Arctic, Antarctic, and Alpine Research*, *47*(1), 27–34. https://doi.org/10.1657/AAAR0014-055

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*(2), 211–218. https://doi.org/10.2307/1552473

Gould, S. J. (1988). Kropotkin was no crackpot. *Natural History*, *97*(7), 12–21.

Graae, B. J., Pagh, S., & Bruun, H. H. (2004). An Experimental Evaluation of the Arctic Fox (Alopex lagopus) as a Seed Disperser. *Arctic, Antarctic, and Alpine Research*, *36*(4), 468–473. https://doi.org/10.1657/1523-0430(2004)036[0468:AEEOTA]2.0.CO;2

Grünberg, I., Wilcox, E. J., Zwieback, S., Marsh, P., & Boike, J. (2020). Linking tundra vegetation, snow, soil temperature, and permafrost. *Biogeosciences*, *17*(16), 4261–4279. https://doi.org/10.5194/bg-17-4261-2020

Gupta, K., Mukhopadhyay, A., Babb, D. G., Barber, D. G., & Ehn, J. K. (2022). Landfast sea ice in Hudson Bay and James Bay: Annual cycle, variability and trends, 2000–2019. *Elementa: Science of the Anthropocene*, *10*(1), 00073. https://doi.org/10.1525/elementa.2021.00073

Hansen, J. E., Sato, M., Simons, L., Nazarenko, L. S., Sangha, I., Kharecha, P., Zachos, J. C., von Schuckmann, K., Loeb, N. G., Osman, M. B., Jin, Q., Tselioudis, G., Jeong, E., Lacis, A., Ruedy, R., Russell, G., Cao, J., & Li, J. (2023). Global warming in the pipeline. *Oxford Open Climate Change*, *3*(1), kgad008. https://doi.org/10.1093/oxfclm/kgad008

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S., & Wilson, W. G. (2007). Ecosystem engineering in space and time. *Ecology Letters*, *10*(2), 153–164. https://doi.org/10.1111/j.1461-0248.2006.00997.x

He, Q., & Bertness, M. D. (2014). Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, *95*(6), 1437–1443. https://doi.org/10.1890/13-2226.1

He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *ECOLOGY LETTERS*, *16*(5), 695–706. https://doi.org/10.1111/ele.12080

Heijmans, M. M. P. D., Magnússon, R. Í., Lara, M. J., Frost, G. V., Myers-Smith, I. H., van Huissteden, J., Jorgenson, M. T., Fedorov, A. N., Epstein, H. E., Lawrence, D. M., & Limpens, J. (2022). Tundra vegetation change and impacts on permafrost. *Nature*

Reviews Earth & Environment, *3*(1), Article 1. https://doi.org/10.1038/s43017-021-00233-0

Hewitt, R. E., Alexander, H. D., Miller, S. N., & Mack, M. C. (2022). Root-associated fungi not tree density influences stand nitrogen dynamics at the larch forest–tundra ecotone. *Journal of Ecology*, *110*(6), 1419–1431. https://doi.org/10.1111/1365-2745.13882

Hewitt, R. E., DeVan, M. R., Lagutina, I. V., Genet, H., McGuire, A. D., Taylor, D. L., & Mack, M. C. (2020). Mycobiont contribution to tundra plant acquisition of permafrost-derived nitrogen. *New Phytologist*, *226*(1), 126–141. https://doi.org/10.1111/nph.16235

Hicks, L. C., Leizeaga, A., Rousk, K., Michelsen, A., & Rousk, J. (2020). Simulated rhizosphere deposits induce microbial N-mining that may accelerate shrubification in the subarctic. *Ecology*, *101*(9), e03094. https://doi.org/10.1002/ecy.3094

Hobbie, J. E., & Hobbie, E. A. (2006). 15n in Symbiotic Fungi and Plants Estimates Nitrogen and Carbon Flux Rates in Arctic Tundra. *Ecology*, *87*(4), 816–822. https://doi.org/10.1890/0012-9658(2006)87[816:NISFAP]2.0.CO;2

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *ECOLOGICAL MONOGRAPHS*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346–363.

Høye, T. T., Mølgaard Ellebjerg, S., & Philipp, M. (2007). The Impact of Climate on Flowering in the High Arctic—The Case of Dryas in a Hybrid Zone. *Arctic, Antarctic, and Alpine Research*, *39*(3), 412–421. https://doi.org/10.1657/1523-0430(06-018)[HOYE]2.0.CO;2

Høye, T. T., & Sikes, D. S. (2013). Arctic entomology in the 21st century. *The Canadian Entomologist*, *145*(2), 125–130. https://doi.org/10.4039/tce.2013.14

Hudson, J. M. G., & Henry, G. H. R. (2009). Increased Plant Biomass in a High Arctic Heath Community from 1981 to 2008. *Ecology*, *90*(10), 2657–2663.

IPCC. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, Ö. Yelekçi, R. Yu, & B. Zhou, Eds.). Cambridge University Press.

Johnson, N. C., Graham, J. H., & Smith, F. A. (1997). Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *The New Phytologist*, *135*(4), 575–585. https://doi.org/10.1046/j.1469-8137.1997.00729.x

Johnson-Bice, S. M., Baldwin, F. B., Richardson, E., & Roth, J. D. (2024). *Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice*. https://ecoevorxiv.org/repository/view/7384/

Johnson-Bice, S. M., Gable, T. D., Roth, J. D., & Bump, J. K. (2023). Patchy indirect effects of predation: Predators contribute to landscape heterogeneity and ecosystem function via localized pathways. *Oikos*, *2023*(10), e10065. https://doi.org/10.1111/oik.10065

Johnson-Bice, S. M., Roth, J. D., & Markham, J. H. (2023). A Cosmic View of "Tundra Gardens": Satellite Imagery Provides a Landscape-Scale Perspective of Arctic Fox Ecosystem Engineering. *ECOSYSTEMS*, *26*(8), 1670–1684. https://doi.org/10.1007/s10021-023-00857-x

Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., & Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*(12), 1862–1869.

Jones, C. G., Lawton, J. H., & Shachak, M. (1996). Organisms as Ecosystem Engineers. In F. B. Samson & F. L. Knopf (Eds.), *Ecosystem Management: Selected Readings* (pp. 130–147). Springer. https://doi.org/10.1007/978-1-4612-4018-1_14

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kalra, Y. P., & Maynard, D. G. (1991). *Methods manual for forest soil and plant analysis* (Vol. 319E). http://scf.rncan.gc.ca/publications?id=11845

Keuper, F., van Bodegom, P. M., Dorrepaal, E., Weedon, J. T., van Hal, J., van Logtestijn, R. S. P., & Aerts, R. (2012). A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, *18*(6), 1998–2007. https://doi.org/10.1111/j.1365-2486.2012.02663.x

Khan, S. A., Mulvaney, R. L., & Hoeft, R. G. (2000). Direct-Diffusion Methods for Inorganic-Nitrogen Analysis of Soil. *Soil Science Society of America Journal*, *64*(3), 1083–1089. https://doi.org/10.2136/sssaj2000.6431083x

Knops, J. M., & Reinhart, K. (2000). Specific Leaf Area Along a Nitrogen Fertilization Gradient. *The American Midland Naturalist*, *144*(2), 265–272. https://doi.org/10.1674/0003-0031(2000)144[0265:SLAAAN]2.0.CO;2

Kohls, S. J., Thimmapuram, J., Buschena, C. A., Paschke, M. W., & Dawson, J. O. (1994). Nodulation patterns of actinorhizal plants in the family rosaceae. *Plant and Soil*, *162*(2), 229–239. https://doi.org/10.1007/BF01347710

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring Beta Diversity for Presence-Absence Data. *Journal of Animal Ecology*, *72*(3), 367–382.

Kropotkin, P. (1902). *Mutual Aid: A Factor of Evolution*. McClure Phillips & Co.

Kudo, G., Molau, U., & Wada, N. (2001). Leaf-trait Variation of Tundra Plants along a Climatic Gradient: An Integration of Responses in Evergreen and Deciduous Species. *Arctic, Antarctic, and Alpine Research*, *33*(2), 181–190. https://doi.org/10.1080/15230430.2001.12003421

Kushner, P. J., Mudryk, L. R., Merryfield, W., Ambadan, J. T., Berg, A., Bichet, A., Brown, R., Derksen, C., Déry, S. J., Dirkson, A., Flato, G., Fletcher, C. G., Fyfe, J. C., Gillett, N., Haas, C., Howell, S., Laliberté, F., McCusker, K., Sigmond, M., … Zwiers, F. W. (2018). Canadian snow and sea ice: Assessment of snow, sea ice, and related climate processes in Canada's Earth system model and climate-prediction system. *The Cryosphere*, *12*(4), 1137–1156. https://doi.org/10.5194/tc-12-1137-2018

Landhäusser, S. M., Chow, P. S., Dickman, L. T., Furze, M. E., Kuhlman, I., Schmid, S., Wiesenbauer, J., Wild, B., Gleixner, G., & Hartmann, H. (2018). Standardized protocols and procedures can precisely and accurately quantify non-structural carbohydrates. *Tree Physiology*, *38*(12), 1764–1778.

Liu, Y., Riley, W. J., Keenan, T. F., Mekonnen, Z. A., Holm, J. A., Zhu, Q., & Torn, M. S. (2022). Dispersal and fire limit Arctic shrub expansion. *Nature Communications*, *13*(1), 3843. https://doi.org/10.1038/s41467-022-31597-6

Markham, J. H. (2009). Does Dryas integrifolia fix nitrogen? *Botany*, *87*(11), 1106–1109. https://doi.org/10.1139/B09-071

Marschner, P., & Rengel, Z. (Eds.) (with Stark, S.). (2007). *Nutrient Cycling in Terrestrial Ecosystems* (Vol. 10). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-68027-7

Martinez Arbizu, P. (2021). *pairwiseAdonis: Pairwise multilevel comparison using adonis* [R package version 0.4]. https://github.com/pmartinezarbizu/pairwiseAdonis

Martini, I. P. (1989). The Hudson Bay Lowland: Major geologic features and assets. In W. J. M. van der Linden, S. A. P. L. Cloetingh, J. P. K. Kaasschieter, W. J. E. van de Graaff, J. Vandenberghe, & J. A. M. van der Gun (Eds.), *Coastal Lowlands: Geology and Geotechnology* (pp. 25–34). Springer Netherlands. https://doi.org/10.1007/978-94-017-1064-0_2

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1991). Primary and Secondary Production in Terrestrial Ecosystems. In J. Cole, G. Lovett, & S. Findlay (Eds.), *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories* (pp. 120–139). Springer. https://doi.org/10.1007/978-1-4612-3122-6_7

Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C., & Grant, R. F. (2021). Arctic tundra shrubification: A review of mechanisms and impacts on ecosystem carbon balance. *Environmental Research Letters*, *16*(5), 053001. https://doi.org/10.1088/1748-9326/abf28b

Meltofte, H., Barry, T., Berteaux, D., Bültmann, H., Christiansen, J. S., Cook, J. A., Dahlberg, A., Daniëls, F. J. A., Ehrich, D., Fjeldså, J., Friðriksson, F., Ganter, B., Gaston, A. J., Gillespie, L. J., Grenoble, L., Hoberg, E. P., Hodkinson, I. D., Huntington, H. P., Ims, R. A., … Wrona, F. J. (2013). *Arctic Biodiversity Assessment: Status and trends in Arctic biodiversity*. Conservation of Arctic Flora and Fauna (CAFF). https://oaarchive.arctic-council.org/handle/11374/232

Michelsen, A., Quarmby, C., Sleep, D., & Jonasson, S. (1998). Vascular plant 15N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia*, *115*(3), 406–418. https://doi.org/10.1007/s004420050535

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013a). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013b). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Monk, J. D., & Schmitz, O. J. (2022). Landscapes shaped from the top down: Predicting cascading predator effects on spatial biogeochemistry. *Oikos*, *2022*(5), e08554. https://doi.org/10.1111/oik.08554

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20152434. https://doi.org/10.1098/rspb.2015.2434

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A., Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., … Wipf, S. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, *10*(2), Article 2. https://doi.org/10.1038/s41558-019-0688-1

Natali, S. M., Watts, J. D., Rogers, B. M., Potter, S., Ludwig, S. M., Selbmann, A.-K., Sullivan, P. F., Abbott, B. W., Arndt, K. A., Birch, L., Björkman, M. P., Bloom, A. A., Celis, G., Christensen, T. R., Christiansen, C. T., Commane, R., Cooper, E. J., Crill, P., Czimczik, C., … Zona, D. (2019). Large loss of CO2 in winter observed across the northern permafrost region. *Nature Climate Change*, *9*(11), 852–857. https://doi.org/10.1038/s41558-019-0592-8

Nielsen, S. M., Pedersen, V., & Klitgaard, B. B. (1994). Arctic Fox (Alopex lagopus) Dens in the Disko Bay Area, West Greenland. *Arctic*, *47*(4), 327–333.

Oksanen, J. (2022, October 11). *Package "vegan."* CRAN. https://github.com/vegandevs/vegan

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). The vegan package. *Community Ecology Package*, *10*(631–637), 719.

Olsen, S. R. (1954). *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*. U.S. Department of Agriculture.

Pandey, D., Kehri, H. K., Zoomi, I., Akhtar, O., & Singh, A. K. (2019). Mycorrhizal Fungi: Biodiversity, Ecological Significance, and Industrial Applications. In A. N. Yadav, S. Mishra, S. Singh, & A. Gupta (Eds.), *Recent Advancement in White Biotechnology Through Fungi: Volume 1: Diversity and Enzymes Perspectives* (pp. 181–199). Springer International Publishing. https://doi.org/10.1007/978-3-030-10480-1_5

Paradis, M., Lévesque, E., & Boudreau, S. (2016). Greater effect of increasing shrub height on winter versus summer soil temperature. *Environmental Research Letters*, *11*(8), 085005. https://doi.org/10.1088/1748-9326/11/8/085005

Parrot. (2021). *Parrot Sequoia+ multispectral drone camera*. Parrot. https://www.parrot.com/en/support/documentation/sequoia

Parsons, A. N., Welker, J. M., Wookey, P. A., Press, M. C., Callaghan, T. V., & Lee, J. A. (1994). Growth Responses of Four Sub-Arctic Dwarf Shrubs to Simulated Environmental Change. *Journal of Ecology*, *82*(2), 307–318. https://doi.org/10.2307/2261298

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*(7), Article 7. https://doi.org/10.1038/nclimate1858

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, *46*(1), 15–27. https://doi.org/10.3354/cr00936

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change.

Trends in Ecology & Evolution, *20*(9), 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Pix4D. (2023a). *Pix4Dcapture* [Windows]. Pix4D SA. https://www.pix4d.com/product/pix4dcapture/

Pix4D. (2023b). *Pix4Dfields* [Windows]. Pix4D SA. https://www.pix4d.com/product/pix4dfields/

Poorter, H., & Evans, J. R. (1998). Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia*, *116*(1), 26–37. https://doi.org/10.1007/s004420050560

Poorter, H., & Ryser, P. (2015). The limits to leaf and root plasticity: What is so special about specific root length? *The New Phytologist*, *206*(4), 1188–1190.

Prabhu, N., Borkar, S., & Garg, S. (2019). Chapter 11 - Phosphate solubilization by microorganisms: Overview, mechanisms, applications and advances. In S. N. Meena & M. M. Naik (Eds.), *Advances in Biological Science Research* (pp. 161–176). Academic Press. https://doi.org/10.1016/B978-0-12-817497-5.00011-2

Prestrud, P. (1992). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Svalbard. *Arctic*, *45*(2), 154–158.

QGIS Development team. (2023). *QGIS Geographic Information System* (3.30.3) [Windows]. QGIS Association. https://www.qgis.org/

Rasband, W. S. (1997). *ImageJ* [Computer software]. U. S. National Institutes of Health. https://imagej.nih.gov/ij/

Rasmussen, L. H., Zhang, W., Ambus, P., Michelsen, A., Jansson, P.-E., Kitzler, B., & Elberling, B. (2022). Nitrogen transport in a tundra landscape: The effects of early and late growing

season lateral N inputs on arctic soil and plant N pools and N2O fluxes. *Biogeochemistry*, *157*(1), 69–84. https://doi.org/10.1007/s10533-021-00855-y

Read, D. J., Leake, J. R., & Perez-Moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany*, *82*(8), 1243–1263. https://doi.org/10.1139/b04-123

Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, *157*(3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P. B., Ellsworth, D. S., & Walters, M. B. (1998). Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: Evidence from within and across species and functional groups. *Functional Ecology*, *12*(6), 948–958. https://doi.org/10.1046/j.1365-2435.1998.00274.x

Reimchen, T. E. (2017). Diverse Ecological Pathways of Salmon Nutrients Through an Intact Marine-terrestrial Interface. *The Canadian Field-Naturalist*, *131*(4), Article 4. https://doi.org/10.22621/cfn.v131i4.1965

Reimchen, T. E., & Fox, C. H. (2013). Fine-scale spatiotemporal influences of salmon on growth and nitrogen signatures of Sitka spruce tree rings. *BMC Ecology*, *13*(1), 38. https://doi.org/10.1186/1472-6785-13-38

Richardson, S. J., Press, M. C., Parsons, A. N., & Hartley, S. E. (2002). How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a

sub-Arctic heath. *Journal of Ecology*, *90*(3), 544–556. https://doi.org/10.1046/j.1365-2745.2002.00681.x

Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, *145*(1), 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Rosenzweig, M. L., & MacArthur, R. H. (1963). Graphical Representation and Stability Conditions of Predator-Prey Interactions. *The American Naturalist*, *97*(895), 209–223. https://doi.org/10.1086/282272

Roth, J. D. (2002). Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*, *133*(1), 70–77. https://doi.org/10.1007/s00442-002-1004-7

Roth, J. D. (2003). Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology*, *72*(4), 668–676. https://doi.org/10.1046/j.1365-2656.2003.00739.x

Roy, A., Gough, L., Boelman, N. T., Rowe, R. J., Griffin, K. L., & McLaren, J. R. (2022). Small but mighty: Impacts of rodent-herbivore structures on carbon and nutrient cycling in arctic tundra. *Functional Ecology*, *36*(9), 2331–2343. https://doi.org/10.1111/1365-2435.14127

Schimel, J. P., Bilbrough, C., & Welker, J. M. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, *36*(2), 217–227. https://doi.org/10.1016/j.soilbio.2003.09.008

Schmidt, N. M., Ims, R. A., Høye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhamme, M. C., & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proceedings: Biological Sciences*, *279*(1746), 4417–4422.

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. https://doi.org/10.1111/j.1461-0248.2010.01511.x

Scott, D., Malcolm, J. R., & Lemieux, C. (2002). Climate change and modelled biome representation in Canada's national park system: Implications for system planning and park mandates. *Global Ecology and Biogeography*, *11*(6), 475–484. https://doi.org/10.1046/j.1466-822X.2002.00308.x

Serreze, M. C., Walsh, J. E., Chapin, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., & Barry, R. G. (2000). Observational Evidence of Recent Change in the Northern High-Latitude Environment. *Climatic Change*, *46*(1), 159–207. https://doi.org/10.1023/A:1005504031923

Shaver, G. R., & Chapin, F. S. (1991). Production: Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs*, *61*(1), 1–31. https://doi.org/10.2307/1942997

Shevtsova, A., Ojala, A., Neuvonen, S., Vieno, M., & Haukioja, E. (1995). Growth and Reproduction of Dwarf Shrubs in a Subarctic Plant Community: Annual Variation and Above-Ground Interactions with Neighbours. *Journal of Ecology*, *83*(2), 263–275. https://doi.org/10.2307/2261565

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de L. Dantas, V., de Bello, F., Duarte,

L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

Simpson, E. H. (1949). Measurement of Diversity. *Nature*, *163*(4148), 688–688. https://doi.org/10.1038/163688a0

Skrede, I., Eidesen, P. B., PorTELa, R. P., & Brochmann, C. (2006). Refugia, differentiation and postglacial migration in arctic-alpine Eurasia, exemplified by the mountain avens (Dryas octopetala L.). *Molecular Ecology*, *15*(7), 1827–1840. https://doi.org/10.1111/j.1365-294X.2006.02908.x

Smith, C. A. S., Smits, C. M. M., & Slough, B. G. (1992). Landform Selection and Soil Modifications Associated with Arctic Fox (Alopex lagopus) Den Sites in Yukon Territory, Canada. *Arctic and Alpine Research*, *24*(4), 324–328. https://doi.org/10.1080/00040851.1992.12002964

Smits, C. M. M., Smith, C. A. S., & Slough, B. G. (1988). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Northern Yukon Territory, Canada. *Arctic*, *41*(1), 12–16.

Standen, K. M., Sniderhan, A. E., Sonnentag, O., Voigt, C., & Baltzer, J. L. (2024). Response of Boreal Plant Communities and Forest Floor Carbon Fluxes to Experimental Nutrient Additions. *Ecosystems*. https://doi.org/10.1007/s10021-023-00899-1

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press.

Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J., & Romanovsky, V. E. (2005). Winter Biological Processes Could Help

Convert Arctic Tundra to Shrubland. *BioScience*, *55*(1), 17–26. https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Sullivan, P. F., Ellison, S. B. Z., McNown, R. W., Brownlee, A. H., & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, *96*(3), 716–727. https://doi.org/10.1890/14-0626.1

Swann, A. L., Fung, I. Y., Levis, S., Bonan, G. B., & Doney, S. C. (2010). Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. *Proceedings of the National Academy of Sciences*, *107*(4), 1295–1300. https://doi.org/10.1073/pnas.0913846107

Tannerfeldt, M., & Angerbjörn, A. (1996). Life history strategies in a fluctuating environment: Establishment and reproductive success in the arctic fox. *Ecography*, *19*(3), 209–220. https://doi.org/10.1111/j.1600-0587.1996.tb01247.x

Tannerfeldt, M., Moehrenschlager, A., & Angerbjörn, A. (2003). Den ecology of swift, kit and arctic foxes: A review. *The Swift Fox: Ecology and Conservation of Swift Foxes in a Changing World*, 167–181.

Thomas, D. B. (2008). Nontoxic Antifreeze for Insect Traps. *Entomological News*, *119*(4), 361–365. https://doi.org/10.3157/0013-872X-119.4.361

Timoney, K., Laroi, G., & Dale, M. (1993). Sub-Arctic Forest-Tundra Vegetation Gradients—The Sigmoid Wave Hypothesis. *Journal of Vegetation Science*, *4*(3), 387–394. https://doi.org/10.2307/3235597

Van Cleve, K., & Alexander, V. (1981). Nitrogen Cycling in Tundra and Boreal Ecosystems. *Ecological Bulletins*, *33*, 375–404.

von Beckerath, X., Benadi, G., Gilg, O., Sittler, B., Yannic, G., Klein, A.-M., & Eitzinger, B. (2022). Long-term monitoring reveals topographical features and vegetation that explain winter habitat use of an Arctic rodent. *Arctic Science*, *8*(2), 349–361. https://doi.org/10.1139/as-2021-0010

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschleger, S. D., & Woodward, F. I. (2014). The relationship of leaf photosynthetic traits – Vcmax and Jmax – to leaf nitrogen, leaf phosphorus, and specific leaf area: A meta-analysis and modeling study. *Ecology and Evolution*, *4*(16), 3218–3235. https://doi.org/10.1002/ece3.1173

Walker, D. A., Epstein, H. E., Raynolds, M. K., Kuss, P., Kopecky, M. A., Frost, G. V., Daniëls, F. J. A., Leibman, M. O., Moskalenko, N. G., Matyshak, G. V., Khitun, O. V., Khomutov, A. V., Forbes, B. C., Bhatt, U. S., Kade, A. N., Vonlanthen, C. M., & Tichý, L. (2012). Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. *Environmental Research Letters*, *7*(1), 015504. https://doi.org/10.1088/1748-9326/7/1/015504

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & Team, C. (2005). The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science*, *16*(3), 267–282.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnússon, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., … Wookey, P. A. (2006). Plant community responses to

experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, *103*(5), 1342–1346. https://doi.org/10.1073/pnas.0503198103

Wang, W., Scali, M., Vignani, R., Spadafora, A., Sensi, E., Mazzuca, S., & Cresti, M. (2003). Protein extraction for two-dimensional electrophoresis from olive leaf, a plant tissue containing high levels of interfering compounds. *ELECTROPHORESIS*, *24*(14), 2369–2375. https://doi.org/10.1002/elps.200305500

Werner, E. E., & Peacor, S. D. (2003). A Review of Trait-Mediated Indirect Interactions in Ecological Communities. *Ecology*, *84*(5), 1083–1100. https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Wielgolaski, F. E., Sømme, L., Thórhallsdóttir, T. E., Grabherr, G., Malinovsky, K. A., Zlotin, R. I., Miehe, G., Hedberg, O., Killick, D. J. B., & Campbell, J. S. (1997). *Polar and alpine tundra*. Elsevier Science Publishing Company, Inc. https://elibrary.ru/item.asp?id=26450837

Wilmers, C. C., Estes, J. A., Edwards, M., Laidre, K. L., & Konar, B. (2012). Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment*, *10*(8), 409–415. https://doi.org/10.1890/110176

Wrigley, R. E., & Hatch, D. R. M. (1976). Arctic Fox Migrations in Manitoba. *Arctic*, *29*(3), 147–158.

Wyant, K. A., Draney, M. L., & Moore, J. C. (2011). Epigeal Spider (Araneae) Communities in Moist Acidic and Dry Heath Tundra at Toolik Lake, Alaska. *Arctic, Antarctic, and Alpine Research*, *43*(2), 301–312. https://doi.org/10.1657/1938-4246-43.2.301

Yang, H., Zhao, X., Liu, C., Bai, L., Zhao, M., & Li, L. (2018). Diversity and characteristics of colonization of root-associated fungi of Vaccinium uliginosum. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-33634-1

Zhao, S.-T., Johnson-Bice, S. M., & Roth, J. D. (2022). Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. *Global Ecology and Conservation*, *40*, e02310. https://doi.org/10.1016/j.gecco.2022.e02310

Zou, K., Thébault, E., Lacroix, G., & Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*, *30*(8), 1454–1465.

Chapter 4: Conclusion

This thesis demonstrates that Arctic foxes do possess the capacity to engineer the terrestrial communities on their dens. Arctic foxes increase the availability of limiting soil resources by concentrating prey-derived nutrients on their dens (Gharajehdaghipour et al., 2016), and I show that this increase can jumpstart ecosystem processes. This alteration of the environment allows for a positive feedback of niche growth and facilitation, increasing primary production and allowing establishment of new plant species that facilitate further community succession, ultimately creating habitat that is preferred by *Dicrostonyx* lemmings. This project confirms a causal link between foxes and den vegetation that has been hypothesized for over half a century (Chesemore, 1969). The effects of this fox-nutrient mechanism have been described by previous studies (Bruun et al., 2005; Chesemore, 1969; Fafard et al., 2020; Gharajehdaghipour et al., 2016; Gharajehdaghipour & Roth, 2018; Johnson-Bice, Roth, et al., 2023; Smith et al., 1992; Zhao et al., 2022) but the mechanism itself has never before been experimentally supported. My thesis fills this small but critical gap in the literature on the ecosystem engineering of Arctic foxes and contributes to the wider study of ecosystem functioning in tundra communities.

In Chapter 2, I studied the effects of an increased N and P deposition rate calculated from Arctic fox activity on a representative plant community and the resultant feedbacks. I examined the affected soil pools, the plant community shift, the parallel effects of snow depth increased by trapped snow, and the cascading second-level trophic effects. I showed that this increased annual deposition of limiting nutrients causes invasion by more productive, taller plants that can accumulate more winter snow and that increased snow cover thickness can accelerate plant community shifts when combined with the nutrient subsidy. These treatments not only drove experimental plot communities to more rapidly diverge from controls when combined, but also

more directly increased the similarity of these communities with the atypical plant communities of Arctic fox dens (Fafard et al., 2020), implying that this specific combination of snow and nutrient deposition shapes those communities. As time progresses, I expect the plot communities that receive only our fertilizer treatment to increase snow depth and their annual increases in similarity to fox dens to accelerate. The increasing abundance and richness of arthropod communities in response to the added nutrients and the greater magnitude of this response with snow/nutrient combination highlights the increasing productivity and functional complexity of these tundra communities. This result adds to the documented responses of sessile species (Fafard et al., 2020) and highly mobile species (Zhao et al., 2022) at these dens and contributes to the understudied ecology of arctic insects (Høye & Sikes, 2013). The lemming sign reported in this chapter serve to further support and clarify the findings of Gharajehdaghipour and Roth (2018); I show a clear preference in lemming space use for the same combination of habitat features but without any questions of deterrence by fox presence and can demonstrate that the combination of snow and nutrients was again preferred. The one caveat of this strong lemming preference is the greater proportional ground cover of *Dryas* shrubs in these plots than at fox dens. This extreme combination of *Dryas* cover dominance and snow depth does not exist naturally and *Dryas* cover is a key food resource for *Dircostonyx* lemmings (von Beckerath et al., 2022).

In Chapter 3, I described the plastic response in leaf economic traits of prostrate shrubs that predate the experiment. These plants dominate *Dryas* heath communities where local Arctic foxes den (Brook & Kenkel, 2002; Johnson-Bice, Roth, et al., 2023) and are the slowest-growing and hardiest of the vascular plants found on these dens (Bliss et al., 1973; Büntgen et al., 2015; Fafard et al., 2020). So, an intraspecific productive response in these plants not only highlights

how a subsidy of limiting nutrients (that these foxes are capable of) can affect growth in the short term but suggests that the invasion of grasses could be in part facilitated by more productive prostrate shrubs (He & Bertness, 2014). Bliss (1962) describes how these plants survive the impact of wind exposure on exposed ridges, and the same conditions that co-facilitate neighboring prostrate shrubs (He & Bertness, 2014; Milbau et al., 2013b; Shevtsova et al., 1995) could protect the roots and basal meristems of those first grass seedlings. It is possible that more productive prostrate shrubs could better stabilize microclimate and develop soils, and 'faster' leaf physiology would help them do both (Reich, 2014). The particular response of *Dryas integrifolia* in this chapter is notable here for its large Nearctic range and underrepresentation in the literature, (Billault-Penneteau et al., 2019; Markham, 2009; Skrede et al., 2006) as well as the unique deciduous leaf strategy, ability to melanize otherwise mineral soils, ectomycorrhizal associations, and responsive flower phenology of its genus (Billault-Penneteau et al., 2019; Bjorbækmo et al., 2010; Høye et al., 2007; Kudo et al., 2001; Skrede et al., 2006; Wielgolaski et al., 1997). Simply put, it could potentially be a foundation species (Dayton, 1972) for dry heath communities across North America and we would not know. Specific characteristics aside, I would speculate that this relatively high degree of leaf plasticity in prostrate shrubs is more likely to occur in deciduous than evergreen shrubs; these plants exhibit higher rates of respiration and productivity to begin with and annual leaves allow for more efficient resource investment under variable conditions (Bliss, 1962; Kudo et al., 2001). Previous studies have used total leaf N content to approximate N investment in photosynthesis, which appears to increase with SLA (Chapin et al., 1995; Evans, 1989; Kudo et al., 2001). The inverse relationship I found between SLA and soluble leaf protein in this productive leaf response raises so many questions it must be studied further: is it real, limited to *Dryas*, an arctic adaptation, a prostrate shrub strategy, etc.

Repeating the analyses with the addition of leaf N and comparing *D. integrifolia* leaves from 'productive' fox dens and 'unproductive' reference sites in Wapusk could be a good starting point with an easily larger sample size.

Together, these chapters detail the process by which Arctic foxes act as ecosystem engineers in the Hudson Bay Lowlands, lay out the theoretical foundations by which we understand it, and support the ability of Arctic foxes to act as ecosystem engineers in dry tundra heaths. More broadly, I connect this process to the overarching importance of consumers in Arctic nutrient cycling, the role of biogeochemical processes in facilitation and succession, and the contribution of local processes to the complex spatial patterns of greening observed in the Arctic. While the subarctic conditions and low latitude likely contributed to the responsiveness of these communities (Büntgen et al., 2015; Chapin et al., 1986; He & Bertness, 2014; Milbau et al., 2013b; D. A. Walker et al., 2012), these findings do suggest, through the processes at play, that key vegetation metrics (SLA, NDVI, and increasing cover dominance of one prostrate shrub species) could be used to predictively model the probability of invasion and community succession in tundra heath ecosystems with further study.

I was unable to directly assess the contribution of productive prostrate shrub responses to community NDVI and it should be examined in the future. The community effects of Arctic fox ecosystem engineering are far from fully described, and they provide an opportunity to study both the wildlife ecology of an ecosystem engineer in a changing environment and the foundational processes of functional ecology at a terrestrial extreme. Due to the 5-year scope of these analyses, none of the experimental plot communities can be said to mimic those of fox dens yet, but the progression is underway. I predict that the plant species composition of plot communities receiving fertilizer will become statistically similar to that of fox den communities

in the coming years, with plots receiving only fertilizer to reach this threshold more slowly than those with both fence and fertilizer treatments. These results demonstrate the dynamics and feedbacks that were hypothesized to change low-productivity tundra into high-productivity fox dens and show that they can be induced by nutrient additions on par with the deposition increased by Arctic fox activity. This thesis settles the "chicken or the egg" question of arctic foxes and den vegetation and provides a theoretical basis for future research.

4.1 References

Aleksandrova, V. D. (1970). The Vegetation of the Tundra Zones in the USSR and Data about its Productivity. *Productivity and Conservation in Northern Circumpolar Lands*.

An, T., Wang, F., Ren, L., Ma, S., Li, S., Liu, L., & Wang, J. (2022). Ratio of nitrate to ammonium mainly drives soil bacterial dynamics involved in nitrate reduction processes. *Applied Soil Ecology*, *169*, 104164. https://doi.org/10.1016/j.apsoil.2021.104164

Andresen, L. C., Bodé, S., Björk, R. G., Michelsen, A., Aerts, R., Boeckx, P., Cornelissen, J. H. C., Klanderud, K., van Logtestijn, R. S. P., & Rütting, T. (2022). Patterns of free amino acids in tundra soils reflect mycorrhizal type, shrubification, and warming. *Mycorrhiza*, *32*(3), 305–313. https://doi.org/10.1007/s00572-022-01075-4

Angerbjörn, A., Hersteinsson, P., & Tannerfeldt, M. (2004). Arctic foxes: Consequences of resource predictability in the Arctic fox—Two life history strategies. In D. W. MacDonald & C. Sillero-Zubiri (Eds.), *The Biology and Conservation of Wild Canids* (pp. 163–172). Oxford University Press.

Angerbjorn, A., Tannerfeldt, M., & Erlinge, S. (1999). Predator–prey relationships: Arctic foxes and lemmings. *Journal of Animal Ecology*, *68*(1), 34–49. https://doi.org/10.1046/j.1365-2656.1999.00258.x

Armstrong McKay, D. I., Staal, A., Abrams, J. F., Winkelmann, R., Sakschewski, B., Loriani, S., Fetzer, I., Cornell, S. E., Rockström, J., & Lenton, T. M. (2022). Exceeding 1.5°C global warming could trigger multiple climate tipping points. *Science*, *377*(6611), eabn7950. https://doi.org/10.1126/science.abn7950

Beck, P. S. A., & Goetz, S. J. (2011). Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: Ecological variability and regional differences. *Environmental Research Letters*, *6*(4), 045501. https://doi.org/10.1088/1748-9326/6/4/045501

Bergman, C. M., & Krebs, C. J. (1993). Diet overlap of collared lemmings and tundra voles at Pearce Point, Northwest Territories. *Canadian Journal of Zoology*, *71*(9), 1703–1709. https://doi.org/10.1139/z93-241

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Bieleski, R. L. (1973). Phosphate Pools, Phosphate Transport, and Phosphate Availability. *Annual Review of Plant Biology*, *24*(Volume 24, 1973), 225–252. https://doi.org/10.1146/annurev.pp.24.060173.001301

Billault-Penneteau, B., Sandré, A., Folgmann, J., Parniske, M., & Pawlowski, K. (2019). Dryas as a Model for Studying the Root Symbioses of the Rosaceae. *Frontiers in Plant Science*, *10*. https://www.frontiersin.org/article/10.3389/fpls.2019.00661

Bjorbækmo, M. F. M., Carlsen, T., Brysting, A., Vrålstad, T., Høiland, K., Ugland, K. I., Geml, J., Schumacher, T., & Kauserud, H. (2010). High diversity of root associated fungi in both alpine and arctic Dryas octopetala. *BMC Plant Biology*, *10*(1), 244. https://doi.org/10.1186/1471-2229-10-244

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., … Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, *562*(7725), 57–62. https://doi.org/10.1038/s41586-018-0563-7

Bledsoe, C., Klein, P., & Bliss, L. C. (1990). A survey of mycorrhizal plants on Truelove Lowland, Devon Island, N.W.T., Canada. *Canadian Journal of Botany*, *68*(9), 1848–1856. https://doi.org/10.1139/b90-242

Bleicher, S. S. (2017). The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ*, *5*, e3772. https://doi.org/10.7717/peerj.3772

Bliss, L. C. (1962). Adaptations of Arctic and Alpine Plants to Environmental Conditions. *Arctic*, *15*(2), 117–144.

Bliss, L. C., Courtin, G. M., Pattie, D. L., Riewe, R. R., Whitfield, D. W. A., & Widden, P. (1973). Arctic Tundra Ecosystems. *Annual Review of Ecology and Systematics*, *4*(1), 359–399. https://doi.org/10.1146/annurev.es.04.110173.002043

Bray, R. H., & Kurtz, L. T. (1945). DETERMINATION OF TOTAL, ORGANIC, AND AVAILABLE FORMS OF PHOSPHORUS IN SOILS. *Soil Science*, *59*(1), 39.

Bronstein, J. L. (2009). The evolution of facilitation and mutualism. *Journal of Ecology*, *97*(6), 1160–1170. https://doi.org/10.1111/j.1365-2745.2009.01566.x

Brook, R. K. (2001). *Structure and dynamics of the vegetation in Wapusk National Park and the Cape Churchill Wildlife Management Area of Manitoba, community and landscape scales* [Thesis, University of Manitoba]. http://hdl.handle.net/1993/2724

Brook, R. K., & Kenkel, N. C. (2002). A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing*, *23*(21), 4761–4776. https://doi.org/10.1080/01431160110113917

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., … Michalet, R. (2008). Facilitation in Plant Communities: The Past, the Present, and the Future. *Journal of Ecology*, *96*(1), 18–34.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, *18*(3), 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

Bruun, H. H., Österdahl, S., Moen, J., & Angerbjörn, A. (2005). Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography*, *28*(1), 81–87. https://doi.org/10.1111/j.0906-7590.2005.04033.x

Bucher, M. (2007). Functional Biology of Plant Phosphate Uptake at Root and Mycorrhiza Interfaces. *The New Phytologist*, *173*(1), 11–26.

Bulleri, F., Bruno, J. F., Silliman, B. R., & Stachowicz, J. J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, *30*(1), 70–78. https://doi.org/10.1111/1365-2435.12528

Büntgen, U., Hellmann, L., Tegel, W., Normand, S., Myers-Smith, I., Kirdyanov, A. V., Nievergelt, D., & Schweingruber, F. H. (2015). Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *Journal of Ecology*, *103*(2), 489–501.

Byers, J. E., & Noonburg, E. G. (2003). Scale Dependent Effects of Biotic Resistance to Biological Invasion. *Ecology*, *84*(6), 1428–1433. https://doi.org/10.1890/02-3131

Cairney, J. W. G. (2011). Ectomycorrhizal fungi: The symbiotic route to the root for phosphorus in forest soils. *Plant and Soil*, *344*(1), 51–71. https://doi.org/10.1007/s11104-011-0731-0

Callaway, R. M. (1995). Positive interactions among plants. *The Botanical Review*, *61*(4), 306–349. https://doi.org/10.1007/BF02912621

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*(6891), Article 6891. https://doi.org/10.1038/nature00812

Chalot, M., & Brun, A. (1998). Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiology Reviews*, *22*(1), 21–44. https://doi.org/10.1111/j.1574-6976.1998.tb00359.x

Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, *17*(7), 881–890. https://doi.org/10.1111/ele.12279

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., & Laundre, J. A. (1995). Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology*, *76*(3), 694–711. https://doi.org/10.2307/1939337

Chapin, F. S., Vitousek, P. M., & Van Cleve, K. (1986). The Nature of Nutrient Limitation in Plant Communities. *The American Naturalist*, *127*(1), 48–58.

Chesemore, D. L. (1969). Den ecology of the Arctic fox in northern Alaska. *Canadian Journal of Zoology*, *47*(1), 121–129. https://doi.org/10.1139/z69-021

Cornelissen, J. H. C., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S. P., Alatalo, J., Stuart Chapin, F., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A. E., Hik, D. S., Hofgaard, A., Jónsdóttir, I. S., Karlsson, S., Klein, J. A., Laundre, J., Magnusson, B., Michelsen, A., … Team, M. O. L. (2007). Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, *10*(7), 619–627. https://doi.org/10.1111/j.1461-0248.2007.01051.x

Craine, J. M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M., & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology*, *16*(5), 563–574. https://doi.org/10.1046/j.1365-2435.2002.00660.x

Dakos, V., Matthews, B., Hendry, A. P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M., & De Meester, L. (2019). Ecosystem tipping points in an evolving world. *Nature Ecology & Evolution*, *3*(3), 355–362. https://doi.org/10.1038/s41559-019-0797-2

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. Murray.

Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. *Proceedings of the Colloquium on Conservation Problems in Antarctica*, 81–96.

De Long, J. R., Sundqvist, M. K., Gundale, M. J., Giesler, R., & Wardle, D. A. (2016). Effects of elevation and nitrogen and phosphorus fertilization on plant defence compounds in subarctic tundra heath vegetation. *Functional Ecology*, *30*(2), 314–325. https://doi.org/10.1111/1365-2435.12493

Deans, C. A., Sword, G. A., Lenhart, P. A., Burkness, E., Hutchison, W. D., & Behmer, S. T. (2018). Quantifying Plant Soluble Protein and Digestible Carbohydrate Content, Using Corn (Zea mays) As an Exemplar. *JoVE (Journal of Visualized Experiments)*, *138*, e58164. https://doi.org/10.3791/58164

DeLuca, T. H., Glanville, H. C., Harris, M., Emmett, B. A., Pingree, M. R. A., de Sosa, L. L., Cerdá-Moreno, C., & Jones, D. L. (2015). A novel biologically-based approach to evaluating soil phosphorus availability across complex landscapes. *Soil Biology and Biochemistry*, *88*, 110–119. https://doi.org/10.1016/j.soilbio.2015.05.016

Disney, R. H. L., Erzinclioglu, Y. Z., Henshaw, D. J. D. C., Howse, D., Unwin, D. M., Withers, P., & Woods, A. (1982). Collecting methods and the adequacy of attempted fauna surveys with reference to the Diptera. *Field Studies*, *5*(4), 607–622.

Dudenhoeffer, M., Roth, J. D., Johnson, L. K., & Petersen, S. D. (2021). Arctic fox winter dietary response to damped lemming cycles estimated from fecal DNA. *Journal of Mammalogy*, *102*(6), 1455–1465. https://doi.org/10.1093/jmammal/gyab115

Dunbar, M. J. (1970). The scientific importance of the circumpolar region, and its flora and fauna. *Productivity and Conservation in Northern Circumpolar Lands*, 71.

Ehrich, D., Schmidt, N. M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., Ecke, F., Eide, N. E., Framstad, E., Frandsen, J., Franke, A., Gilg, O., Giroux, M.-A., Henttonen, H., Hörnfeldt, B., Ims, R. A., Kataev, G. D., Kharitonov, S. P., Killengreen, S. T., … Solovyeva, D. V. (2020). Documenting lemming population change in the Arctic: Can we detect trends? *Ambio*, *49*(3), 786–800. https://doi.org/10.1007/s13280-019-01198-7

Elmhagen, B., Tannerfeldt, M., Verucci, P., & Angerbjörn, A. (2000). The arctic fox (Alopex lagopus): An opportunistic specialist. *Journal of Zoology*, *251*(2), 139–149. https://doi.org/10.1111/j.1469-7998.2000.tb00599.x

Environment and Climate Change Canada. (2019). *Canada's changing climate report.* (E. Bush & D. S. Lemmen, Eds.). http://publications.gc.ca/collections/collection_2019/eccc/En4-368-2019-eng.pdf

Environment and Climate Change Canada. (2024a). *Canadian Climate Normals 1991-2020 Data—Climate—Environment and Climate Change Canada*. Government of Canada. https://climate.weather.gc.ca/climate_normals/results_1991_2020_e.html?searchType=stnName_1991&txtStationName_1991=Churchill&searchMethod=contains&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=2200000000&dispBack=1

Environment and Climate Change Canada. (2024b). *Historical Data—Climate—Environment and Climate Change Canada*. Government of Canada. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Epstein, H. E., Myers-Smith, I., & Walker, D. A. (2013). Recent dynamics of arctic and sub-arctic vegetation. *Environmental Research Letters*, *8*(1), 015040. https://doi.org/10.1088/1748-9326/8/1/015040

Eriksen, B., Bölter, M., Breen, K., Henry, G., Lévesque, E., Mattson, J.-E., Parker, C. L., & Rayback, S. (2006). Environment and site descriptions of an ecological baseline study in the Canadian Arctic: The Tundra Northwest Expedition 1999 (Nunavut and Northwest Territories, Canada). *Polarforschung*, *73*(2/3), 77–88.

Ernst, C. M., Loboda, S., & Buddle, C. M. (2016). Capturing northern biodiversity: Diversity of arctic, subarctic and north boreal beetles and spiders are affected by trap type and habitat. *Insect Conservation and Diversity*, *9*(1), 63–73. https://doi.org/10.1111/icad.12143

Euskirchen, E. S., Bennett, A. P., Breen, A. L., Genet, H., Lindgren, M. A., Kurkowski, T. A., McGuire, A. D., & Rupp, T. S. (2016). Consequences of changes in vegetation and snow cover for climate feedbacks in Alaska and northwest Canada. *Environmental Research Letters*, *11*(10), 105003. https://doi.org/10.1088/1748-9326/11/10/105003

Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, *78*(1), 9–19. https://doi.org/10.1007/BF00377192

Evans, J. R., & Poorter, H. (2001). Photosynthetic acclimation of plants to growth irradiance: The relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell & Environment*, *24*(8), 755–767. https://doi.org/10.1046/j.1365-3040.2001.00724.x

Fafard, P. M., Roth, J. D., & Markham, J. H. (2020). Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. *Journal of Vegetation Science*, *31*(1), 173–179. https://doi.org/10.1111/jvs.12828

Fisher, J. P., Estop-Aragonés, C., Thierry, A., Charman, D. J., Wolfe, S. A., Hartley, I. P., Murton, J. B., Williams, M., & Phoenix, G. K. (2016). The influence of vegetation and

soil characteristics on active-layer thickness of permafrost soils in boreal forest. *Global Change Biology*, *22*, 3127–3140.

Florko, K. R. N., Bernhardt, W., Breiter, C.-J. C., Ferguson, S. H., Hainstock, M., Young, B. G., & Petersen, S. D. (2018). Decreasing sea ice conditions in western Hudson Bay and an increase in abundance of harbour seals (Phoca vitulina) in the Churchill River. *Polar Biology*, *41*(6), 1187–1195. https://doi.org/10.1007/s00300-018-2277-6

Forkel, M., Carvalhais, N., Rödenbeck, C., Keeling, R., Heimann, M., Thonicke, K., Zaehle, S., & Reichstein, M. (2016). Enhanced seasonal CO2 exchange caused by amplified plant productivity in northern ecosystems. *Science*, *351*(6274), 696–699. https://doi.org/10.1126/science.aac4971

Freschet, G. T., Swart, E. M., & Cornelissen, J. H. C. (2015). Integrated plant phenotypic responses to contrasting above- and below-ground resources: Key roles of specific leaf area and root mass fraction. *New Phytologist*, *206*(4), 1247–1260. https://doi.org/10.1111/nph.13352

Gable, T. D., Johnson-Bice, S. M., Homkes, A. T., Windels, S. K., & Bump, J. K. (2020). Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers. *Science Advances*, *6*(46), eabc5439. https://doi.org/10.1126/sciadv.abc5439

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. (2004). Plant Functional Markers Capture Ecosystem Properties During Secondary Succession. *Ecology*, *85*(9), 2630–2637. https://doi.org/10.1890/03-0799

Gharajehdaghipour, T., & Roth, J. D. (2018). Predators attract prey through ecosystem engineering in the Arctic. *Ecosphere*, *9*(1), e02077. https://doi.org/10.1002/ecs2.2077

Gharajehdaghipour, 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

Ghirardo, A., Lindstein, F., Koch, K., Buegger, F., Schloter, M., Albert, A., Michelsen, A., Winkler, J. B., Schnitzler, J.-P., & Rinnan, R. (2020). Origin of volatile organic compound emissions from subarctic tundra under global warming. *Global Change Biology*, *26*(3), 1908–1925. https://doi.org/10.1111/gcb.14935

Gough, L., Bass, H., & McLaren, J. R. (2015). Effects of Increased Soil Nutrients on Seed Rain: A Role for Seed Dispersal in the Greening of the Arctic? *Arctic, Antarctic, and Alpine Research*, *47*(1), 27–34. https://doi.org/10.1657/AAAR0014-055

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*(2), 211–218. https://doi.org/10.2307/1552473

Gould, S. J. (1988). Kropotkin was no crackpot. *Natural History*, *97*(7), 12–21.

Graae, B. J., Pagh, S., & Bruun, H. H. (2004). An Experimental Evaluation of the Arctic Fox (Alopex lagopus) as a Seed Disperser. *Arctic, Antarctic, and Alpine Research*, *36*(4), 468–473. https://doi.org/10.1657/1523-0430(2004)036[0468:AEEOTA]2.0.CO;2

Grünberg, I., Wilcox, E. J., Zwieback, S., Marsh, P., & Boike, J. (2020). Linking tundra vegetation, snow, soil temperature, and permafrost. *Biogeosciences*, *17*(16), 4261–4279. https://doi.org/10.5194/bg-17-4261-2020

Gupta, K., Mukhopadhyay, A., Babb, D. G., Barber, D. G., & Ehn, J. K. (2022). Landfast sea ice in Hudson Bay and James Bay: Annual cycle, variability and trends, 2000–2019. *Elementa: Science of the Anthropocene*, *10*(1), 00073. https://doi.org/10.1525/elementa.2021.00073

Hansen, J. E., Sato, M., Simons, L., Nazarenko, L. S., Sangha, I., Kharecha, P., Zachos, J. C., von Schuckmann, K., Loeb, N. G., Osman, M. B., Jin, Q., Tselioudis, G., Jeong, E., Lacis, A., Ruedy, R., Russell, G., Cao, J., & Li, J. (2023). Global warming in the pipeline. *Oxford Open Climate Change*, *3*(1), kgad008. https://doi.org/10.1093/oxfclm/kgad008

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S., & Wilson, W. G. (2007). Ecosystem engineering in space and time. *Ecology Letters*, *10*(2), 153–164. https://doi.org/10.1111/j.1461-0248.2006.00997.x

He, Q., & Bertness, M. D. (2014). Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, *95*(6), 1437–1443. https://doi.org/10.1890/13-2226.1

He, Q., Bertness, M. D., & Altieri, A. H. (2013). Global shifts towards positive species interactions with increasing environmental stress. *ECOLOGY LETTERS*, *16*(5), 695–706. https://doi.org/10.1111/ele.12080

Heijmans, M. M. P. D., Magnússon, R. Í., Lara, M. J., Frost, G. V., Myers-Smith, I. H., van Huissteden, J., Jorgenson, M. T., Fedorov, A. N., Epstein, H. E., Lawrence, D. M., & Limpens, J. (2022). Tundra vegetation change and impacts on permafrost. *Nature Reviews Earth & Environment*, *3*(1), Article 1. https://doi.org/10.1038/s43017-021-00233-0

Hewitt, R. E., Alexander, H. D., Miller, S. N., & Mack, M. C. (2022). Root-associated fungi not tree density influences stand nitrogen dynamics at the larch forest–tundra ecotone. *Journal of Ecology*, *110*(6), 1419–1431. https://doi.org/10.1111/1365-2745.13882

Hewitt, R. E., DeVan, M. R., Lagutina, I. V., Genet, H., McGuire, A. D., Taylor, D. L., & Mack, M. C. (2020). Mycobiont contribution to tundra plant acquisition of permafrost-derived nitrogen. *New Phytologist*, *226*(1), 126–141. https://doi.org/10.1111/nph.16235

Hicks, L. C., Leizeaga, A., Rousk, K., Michelsen, A., & Rousk, J. (2020). Simulated rhizosphere deposits induce microbial N-mining that may accelerate shrubification in the subarctic. *Ecology*, *101*(9), e03094. https://doi.org/10.1002/ecy.3094

Hobbie, J. E., & Hobbie, E. A. (2006). 15n in Symbiotic Fungi and Plants Estimates Nitrogen and Carbon Flux Rates in Arctic Tundra. *Ecology*, *87*(4), 816–822. https://doi.org/10.1890/0012-9658(2006)87[816:NISFAP]2.0.CO;2

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *ECOLOGICAL MONOGRAPHS*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346–363.

Høye, T. T., Mølgaard Ellebjerg, S., & Philipp, M. (2007). The Impact of Climate on Flowering in the High Arctic—The Case of Dryas in a Hybrid Zone. *Arctic, Antarctic, and Alpine Research*, *39*(3), 412–421. https://doi.org/10.1657/1523-0430(06-018)[HOYE]2.0.CO;2

Høye, T. T., & Sikes, D. S. (2013). Arctic entomology in the 21st century. *The Canadian Entomologist*, *145*(2), 125–130. https://doi.org/10.4039/tce.2013.14

Hudson, J. M. G., & Henry, G. H. R. (2009). Increased Plant Biomass in a High Arctic Heath Community from 1981 to 2008. *Ecology*, *90*(10), 2657–2663.

IPCC. (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, Ö. Yelekçi, R. Yu, & B. Zhou, Eds.). Cambridge University Press.

Johnson, N. C., Graham, J. H., & Smith, F. A. (1997). Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *The New Phytologist*, *135*(4), 575–585. https://doi.org/10.1046/j.1469-8137.1997.00729.x

Johnson-Bice, S. M., Baldwin, F. B., Richardson, E., & Roth, J. D. (2024). *Marine resources alter tundra food web dynamics by subsidizing a terrestrial predator on the sea ice*. https://ecoevorxiv.org/repository/view/7384/

Johnson-Bice, S. M., Gable, T. D., Roth, J. D., & Bump, J. K. (2023). Patchy indirect effects of predation: Predators contribute to landscape heterogeneity and ecosystem function via localized pathways. *Oikos*, *2023*(10), e10065. https://doi.org/10.1111/oik.10065

Johnson-Bice, S. M., Roth, J. D., & Markham, J. H. (2023). A Cosmic View of "Tundra Gardens": Satellite Imagery Provides a Landscape-Scale Perspective of Arctic Fox Ecosystem Engineering. *ECOSYSTEMS*, *26*(8), 1670–1684. https://doi.org/10.1007/s10021-023-00857-x

Jones, C. G., Gutiérrez, J. L., Byers, J. E., Crooks, J. A., Lambrinos, J. G., & Talley, T. S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*(12), 1862–1869.

Jones, C. G., Lawton, J. H., & Shachak, M. (1996). Organisms as Ecosystem Engineers. In F. B. Samson & F. L. Knopf (Eds.), *Ecosystem Management: Selected Readings* (pp. 130–147). Springer. https://doi.org/10.1007/978-1-4612-4018-1_14

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and Negative Effects of Organisms as Physical Ecosystem Engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kalra, Y. P., & Maynard, D. G. (1991). *Methods manual for forest soil and plant analysis* (Vol. 319E). http://scf.rncan.gc.ca/publications?id=11845

Keuper, F., van Bodegom, P. M., Dorrepaal, E., Weedon, J. T., van Hal, J., van Logtestijn, R. S. P., & Aerts, R. (2012). A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, *18*(6), 1998–2007. https://doi.org/10.1111/j.1365-2486.2012.02663.x

Khan, S. A., Mulvaney, R. L., & Hoeft, R. G. (2000). Direct-Diffusion Methods for Inorganic-Nitrogen Analysis of Soil. *Soil Science Society of America Journal*, *64*(3), 1083–1089. https://doi.org/10.2136/sssaj2000.6431083x

Knops, J. M., & Reinhart, K. (2000). Specific Leaf Area Along a Nitrogen Fertilization Gradient. *The American Midland Naturalist*, *144*(2), 265–272. https://doi.org/10.1674/0003-0031(2000)144[0265:SLAAAN]2.0.CO;2

Kohls, S. J., Thimmapuram, J., Buschena, C. A., Paschke, M. W., & Dawson, J. O. (1994). Nodulation patterns of actinorhizal plants in the family rosaceae. *Plant and Soil*, *162*(2), 229–239. https://doi.org/10.1007/BF01347710

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring Beta Diversity for Presence-Absence Data. *Journal of Animal Ecology*, *72*(3), 367–382.

Kropotkin, P. (1902). *Mutual Aid: A Factor of Evolution*. McClure Phillips & Co.

Kudo, G., Molau, U., & Wada, N. (2001). Leaf-trait Variation of Tundra Plants along a Climatic Gradient: An Integration of Responses in Evergreen and Deciduous Species. *Arctic, Antarctic, and Alpine Research*, *33*(2), 181–190. https://doi.org/10.1080/15230430.2001.12003421

Kushner, P. J., Mudryk, L. R., Merryfield, W., Ambadan, J. T., Berg, A., Bichet, A., Brown, R., Derksen, C., Déry, S. J., Dirkson, A., Flato, G., Fletcher, C. G., Fyfe, J. C., Gillett, N., Haas, C., Howell, S., Laliberté, F., McCusker, K., Sigmond, M., … Zwiers, F. W. (2018). Canadian snow and sea ice: Assessment of snow, sea ice, and related climate processes in Canada's Earth system model and climate-prediction system. *The Cryosphere*, *12*(4), 1137–1156. https://doi.org/10.5194/tc-12-1137-2018

Landhäusser, S. M., Chow, P. S., Dickman, L. T., Furze, M. E., Kuhlman, I., Schmid, S., Wiesenbauer, J., Wild, B., Gleixner, G., & Hartmann, H. (2018). Standardized protocols and procedures can precisely and accurately quantify non-structural carbohydrates. *Tree Physiology*, *38*(12), 1764–1778.

Liu, Y., Riley, W. J., Keenan, T. F., Mekonnen, Z. A., Holm, J. A., Zhu, Q., & Torn, M. S. (2022). Dispersal and fire limit Arctic shrub expansion. *Nature Communications*, *13*(1), 3843. https://doi.org/10.1038/s41467-022-31597-6

Markham, J. H. (2009). Does Dryas integrifolia fix nitrogen? *Botany*, *87*(11), 1106–1109. https://doi.org/10.1139/B09-071

Marschner, P., & Rengel, Z. (Eds.) (with Stark, S.). (2007). *Nutrient Cycling in Terrestrial Ecosystems* (Vol. 10). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-68027-7

Martinez Arbizu, P. (2021). *pairwiseAdonis: Pairwise multilevel comparison using adonis* [R package version 0.4]. https://github.com/pmartinezarbizu/pairwiseAdonis

Martini, I. P. (1989). The Hudson Bay Lowland: Major geologic features and assets. In W. J. M. van der Linden, S. A. P. L. Cloetingh, J. P. K. Kaasschieter, W. J. E. van de Graaff, J. Vandenberghe, & J. A. M. van der Gun (Eds.), *Coastal Lowlands: Geology and Geotechnology* (pp. 25–34). Springer Netherlands. https://doi.org/10.1007/978-94-017-1064-0_2

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1991). Primary and Secondary Production in Terrestrial Ecosystems. In J. Cole, G. Lovett, & S. Findlay (Eds.), *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories* (pp. 120–139). Springer. https://doi.org/10.1007/978-1-4612-3122-6_7

Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C., & Grant, R. F. (2021). Arctic tundra shrubification: A review of mechanisms and impacts on ecosystem carbon balance. *Environmental Research Letters*, *16*(5), 053001. https://doi.org/10.1088/1748-9326/abf28b

Meltofte, H., Barry, T., Berteaux, D., Bültmann, H., Christiansen, J. S., Cook, J. A., Dahlberg, A., Daniëls, F. J. A., Ehrich, D., Fjeldså, J., Friðriksson, F., Ganter, B., Gaston, A. J.,

Gillespie, L. J., Grenoble, L., Hoberg, E. P., Hodkinson, I. D., Huntington, H. P., Ims, R. A., … Wrona, F. J. (2013). *Arctic Biodiversity Assessment: Status and trends in Arctic biodiversity*. Conservation of Arctic Flora and Fauna (CAFF). https://oaarchive.arctic-council.org/handle/11374/232

Michelsen, A., Quarmby, C., Sleep, D., & Jonasson, S. (1998). Vascular plant 15N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia*, *115*(3), 406–418. https://doi.org/10.1007/s004420050535

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013a). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Milbau, A., Shevtsova, A., Osler, N., Mooshammer, M., & Graae, B. J. (2013b). Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems. *New Phytologist*, *197*(3), 1002–1011. https://doi.org/10.1111/nph.12054

Monk, J. D., & Schmitz, O. J. (2022). Landscapes shaped from the top down: Predicting cascading predator effects on spatial biogeochemistry. *Oikos*, *2022*(5), e08554. https://doi.org/10.1111/oik.08554

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20152434. https://doi.org/10.1098/rspb.2015.2434

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A., Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., … Wipf, S. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, *10*(2), Article 2. https://doi.org/10.1038/s41558-019-0688-1

Natali, S. M., Watts, J. D., Rogers, B. M., Potter, S., Ludwig, S. M., Selbmann, A.-K., Sullivan, P. F., Abbott, B. W., Arndt, K. A., Birch, L., Björkman, M. P., Bloom, A. A., Celis, G., Christensen, T. R., Christiansen, C. T., Commane, R., Cooper, E. J., Crill, P., Czimczik, C., … Zona, D. (2019). Large loss of CO2 in winter observed across the northern permafrost region. *Nature Climate Change*, *9*(11), 852–857. https://doi.org/10.1038/s41558-019-0592-8

Nielsen, S. M., Pedersen, V., & Klitgaard, B. B. (1994). Arctic Fox (Alopex lagopus) Dens in the Disko Bay Area, West Greenland. *Arctic*, *47*(4), 327–333.

Oksanen, J. (2022, October 11). *Package "vegan."* CRAN. https://github.com/vegandevs/vegan

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). The vegan package. *Community Ecology Package*, *10*(631–637), 719.

Olsen, S. R. (1954). *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*. U.S. Department of Agriculture.

Pandey, D., Kehri, H. K., Zoomi, I., Akhtar, O., & Singh, A. K. (2019). Mycorrhizal Fungi: Biodiversity, Ecological Significance, and Industrial Applications. In A. N. Yadav, S. Mishra, S. Singh, & A. Gupta (Eds.), *Recent Advancement in White Biotechnology*

Through Fungi: Volume 1: Diversity and Enzymes Perspectives (pp. 181–199). Springer International Publishing. https://doi.org/10.1007/978-3-030-10480-1_5

Paradis, M., Lévesque, E., & Boudreau, S. (2016). Greater effect of increasing shrub height on winter versus summer soil temperature. *Environmental Research Letters*, *11*(8), 085005. https://doi.org/10.1088/1748-9326/11/8/085005

Parrot. (2021). *Parrot Sequoia+ multispectral drone camera*. Parrot. https://www.parrot.com/en/support/documentation/sequoia

Parsons, A. N., Welker, J. M., Wookey, P. A., Press, M. C., Callaghan, T. V., & Lee, J. A. (1994). Growth Responses of Four Sub-Arctic Dwarf Shrubs to Simulated Environmental Change. *Journal of Ecology*, *82*(2), 307–318. https://doi.org/10.2307/2261298

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*(7), Article 7. https://doi.org/10.1038/nclimate1858

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, *46*(1), 15–27. https://doi.org/10.3354/cr00936

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, *20*(9), 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Pix4D. (2023a). *Pix4Dcapture* [Windows]. Pix4D SA. https://www.pix4d.com/product/pix4dcapture/

Pix4D. (2023b). *Pix4Dfields* [Windows]. Pix4D SA. https://www.pix4d.com/product/pix4dfields/

Poorter, H., & Evans, J. R. (1998). Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia*, *116*(1), 26–37. https://doi.org/10.1007/s004420050560

Poorter, H., & Ryser, P. (2015). The limits to leaf and root plasticity: What is so special about specific root length? *The New Phytologist*, *206*(4), 1188–1190.

Prabhu, N., Borkar, S., & Garg, S. (2019). Chapter 11 - Phosphate solubilization by microorganisms: Overview, mechanisms, applications and advances. In S. N. Meena & M. M. Naik (Eds.), *Advances in Biological Science Research* (pp. 161–176). Academic Press. https://doi.org/10.1016/B978-0-12-817497-5.00011-2

Prestrud, P. (1992). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Svalbard. *Arctic*, *45*(2), 154–158.

QGIS Development team. (2023). *QGIS Geographic Information System* (3.30.3) [Windows]. QGIS Association. https://www.qgis.org/

Rasband, W. S. (1997). *ImageJ* [Computer software]. U. S. National Institutes of Health. https://imagej.nih.gov/ij/

Rasmussen, L. H., Zhang, W., Ambus, P., Michelsen, A., Jansson, P.-E., Kitzler, B., & Elberling, B. (2022). Nitrogen transport in a tundra landscape: The effects of early and late growing season lateral N inputs on arctic soil and plant N pools and N2O fluxes. *Biogeochemistry*, *157*(1), 69–84. https://doi.org/10.1007/s10533-021-00855-y

Read, D. J., Leake, J. R., & Perez-Moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany*, *82*(8), 1243–1263. https://doi.org/10.1139/b04-123

Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, *157*(3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Reich, P. B., Ellsworth, D. S., & Walters, M. B. (1998). Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: Evidence from within and across species and functional groups. *Functional Ecology*, *12*(6), 948–958. https://doi.org/10.1046/j.1365-2435.1998.00274.x

Reimchen, T. E. (2017). Diverse Ecological Pathways of Salmon Nutrients Through an Intact Marine-terrestrial Interface. *The Canadian Field-Naturalist*, *131*(4), Article 4. https://doi.org/10.22621/cfn.v131i4.1965

Reimchen, T. E., & Fox, C. H. (2013). Fine-scale spatiotemporal influences of salmon on growth and nitrogen signatures of Sitka spruce tree rings. *BMC Ecology*, *13*(1), 38. https://doi.org/10.1186/1472-6785-13-38

Richardson, S. J., Press, M. C., Parsons, A. N., & Hartley, S. E. (2002). How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a sub-Arctic heath. *Journal of Ecology*, *90*(3), 544–556. https://doi.org/10.1046/j.1365-2745.2002.00681.x

Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, *145*(1), 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Rosenzweig, M. L., & MacArthur, R. H. (1963). Graphical Representation and Stability Conditions of Predator-Prey Interactions. *The American Naturalist*, *97*(895), 209–223. https://doi.org/10.1086/282272

Roth, J. D. (2002). Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. *Oecologia*, *133*(1), 70–77. https://doi.org/10.1007/s00442-002-1004-7

Roth, J. D. (2003). Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology*, *72*(4), 668–676. https://doi.org/10.1046/j.1365-2656.2003.00739.x

Roy, A., Gough, L., Boelman, N. T., Rowe, R. J., Griffin, K. L., & McLaren, J. R. (2022). Small but mighty: Impacts of rodent-herbivore structures on carbon and nutrient cycling in arctic tundra. *Functional Ecology*, *36*(9), 2331–2343. https://doi.org/10.1111/1365-2435.14127

Schimel, J. P., Bilbrough, C., & Welker, J. M. (2004). Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, *36*(2), 217–227. https://doi.org/10.1016/j.soilbio.2003.09.008

Schmidt, N. M., Ims, R. A., Høye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhamme, M. C., & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proceedings: Biological Sciences*, *279*(1746), 4417–4422.

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, *13*(10), 1199–1209. https://doi.org/10.1111/j.1461-0248.2010.01511.x

Scott, D., Malcolm, J. R., & Lemieux, C. (2002). Climate change and modelled biome representation in Canada's national park system: Implications for system planning and park mandates. *Global Ecology and Biogeography*, *11*(6), 475–484. https://doi.org/10.1046/j.1466-822X.2002.00308.x

Serreze, M. C., Walsh, J. E., Chapin, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., & Barry, R. G. (2000). Observational Evidence of Recent Change in the Northern High-Latitude Environment. *Climatic Change*, *46*(1), 159–207. https://doi.org/10.1023/A:1005504031923

Shaver, G. R., & Chapin, F. S. (1991). Production: Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs*, *61*(1), 1–31. https://doi.org/10.2307/1942997

Shevtsova, A., Ojala, A., Neuvonen, S., Vieno, M., & Haukioja, E. (1995). Growth and Reproduction of Dwarf Shrubs in a Subarctic Plant Community: Annual Variation and Above-Ground Interactions with Neighbours. *Journal of Ecology*, *83*(2), 263–275. https://doi.org/10.2307/2261565

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de L. Dantas, V., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of

intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

Simpson, E. H. (1949). Measurement of Diversity. *Nature*, *163*(4148), 688–688. https://doi.org/10.1038/163688a0

Skrede, I., Eidesen, P. B., Por^{TEL}a, R. P., & Brochmann, C. (2006). Refugia, differentiation and postglacial migration in arctic-alpine Eurasia, exemplified by the mountain avens (Dryas octopetala L.). *Molecular Ecology*, *15*(7), 1827–1840. https://doi.org/10.1111/j.1365-294X.2006.02908.x

Smith, C. A. S., Smits, C. M. M., & Slough, B. G. (1992). Landform Selection and Soil Modifications Associated with Arctic Fox (Alopex lagopus) Den Sites in Yukon Territory, Canada. *Arctic and Alpine Research*, *24*(4), 324–328. https://doi.org/10.1080/00040851.1992.12002964

Smits, C. M. M., Smith, C. A. S., & Slough, B. G. (1988). Physical Characteristics of Arctic Fox (Alopex lagopus) Dens in Northern Yukon Territory, Canada. *Arctic*, *41*(1), 12–16.

Standen, K. M., Sniderhan, A. E., Sonnentag, O., Voigt, C., & Baltzer, J. L. (2024). Response of Boreal Plant Communities and Forest Floor Carbon Fluxes to Experimental Nutrient Additions. *Ecosystems*. https://doi.org/10.1007/s10021-023-00899-1

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press.

Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J., & Romanovsky, V. E. (2005). Winter Biological Processes Could Help Convert Arctic Tundra to Shrubland. *BioScience*, *55*(1), 17–26. https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Sullivan, P. F., Ellison, S. B. Z., McNown, R. W., Brownlee, A. H., & Sveinbjörnsson, B. (2015). Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska. *Ecology*, *96*(3), 716–727. https://doi.org/10.1890/14-0626.1

Swann, A. L., Fung, I. Y., Levis, S., Bonan, G. B., & Doney, S. C. (2010). Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. *Proceedings of the National Academy of Sciences*, *107*(4), 1295–1300. https://doi.org/10.1073/pnas.0913846107

Tannerfeldt, M., & Angerbjörn, A. (1996). Life history strategies in a fluctuating environment: Establishment and reproductive success in the arctic fox. *Ecography*, *19*(3), 209–220. https://doi.org/10.1111/j.1600-0587.1996.tb01247.x

Tannerfeldt, M., Moehrenschlager, A., & Angerbjörn, A. (2003). Den ecology of swift, kit and arctic foxes: A review. *The Swift Fox: Ecology and Conservation of Swift Foxes in a Changing World*, 167–181.

Thomas, D. B. (2008). Nontoxic Antifreeze for Insect Traps. *Entomological News*, *119*(4), 361–365. https://doi.org/10.3157/0013-872X-119.4.361

Timoney, K., Laroi, G., & Dale, M. (1993). Sub-Arctic Forest-Tundra Vegetation Gradients—The Sigmoid Wave Hypothesis. *Journal of Vegetation Science*, *4*(3), 387–394. https://doi.org/10.2307/3235597

Van Cleve, K., & Alexander, V. (1981). Nitrogen Cycling in Tundra and Boreal Ecosystems. *Ecological Bulletins*, *33*, 375–404.

von Beckerath, X., Benadi, G., Gilg, O., Sittler, B., Yannic, G., Klein, A.-M., & Eitzinger, B. (2022). Long-term monitoring reveals topographical features and vegetation that explain

winter habitat use of an Arctic rodent. *Arctic Science*, *8*(2), 349–361. https://doi.org/10.1139/as-2021-0010

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschleger, S. D., & Woodward, F. I. (2014). The relationship of leaf photosynthetic traits – Vcmax and Jmax – to leaf nitrogen, leaf phosphorus, and specific leaf area: A meta-analysis and modeling study. *Ecology and Evolution*, *4*(16), 3218–3235. https://doi.org/10.1002/ece3.1173

Walker, D. A., Epstein, H. E., Raynolds, M. K., Kuss, P., Kopecky, M. A., Frost, G. V., Daniëls, F. J. A., Leibman, M. O., Moskalenko, N. G., Matyshak, G. V., Khitun, O. V., Khomutov, A. V., Forbes, B. C., Bhatt, U. S., Kade, A. N., Vonlanthen, C. M., & Tichý, L. (2012). Environment, vegetation and greenness (NDVI) along the North America and Eurasia Arctic transects. *Environmental Research Letters*, *7*(1), 015504. https://doi.org/10.1088/1748-9326/7/1/015504

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & Team, C. (2005). The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science*, *16*(3), 267–282.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnússon, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., … Wookey, P. A. (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, *103*(5), 1342–1346. https://doi.org/10.1073/pnas.0503198103

Wang, W., Scali, M., Vignani, R., Spadafora, A., Sensi, E., Mazzuca, S., & Cresti, M. (2003). Protein extraction for two-dimensional electrophoresis from olive leaf, a plant tissue containing high levels of interfering compounds. *ELECTROPHORESIS*, *24*(14), 2369–2375. https://doi.org/10.1002/elps.200305500

Werner, E. E., & Peacor, S. D. (2003). A Review of Trait-Mediated Indirect Interactions in Ecological Communities. *Ecology*, *84*(5), 1083–1100. https://doi.org/10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Wielgolaski, F. E., Sømme, L., Thórhallsdóttir, T. E., Grabherr, G., Malinovsky, K. A., Zlotin, R. I., Miehe, G., Hedberg, O., Killick, D. J. B., & Campbell, J. S. (1997). *Polar and alpine tundra*. Elsevier Science Publishing Company, Inc. https://elibrary.ru/item.asp?id=26450837

Wilmers, C. C., Estes, J. A., Edwards, M., Laidre, K. L., & Konar, B. (2012). Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment*, *10*(8), 409–415. https://doi.org/10.1890/110176

Wrigley, R. E., & Hatch, D. R. M. (1976). Arctic Fox Migrations in Manitoba. *Arctic*, *29*(3), 147–158.

Wyant, K. A., Draney, M. L., & Moore, J. C. (2011). Epigeal Spider (Araneae) Communities in Moist Acidic and Dry Heath Tundra at Toolik Lake, Alaska. *Arctic, Antarctic, and Alpine Research*, *43*(2), 301–312. https://doi.org/10.1657/1938-4246-43.2.301

Yang, H., Zhao, X., Liu, C., Bai, L., Zhao, M., & Li, L. (2018). Diversity and characteristics of colonization of root-associated fungi of *Vaccinium uliginosum*. *Scientific Reports*, *8*(1), Article 1. https://doi.org/10.1038/s41598-018-33634-1

Zhao, S.-T., Johnson-Bice, S. M., & Roth, J. D. (2022). Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. *Global Ecology and Conservation*, *40*, e02310. https://doi.org/10.1016/j.gecco.2022.e02310

Zou, K., Thébault, E., Lacroix, G., & Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*, *30*(8), 1454–1465.