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Understanding The Role Of Small Mammals In Arctic Biogeochemical Cycling

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UNDERSTANDING THE ROLE OF SMALL MAMMALS IN ARCTIC BIOGEOCHEMICAL
CYCLING

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Dedication

This dissertation is dedicated to my wife Anna, my mentors along the way, and the small mammals of course!

UNDERSTANDING THE ROLE OF SMALL MAMMALS IN ARCTIC BIOGEOCHEMICAL
CYCLING

by

AUSTIN N. ROY, B.S.

DISSERTATION

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Abstract

Small mammals play an integral role in their ecosystems. This is especially true in northern ecosystems, where small mammals represent both top-down and bottom-up forces and can have strong effects on ecosystem function through affecting biogeochemical cycling. Despite these important effects, the role of small mammals in influencing biogeochemical cycling has been largely underappreciated in the understanding of arctic ecosystems, leading to a call to better understand how small mammal herbivores impact ecosystem processes including carbon cycling. The overarching goal of this dissertation is to assess how biogeochemical cycling is affected by small mammal herbivore presence, behavior, and population dynamics in the arctic tundra of northern Alaska, USA. To achieve this, I present four chapters that examine the different ways that small mammals can influence arctic biogeochemical cycling. In the first chapter, I differentiate the roles of small mammal and large mammal herbivores in affecting above- and below-ground responses in arctic tundra after 20 years of exclusion. In Chapter 2, I explore how structure building activities of small mammals can influence soils and plants. I then discuss how small mammal population cycles may impact ecosystem function in Chapter 4. Finally, in the last data chapter, I examine how changes in animal density and diet during different phases of the small mammal population cycle may affect nutrient limitation in tundra systems. This dissertation provides a more comprehensive analysis of the different ways that small mammals influence arctic ecosystems and updates the understanding of their roles in contemporary tundra environments. Furthermore, this dissertation contributes to a growing interest in linking multiple ecological levels and can be used to better understand the future of ecological conditions in the Arctic.

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Chapter 1: Introduction: a background in small mammals' influence on soils and biogeochemical cycling

Herbivores, such as small mammals, can have important influences on ecosystem functioning through their top-down (herbivory) and bottom-up regulation of the physical and biogeochemical environment. Through these impacts, small mammal herbivores can alter ecosystem properties such as hydrology (Jones et al. 1994), light availability (Borer et al. 2014), albedo (Detling and Painter 1983), vegetation community (Ylanne et al. 2015), and primary productivity (Olofsson et al. 2001). Despite the importance of these species in ecosystems, a better understanding of the influence of small mammal herbivores on soils and nutrient cycling is needed due to the further potential impacts on other ecological processes. This is especially true in rapidly changing ecosystems, such as the Arctic, where changes in herbivore impacts might have compounding or alleviating influences on climate-change driven changes in global biogeochemical cycling and carbon storage.

SMALL MAMMAL INFLUENCES ON NUTRIENT CYCLING AND ECOSYSTEM FUNCTION

Here I describe the importance of small mammal herbivores as influencers of soils and their regulation of nutrient cycling. I provide examples of how small mammals (or other herbivores when small mammal examples are not available) influence soils and nutrient cycling through consumption (herbivory) and non-consumption activity types and highlight the factors affecting the roles of small mammals in ecosystems.

1.1 Effects as consumers

As consumers, small mammal herbivores can impose both top-down and bottom-up forces in ecosystems by affecting plant communities and soil nutrient availability. Through herbivory, small mammals can have strong influences vegetation cover and plant species abundance. For example, at the peak of their population cycle, lemmings can consume approximately 50% of summer standing forage (Batzli et al. 1980) and 80% of available winter vegetation (McKendrick et al. 1980). Selective foraging not only alters overall vegetation cover, but may also change the representation of species within the vegetation community by increasing the abundance of preferred forage species in some cases (Johnson et al. 2011) or non-preferred species in other cases (Cahoon et al. 2012).

By controlling both plant biomass and plant community assemblage, small mammals can impact top-down regulation of ecosystem functioning. Increases or decreases in the total amount

of vegetation on the landscape alters the amount of carbon (C) stored in plant biomass and the amount of primary productivity occurring within an ecosystem (Tanentzap and Coomes 2012; Falk et al. 2014). Additionally, by controlling the representation of different plant species in vegetation communities, small mammals may shift plant communities towards communities with more productive species (Johnson et al. 2011, Tuomi et al. 2019). Lastly, herbivory by small mammals might induce compensatory growth or alter nutrient concentrations in plant tissues within individual plants that may feedback to alter biogeochemical cycling and ecosystem functioning (McNaughton 1979, Petit Bon et al. 2020).

Herbivory by small mammals can also affect bottom-up forces in ecosystems. By controlling which plant species are dominant in a system, they may aid in regulating which plant species contribute to the litter pool and resulting nutrient availability in soils. For example, brown lemmings (*Lemmus trimucronatus*) primarily consume graminoids (Batzli and Pitelka 1983) and can greatly reduce graminoid abundance during the peak of their population cycle (Batzli and Jung 1980). An extended reduction in graminoid biomass could allow for non-graminoid species such as shrubs to have a disproportionate representation in the litter pool. Since shrub litter can be more or less recalcitrant than graminoid litter (Myers-Smith et al. 2011, McLaren et al. 2017a), this may lead to altered decomposition and carbon sequestration rates (Couëteaux et al. 1995, Cornelissen et al. 2007). Furthermore, herbivory by small mammals may increase C allocation to plant roots and root exudates (Holland et al. 1996), which may in turn stimulate carbon cycling in soils. Depending on which small mammal species are contributing to nutrient cycling, the rates of ecosystem processes may increase or decrease (Tuomi et al. 2019, Ylänne and Stark 2019). In addition to altering which species contribute to the litter pool, small mammals also influence the quality of litter derived from a single plant species. Herbivory can increase nitrogen concentration in plants (Jefferies et al. 1994, Ouellet et al. 1994, Bardgett and Wardle 2003, Peek and Forseth 2003), thus increasing the quality of potential leaf litter within a given forage species. Such changes in litter quality and resulting soil nutrient availability can influence nutrient limitation and control primary productivity within an ecosystem.

Small mammals can also influence below-ground nutrient cycling through the acts of consuming and digesting forage. First, while consuming vegetation, not all plant material is used by herbivores (Lindeman 1942), as some portion is lost and becomes part of the litter pool. This unconsumed material (vegetation clippings) tends to have higher nutrient concentrations and

faster decomposition rates compared to litter material that falls during senescence (Chapin et al. 1980, McLaren & Roy, unpublished data), thus increasing nutrient availability within ecosystems. The second way small mammals can alter nutrient cycling is by increasing soil organic matter (SOM) pool and nutrient availability via waste material (feces and urine). The production of feces and urine provides microbes and plants access to nutrients more quickly than if the consumed materials were to decompose without herbivore facilitation (Hobbs 1996, Bardgett and Wardle 2003). Waste production may have particular importance in ecosystem functioning due to links with alleviating nutrient limitation (Elser and Urabe 1999) and herbivore-induced variations in nutrient availability through space and time. Herbivore identity and forage type can influence the ratio and concentration of nutrients released by herbivores, with feedbacks on primary production and producer assemblage (Sturner 1990). The seasonal use of certain forage species may also alter the nutrients released by herbivores over time and thus create heterogeneous nutrient availability across time. Additionally, resource requirements of organisms vary through time (Warne 2014), and the nutrients released by herbivores vary due to the biological needs of organisms (Elser and Urabe 1999). Finally, small herbivores may consume material in one location and deposit waste material in another (McKendrick et al. 1980). This movement of nutrients can alter the spatial heterogeneity of nutrient availability among and between landscapes (Sitters et al. 2017, Veldhuis et al. 2018, Doughty et al. 2020) and has the potential to influence ecosystem functioning across multiple scales.

1.2 Effects as structure builders

Structure building is an important aspect of how small mammals influence their environments. Here I define structure building as the physical alteration of the environment for secondary purposes and not solely as a byproduct of activities such as forage consumption or habitat use. Examples of structures built by herbivores include nests, haypiles, trails, burrows, baths, and beds. Structure-building activities are common within small mammal guilds and can notably be observed in pikas (*Ochotona* spp, hay piles, Aho et al. 1998), arvicoline rodents (e.g., *Lemmus* spp., *Microtus* spp., trails and burrows, McKendrick et al. 1980), and degus (*Octodon* spp.) and kangaroo rats (*Dipodomys* spp., dust baths, Culbertson 1946, Woods and Boraker 1975). These structures provide resources for the small mammal but also alter resources for other organisms and impact ecosystem function by providing unique microclimates, providing habitat, and influencing nutrient cycling.

1.2.1 Nests and hay piles

Nests and hay piles are created by small mammals for shelter, young-rearing, and food resources. Small mammal nests and haypiles are constructed by gathering specific vegetation resources into particular areas, essentially creating unique litter piles across the landscape. This litter collection might influence both the density of plant litter (e.g., more litter at nest sites) and which plant species are contributing to litter decomposition (e.g., only certain species used in nest construction), with resulting effects on soils. For example, soils under nests have been shown to have greater SOM compared to control locations away from nests (Whitford and Steinberger 2010). Additionally, since herbivores may spend a large amount of time in the nest, including time defecating, nests can be manure and nutrient hotspots within a landscape (Taylor 1935). This influence of decomposing organic matter from building and using nests can lead to higher nitrogen mineralization under nest locations (Whitford and Steinberger 2010). Similar to nest construction, haypiles concentrate plant material into localized areas. As haypiles are not usually completely consumed (see Chapter 3), they provide areas where decomposing biomass can accumulate and result in higher soil and plant C and N concentrations at hay piles compared to control sites (Aho et al. 1998). Changes in plant nutrients due to hay piles may influence forage quality for other organisms. However, the plant species composition of these structures likely influences the magnitude of effect they have, indicating that small mammal vegetation preference may play a role in ecosystem function. A more thorough examination of the factors influencing how hay piles and next affect soils and nutrient availability will allow for a better understanding of the role they play in ecosystem function.

1.2.2 Trails and runways

The creation of trails and the movement of small mammals can have important influence ecosystems as individuals may travel and trample up to 20% of the area used in a given day (Hobbs and Searle 2005). Different from game trails, runways are trails used by small mammals which are actively maintained through trail grooming. By repeatedly using these runways, small mammals can influence ecosystem processes by affecting soils and plants. Trampling and soil compaction by animals often influences soils by reducing soil pore volume (Ruser et al. 2006), reducing soil fauna diversity (Beylich et al. 2010), and increasing water-logging in soil (van Klink et al. 2015). The creation of runways and trampling can also influence plant diversity. By removing vegetation biomass to create pathways, herbivores can reduce competition among

plants for light, resulting in increases in plant diversity (Borer et al. 2014). Additionally, trampling along pathways can change vegetation communities by physically damaging plants (Egelkraut et al. 2020). These changes in plant communities would likely feedback and influence soil properties and functions such as altering the quality and diversity of the litter pool. The maintenance and use of runways can also influence soil temperatures as trail grooming may allow more light to penetrate to the soil surface (Pastor et al. 1993) and trampling can remove insulating plant material (Van der Wal et al. 2001). While the effects of trails are often attributed to larger herbivores (e.g., (Bakker et al. 2004, Egelkraut et al. 2020), smaller herbivores, such as lemmings, might also compact soils by using the same runways over multiple decades (McKendrick et al. 1980), resulting in long-term impacts within the ecosystem.

In addition to effects on soil properties, runways may affect the biogeochemical cycling (e.g., cycling of C, N, and P). Soil compaction within runways may greatly influence soil biogeochemical processes by decreasing CO₂ efflux and N mineralization rates (Beylich et al. 2010). This is likely due to water logging within trails and the creation of anoxic conditions, which may slow down decomposition (Schrama et al. 2013, van Klink et al. 2015). Alternatively, trampling and increases in soil temperatures within runways can increase the rate of physical decomposition and the turnover rate of plant litter (Falk et al. 2015). Additionally, by regulating litter inputs along runways, small mammals may influence decomposition and soil nutrient availability, as described earlier. Such changes in soil conditions and nutrient cycling may feedback to affect additional ecosystem processes near rodent runways (Ross et al. 2007).

1.2.3 Digging, burrowing, and soil movement

Herbivores show digging behavior for a variety of reasons including creating burrows for shelter, creating caches to store food, and digging pits in search of food. Such activities create disturbance and heterogeneity within landscapes (Tang et al. 2019), and the level of disturbance caused by digging activities can be ecologically significant, with some mammals moving between 0.5 - 450 t soil ha⁻¹ (Eldridge et al. 2012). These soil movement activities can influence both soil structure and ecosystem functioning.

Soil movement by small mammals provides a critical link between soil surface and deeper soil processes. Digging transfers materials from the subsurface to the surface, making previously inaccessible resources available at the soil surface (Hull Sieg 1987, Ballová et al. 2019). Alternatively, burrowing activities can also move organic material from the surface into

deeper soil layers via bedding material, feces, and food caches (Hansell 1993). The transfer of material between soil profiles can alter limiting nutrient ratios and microbial process and nutrient cycling rates (Ayarbe and Kieft 2000, Canals and Sebastià 2000, Fontaine et al. 2007).

Digging and burrowing also influences ecosystems by altering soil conditions. Burrows provide unique temperature clines and may provide a buffer between temperature extremes (Burda et al. 2007). Burrow conditions may also provide unique atmospheric conditions compared to the surface and surrounding soils due to reduced air flow in burrows and the metabolisms of organisms using the burrow (Roper et al. 2001). Furthermore, digging also influences other physical properties such as water availability within soils by increasing the amount and depth of water infiltration (Grant 1974, Laundre 1993). Other digging activities, such as the creation of soil pits, can alter soil structure resulting in increased soil moisture and evapotranspiration (Koford 1958, Whitford and Kay 1999). These changes in soil conditions as a result of digging may be important to ecosystem functioning due to their impacts on chemical reactions and decomposition (Laundre 1993). Changes in soil conditions are also important for their ability to create unique ecological opportunities within the larger landscape.

While digging has important effects on local conditions, it can also have impacts at higher scales. As burrows and digging locations may be dispersed on the landscape, they may create hot spots or areas of unique conditions within the larger landscape (Fafard et al. 2019, Louw et al. 2019, Mayengo et al. 2020). Digging also influences microtopography which can trap organic (e.g., litter, spores, seeds) and inorganic material (e.g., dust, Whitford and Kay 1999). Furthermore, when soils are brought to the soil surface, they can be eroded and dispersed through the ecosystem. Some soil movement activities may even create novel habitats within ecosystems (e.g., ephemeral wetland-type habitats, Coppedge et al. 1999). These spatial effects may affect the distribution of resources, spatial heterogeneity of ecosystem processes, and the biogeography of organisms within an ecosystem (Eldridge and Myers 2001, Bagchi et al. 2006, Fafard et al. 2019, Louw et al. 2019, Tang et al. 2019).

1.3. Herbivore identity and impacts on ecosystems

A single individual may have small or large impacts on their ecosystem, understanding what drives the magnitude of herbivore impacts is important to examining their role in ecosystems. Many factors about herbivores influence the effects they impose on ecosystems. Important factors include herbivore body size, behavior, and population size.

1.3.1 Herbivore body size

Herbivore body size is one important characteristic which influences herbivore impacts on ecosystems. For example, larger bodied herbivore species tend to have larger trampling effects than those of smaller bodied herbivore communities (Cumming and Cumming 2003). Body size can also influence the impacts of burrows, with the size and depth of burrow structures varying with species, contributing to above-ground burrow mounds ranging from 0.5-700 m² (Davidson et al. 2012). Body size can also be important to the effects of herbivores on nutrient cycling. In comparing small mammals and larger mammals (ungulates), researchers found that areas exposed to large herbivores had lower N mineralization rates, NO₃ availability, pH and increased total C compared to areas exposed to small mammal herbivores (Bakker et al. 2004). However, some have argued that small mammal herbivores are more efficient in influencing mineralization rates than other herbivores (large mammal and insect, Hull Sieg 1987) and may have larger impacts on their ecosystems than other herbivore types.

1.3.2 Behavior and sociality

Behaviors and social structures of different species are also important in determining influences of herbivores. Whether species are migratory or resident is important; migratory species (e.g., caribou) may utilize areas in high density for short periods of time, while other resident species using the same habitats (e.g., voles and lemmings) use the same area year round. Due to their persistent impacts on ecosystems, especially if the species reaches high density, resident species are likely more important at regional scales in influencing their ecosystems than migratory species. Sociality within a species is an additional important characteristic, with social or colonial herbivores likely having larger impacts than less social species. Social herbivores tend to reach higher densities and have greater impacts such as creating distinct habitat patches within ecosystems (Davidson et al. 2012). Relatedly, population size of a species may have beneficial or detrimental impacts on systems. Due to the increase in the number individuals and densities, higher population sizes will likely have greater numerical impacts on a system than smaller populations. Research has shown that population “explosions” in small mammals influence vegetation diversity and cover (McKendrick et al. 1980, Hull Sieg 1987), which may in turn influence soil properties such as light and moisture penetration, soil temperature, and nutrient cycling as discussed earlier. Other research has suggested that moderate levels of herbivore

activity may be most beneficial for soil and ecosystem functioning (Biondini et al. 1998, Cao et al. 2004).

SMALL MAMMALS IN THE ARCTIC TUNDRA

Small mammals in the arctic tundra include members of three different orders (Soricomorpha, Lagomorpha, and Rodentia) and seven families (Soricidae, Leporidae, Castoridae, Erethizontidae, Sciuridae, Dipodidae, and Cricetidae). This includes 16 species of shrew (*Sorex* spp.), four species of rabbits and hares (*Lepus* spp.), two species of beaver (*Castor* spp.), the North American porcupine (*Erethizon dorsatum*), four species of squirrels (*Marmota* spp. and *Uroditellus* spp.), and one mouse species (*Sicista betulina*, Elias 2019, Hope 2019). The most numerous and diverse group of arctic small mammals are the members of the subfamily Arvicolinae. These Arvicoline rodents include the muskrat (*Ondatra zibethicus*), 10 species of lemmings (*Dicrostonyx* spp., *Lemmus* spp., *Myopus* sp., and *Synaptomys* sp.), and 14 species of voles (*Arvicola* spp., *Lasiopodomys* sp., *Microtus* spp., and *Myodes* spp., Elias 2019, Hope 2019, Ehrlich et al. 2020).

2.1 Arvicoline rodents as important herbivores

Of all the mammalian herbivore species present in the Arctic, Arvicoline rodents are arguably the most important in terms of their influences on soils and ecosystem functioning. This importance is due, in part, to their biology and ecology in arctic systems. While other rodents (e.g., arctic ground squirrels, *Uroditellus* spp.) are present in the system and are important soil movers (Tikhomirov 1959), these other species are not active year-round, hibernating in winter (Morrison and Galster 1975). Arvicoline rodents, however, are active year-round. This ability to influence the ecosystem continuously means that these species affect the system not only during the growing season, when carbon is being sequestered as plant biomass, but also during winter and influencing resource availability at snow melt and affecting how arctic systems recover from winter disturbances. Additionally, voles and lemmings can exert large influences on their habitats due to the high densities that they can reach. Near Utqiagvik, Alaska, brown lemming (*Lemmus trimucronatus*) densities have been recorded as high as 225 individuals ha⁻¹ (Batzli et al. 1980). The ability to reach high densities is not unique to voles and lemmings though. Other herbivore species such as caribou (*Rangifer tarandus*) also reach high densities and do not hibernate. While caribou may use areas at high density, it is usually only for a short period of time as the species is migratory, whereas resident species such as voles and lemmings are present

and active in arctic systems continuously. Furthermore, due to their abundance, species such as lemmings may have increased impacts on ecosystems than larger herbivores because of their ability to consume more vegetation than these larger species (Batzli et al. 1980, Ehrich et al. 2020), especially when at high density.

A key characteristic of Arvicoline rodents that makes them so important in the Arctic are their population cycles. While these species may be quite abundant in one year, they may be nearly absent from the ecosystem the following year(s). These population cycles may occur synchronously between populations and species (Krebs 2013a), showing these rodents can have large spatial impacts (Olofsson et al. 2012). These population cycles have been documented and researched for over a century (Collett 1895), however, the exact drivers behind these cycles remain relatively unknown. Current research suggests that multifactorial interactions between resource availability, climate, competition, predation, and disease likely drive the regular cycles that have been documented in the past (Krebs 2013b).

While small mammal population cycles have been relatively predictable in the past, the cycles of Arvicoline rodents may be shifting from historic patterns, at least partly due to changing environmental factors. Research in Europe has suggested that lemming and vole population cycles may have crashed or become suppressed due to climate change (Ims et al. 2008, Kausrud et al. 2008, Cornulier et al. 2013), although these patterns have not been observed in other arctic locales (Ehrich et al. 2020). While not as thoroughly studied, in the North American Arctic, a similar trend may be occurring. Near Utqiagvik, AK, lemming populations historically peaked every 3-5 years (Batzli et al. 1980), but no large population peaks have been observed in at least the last 10 years (Ott and Currier 2012, Ott 2017). Although, recent research may also show that population levels are increasing in some areas due to climate change, with some Arvicoline species benefiting from changing conditions more than other species (Krebs et al. 2019). These changes in environmental conditions may not only alter population cycles, but also which species may be dominant on future arctic landscapes. These changes in the density of arctic herbivores are likely to alter how arctic ecosystems function in the future.

A BRIEF HISTORY OF ARCTIC SMALL MAMMAL-ECOLOGICAL RESEARCH

Ever since the work of Elton (1924), understanding small mammal population cycles and their roles in ecosystems has been a core concept in western ecological thought; although the importance of small mammals in ecosystems and cultures was of interest to many peoples well

before the early 1900's. Beginning in the 1950's, this interest in small mammal ecology was paired with an international interest in arctic ecosystems during the International Biological Program (IBP). In the North American Arctic, research projects funded under the IBP started with studies understanding the physiology of arctic species and their persistence in extreme environments (Rausch 2001), and eventually expanded into understanding the roles of small mammals within arctic ecosystems (Batzli et al. 1980). The IBP project was followed by additional experiments through the 1980's, including the Research in Arctic Tundra Environments (RATE) experiment (e.g., Batzli and Jung 1980), amongst others. These research projects provided novel information on small mammal population cycles, physiology, diet, and impacts on tundra vegetation (Batzli et al. 1980). The methods used in these studies often relied on enclosure fencing, live-trapping, and *ex situ* experimentation of animals (Batzli et al. 1980). While these studies expanded the knowledge of small mammals in the Arctic, there were no successful studies manipulating arctic small mammal population densities (Batzli and Jung 1980) and few descriptions of the non-herbivory impacts of small mammals on ecosystem processes and soils (although see Bee and Hall 1956, McKendrick et al. 1980).

Following the IBP and RATE experiments, research examining arctic small mammals continued relatively sporadically over the following decades, continuing to establish and monitor historic enclosure fencing (e.g., Gough et al. 2008, Johnson et al. 2012) and examining the impacts of small mammals on other species (e.g., Schmidt 2012). During this time, researchers continued to expand upon the effects of small mammals on vegetation communities (e.g., Gough et al. 2012, Olofsson et al. 2012) but also began to include more studies examining soils and biogeochemical cycling (Stark and Grellmann 2002, Lara et al. 2016). This is notable as small mammal effects on below ground processes and nutrient availability may feedback to aid in regulating other ecosystem processes, as described in Section 1.

With a stronger recognition of climate change and a focus on the importance of stored C in arctic tundra, there has been a renewed interest in understanding arctic ecosystem function in more ways (Chapin et al. 1995). At the same time, there has been a call for a more thorough understanding on C-cycling and an expressed need to understand the role of herbivores in C-cycling and include them in ecosystem models (Schmitz et al. 2014, Rastetter et al. 2022). This is of particular importance because small mammals, as locally important herbivores, are likely to interact with their ecosystems differently under novel environmental conditions compared to the

past. While continued examination of historic exclosure studies remain informative of herbivore impacts over long periods, additional experimental methods are needed to understand more short-term impacts replicating modern conditions to begin to fill research needs. Furthermore, small mammals interact with their environments through more than just their roles as herbivore consumers. To fully understand the roles of small mammals in arctic environments, more information is needed on small mammal direct and cumulative impacts as well as linking the multiple interactions between small mammals and their habitats to better understand future tundra ecosystem processes.

DISSERTATION: UNDERSTANDING THE ROLE OF SMALL MAMMALS IN ARCTIC NUTRIENT CYCLING AND ECOSYSTEM FUNCTION

The Arctic is a key ecosystem in the global carbon cycle in part due to its ability to hold a large amount of stored soil carbon relative to its area (Ping et al. 2008). The capacity for arctic tundra to hold carbon stems from its dry and cold climate which slows decomposition and other ecosystem processes. Historically, arctic tundra has been a carbon sink, absorbing more carbon through photosynthesis than it emits; however, changes to the ecosystem due to warming have accelerated decomposition, changing the tundra from a carbon sink to a potential carbon source (Oechel et al. 1993). Attempts to understand and predict the future of carbon cycling in the Arctic have largely ignored the role of herbivores (Schmitz et al. 2014). Incorporating herbivores in our understanding of arctic ecosystem processes is especially important because of concurrent changes in herbivore populations and changing arctic conditions. These simultaneous changes in ecological processes and herbivore dynamics may interact and create feedbacks which further influence ecosystem processes including carbon and nutrient cycles (Wookey et al. 2009). Because of this, there have been calls to incorporate the activities and effects of herbivores in ecosystem and carbon cycling models (Schmitz et al. 2014, Moorhead et al. 2017)

However, the understanding of the role of small mammals in the Arctic is limited; previous studies examining the influence of voles and lemmings have lacked breadth. Many experiments have examined the general impacts of these herbivores on ecosystem properties without teasing apart the roles of different herbivore activities or did not separate the impacts of different herbivore types (although, see McKendrick et al. 1980, Grellmann 2002, Roy et al. 2020). Additionally, the focus on the impact of small mammals on soil processes has been limited, even though soils regulate many broader ecosystem processes. When studies have

researched the impacts of Arvicoline rodent activities in the Arctic, they have been limited to few activity types (e.g., only runways), their effects on single nutrients (e.g., Phosphorus), or have not incorporated population cycles (McKendrick et al. 1980). Furthermore, most studies in North America occurred 30-50 years ago (although, see Gough et al. 2008, Johnson et al. 2011, Lara et al. 2016, Ehrlich et al. 2020) and environmental conditions in the Arctic continue to change, exemplifying the need to provide current information on the roles of small mammals in this system and to understand how changing small mammal population dynamics influence arctic ecosystem processes.

Small mammals play an integral role in the functioning of arctic ecosystems. Though some have explored the importance of these herbivores in the arctic and examined changes in their population cycles, few have linked these two processes together. The overarching goal of this collection of studies is to assess how nutrient cycling is affected by small mammal herbivore presence, behavior, and population dynamics in the arctic tundra of northern Alaska, USA. This dissertation addresses knowledge gaps by examining interactions between small mammals, their cycles, and ecosystem properties.

Dissertation summary

In the following chapters, I begin to fill in these gaps in knowledge and provide a clearer understanding of the role of small mammal herbivores in Arctic nutrient cycling and ecosystem functioning.

In Chapter 2, we investigate the influences of long-term reduced herbivore activity on above- and belowground processes. Arctic herbivores can influence ecosystems by altering plant communities and soil processes, which may regulate ecosystem process rates (Tuomi et al. 2019). Long-term herbivore exclosures have been provided insights into the chronic impact of herbivores on arctic ecosystems. However, most experiments have not examined the impact of excluding different herbivore guilds (e.g., rodents vs. ungulates) and/or have not focused on the long-term impacts of herbivores on soil nutrient pools and microbial processes. To study this, we sampled 20-year old fencing in two tundra vegetation types located at the Arctic-LTER near Toolik Lake, Alaska. For this study we examined soil nutrient pools and changes in vegetation in all mammal and large mammal only exclosures to evaluate how vegetation community and soil nutrient pools respond as a function of long-term herbivore exclusion and herbivore guild membership.

In Chapter 3, we evaluate how different types of small mammal-built structures affect arctic soil and plant CNP cycling. Individual structure types built by Arctic herbivores likely have different impacts on ecosystem properties such as changes in plant communities, and nutrient movement and availability in soils. We sampled soils underneath different lemming and vole structure types (hay piles, runways, latrines, and burrows). For this chapter we examined how soil nutrient levels vary between Arvicoline rodent activity types and whether small mammal structure effects were ubiquitous between tundra habitats across northern Alaska.

In Chapter 4, we study the effect of varying small mammal population scenarios on vegetation community structure and soil nutrient pools. Different densities of rodents, at different phases of their population cycle, are likely to have different impacts on arctic ecosystem functions. Here we utilize lemming enclosures, exclosures, and control sites located on the Barrow Ecological Observatory near Utqiagvik, Alaska which mimic different phases of the lemming population cycle. We sampled soils and vegetation from these treatments to determine how ecosystem properties are influenced by lemming cycles and recovery from a population peak.

In Chapter 5, we examine how consumer-driven nutrient recycling and lemming population cycles influence nutrient availability in the Arctic. Due to changes in forage quality or composition, the nutrients recycled back to the environment through feces at these different points of the population cycle may impact nutrient availability for primary productivity. In this chapter, we analyze the nutrients available from feces at different phases of the lemming population cycle, how nutrients change with variable diets, and the rate at which nutrients are released back to the environment.

Finally, Chapter 6 provides a summary of our findings, conclusions on the role of small mammals in arctic ecosystems and aims for future research involving small mammal ecology.

Chapter 2: Above- and below-ground responses to long-term herbivore exclusion

Abstract

Herbivores can play an important role in determining arctic ecosystem function with effects determined in part by herbivore identity. We examined the impact of long-term (22 years) small and large mammal herbivore exclusion in two arctic plant communities in northern Alaska: dry heath (DH) and moist acidic tundra (MAT). Our aims were to examine how herbivore exclusion influences (1) plant communities and (2) soil nutrient pools and microbial processes. While herbivore absence increased moss and decreased evergreen shrub cover in MAT, there were few other significant effects on vegetation in either community. We also observed no influence of exclusion on most soil properties. However, in DH, phosphatase activity was greater in areas where small mammals alone were present, suggesting that they are altering phosphorus (P) availability, perhaps through herbivores' influence on the plant community and subsequently on competition for P with the microbial community. We conclude that herbivore impacts in the Arctic are dependent on both the plant community and herbivore identity (size). We show the importance of understanding the roles of herbivores in the Arctic and contribute to a growing number of herbivore studies in a biome likely to experience future changes in herbivore communities and ecosystem function.

Introduction

Herbivores can have strong influences on ecosystem properties and processes, with their impact depending on the identity of the herbivores present. Communities of larger-bodied herbivores have been described as having larger impacts than communities of smaller-bodied herbivores (Cumming and Cumming 2003), although a number of studies have shown important effects of small herbivores on ecosystem properties (Howe and Brown 1999, Bakker et al. 2004, Johnson et al. 2011) and even similarly sized effects as large mammals on nitrogen (N) cycling (Clark et al. 2005). Additionally, herbivore identity as either a migrant or resident species may be an important control on the impacts of herbivores on ecosystems, especially in the Arctic. Migratory species such as caribou (*Rangifer tarandus*) may use areas at high densities for a short period of time; in contrast, resident species such as voles (*Microtus* spp.) and lemmings (*Lemmus* spp.) have relatively small home-ranges and are present and active year-round. Some resident herbivore species may also go through large population increases and crashes (Batzli et al. 1980,

Ims et al. 2011), with these species being more important at local scales during times of high abundance.

Arctic herbivores can influence ecosystems by altering plant communities and soil processes. Small and large arctic herbivores may influence vegetation abundance and cover (Johnson et al. 2011, Cahoon et al. 2012), plant biomass (Olofsson et al. 2012), light limitation (Borer et al. 2014), plant nutrient levels (Jefferies et al. 1994, Tuomi et al. 2019), photosynthetic potential (Li et al. 2018), and productivity and plant senescence (Chew 1974, Batzli 1978, Mosbacher et al. 2018). In addition to influencing vegetation, herbivores can also have both direct and indirect effects on soil processes. Arctic mammalian herbivores can redistribute soil (Tikhomirov 1959, McKendrick et al. 1980) and may influence carbon (C) and nutrient cycling by bringing material from lower soil layers to the soil surface (Ballová et al. 2019) where it can be accessed by microbes and plants. Herbivores can also influence soil properties and nutrient cycling by producing feces and urine (Clark et al. 2005), influencing the composition of the litter pool (Wardle et al. 2002), altering soil temperatures (Van der Wal et al. 2001, Borer et al. 2014), and affecting soil pore space and soil moisture (van Klink et al. 2015). These interactions between herbivores and arctic ecosystem functions have the potential to influence this ecosystem over long time periods.

Long-term herbivore exclosures have provided insights into the chronic impact of herbivores on arctic ecosystems. For example, in one of the longest running exclosure experiments on the north coast of Alaska, data showed higher graminoid abundance and lower lichen abundance in control sites compared to herbivore exclusion sites after 50 years of lemming exclusion (Johnson et al. 2011), implying that there may be a positive relationship between herbivore activity and plant biomass. While most research examining arctic herbivores has observed decreases in plant biomass due to herbivory (Moen and Oksanen 1998, Olofsson et al. 2002, Post et al. 2008, Olofsson et al. 2009), other studies have shown increases (Johnson et al. 2011) or no difference (Olofsson et al. 2002) in plant biomass; suggesting that the effects of herbivores may vary by vegetation community. Differences in effects of herbivory may in part be due to differences in vegetation communities (Moen and Oksanen 1998) or the length of time the experiment has been running and possible transient effects of herbivory (Tilman 1988, Mallen-Cooper et al. 2019). Long-term exclosures in the Arctic have also shown a relationship between herbivores and landscape level ecosystem functions such as albedo, methane (CH₄) flux,

ecosystem respiration, net ecosystem exchange, and C storage (Cahoon et al. 2012, Väisänen et al. 2014, Lara et al. 2016, Ylänne and Stark 2019). These enclosure experiments have been informative about herbivore-ecosystem interactions, but most experiments excluded either all herbivores or a specific size class of herbivores, and did not examine the potential differential impacts between herbivore guilds (e.g., ungulates vs. rodents; although see Pastor and Naiman 1992, Grellmann 2002, Olofsson et al. 2009).

Herbivore enclosures constructed in the 1990s at the Arctic Long-Term Ecological Research site near Toolik Lake, Alaska provide an opportunity to examine the long-term impacts of herbivores and begin to understand how different herbivore guilds influence ecosystem structure. These enclosures have increased the understanding of the interaction between herbivores and vegetation communities (Gough et al. 2007, Gough et al. 2008) and soil food webs (Gough et al. 2012). While these enclosures were monitored for the past 20 years, the impact of herbivore exclusion on soil biogeochemical and physical processes remains unexamined. Furthermore, most studies have focused on the influence of herbivory on arctic vegetation and ecosystem level processes, and fewer studies have assessed the long-term impacts of arctic herbivores on soil nutrient pools and microbial processes (although see Stark and Grellmann 2002, Olofsson et al. 2004b, Sitters et al. 2017, Sitters et al. 2019, Stark et al. 2019). This has led to the need to have a better understanding of the role of herbivores in systems with slow nutrient cycling. Our goal was to examine how the vegetation community and soil nutrient pools respond to long-term reduced herbivore activity in two arctic plant communities. The specific questions we aimed to answer were:

1. What are the long-term impacts of reduced mammal activity on vegetation community structure and soil nutrient pools in two arctic plant communities?
2. How does the guild of mammalian herbivores (rodent vs. caribou) affect vegetation community and soil processes?

Materials and Methods

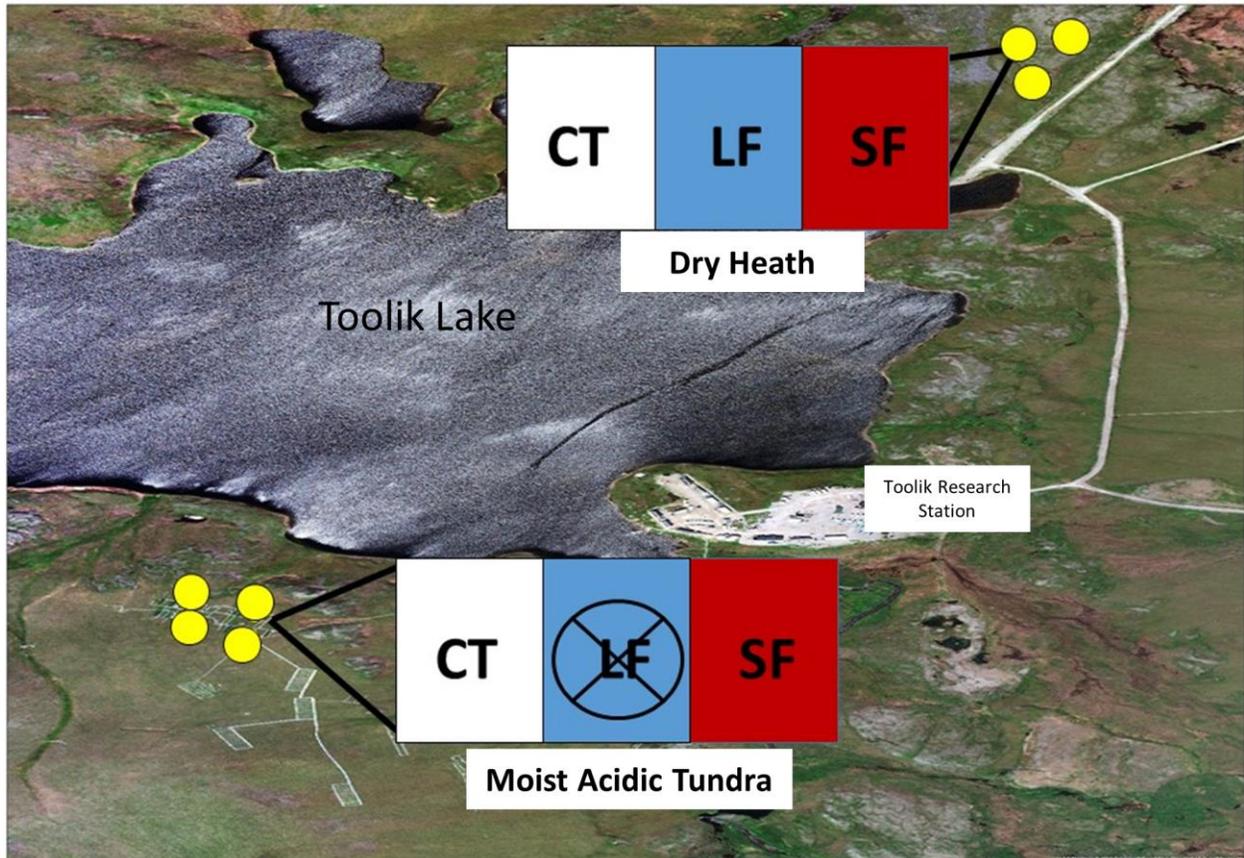


Figure 2.1: Overview of study area located in two types of arctic tundra near Toolik Lake, Alaska. Yellow dots represent locations of experimental herbivore exclosures, with three fencing blocks in HD, and four in MAT. Each block included a CT (no herbivores excluded), an SF (large and small herbivores excluded), and an LF (large herbivores only excluded). The fencing block designs are inlayed..

Study Site – We conducted this study in long-term herbivore exclosures located in moist acidic tundra (MAT) and dry heath (DH) tundra at the Arctic Long-Term Ecological Research (ARC-LTER) site near Toolik Lake, Alaska during the summer of 2017. The ARC-LTER is located north of the Brooks Range along the Dalton Highway (68°37'40''N, 149°35'41''W). The MAT experimental site is located along the southern side of Toolik Lake at an elevation of 755 m, and the DH site is located along the northeastern side of the lake at an elevation of 720 m. Vegetation at the MAT site is equally represented by evergreen shrubs (*Rhododendron palustre*, *Vaccinium*

vitis-idaea), deciduous shrubs (*Betula nana*, *Rubus chamaemorus*), and graminoids (*Eriophorum vaginatum*, *Carex bigelowii*) with abundant *Sphagnum* mosses (Gough et al. 2007, Gough et al. 2012, McLaren et al. 2017a) while the DH site is dominated by evergreen shrubs (*Loiseleuria procumbens*, *Ledum palustre*, *Empetrum nigrum*, *V. vitis-idaea*) and lichens (Gough et al. 2002, Gough et al. 2012). For a complete list of plant species in both plant communities, please see our online data (data accessibility section). Both sites are underlain by continuous permafrost (Shaver et al. 2014). At Toolik Field Station (< 1 km from either experimental site), air temperatures range from -57.6 to 28.2°C (mean annual air temperature = -6.8), soil surface temperatures range from -25.7 to 33.0°C (mean annual soil temperature = -0.6), and yearly mean precipitation is 256.7 mm (Environmental Data Center 2017). Local mammalian dominant resident herbivores include singing voles (*Microtus miurus*) and tundra voles (*M. oeconomus*), with additional herbivores including collared lemmings (*Dicrostonyx groenlandicus*), red-backed voles (*Clethrionomys rutilus*), arctic ground squirrels (*Spermophilus parryii*), and migratory caribou (Batzli and Henttonen 1990, Gough et al. 2008). Plant species important for local small mammal herbivores include tussock cotton grass (*Eriophorum vaginatum*) for tundra voles and willows (*Salix* spp.) for singing voles (Batzli and Lesieutre 1991). Lichens, shrubs, and tussock cotton grass are important local forage species for caribou (Walsh et al. 1997, Walker et al. 2001, Joly et al. 2009).

Experimental herbivore exclosures were established within each vegetation community in 1996 (Figure 2.1) within an existing experimental layout consisting of three (DH) or four (MAT) blocks of 5 x 20 m plots separated by 2 m walkways. At each block there is a fencing plot (5 x 20 m each), with a series of 5 x 5 m fences and control sites. Each block consists of a large herbivore exclosure (LF, 15.2 x 15.2 m mesh), a large and small herbivore exclosure (SF, 1.3 m x 1.3 m mesh), and a control (CT, no fencing) plot (Gough et al. 2007). Each exclosure is approximately 2 m tall to prevent herbivores from feeding over the exclosures and has approximately 10 cm of the exclosures buried into the soil to prevent small mammals from burrowing under the exclosures. Although all three treatments are present at both sites, the LF plots in the MAT were not sampled for this study.

Vegetation community – In late July 2017, we assessed the vegetation community within each experimental plot at the DH and MAT sites. We used 1 x 1 m quadrats to quantify the percent cover of vascular and non-vascular plants, bare ground, and plant litter in eight

contiguous replicates within each plot. Vascular plants were identified to species while mosses and lichens were grouped across species. For analysis we determined proportional cover by summing the percent cover of all plants and then calculating the relative abundance of each group to standardize across plots. Most analyses were conducted on plant growth forms (graminoids, evergreen shrubs, deciduous shrubs, forbs, lichens, mosses) rather than individual species.

Soil analysis – We collected soil samples from each treatment in the DH on 22-Jul-2017 and MAT on 24-Jul-2017. For the DH, we collected three randomly located samples per plot; using a serrated bread knife we collected 10 x 10 cm columns of the organic horizon to a depth of 5 cm. For the DH, the mineral layer was shallow (~ 5cm depth) so we only sampled the upper organic layer of soil (top five cm of the organic layer). Additionally, because the mineral layer had numerous rocks and would thus require large volumes of soil sampled for analysis, in this community we did not sample this layer in order to minimize destructive impacts in these long term enclosures. In the MAT, three 10 x 10 cm columns of soils were cut from each plot to a depth of approximately 30 cm or to the depth of active layer (i.e., frozen soil was not sampled), whichever was less. We separated each column of MAT soil into the upper organic layer (top 5 cm, as above), the lower organic layer (the remaining depth of the organic column), and the top five cm of the mineral layer (when accessible) in the field. We separated the top 5 cm from the rest of the organic layer to enable comparison between the two ecosystem types, and also to follow sampling protocols from other previously published studies at these sites (Mack et al. 2004, McLaren and Buckeridge 2019).

For each soil column and depth, we dried a subsample of each core (approximately 5 cm³) at 50°C for 48 hours to assess bulk density (BD) and gravimetric water content (GWC). When volume could not be accurately assessed only GWC measurements were taken. Subsequently, we individually homogenized each soil sample by hand, removing all large roots (> 1mm diameter), and partitioned samples for analysis within two days of collection, and then froze samples before shipping to the University of Texas at El Paso, where they were stored at -20°C until analysis.

We analyzed soil samples for total % C (%C) and total % N (%N), inorganic nutrients (NH₄⁺, NO₃⁻, PO₄³⁻); organic nutrients (extractable organic C (EOC), extractable total N (ETN),

extractable organic P (EOP)); microbial biomass C, N, P; and extracellular enzyme activity using the following methods.

We dried, ground, and processed soil subsamples for % C and % N content using a dry combustion C and N analyzer (ElementarPyroCube®). To determine soil inorganic nutrients, we thawed and extracted frozen subsamples (5 g) in 25 ml of 0.5 M K₂SO₄ for 2 hours, filtered through glass filter paper and analyzed extractant using colorimetric microplate assays (BioTEK Synergy HT microplate reader, Winooski, Vermont, USA). NH₄⁺-N (NH₄⁺) was determined using a modified Berlethot assay (Rhine et al. 1998), NO₃⁻-N (NO₃⁻) using a modified Griess assay (Doane and Horwath 2003), and PO₄³⁻-P (PO₄³⁻) using a malachite green assay (D'Angelo et al. 2001).

EOC was determined colorimetrically after an Mn (III)-reduction assay (Bartlett and Ross 1988). ETN and EOP were determined using a modified alkaline persulfate digestion using a 1:1 ratio of oxidizing reagent to sample and autoclaved for 40 min at 121°C (Lajtha et al. 1999) followed by analysis for NO₃⁻ and PO₄³⁻ respectively as above. To determine microbial biomass C, N, and P, we conducted the above assays on samples using a direct chloroform-addition modification of the fumigation-extraction method (Brookes et al. 1985, Voroney et al. 2006), where 5 g of thawed soil was incubated for 24 hours with 2 mL of ethanol-free chloroform, followed by extraction in 25 mL of 0.5 M K₂SO₄. We calculated microbial biomass for C, N, and P (MBC, MBN, and MBP) by subtracting ETN, EOP or EOC respectively of non-fumigated samples from that of fumigated samples. No correction factor was applied for incomplete CHCl₃-release, or sorption of P because these values are not known for K₂SO₄-extraction for these two ecosystems.

Extracellular enzyme (exoenzyme) activity was assessed for 10 exoenzymes involved in the microbial acquisition of C, N, and P: C-acquiring enzymes (β -glucosidase, β -cellobiosidase, β -xylosidase, α -glucosidase), N-acquiring enzymes (N-acetyl-glucosaminidase (NAG), leucine amino peptidase (LAP)) and P-acquiring enzymes (phosphatase, phosphodiesterase), as well as the oxidative enzymes phenol oxidase and peroxidase. One g of soil was blended with a sodium acetate buffer to reflect natural soil conditions (pH = 5), and pipetted onto 96 well plates with eight replicates per soil. Substrate tagged with fluorescing 4-methylumbelliferone (MUB) or 7-amido-4-methyl coumarin (MC) (LAP only) was added to soil slurries. Samples were incubated at 20°C and enzyme activity (fluorescence) measured every 30 minutes for 3.5 hours following

methods adapted from Sayia-Cork et al. (2002) and McLaren et al. (2017a). For each substrate, we measured the background fluorescence of soils and substrate and the quenching of MUB or MC by soils and used standard curves of MUB or MC to calculate the rate of substrate hydrolyzed. Fluorescence was measured at 365 nm excitation and 450 nm emission using a BioTek Synergy HT microplate reader (BioTek Instruments Inc., Winooski, VT, USA). Oxidative enzyme analysis was performed using an L-3,4-dihydroxyphenylalanine (L-DOPA) substrate for phenol oxidase and peroxidase. Color absorbance was measured at 460 nm using a reader after 24 hours of incubation.

Statistical methods – We performed statistical analyses with the program R (R Core Team 2018) with a cutoff of $p < 0.05$ for inferring statistical significance. In all analyses, sites were analyzed separately. In DH, there were three treatment blocks with three types of fencing treatments (CT, LF, SF), whereas in MAT there were four blocks and two fencing treatments (CT, SF). A block factor was included to reflect the field experimental design.

To assess changes in plant communities we used the package *vegan* (Oksanen et al. 2019) to calculate Shannon diversity indices for each treatment at each site; Pielou's evenness was then calculated from the diversity values. Differences in diversity, evenness, and species richness between treatments in each vegetation community were examined using ANOVA or t-tests as appropriate. To determine if there was an effect of exclosures on percent cover, we used a blocked Multivariate Analysis of Variance (MANOVA) with Pillai's trace test statistic, and an experimental block as our blocking factor for each site. In the MANOVA, we used percent cover of each plant growth form (graminoid, evergreen shrub, deciduous shrub, forb, lichen, moss, bare ground) as the dependent variable and exclosure treatment (CT, SF, LF) as the independent variable.

Differences in soil variables between treatments and soil depth were determined using ANOVA or t-tests as appropriate, with nutrient concentrations, microbial biomass, and enzyme activity as response variables and exclosure type and soil depth as independent variables. When data could not be normalized, Kruskal-Wallis and Wilcoxon tests were used. For soil response variables, vegetation communities were analyzed separately, with soil depth only analyzed in MAT and guild identity (SF and LF treatments) only analyzed in DH.

Results

Vegetation – In dry heath (DH) tundra, we observed changes in the vegetation structure due to herbivory presence and the identity of the herbivore present in the system. Shannon diversity indices varied between the fencing treatments ($F_{2,6} = 5.19$, $p = 0.05$). Tukey post hoc tests showed that diversity in the large herbivore only enclosure (LF) trended lower than controls (CT) ($p = 0.08$) and all herbivore enclosures (SF) ($p = 0.07$), while there was no difference in diversity between SF and CT ($p > 0.10$, Table 2.1). Similar to diversity, evenness values varied among treatments ($F_{2,6} = 9.98$, $p = 0.01$), again with LF being lower than CT ($p = 0.02$) and SF ($p = 0.02$, Table 2.1). There were no differences among treatments for species richness ($F_{2,6} = 2.68$, $p = 0.15$, Table 2.1). Although the mean abundance of some plant groups appeared to differ across fencing treatments, particularly lichens which had lower abundance in CT than SF and LF (Figure 2.2), the MANOVA found no significant effect of fencing on the plant community overall ($F_{2,6} = 0.97$, $p = 0.54$) or for any individual growth forms ($p > 0.05$).

In the moist acidic tundra (MAT), in contrast with DH, we found no difference in Shannon diversity between the SF treatment and the CT ($t_{4,86} = 1.28$, $p = 0.18$). Furthermore, we found no differences in evenness ($t_{3,95} = -0.24$, $p = 0.82$) or richness ($t_{5,46} = 1.70$, $p = 0.15$) between treatments (Table 2.1). Again, we found no significant effect of fencing on plant community composition overall ($F_{1,6} = 0.97$, $p = 0.28$, Figure 2.2). However, when analyzing each growth form independently, we found that herbivore exclusion significantly increased moss cover ($F_{2,6} = 13.00$, $p = 0.01$) and reduced evergreen shrub cover ($F_{1,6} = 10.00$, $p = 0.01$). There was also a trend towards greater graminoid cover inside the SF treatment ($F_{1,6} = 2.70$, $p = 0.15$).

Soil nutrient pools - Generally, there were significant differences in soil variables between sites, with MAT having higher CNP pool concentrations and enzyme activities than DH (Supplemental Table 2.1). There were no significant responses to long-term herbivore exclusion for % C and N, inorganic N and P pools, extractable CNP pools, or microbial biomass CNP pools in either vegetation community (Table 2.2, Supplemental Table 2.2, Figure 2.3 and Supplemental Figures 2.1-2.3). Small mammal activity did not affect soil exoenzyme activity in the MAT (Supplementary Table 2.3, Supplemental Figure 2.5). In the MAT, most soil variables differed by depth ($p < 0.01$, Supplementary Table 2.2, Supplemental Figures 2.6-2.7), but not by treatment ($p = 0.05$). In the DH, there were few effects of herbivore exclusion on exoenzyme activity (Supplemental Figure 2.4, Supplemental Table 2.3). We did observe that areas that were

Table 2.1: Mean and standard error for species diversity, species richness, and evenness of plant communities in 2017 from an herbivore exclosure experiment in two different tundra types: DH and MAT.

Site	Treatment	Shannon Diversity	SE of Diversity	Species Richness	SE of Richness	Evenness	SE of Evenness
DH	CT	1.53	0.01	6.08	0.26	0.66	0.09
	LF	1.52	0.04	6.79	0.19	0.64	0.15
	SF	1.55	0.01	6.04	0.24	0.67	0.16
MAT	CT	1.57	0.01	9.31	0.26	0.58	0.06
	SF	1.42	0.01	9.31	0.18	0.52	0.03

Table 2.2: The impact of herbivores on soil variables after 20 years of exclusion. ANOVA and Kruskal-Wallis summary results from comparisons of soil variables between exclosures (SF (large and small herbivores excluded) treatment) in dry heath (DH) and Moist Acidic Tundra (MAT)

	DH			MAT		
	Fence			Fence		
	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>
% C	$F = 0.39$	0.69	2,6	$W = 78$	0.76	1
% N	$F = 0.36$	0.71	2,6	$F = 0.68$	0.42	1,6
C:N	$F = 0.20$	0.82	2,6	$F = 0.25$	0.62	1,6
NH ₄	$F = 0.16$	0.86	2,6	$W = 75.5$	0.86	1
NO ₃	$X^2 = 2.00$	0.37	2	$W = 68$	0.83	1
PO ₄	$X^2 = 0.80$	0.67	2	$W = 85$	0.47	1
EOC	$F = 0.53$	0.61	2,6	$W = 89$	0.35	1
ETN	$F = 0.36$	0.71	2,6	$W = 69$	0.89	1
EOP	$X^2 = 0.83$	0.66	2	$W = 79$	0.71	1
MBC	$X^2 = 0.62$	0.73	2	$W = 64$	0.30	1
MBN	$X^2 = 0.80$	0.67	2	$W = 79$	0.44	1
MBP	$X^2 = 0.36$	0.84	2	$W = 66$	0.75	1

only accessed by small mammal herbivores (LF) had significantly higher phosphodiesterase activity ($F_{2,6} = 8.66$, $p = 0.02$) than areas which could be accessed by both large and small herbivores and herbivore-free exclosures (Figure 2.3).

Discussion

Overall, we found few effects of long-term reductions in herbivore activity on vegetation in two arctic plant communities. Although the effects were not large, herbivore presence did alter each plant community differently. In the moist acidic tundra (MAT), mosses were more abundant and evergreen shrubs were less abundant in areas where herbivores were excluded compared with controls, similar to effects found after a shorter period of herbivore exclusion in these same plots (Gough et al. 2007, Gough et al. 2012). Herbivore activity in MAT negatively affected graminoids; thus, when herbivores were removed, graminoid cover increased and evergreen shrubs may have experienced greater competition resulting in a decline in evergreen relative abundance. While Gough et al. (2007) showed that herbivory became more important under fertilized conditions, our data show that even without fertilization, herbivory can play a role in regulating some forage species. The increase in mosses with reduced caribou and vole activity has also been seen in other studies (Rydgren et al. 2007) and is likely due to voles using mosses as winter forage (Batzli and Lesieutre 1991) and potentially disturbing the mosses through trampling (Van der Wal et al. 2001) and creating runways. Such increases in moss cover may also negatively influence evergreen shrub establishment and growth (Holmgren et al. 2015) and may additionally partially explain the reduced evergreen shrub cover we observed in the MAT. Even though we did not observe exclusion effects on soil properties in the MAT, changes in moss cover due to herbivory may influence system properties such as nutrient availability (Olofsson et al. 2009, Bueno et al. 2016) and soil temperatures (Gornall et al. 2011) in the future.

Our results from the dry heath (DH) sites show that herbivores influence this plant community differently from the MAT, by decreasing plant diversity and evenness when caribou alone are excluded, and that interactions between types of herbivores may be important. Although there were no statistical differences in plant growth form abundance among treatments, likely due to low replication at the block level and therefore low statistical power, there was greater lichen cover in large mammal exclusion (LF) plots ($37\% \pm 7$) compared to areas where all herbivores access (CT) plots ($24\% \pm 3$) in the DH which corresponds with increases in lichen cover with caribou exclusion found in other studies (Olofsson et al. 2004b, Gough et al. 2008,

Pajunen et al. 2008). However, this observed increase was not present when small mammals were also excluded (SF plots 30% ± 9). While this increase in lichen cover was not observed in a European heath community when herbivores were excluded (Grellmann 2002), it suggests that there may be an interaction between the activity of different herbivore guilds; Lichen cover may increase due to the absence of caribou, but small mammal activity or foraging on vascular plants could also potentially alleviate competition pressure on lichens by reducing vascular plant abundance.

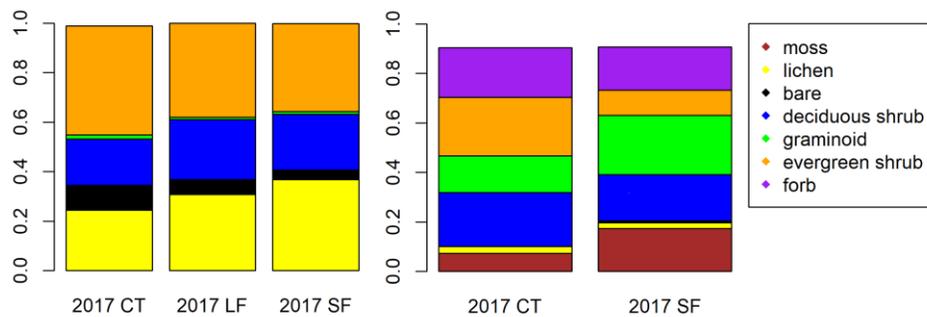


Figure 2.2: Relative abundance of vegetation growth forms from an herbivore exclusion experiment located in MAT ($n = 4$) and DH ($n = 3$) tundra at the ARC-LTER located at Toolik Lake, Alaska. Data were collected in July 2017.

In addition to differing effects on the vegetation communities, we also found that herbivore guilds may impact soils differently. In the DH site, we found higher phosphodiesterase activity in areas where large, but not small, mammals were excluded, compared to control sites (all herbivores present) and all herbivore exclusion. An increase in phosphatases suggests that microbes are experiencing P-limitation, and the trend of increases in PO_4^{3-} in the large herbivore exclusion (LF) treatments (Supplemental Figure 2.2) further suggests that this increase in phosphatases may be increasing P availability in the soil. Thus, increases in phosphatases in the DH indicate that large mammals may be regulating P availability but only when small mammals are not present. In contrast to Sitters et al. (2019), which found that heavy reindeer grazing created more P-limited conditions, our results support the opposite trend - that reduced caribou activity creates P-limited conditions. Our observed increase in lichens in the LF

treatments may partially explain increased phosphatases. As P can be limiting to lichens (Makkonen et al. 2007) and lichens can produce their own phosphatases (Hogan et al. 2010), increases in lichen abundance may directly result in increases in phosphatase activity. Alternatively, changes in the vegetation community may alter competition for P in the microbial community and in turn influence phosphatase production.

Although the purpose of this paper was to compare herbivore impacts between each plant community, and we thus focus on shallow soils, we did observe generally higher carbon and nutrient concentrations in the organic soils than mineral soils in the MAT (Supplemental Table 2.2 and 2.3). The impacts of herbivores (urine, feces, litter inputs) are likely concentrated in the upper portion of soil layers and then cycle between the organic layers. This is supported by the few differences we observed between the organic layers. While the mineral layer differed from the organic layers, we found few responses in the mineral layer due to herbivore treatments, suggesting that the impacts of herbivores may be immediate and not persist over long time periods. Though we did not sample at depth in the DH, we expect that we would see similar deep soil responses to herbivores as in the MAT.

Our sampling is part of an ongoing effort examining how herbivores influence ecosystem dynamics in these long-term exclosures (Gough et al. 2007, Gough et al. 2008, Gough et al. 2012). Our data show little change from previous samplings, which also show relatively few changes over time (Gough and Johnson 2017), and provide valuable additional timepoints for this experiment and the examination of ecosystem functions in a changing arctic environment. Interestingly, in a study design similar to ours in another heath community, but also including fertilization (Stark and Grellmann 2002), slower nutrient cycling under grazing after seven years of exclusion was reported. Their research found that excluding herbivores influenced microbial biomass carbon (MBC) and microbial respiration, but microbial biomass nitrogen (MBN) was only affected by exclusion + fertilization (Stark and Grellmann 2002). The fact that we did not detect any changes in soil nutrient pools 21 years after treatment began (Supplemental Table 2.3) indicates that influences of herbivores may be transient. Many of the variables we examined (e.g., available nutrients) show strong variation seasonally (McLaren et al. 2017b) and between

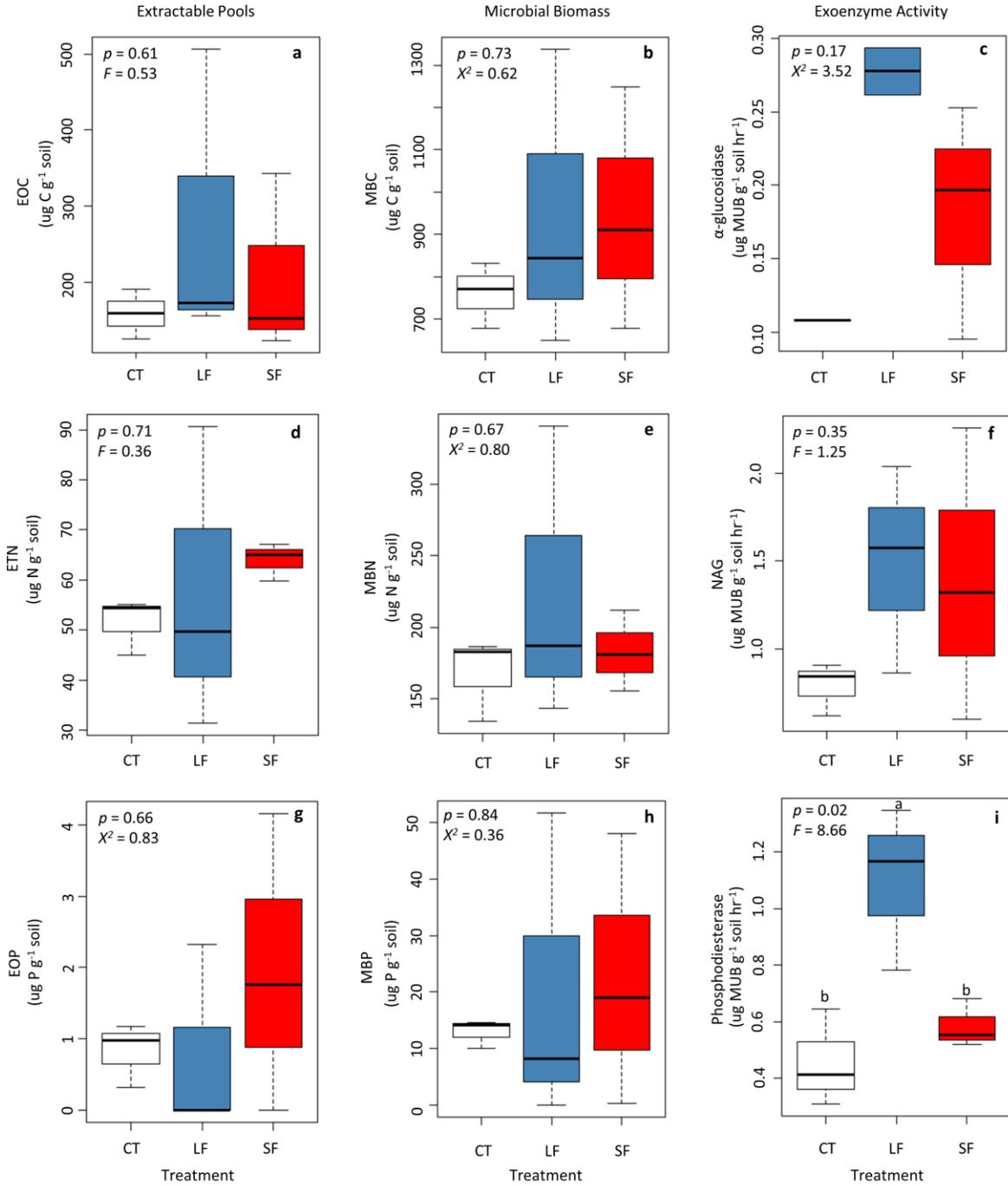


Figure 2.3: Boxplots showing the impact of herbivores on (a), (d), (g) extractable organic nutrients, (b), (e), (h) microbial biomass, and (c), (f), (i) potential enzyme activity in soils collected in July 2017 from an herbivore exclusion experiment in DH ($n = 3$) tundra at the ARC-LTER located at Toolik Lake, Alaska.

years (Edwards and Jefferies 2013), and with a single sampling it is possible that we missed transient effects that occurred during other parts of the growing season or during other years. Alternatively, studies have found that herbivore impacts may increase through time (Mallen-Cooper et al. 2019), and due to slow ecosystem processes in the Arctic, it may take greater than 20 years to see effects. As the impacts of herbivores in the Arctic can persist for greater than 150 years (Egelkraut et al. 2018), their impacts are likely to change over time (Mallen-Cooper et al. 2019), and more work is needed tracking the legacy level effects of herbivory within arctic ecosystems.

The level and intensity of herbivore activity may also influence arctic ecosystem processes. Some studies have shown that heavy grazing can increase N cycling and primary productivity, and moderate grazing may decrease these properties (Zamin and Grogan 2013), whereas others have shown the opposite (Pastor and Naiman 1992). Regardless, changes in herbivore density may have lasting effects on ecosystem functions and may be especially important with species with cyclic population densities such as voles. In the year of this study, and the years immediately preceding it, vole abundance was low (Maguire and Rowe 2017, Rowe and Steketee (unpublished data)), and vole densities inside the exclosures may have not differed greatly from that outside the exclosures. In addition to low densities of voles, the activities of these herbivores are particularly localized (e.g., latrine sites) and thus our randomized soil sampling may have missed sites where herbivore activities do affect soil nutrient cycling. Although we found few effects during a potential low phase of the local vole population cycle, the effect of voles on ecosystem functions during the high point in their population cycle has been documented in other ecosystems (Olofsson et al. 2012), suggesting the effects of voles in this ecosystem are density dependent. Potential suppression in arctic herbivore population cycles (Ims et al. 2008) may thus alter the role of herbivores in arctic systems in the future.

Here we described the influence of herbivores on vegetation and soil function in two arctic plant communities after 20 years of herbivore exclusion. We found that herbivory pressure altered moss cover and evergreen shrub abundance in the MAT and influenced P-acquiring enzyme activity in the DH. We provide evidence of differing impacts between different herbivore guilds for both vegetation and soil properties. Although other studies found stronger effects of herbivores under increased nutrient or warmed conditions, our data, collected under ambient conditions, may provide a baseline with which to examine the impacts of herbivores in a

changing arctic environment. Future changes in arctic systems may alter herbivore populations and communities as well as their influences on ecosystem ecology. While our replicate numbers were low, we believe that our results are representative of the potential impacts of herbivores in these two Alaskan arctic plant communities. However, the impacts of herbivores on these processes are likely to vary among the major regional vegetation types and we recommend that further studies incorporate additional systems to better elucidate the impacts of herbivores in the Arctic as a whole. Future work should also examine how potential changes in herbivore population dynamics and species assemblages of herbivores may influence ecosystem functions.

Data Accessibility

Data from this project will be made available on the Arctic Data Center. McLaren et al. 2019, Soil biogeochemical variables collected on the Arctic LTER experimental plots in moist acidic and dry heath tundra, Arctic LTER Toolik Field Station, Alaska 2017.

(<https://doi.org/10.6073/pasta/5a5cbb785bde48522bde7b87c65d3c13>). Gough 2019, Relative percent cover of plant species for years 2012-2017 in the Arctic Long-term Ecological Research (ARC-LTER) 1989 moist acidic tundra (MAT89) experimental plots, Toolik Field Station, Alaska. Environmental Data Initiative.

(<https://doi.org/10.6073/pasta/f31def760db3f8e6cfee5fee07cc693e>). Gough L. 2019. *Relative percent cover of plant species for years 2013 2014 2016 2017 in LTER dry heath tundra experimental plots established in 1989, Arctic LTER Toolik, Field Station Alaska*. Environmental Data Initiative. <https://doi.org/10.6073/pasta/25d3f0db55e9df6f99fc3e9596433090>.

Author Contributions

This chapter has been published in *Arctic, Antarctic, and Alpine Research* (Roy et al. 2020), and was co-authored by Austin Roy (AR), Matthew Suchocki (MS), Laura Gough (LG), and Jennie McLaren (JRM). JRM and LG co-conceived the larger study of which this study was led by AR; LG and JRM conceived the ideas and designed the methodology; AR and MS collected and analyzed the data; AR and JRM interpreted the results; AR led the writing of the manuscript. All authors contributed critically.

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Chapter 3: Impacts of herbivore structures on carbon and nutrient cycling in arctic tundra

Abstract

1. Understanding arctic ecosystem function is key to understanding future global carbon (C) and nutrient cycling processes. However, the effects small mammal herbivores have on ecosystems as structure builders have been underrepresented in the understanding of arctic systems.
2. We examined the impact of small mammal-engineered structures (hay piles, runways, latrines, burrows) and carcasses on soils and plants in three arctic tundra regions near Utqiagvik, Toolik Lake, and Nome, Alaska. Our aims were to 1) examine how vole and lemming structures influence plant and soil nutrient pools and microbial processes, 2) elucidate potential mechanisms by which these structures influence nutrient cycling, 3) determine if structure effects were similar across tundra system types, and 4) understand how changes in the abundance of these structures during different phases of small mammal multi-annual population cycles might influence nutrient cycling.
3. In general, small mammal structures increased nitrogen (N) availability in soils, although these effects varied with study region. Across study regions, hay piles were relatively uncommon but increased multiple soil N pools, C- and N-acquiring enzyme activities, and leaf phosphorus (P) concentrations, with the nutrient variables and size of the effects varying by region. Small mammal carcasses, although likely also rare on the landscape, provided nutrient-rich hotspots by increasing C, N, and P in soils. Runways and latrines had the highest percent cover of all activity types on the landscape but increased fewer N and P pools. The effects of different structures were regulated by different mechanisms, with the effects of hay piles likely influenced by higher N-mineralization rates of green litter material, and runways, latrines, and burrows influenced by higher soil temperatures compared to controls. Small mammal structures seemed to have no effect on vegetation community composition.
4. We conclude that by influencing soil nutrient availability and biogeochemical cycling, small mammal structures can influence bottom-up regulation of ecosystem function, particularly during the high phase of the small mammal population cycle, but that future changes in these population cycles might alter the role of small mammals in the Arctic and have lasting effects on system processes.

Introduction

Multiple mechanisms that control ecosystem processes have been explored to predict how the Arctic might function into the future; however, the role of herbivores and their structure building activities have been under appreciated. Herbivores are known to regulate ecosystem processes in other ecosystems (Jones et al. 1994, Wright et al. 2002, Kielland et al. 2006, Clark et al. 2016), resulting in a growing interest in the effects of these organisms on ecosystem processes and biogeochemical cycling in arctic ecosystems (Schmitz et al. 2014, Moorhead et al. 2017, Rastetter et al. 2022). To date, herbivore research in the Arctic has focused on the impact of herbivore presence and abundance on the ecosystem (Olofsson et al. 2012, Siewert and Olofsson 2021). Here, we expand these efforts by distinguishing between ecosystem impacts of consumptive (e.g., herbivory) vs non-consumptive (e.g., structure building) behaviors exhibited by these organisms.

Herbivores are traditionally thought of as having top-down controls on ecosystems through consumption, but these species may also have bottom-up controls by influencing biogeochemical cycling and nutrient availability. As the Arctic is known to be nutrient limited (Jonasson et al. 1999, McLaren and Buckeridge 2019, Tuomi et al. 2019), any changes in nutrient availability due to structure building activities could alter ecosystem processes and function (Egelkraut et al. 2018, Egelkraut et al. 2020). While engineered structures likely influence biogeochemical cycling at local scales, these local impacts can be scaled up to predict ecosystem function at broader scales. Current research on arctic biogeochemical cycling has highlighted the role of herbivory-induced changes in plant communities (Sitters et al. 2019, Stark et al. 2019, Yläne and Stark 2019) and burrowing activities (Louw et al. 2019). While these factors are impactful, other behaviors and structures might also be important (Egelkraut et al. 2020). For example, the production of feces adds readily accessible nutrients to soil organic matter (Sitters and Olde Venterink 2021b) and may alter nutrient limitation in soils (Sitters et al. 2017). Additionally, the creation of latrines (used by many arctic small mammals) may create spatially non-uniform effects of feces on nutrient cycling within landscapes. Runways built and used by small mammal herbivores may alter light-availability (Mossman 1955, Borer et al. 2014), nutrient cycling (Schrama et al. 2013), and water retention (van Klink et al. 2015) at local scales. Some activities or structures can increase or decrease soil temperatures (Coppedge et al. 1999, Burda et al. 2007, Whitford and Steinberger 2010), which can alter nutrient cycling rates.

While herbivores have been classically described as having top-down controls on ecosystem function (although see Turkington 2009), the structures built by small mammals show the potential for these species to have bottom-up effects on ecosystems by controlling the size and proportion of nutrient pools that are available to plants and microbes. Changes in soil nutrient pools and vegetation (Tang et al. 2019) can feedback to influence other ecosystem properties such as plant nutrient allocation and C-cycling (Wookey et al. 2009, Min et al. 2021), photosynthetic and primary productivity (Chapin et al. 2002a, van Wijk et al. 2005), vegetation community composition (Gough et al. 2008, Gough et al. 2012), and alter ecosystem process rates (Tuomi et al. 2019, Ylänne and Stark 2019). A clearer understanding of how small herbivore-built structures influence ecosystem form and function will better elucidate the multiple roles of these species in arctic systems (Fafard et al. 2019, Louw et al. 2019).

In the Arctic, arvicoline rodents, such as lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) and voles (*Microtus* spp. and *Myodes* spp.), have been described as locally important herbivores (Roy et al. 2020) because they are active year-round (i.e., do not hibernate), are resident species (i.e., do not migrate), and can be found at high densities. These herbivores can go through 3-5-year population cycles, resulting in extreme increases in animal density from the population cycle low to peak (Batzli et al. 1980). The accompanying increases in small mammal structures in a year of peak population density might be important over larger spatial-temporal scales, especially if the structures have persistent effects on ecosystem processes (e.g., decomposition). Some researchers have hypothesized that recent population cycles have been suppressed or crashed because of climate change effects (Ims et al. 2008, Cornulier et al. 2013, but see Ehrlich et al. 2020), which might change the level of impact herbivores exert in the Arctic. Such changes in herbivore density will influence the number of structures on the landscape and potentially affect ecosystem function at spatiotemporal scales.

The next step to improving knowledge of the impact of herbivores in the Arctic is understanding how the different structures built by the dominant mammalian herbivores (small mammals) and changes in structure abundance influence biogeochemical cycles. The overarching goal of this study was to examine the influences of specific small mammal structures on C, nitrogen (N), and phosphorus (P) cycles in arctic tundra. Our specific objectives were to 1) compare C, N, and P pools of soils and plants at arvicoline structure sites to control sites, 2) identify potential mechanisms driving the effects of structures on nutrient pools, 3) examine the

effects of small mammal structures across three tundra systems, and 4) determine the relative percent cover of different structure types during the high phase compared to the low phase of a population cycle.

Materials and Methods

Study site

We conducted this study at arctic tundra regions located near Utqiagvik (formerly Barrow, 71.290°, -156.788°, elevation 5 m), Toolik Lake (68.627°, -149.594°, elevation 750-900 m), and Nome (64.501°, -165.406°, elevation 45-100 m), Alaska (Figure 3.1a). Within each region, samples were collected from three sites separated by a minimum of 750 m. Sample sites at Utqiagvik were within a high-centered polygon tundra ecosystem dominated by graminoids, dwarf shrubs, and lichens, and the dominant small mammals were brown lemmings (*Lemmus trimucronatus*), with additional small mammal species present including collared lemmings (*Dicrostonyx groenlandicus*) and shrews (*Sorex* spp., Batzli et al. 1980). Sample sites at Toolik and Nome were within moist acidic tussock tundra ecosystems, dominated by sedges, deciduous shrubs, and evergreen shrubs (Racine et al. 1987, Roy et al. 2020) and the small mammal species used in this study were tundra voles (*Microtus oeconomus*), with additional small mammal species present including collared lemmings, singing voles (*M. miurus*), red-backed voles (*Myodes rutilus*), arctic ground squirrels (*Urocitellus parryii*), and shrews (Quay 1951, Batzli and Henttonen 1990).

Sampling of small mammal structure types

Soils: We collected soil from the Utqiagvik and Toolik Lake sites in the summer of 2018, and the Nome sites in the summer of 2019. From each site within each region, we collected five soil samples using a serrated bread knife from the soil organic layer to a depth of 5 cm (approximately 5 x 5 x 5 cm) under four small mammal structure types: hay piles or winter nests (hereafter hay piles), runways, latrines, burrow entrances (hereafter burrows), and control locations (Figure 3.1b-f) at each site. Only structures with fresh sign (e.g., active burrow or runway) were sampled, however as some structures can be used for multiple years (McKendrick et al. 1980) the age of a structure was not assessed. In Utqiagvik, hay piles were lemming winter nests, and controls were areas 1 m from a hay pile which lacked any visible small mammal activity. At Toolik Lake and Nome, hay piles were piles of clipped *Eriophorum vaginatum* near tussocks, and controls were areas 1 m from hay piles and near tussocks not showing vole

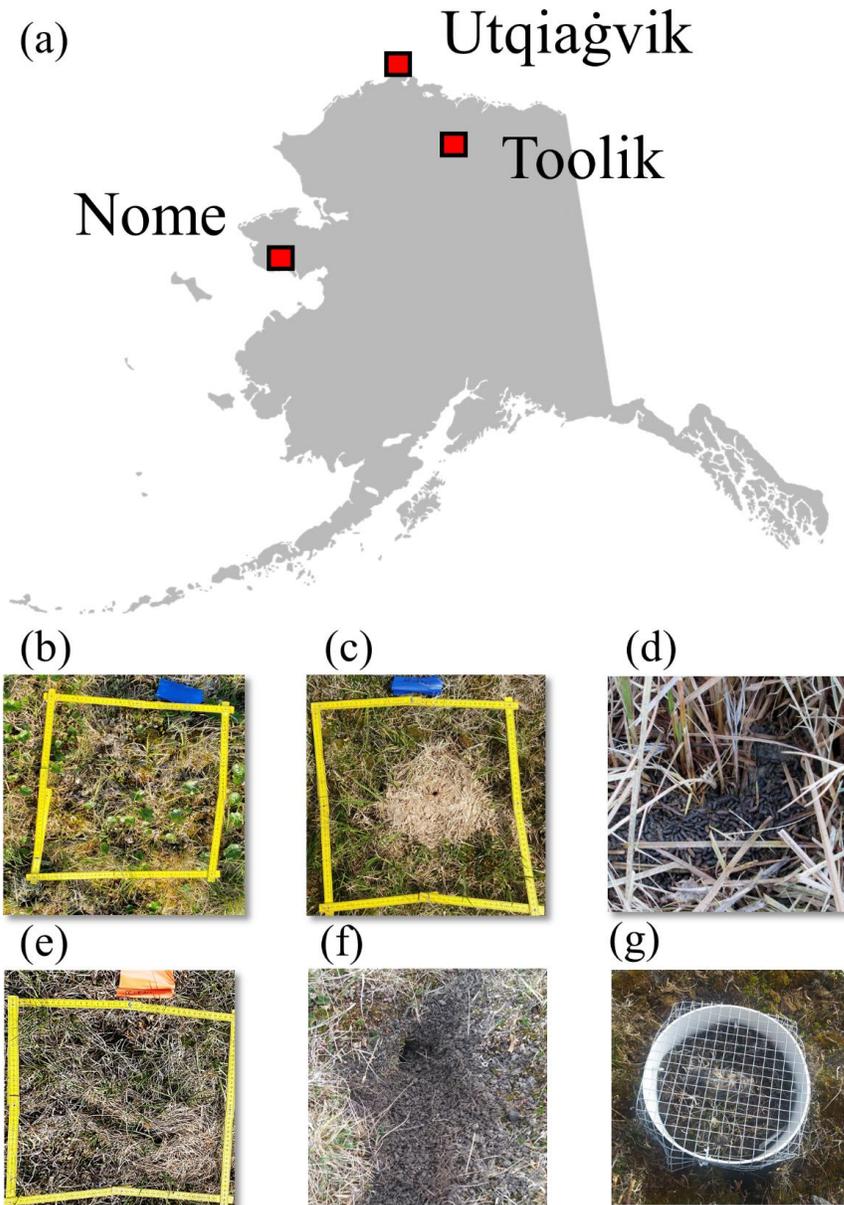


Figure 3.1: (a) Overview of study areas located in arctic tundra in northern Alaska, USA, and examples structures built by small mammals: (b) control plot, (c) hay pile, (d) latrine, (e) runway, (f) burrow, and (g) carcass.

damage. At the Nome sites, only hay piles and controls were sampled as other structure types could not be located.

At Utqiagvik we conducted two additional studies not done at Toolik or Nome. We recorded upper organic layer soil (2.5 cm depth) temperatures under five replicates of each structure type using a digital probe thermometer (Yard Mastery, FL, USA). We also tested the effect of lemming carcasses on soil nutrient pools. In the summer of 2018, lemming carcasses (received from D. Holt, Alaska Fish & Wildlife Permit #18-089) were placed in the center of high-centered polygons. Five carcasses were placed directly on the soil surface and enclosed with a PVC collar (Figure 3.1g). Three control sites with collars were also installed adjacent to the carcasses. Carcasses decomposed for approximately 1 year and in 2019 were removed, and soils sampled beneath each carcass and control plots following the same protocol described above.

For each soil sample, we dried a subsample of known volume at 50 °C for 48 hours to assess bulk density and volumetric water content. Subsequently, we homogenized each remaining soil sample by hand, removing all large roots (>1 mm diameter), and partitioned samples for analysis within two days of collection. Soil samples were then shipped to the University of Texas at El Paso, where they were either processed immediately or frozen at -80°C until analysis (enzyme samples only).

Plants: We conducted plant sampling only at the Utqiagvik sites. To assess the influence of small mammal structures on plant communities we assessed the vegetation community at each structure location in 2018. We used a 40 cm x 40 cm quadrat and Daubenmire values (Coulloudon et al. 1999) to quantify percent cover of vascular and nonvascular plants, bare ground, and plant litter at each structure and control location, with no overlap between sampling areas. Vascular plants were identified to species, and mosses and lichens were grouped across species. For analysis, plant species were grouped into functional groups (graminoid, shrub, moss, lichen, bare ground, litter). Additionally, in summer 2020 we sampled live *Carex aquatilis* leaves during the peak growing season from plants growing within or immediately adjacent to five hay piles, runways, latrines, burrows, and control locations. Samples were immediately dried at 50 °C for 48 hours before analysis for C, N, and P content.

Soil and plant analysis

We analyzed dried soil and plant samples for total C, N, and P, fresh soil samples for inorganic nutrients (NH_4^+ , NO_3^- , PO_4^{3-}); total extractable nutrients (extractable organic C (EOC), extractable total N (ETN)); and microbial biomass C, N, and P; and frozen soil samples for extracellular enzyme activity.

We ground and processed dry plant and soil subsamples for total C and N content using a dry combustion C and N analyzer (PyroCube®, Elementar, Langenselbold, Germany). Total P content was determined after ashing samples at 500 C, digesting using 6M HCl, then analyzing PO_4^{3-} content using a malachite green assay (D'Angelo et al. 2001). To determine soil inorganic nutrients, we extracted subsamples in 0.5 M K_2SO_4 and analyzed extractant using colorimetric microplate assays (BioTEK Synergy HT microplate reader, Winooski, Vermont, USA). NH_4^+ -N (NH_4^+) was determined using a modified Berlethot assay (Rhine et al. 1998), NO_3^- -N (NO_3^-) using a modified Griess assay (Doane and Horwath 2003), and PO_4^{3-} -P (PO_4^{3-}) using a malachite green assay (D'Angelo et al. 2001).

EOC and ETN were determined for the extracts mentioned above using an EOC/ETN analyzer (TOC-V Series CN analyzer, Shimadzu Corporation, Kyoto, Japan). To determine microbial biomass C, N, and P, we conducted the above EOC and ETN assays on samples after a direct chloroform-addition modification of the fumigation-extraction method (Brookes et al. 1985, Voroney et al. 2006) prior to extraction. We calculated microbial biomass for C, N, and P (MBC, MBN, and MBP) by subtracting EOC, ETN, or PO_4^{3-} respectively of non-fumigated samples from that of fumigated samples.

Extracellular enzyme (exoenzyme) activity was assessed for 10 exoenzymes involved in the microbial acquisition of C, N, and P (as in Roy et al. 2020): C-acquiring enzymes (β -glucosidase, β -cellobiosidase, β -xylosidase, α -glucosidase), N-acquiring enzymes (N-acetyl-glycosaminidase (NAG), leucine amino peptidase (LAP)) and P-acquiring enzymes (phosphatase, phosphodiesterase), as well as the oxidative enzymes phenol oxidase and peroxidase. One g of soil was blended with a sodium acetate buffer to reflect natural soil conditions (pH = 4). Samples were incubated at 20°C and enzyme activity (fluorescence) measured every 30 minutes for 3.5 hours following methods adapted from Sayia-Cork et al. (2002) and McLaren et al. (2017a). Oxidative enzyme analysis was performed using an L-3,4-

dihydroxyphenylalanine (L-DOPA) substrate for phenol oxidase and peroxidase. Color absorbance was measured at 460 nm using a reader after 24 hours of incubation at 6 °C.

N-mineralization rates

As small mammal structures, in particular hay piles, may influence litter input by increasing the amount of green litter entering the litter pool, we examined how soil N-mineralization rates were influenced by cover of different types of litter using an intact core mineralization experiment (DeMarco et al. 2011), modified from Aguirre et al. (2021). In the fall of 2018, we installed 28 mineralization cores at one site within each study region. At each site, soil cores were assigned to one of four litter treatments: 1) hayed litter (clipped, green, preferred forage material), 2) senesced litter (clipped, senesced, preferred forage material), 3) senesced non-preferred forage (clipped, senesced, non-preferred plant material) placed directly on top of the soil or 4) no litter (controls). Green leaf material was collected during the middle of the growing season (July) and senesced material was collected in early Fall (September). At each site the preferred species (Utqiagvik - *C. aquatilis*, Toolik and Nome - *Eriophorum vaginatum*) and the non-preferred species (Utqiagvik - *Petasites frigidus*, Toolik and Nome - *Betula nana*) were chosen based on small mammal diet preferences (Batzli et al. 1983, Batzli and Lesieutre 1991) and the species' dominance in the vegetation community. All plant material was cut into 2.5 cm segments and dried at 50 C for 48 hours prior to use in the mineralization cores. Mineralization cores were incubated *in situ* for approximately one year. Wildlife disturbed all mineralization cores at Utqiagvik, and these cores could not be analyzed. For the remaining cores, resin bags and soils were removed from each tube, soils homogenized, and frozen until analysis.

Soils and resin bags were analyzed for NH_4^+ and NO_3^- . Net N-mineralization was calculated as the differences between DIN ($\text{NH}_4^+ + \text{NO}_3^-$) in the initial soil sample and DIN in the final soil core plus the DIN accumulated in the resin bag immediately below soils (DeMarco et al. 2011). Mineralization rates were calculated as net N-mineralization divided by the number of incubation days in the field.

Cover of small mammal structures

To assess the relative percent cover of small mammal structures during different phases of the small mammal population cycle we visually estimated percent coverage of each structure type (hay piles, runways, latrines, burrows) within eight 1 m² adjacent quadrats in enclosures (20 x 20 m) and enclosure fences (8 x 8 m) installed for a separate experiment located adjacent to our soil

sample locations. There were three replicates of each enclosure and enclosure fence, each replicate set was separated by at least 750 m, within each of our study regions. Enclosure fences were established and stocked with four individual small mammals (voles at Toolik and Nome and lemmings at Utqiagvik) per enclosure in the summer of 2018 in Utqiagvik and Toolik, and 2019 in Nome. This stocking density mimics the expected population density of small mammals during the high phase of their cycle (Batzli et al. 1980, Batzli and Henttonen 1990). Enclosure fences excluded small mammals and represented the low phase of the population cycle. We collected percent cover data within each fencing treatment in July of 2018 and 2019, with the percent cover of each small mammal structure type averaged among quadrats within each fencing treatment (high phase and low phase).

Statistical analysis

We performed statistical analysis using program R (R Core Team 2018) with a cutoff of $p < 0.05$ for inferring statistical significance.

Effects of small mammal structures on soil nutrient cycling – At Utqiagvik and Barrow, where multiple small mammal structure types were sampled, differences in soil variables due to structure types (hay piles, runways, latrines, burrows) were determined using two-way ANOVAs or student's t-tests (Carcass study) as appropriate, with nutrient concentrations, microbial biomass, and enzyme activity as the response variables and sample region and structure type as independent variables. Similarly, we examined differences in N-mineralization using two-way ANOVAs with mineralization rates as response variables and sample region and litter type as independent variables. To examine effects of structures on individual, pooled nutrient-acquiring (e.g., all C-acquiring enzymes), and total enzyme activity, individual enzyme activities were standardized (activity/maximum activity) before pooling. When data could not be normalized, Kruskal-Wallis and Wilcoxon rank sum tests were used. Because the only structures sampled at Nome were hay piles, we also compared the effect of hay piles to controls across all three study regions (Utqiagvik, Toolik, Nome) using two-way ANOVAs with soil variables as the dependent variable and structure type and region as the independent variables.

Soil temperatures – To determine the influence of structures on soil temperatures, we used a Kruskal-Wallis test, with temperature as the dependent variable and structure type as the independent variable.

Plant CNP – Differences in leaf C, N, and P were analyzed individually using a one-way ANOVA or Kruskal-Wallis when appropriate. Structure type was used as the independent variable and plant CNP were used as dependent variables.

Vegetation community – To examine the influence of structure type on vegetation community, we used the package *vegan* (Oksanen et al. 2019) to calculate Shannon diversity indices using plant species identified at each structure type. Differences in diversity indices were compared between each structure type using a Kruskal Wallis test with Shannon diversity indices as the dependent variable and structure type as the independent variable, followed by a Dunn's post hoc test. We also compared the percent cover of plant functional groups at structure sites using two-way ANOVAs, with percent cover of each functional group as the dependent variable and structure type as the independent variable.

Small mammal structure cover – Mean percent cover of each structure type was compared between lemming high phase (enclosure) and low phase (exclosure) fences using a two-way ANOVA with population phase and region as the independent variable and cover of each structure type as the dependent variables.

Results

Small mammal structure type and soil nutrients

At Utqiagvik and Toolik, we observed multiple effects of small mammal structures on nutrient pools, with hay piles and latrines having the largest and most consistent effects (Figure 3.2). Hay piles mainly affected N pools, while latrines affected C, N, and P pools (Figure 3.2). For NH_4^+ and ETN, there were significant treatment x region interactions (Table 3.1), with higher NH_4^+ under hay piles than controls ($p < 0.001$, Supplemental Table 3.1) and a trend for higher ETN under hay piles than controls ($p = 0.074$) at Utqiagvik, but no significant effects for either variable under hay piles at Toolik (Figure 3.2). MBN varied by structure type but not by region (Table 3.1) and showed that hay piles ($p = 0.025$) and runways ($p = 0.013$) had higher MBN concentrations than controls. The only enzyme activity affected by small mammal structures was β -xylosidase ($p = 0.059$, $\chi^2 = 7.43$), and the effect was only marginal with activity trending higher under hay piles ($p = 0.098$) than controls (Figure 3.2f). Additionally, we observed a treatment x region interaction for EOC (Table 3.1) and PO_4^{3-} (Table 3.1), where EOC (Figure 3.2d) and PO_4^{3-} (Supplemental Figure 3.3) concentrations were higher under latrines than controls at Toolik ($p < 0.05$, Supplemental Table 3.1), but there were no effects seen in either

variable at Utqiaġvik. Additionally, ETN trended higher ($p = 0.06$) under latrines than controls at Toolik (Figure 3.2c, Table 3.1, Supplemental Table 3.1).

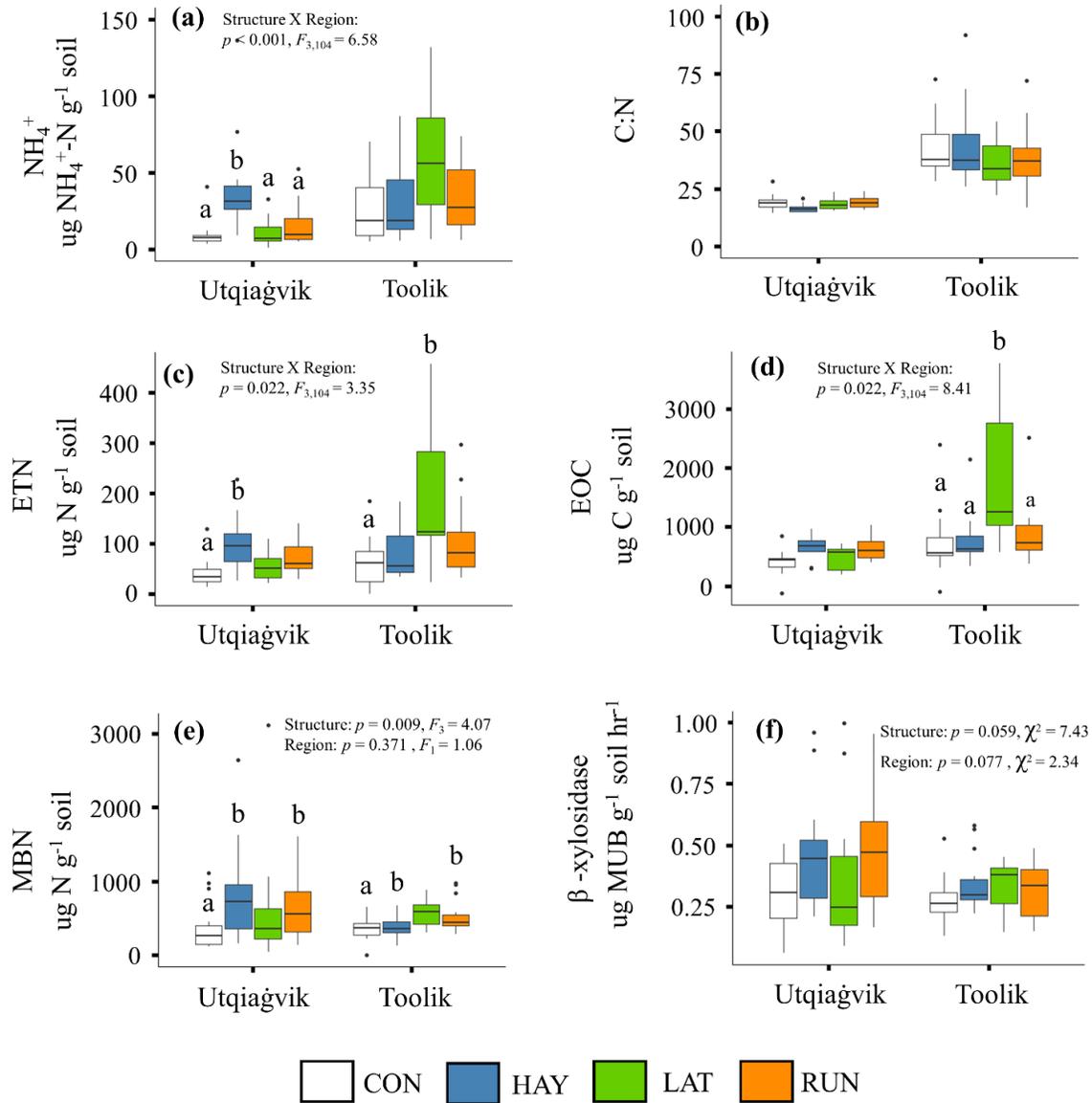


Figure 3.2: Boxplots showing the relative impacts of small mammal structures (CON = control, HAY = hay pile, RUN = runway, LAT = latrine) on (a) ammonium (NH_4^+), (b) extractable total N (ETN), (c) microbial biomass N (MBN), (d) C:N ratios, (e) extractable organic C (EOC), and (f) potential β -xylosidase activity in soils collected in 2018 from beneath small mammal structures at the Utqiaġvik and Toolik study sites.

Table 3.1: Statistical impact of small mammal structures on soil variables (total % carbon (C), nitrogen (N), and phosphorus (P) content (TC, TN, TP); ammonium (NH₄⁺); nitrate (NO₃⁻); phosphate (PO₄³⁻); extractable organic C (EOC); extractable total N (ETN); extractable inorganic N (EIN); extractable organic N (EON); microbial biomass C, N, and P (MBC, MBN, MBP)). Summary results from statistical comparisons of soil variables between small mammal structure types and study regions. ANOVA tests were used when possible and Wilcoxon rank sum tests and Kruskal-Wallis were used when data could not be normalized.

Variable	Structure			Region			Structure x Region		
	<u>Stat</u>	<u>p</u>	<u>df</u>	<u>Stat</u>	<u>p</u>	<u>df</u>	<u>Stat</u>	<u>p</u>	<u>df</u>
TC	<i>F</i> = 1.96	0.124	3	<i>F</i> = 106.98	<0.001	1	<i>F</i> = 4.35	0.006	3, 104
TN	$\chi^2 = 2.77$	0.429	3	<i>W</i> = 2732	<0.001	1	----	----	----
TP	$\chi^2 = 2.48$	0.479	3	<i>W</i> = 2858	<0.001	1	----	----	----
CN	$\chi^2 = 3.31$	0.346	3	<i>W</i> = 54.06	<0.001	1	----	----	----
CP	$\chi^2 = 3.68$	0.298	3	<i>W</i> = 163	<0.001	1	----	----	----
NP	$\chi^2 = 3.59$	0.310	3	<i>W</i> = 778	<0.001	1	----	----	----
NH ₄ ⁺	<i>F</i> = 4.98	0.003	3	<i>F</i> = 21.08	<0.001	1	<i>F</i> = 6.58	<0.001	3, 104
NO ₃ ⁻	$\chi^2 = 4.91$	0.179	3	<i>W</i> = 1664	0.060	1	----	----	----
PO ₄ ³⁻	<i>F</i> = 1.21	0.310	3	<i>F</i> = 74.83	<0.001	1	<i>F</i> = 4.29	0.007	3, 104
EOC	<i>F</i> = 2.54	0.061	3	<i>F</i> = 25.06	<0.001	1	<i>F</i> = 8.41	<0.001	3, 104
ETN	<i>F</i> = 5.25	0.002	3	<i>F</i> = 3.07	0.083	1	<i>F</i> = 3.54	0.022	3, 104
EIN	<i>F</i> = 5.12	0.002	3	<i>F</i> = 20.56	<0.001	1	<i>F</i> = 6.59	<0.001	3, 104
EON	<i>F</i> = 3.62	0.014	3	<i>F</i> = 1.03	0.313	1	<i>F</i> = 3.25	0.025	3, 103
MBC	$\chi^2 = 5.68$	0.128	3	<i>W</i> = 1509	0.959	1	----	----	----
MBN	<i>F</i> = 4.07	0.009	3	<i>F</i> = 1.21	0.273	1	<i>F</i> = 1.06	0.371	3, 102
MBP	$\chi^2 = 1.03$	0.794	3	<i>W</i> = 310	<0.001	1	----	----	----

There were further effects of small mammal structures on soil nutrient pools for the two structure types collected only at Utqiagvik (Table 3.2, Supplemental Table 3.3). Burrows had higher NH_4^+ ($p = 0.028$) and ETN ($p = 0.021$) concentrations compared to controls (Supplemental Figures 3.10 and 3.11), and carcasses had higher NH_4^+ (Table 3.2, Figure 3.3a), ETN (Table 3.2, Figure 3.3b), and EIN (Table 3.2, Supplemental Figure 3.11, Supplemental Table 3.4) than controls. In addition to N pools, carcasses also influenced C and P pools by having higher EOC and PO_4^{3-} than controls (Figure 3.3c-d, Table 3.2, Supplemental Table 3.4).

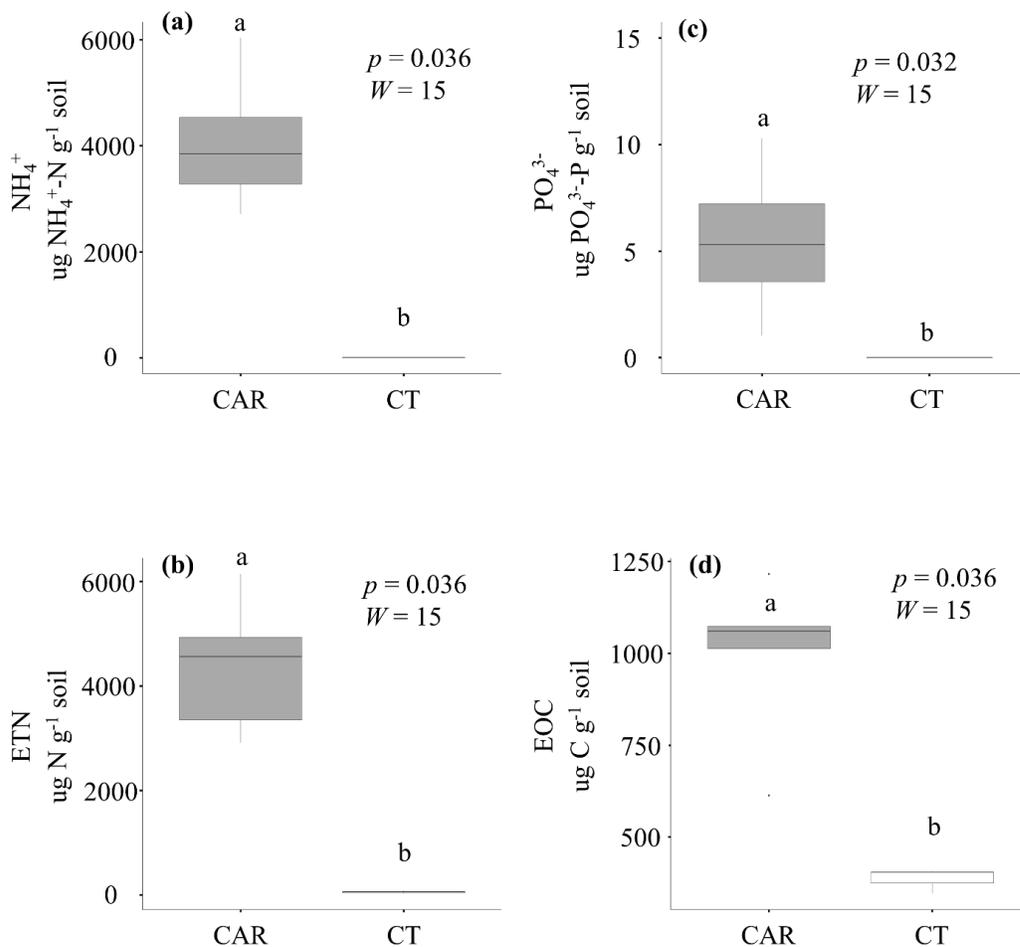


Figure 3.3: Boxplots showing the relative impacts of lemming carcasses (CAR) on soil (a) NH_4^+ , (b) ETN, (c) PO_4^{3-} , and (d) EOC compared to control (CT) sites. Soils were collected from beneath CAR and CT sites near Utqiagvik, Alaska, USA, after one year of decomposition. See Figure 3.2 for variable definitions.

Table 3.2: Mean (standard error) of total percent % carbon (TC), total % nitrogen (TN), total % phosphorus (TP), C:N ratio, C:P ratio, N:P ratio, inorganic nutrient (NH_4^+ , NO_3^- , PO_4^{3-}) concentrations, extractable organic nutrients (EOC, ETN, EIN), and microbial biomass CNP (MBC, MBN, MBP) in soils collected at control (CT) and lemming carcass (CAR) sites near Utqiagvik, Alaska, USA in 2019. Wilcoxon rank sum test results from comparisons of soil variables between control and carcass sites. See Table 1 for variable definitions.

Variable	Treatment		Statistics	
	CT	CAR	<i>W</i>	<i>p</i>
TC	41.56 (1.29)	42.88 (0.43)	11	0.393
TN	1.43 (0.20)	1.47 (0.15)	7	1.000
TP	0.13 (0.02)	0.16 (0.02)	12	0.250
CN	30.71 (5.81)	31.01 (4.63)	9	0.786
CP	335.43 (50.61)	301.48 (67.96)	4	0.393
NP	11.73 (2.80)	9.41 (0.69)	6	0.786
NH_4^+	5.08 (2.18)	4082.12 (573.94)	15	0.036
NO_3^-	1.77 (1.45)	1.04 (0.31)	8	1.000
PO_4^{3-}	0 (0)	16.90 (11.51)	15	0.032
EOC	385.32 (19.75)	995.28 (101.40)	15	0.036
ETN	52.74 (17.06)	4377.08 (576.58)	15	0.036
EIN	6.85 (2.29)	4083.16 (573.75)	15	0.036
EON	45.89 (14.88)	293.93 (198.58)	11	0.393
MBC	1526.28 (57.92)	2177.23 (342.02)	12	0.250
MBN	884.65 (682.05)	135.65 (122.94)	2	0.127
MBP	3.30 (1.91)	46.06 (17.53)	12	0.250

Hay piles across multiple arctic sites

In comparing the effects of hay piles among our three study regions, we documented hay pile effects on C and N, but not P, pools along with general differences among regions (Figure 3.4, Supplemental Table 3.5). We observed a trend for higher EOC under hay piles than controls ($p = 0.075$, $F_1 = 3.249$, Supplemental Figure 3.4). We also saw effects of hay piles on C-acquiring enzymes, with higher β -glucosidase ($p = 0.040$, $W = 1188$), β -cellobiosidase ($p = 0.010$, $F_1 = 7.014$), β -xylosidase ($p = 0.044$, $W = 1236$, Supplemental Figure 3.7, Supplemental Table 3.6). Hay piles influenced N pools by having higher ETN ($p = 0.004$, $F_1 = 8.668$, Figure 3.4c), MBN

($p = 0.011$, $F_1 = 6.723$, Figure 3.4b) and NAG enzyme activity ($p = 0.002$, $F_1 = 10.368$, Supplemental Figure 73.) than controls across all regions. Soils under hay piles also had higher NH_4^+ concentrations compared to controls, but only at the Utqiagvik sites ($p = 0.001$, Figure 3.4a). Lastly, we observed trends for higher EON ($p = 0.062$, $W = 1244$) under hay piles than controls (Supplemental Figure 3.4).

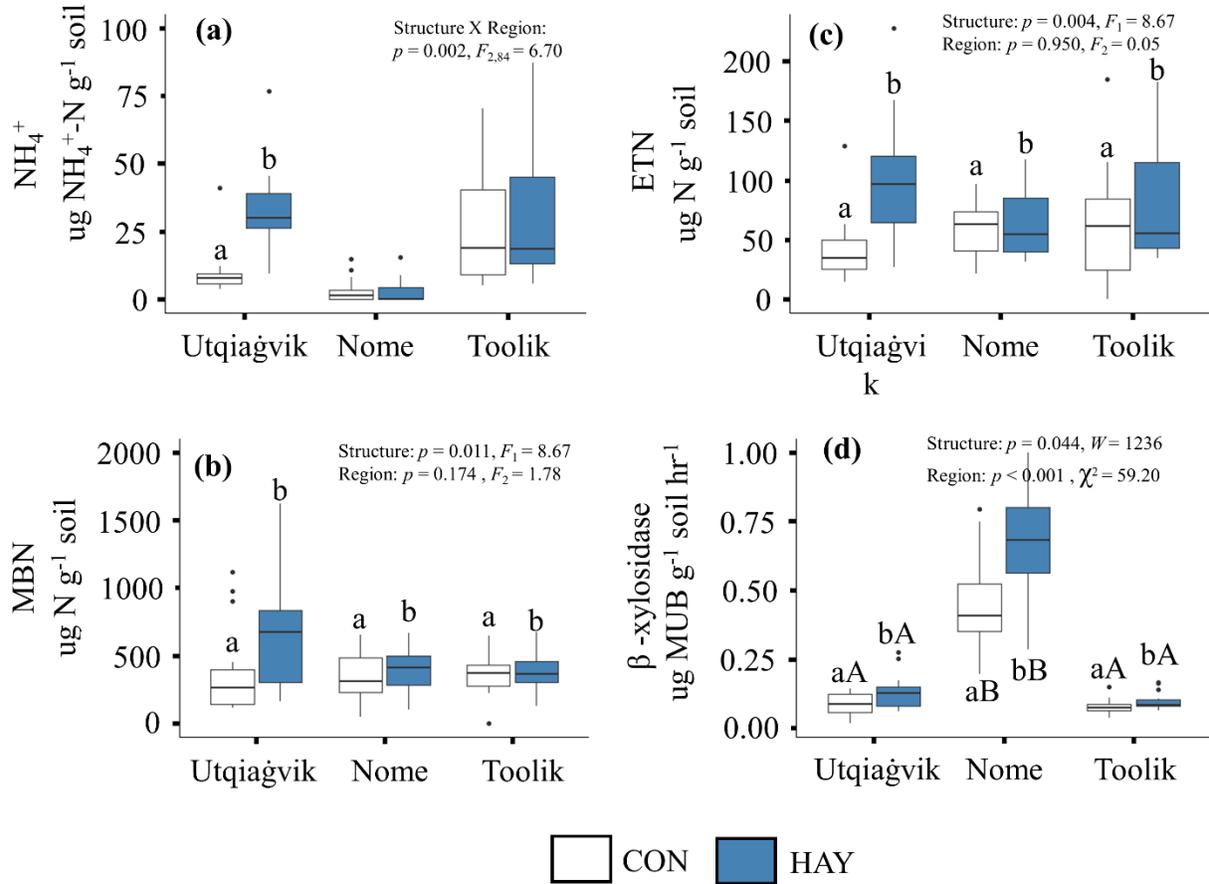


Figure 3.4: Boxplots showing (a) NH_4^+ , (b) ETN, (c) MBN, and (d) potential β -xylosidase activity in soils beneath hay piles (HAY) and control sites (CON). Soils were collected at the Utqiagvik (2018), Toolik (2018), and Nome (2019) study sites. Uppercase letters represent differences between study regions and lowercase letters represent differences between treatments. See Figure 3.2 for variable definitions.

N-mineralization rates

Net N-mineralization rates varied by litter type ($p < 0.001$, $F_3 = 10.533$), but not by region ($p = 0.688$, $F_1 = 0.063$, Supplemental Table 3.7). Soils under hayed litter had higher net N-mineralization than controls and all other treatments ($p < 0.001$, Figure 3.5a)

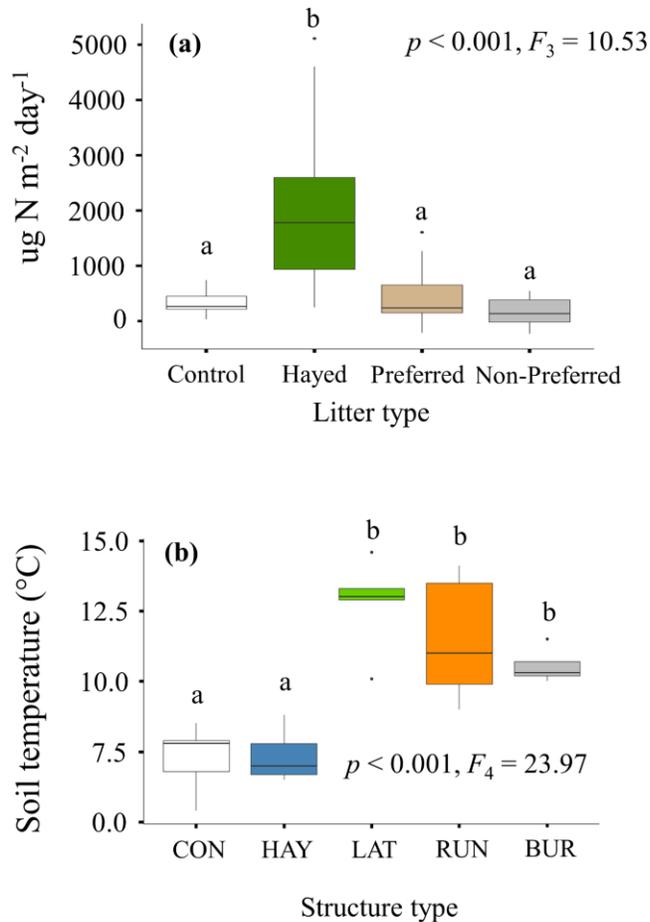


Figure 3.5: Boxplots showing the relative impact of small mammals on mechanisms influencing biogeochemical cycling in arctic tundra. (a) N-mineralization rates observed under hayed preferred forage litter (green *E. vaginatum*), senesced preferred forage litter (senesced *E. vaginatum*), and senesced non-preferred forage litter (senesced *B. nana*); after one year *in situ* near Toolik and Nome, Alaska, USA. (b) Soil temperatures collected under control (CON) and lemming structure sites (HAY = hay pile, LAT = latrine, RUN = runway, BUR = burrow) in 2020 near Utqiagvik, Alaska, USA.

Soil temperatures

Lemming structure type influenced soil temperatures ($p < 0.001$, $F_1 = 23.97$, Figure 3.5b). Latrines ($p < 0.001$), burrows ($p = 0.014$), and runways ($p = 0.001$) sites had higher temperatures than controls, while there was no difference in soil temperatures between hay piles and control sites ($p = 0.999$).

Small mammal structures and plant nutrients

The only effect of lemming structures on *C. aquatilis* leaf tissue total C, N, and P and elemental ratios was caused by hay piles (Supplemental Table 3.8). Hay piles had lower total C ($p = 0.017$), higher total P ($p < 0.001$), and lower C:P than controls ($p = 0.003$, Figure 3.6, Supplemental Figure 3.9).

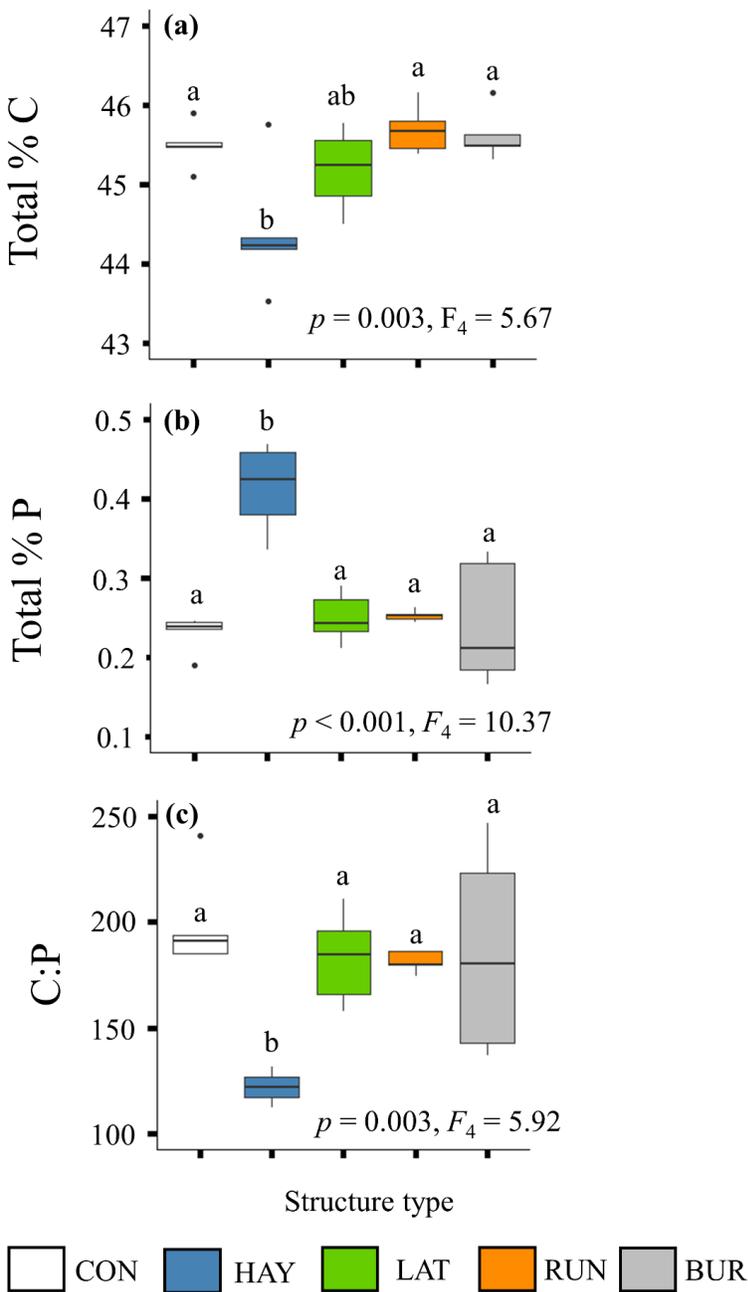


Figure 3.6: Boxplots showing the relative impact of lemming structures on vegetation (a) total % C, (b) total % P, and (c) C:P. *C. aquatilis* leaf tissues were collected from within, or adjacent to, active lemming structures near Utqiagvik, Alaska, USA in 2020.

Vegetation percent cover

Shannon diversity indices varied by structure type ($p = 0.034$, $\chi^2 = 8.70$), with post hoc tests showing that diversity was higher at burrows than hay piles (Utqiagvik only, $p = 0.025$), although there were no differences in diversity indices between lemming structures and controls ($p > 0.05$). While we observed no significant differences in the mean percent cover of functional groups between structure sites and controls ($p = 0.959$, $F_4 = 0.16$), some functional groups were unique to certain structure types (Supplemental Figure 3.13). Bare ground was only observed at runways, burrows, and latrines, and evergreen shrubs were only observed at latrines.

Small mammal structure percent cover

We did not observe any small mammal structures in the low phase treatment fence within any region. Within the high phase treatment and across all study regions, percent cover varied by structure type ($p < 0.001$, $F_3 = 9.468$) and region ($p = 0.0316$, $F_2 = 2.375$). Region-wide, runways and latrines had the highest percent cover (1.4%), followed by hay piles (0.6%, Figure 3.7).

While there were no region x structure cover interactions ($p = 0.986$, $F_5 = 0.14$), Utqiagvik had the highest percent cover of structures (12.5%), with runways covering the most area (7.5%), followed by latrines (4.3%), burrows (0.6%), and hay piles (0.1%, Figure 3.7). Toolik had the second highest percent cover of small mammal structures (1.7%), with hay piles having the highest cover at 1.1%, followed by runways (0.6%), and latrines were not observed (Figure 3.7).

Finally, Nome had the lowest percent cover of small mammal structures (1.3 %); again, runways had the highest cover (0.7%), followed by hay piles (0.6%) and no latrines were observed (Figure 3.7).

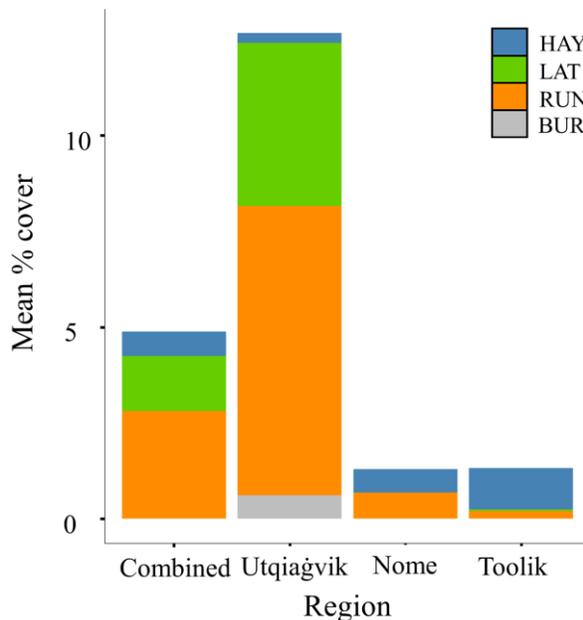


Figure 3.7: Mean percent cover (% cover) of small mammal structures (HAY = hay piles, LAT = latrine, RUN = runway, BUR = burrow) collected within small mammal enclosures (100 individuals ha⁻¹) after 2 years of small mammal presence, located near Utqiagvik, Toolik, and Nome, Alaska, USA.

Discussion

Small mammal-built structures alter nutrient pools

Our study reveals that the structures created by arctic small mammal contribute to the bottom-up regulation of biogeochemical cycling and on ecosystem function. A key result of this study is that different small mammal structures produce unique effects on the carbon (C), nitrogen (N), and phosphorus (P) pools of soils and plants. We found that hay piles were particularly important, having positive effects on soil N pools as well as the activity of C- and N-acquiring enzymes across geographically separated tundra ecosystems. Like hay piles, latrines and carcasses affected pools of multiple resources, including C, N and P, while runways and burrows increased only soil N pools. We also showed that the effects of small mammal structures were relatively ubiquitous across the arctic tundra ecosystems we examined, influencing N pools more than any other biogeochemical variables measured, but that the relative influence of a given structure type varies by ecosystem/region. Together, our findings suggest that the impacts of small mammals during the high phase of their population cycle have the potential to affect nutrient availability at landscape levels.

Our results support the idea that small mammal-built structures can have bottom-up effects on arctic ecosystems by increasing N-availability in soils, and therefore, because of the coupling of C-N cycling in arctic tundra (Jonasson et al. 1999), impact C sink-source dynamics in tundra ecosystems (Min et al. 2021) during the high phase of their population cycle. This conclusion is supported by our observation that increases in N pool size coincide with higher β -xylosidase activity, suggesting that microbes increase their effort to acquire C in response to decrease in N- limitation. In addition, if population peaks result in increases in N-availability this could result in greater C sequestration in arctic tundra via increased photosynthetic potential (Chapin et al. 2002a), total plant and leaf biomass (van Wijk et al. 2005, Gough et al. 2012), and changes in plant community composition (Weintraub and Schimel 2005, Gough et al. 2012). Alternatively, increases in N-availability and changes in plant communities might prime and therefor enhance soil microbial decomposition (Sistla et al. 2012), leading to rapid cycling and loss of C from the system (Sistla et al. 2012, Tuomi et al. 2019). Furthermore, at the peak of their population cycle, small mammals can dramatically reduce above-ground plant biomass by > 80% (Batzli et al. 1980, McKendrick et al. 1980), potentially causing short term decreases in C-sequestration (Sjögersten et al. 2008, Metcalfe and Olofsson 2015).

We also found that by affecting soil nutrient pools, small mammal structures may have bottom-up effects on plant community stoichiometry. In particular, hay piles increased P in plant tissues at our Utqiagvik sites, suggesting that hay piles may influence the relationship between N:P limitation at local scales. As arctic tundra systems can be N and P co-limited (McLaren and Buckeridge 2019), changes in either N or P pools may have consequences for ecosystem function. Our findings that small mammal structures influence plant nutrients support findings from Petit Bon et al. (2020), which showed increases in plant nutrient content where small mammals were present. Similar effects of herbivores on plant community nutrient content have been seen in other arctic locales (Tolvanen et al. 2002, Tuomi et al. 2019) but were associated with the effects of changes in plant community composition due to selective herbivory and nutrient return via excrement (Petit Bon et al. 2020). We show that small mammals can influence plant stoichiometry through both top-down and bottom-up effects.

Our finding that hay piles have similar effects on N-availability at all three tundra regions, and for both small mammal species, affirms the importance of this structure type in tundra ecosystem function. We did find that the strength of hay pile effects varied by region, which may be because dominant small mammal species differed among regions and there are observed differences in hay piles constructed by brown lemmings versus tundra voles. At our sites, tundra voles and brown lemmings construct hay piles from *E. vaginatum* and *Carex* spp., respectively. Differences between these plant species, such as *E. vaginatum* having lower N content (Schimel and Chapin 1996) and faster decomposition rates than *C. aquatilis* (McLaren et al., unpublished data), likely influence the size of effects between regions and small mammal species. Additionally, differences in how each species or individual uses the structure (e.g., nest and/or food source) might also explain the differences we observed. As comparable increases in soil N have been observed under similar structures built by small mammals in other ecosystems (e.g., pika hay piles, Aho et al. 1998; woodrat houses, Whitford and Steinberger 2010), our results suggests that these types of engineered structures might be important to ecosystem function across both herbivore and ecosystem types.

Mechanistic effects of small mammal structures

To gain mechanistic understanding of how small mammals influence soil and plant nutrient pools, we examined how: 1) changes in litter composition affected N-mineralization, 2) herbivore-built structures affected changes in vegetation cover, and 3) small mammal structures

affected soil temperatures. Of these, differences in N-mineralization due to shifts in small mammal-induced litter inputs, had the strongest effects on soil nutrient (N) pools. The increases in N-mineralization in soils covered by green litter might explain the impacts of hay piles, which are typically constructed from green (as opposed to senesced) plant material which is high in N-content (Chapin and Kedrowski 1983), thus providing high quality, rapidly decomposable substrate for microbes (Fonte and Schowalter 2004). We also observed higher soil temperatures under runways, latrines, and burrow sites, perhaps because of slightly higher, although not statistically significant, cover of dark colored bare ground, which in turn might have increased rates of soil biogeochemical cycling (Davidson et al. 2000, Oelbermann et al. 2008) and partially explain the effects we observed on soil nutrients at these sites. We did not observe differences in plant diversity or percent cover of functional groups between lemming structure types and control areas, suggesting that herbivore induced changes in the plant community are not a main driver of the biogeochemical differences we observed. However, our sampling quadrat area (0.16 m²) might have been too large to detect vegetation changes at the scale of the herbivore structure, which typically cover a smaller area (~0.01 m², Roy, personal observation). Additionally, as structures likely varied in age and persistence (e.g., hay piles vs runways) it is unclear if stronger effects would be observed over time. There are additional mechanisms that were beyond the scope of our study, through which small mammal structures have been shown to influence biogeochemical cycling. For example, changes in light penetration and soil moisture can also influence plant communities and nutrient cycling (Borer et al. 2014) and have been shown to be affected by proximity to animal pathways, likely due to vegetation removal and changes in the vegetation community (Borer et al. 2014), soil compaction (Beylich et al. 2010, Schrama et al. 2013) and altered water infiltration (Laundre 1993, van Klink et al. 2015).

Spatiotemporal legacy effects of structures on biogeochemistry

Although we show large effects of hay piles relative to other structures at a localized spatial scale, because of differences in abundance and persistence, non-hay pile structures might be equally or more important at different spatiotemporal scales, with some structures existing on the landscape for only a season and others for several years or decades. Given their high percent cover and persistence up to the decadal time scale (McKendrick et al. 1980), runways, latrines, and burrows are likely to be important structures to ecosystem function over time, even though these structures showed fewer effects than hay piles on nutrient pools. Petit Bon et al. (2020)

showed that the effects of arctic small mammal presence during winter can continue through the entire growing season, and the increased cover of long-lasting structures (e.g., runways) might have legacy effects by influencing nutrient cycling in the years following a population peak. Potential legacy effects of these structures could influence arctic ecosystem processes, even when herbivores are rare on the landscape (Egelkraut et al. 2018) and may partially explain the observed increase in aboveground plant productivity seen in the year(s) following a population peak (Olofsson et al. 2012). Alternatively, structures with shorter persistence, such as carcasses and hay piles, might still have important effects on tundra ecosystems as they affect a wider range of nutrient pools than other structure types. While most lemming carcasses are scavenged, some persist through the winter during the low population phase (Mullen and Pitelka 1972), and, as our data suggest, carcasses provide concentrated nutrients at local scales. Similarly, hay piles might be disturbed or destroyed within a growing season (Roy, personal observation at Utqiagvik, AK) and are rare in some landscapes (Utqiagvik and Nome), but still have important effects on nutrient cycling. While structures might provide pulses of nutrients over a short period that may help explain how arctic systems recover from small mammal population peaks (Pitelka 1964), they also provide N-rich hot spots which can have a lasting effect in such a nutrient-limited system. Such heterogeneity of nutrient availability, through space and time, within the landscape might be an important driver of ecosystem function by affecting vegetation and microbial diversity (Wang et al. 2017, Fafard et al. 2019, Egelkraut et al. 2020) and productivity (Pang and Guo 2017, Tang et al. 2019) and altering patterns of herbivore activity (Davidson et al. 2018, Mayengo et al. 2020).

We have shown that because of their greater percent cover during peaks in small mammal populations, the structures built by small mammals might be particularly important during population peaks. However, traditional population cycles might be changing. Some studies hypothesize a suppression of arvicoline rodent cycles, with lower peaks and longer periods between them (Ims et al. 2008, Cornulier et al. 2013). Such decreases in population density might reduce the impact of these organisms on the landscape, resulting in lower nutrient availability and slower ecosystem process rates in the long term (Tuomi et al. 2019). Alternatively, some research has shown less variability between the peak and low phase of the population cycle, with relatively higher abundances during the nadir in recent years (Krebs et al. 2019). If the latter trend is occurring/occurs in the Arctic, we predict increases in N-availability

due to a more stable abundance of small-mammal structures at decadal time scales. This would lead to changes in plant community composition and productivity, as well as ecosystem function (Arens et al. 2008, Gough et al. 2008, Yu et al. 2017) via potential legacy effects on arctic soils (Egelkraut et al. 2018, Barthelemy et al. 2019). Finally, the contemporary community assemblage of small mammal herbivores might change, and historically dominant species might be replaced with others (Krebs et al. 2019, Ehrich et al. 2020). As our data suggest, structures from different species (albeit at different regions) affect nutrient cycling in different ways, and a better understanding of how individual species and abundances will influence ecosystem processes in the Arctic will aid in the understanding of how this ecosystem might function in the future.

Conclusion

In this paper we describe the influence of small mammal structures on soil and plant nutrient pools in arctic tundra. We found that individual structures influence soil and plant nutrient pools in different ways, with hay piles and carcasses increasing nutrient availability and pool size while runways, latrines, and burrows increased soil temperatures, potentially altering biogeochemical cycling rates. Because of their influence on soil nutrient pools and potential bottom-up controls on ecosystem function we recognize that small mammals are important components of arctic tundra ecosystems in part due to their structure building activities. While past studies usually examined the impacts of herbivory alone, our findings highlight the need to consider the ways in which both small mammal herbivory and structure building interact to impact the cycling of C and N when examining the cumulative impact of these herbivores in the Arctic. As small mammal population dynamics and their environment are changing concurrently, determining the ultimate effects of climate change on ecosystem function requires considering both changing herbivore populations and changing habitats in unison. This is especially true as the effects of warming are often underestimated when herbivores are not included in models examining ecosystem function in the Arctic (Rastetter et al. 2022). Finally, we suggest future work should examine the timeline for persistence of these structures, spatial impacts of their effects on landscapes, and how structures influence nutrient cycling over multiple years, especially immediately following and in between population peaks, to better understand how these organisms influence ecosystem process rates and biogeochemical cycling over time.

Data Accessibility

Data from this project will be made available on the Arctic Data Center: McLaren & Roy 2021a, Soil and plant biogeochemical and soil temperature variables collected at brown lemming (*Lemmus trimucronatus*) and tundra vole (*Microtus oeconomus*) structure sites near Nome, Toolik Lake, and Utqiagvik, Alaska. McLaren & Roy 2021b, Percent cover of vegetation at brown lemming (*Lemmus trimucronatus*) structure sites near Utqiagvik, Alaska. McLaren & Roy 2021c, Soil nitrogen mineralization rate data under different senesced and un-senesced litter types from Nome, Toolik Lake, and Utqiagvik, Alaska. Gough & Roy 2021, Relative percent cover of small mammal structures from the Team Vole experimental plots near Nome, Toolik Lake, and Utqiagvik, Alaska.

Author Contributions

This chapter has been submitted for review in a peer-reviewed journal, and is co-authored by Austin Roy (AR), Natalie Boelman (NTB), Laura Gough (LG), Kevin Griffin (KLG), Rebecca Rowe (RJR), and Jennie McLaren (JRM). NTB, LG, KLG, RJR, and JRM co-conceived the larger study of which this specific study led by ANR is part of; ANR and JRM conceived the ideas and designed the methodology; ANR collected and analyzed the data; ANR and JRM interpreted the results; ANR led the writing of the manuscript. All authors contributed critically and gave final approval for publication.

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Chapter 4: Revisiting the Nutrient Recovery Hypothesis: can contemporary population cycles influence ecosystem functioning

Abstract

Small mammals exhibit strong fluctuations in population abundance which may affect the strength of their influence on biogeochemical cycling and resulting controls on tundra ecosystem functioning. We applied the Nutrient Recovery Hypothesis (NRH), which posits that small mammals can impact environmental conditions to the point where these effects feedback to drive the small mammal population cycle. Because of the effects of small mammal density on plants and soils there are likely consequences on ecosystem processes. Here we examine the NRH in a small mammal-plant-soil system in northern Alaska to better understand how small mammal population cycles influence ecosystems. Our specific aims were to 1) determine if patterns of soil nutrient availability varied at different phases of the population cycle in accordance with the NRH, and 2) examine whether the predictions of the NRH are supported under contemporary conditions. We tested these aspects of the hypothesis by sampling above- and below-ground variables within a series of small mammal fencing treatments representing a contemporary population cycle. In general, we found moderate support of the NRH due to lower cover of lemming forage species and higher summer soil temperatures in our high small mammal-density treatments compared to our low-density exclosures. The NRH was not supported using soil nutrient data, however, as we found few effects of our treatments on soil biogeochemistry, with only microbial biomass carbon (C) being higher where lemmings were present than where they were absent. While the effects we observed were weaker under a contemporary population cycle than expected under a historic, high-density cycle, the effects we observed may have influences on ecosystem functioning through the alteration of biogeochemical availability. Finally, by keeping the system closer to the low-phase predictions of the NRH, contemporary small mammal population densities may potentially strengthen the ability of the Arctic to act as a C-sink in the future.

Introduction

Small mammals, such as lemmings (*Lemmus* spp.) and voles (*Microtus* spp., *Myodes* spp.), are important herbivores in the Arctic (Lara et al. 2012, Box et al. 2019, Myers-Smith et al. 2020) and play multiple roles regarding energy flow between trophic levels (Legagneux et al. 2012), controlling predator dynamics (Schmidt et al. 2012), and, importantly, regulating biogeochemical

availability (Stark et al. 2002, Sitters et al. 2017, Tuomi et al. 2019, Roy et al. 2020). Understandably, changes in the density of arctic small mammals will alter the size of their influence in the Arctic (Batzli et al. 1980, McKendrick et al. 1980). Historically, arctic small mammal populations have been characterized by their regular population cycles, with population peaks occurring approximately every 3-5 years, followed by periods of low abundance (Pitelka and Batzli 2018). Recently there has been a call to better understand how small mammal population cycles affect ecosystem processes (Andreassen et al. 2020) as these population cycles may lead to pulses in the impacts of small mammals on the landscape. Though these cycles have likely been important to arctic ecology since the last glaciation, researchers have documented a “loss” or “collapse” of some small mammal population cycles in northern regions beginning in the 1980’s (Ims et al. 2008). This loss of population cycles, and resulting lower overall abundance, will likely decrease the size of small mammal impacts on arctic system processes and function. As arctic systems are seeing rapid environmental change (Cohen et al. 2014) at the same time population cycles are disappearing, it is particularly important to understand how these novel population dynamics may influence ecosystem functioning into the future.

The Nutrient Recovery Hypothesis (NRH, Figure 4.1, Pitelka 1964) provides a framework to help examine how population cycles influence arctic systems. Developed using brown lemming (*Lemmus trimucronatus*) population cycles in arctic Alaska, the NRH describes how lemmings influence their habitat and how these habitat changes may feedback to drive population cycles. The NRH predicts: 1) During a population peak, small mammals remove vegetation cover which leads to increased soil temperatures and altered soil nutrient cycling, causing changes in the quantity and quality of forage species, and in turn leading to a small mammal population crash. 2) During the low phase of the population cycle, the vegetation recovers until the system can support high densities of lemmings again. These predicted changes in plants and soils also have the potential to influence ecosystem functioning. For example, decreases in vegetation cover and increases in soil temperature can reduce carbon capture (Van Der Wal et al. 2007, Sjögersten et al. 2011), increase the rates of soil biogeochemical cycling (Ylänne and Stark 2019, Ylänne et al. 2020), and increase soil respiration (Fang and Moncrieff 2001), resulting in the system becoming a weaker carbon (C) sink or potential C source during the high phase of the lemming cycle. Alternatively, during the low phase of lemming cycle, when vegetation is recovering from the peak, the system may shift towards a C sink due to

increases in C capture through new plant growth and decreases in soil temperature, nutrient cycling rates, and soil respiration. If the NRH holds true, small mammal population dynamics should be able to induce a cyclicity in C source-sink dynamics in the Arctic.

Support for the NRH has primarily come from long-term small mammal exclusion studies (Grellmann 2002, Stark and Grellmann 2002, Lara et al. 2016) and forage quality models (Barkley et al. 1980). These studies however have been limited by the lack of a direct examination of the impacts of small mammals during different stages of the population cycle, and by the fact that effects on soil nutrients are assumed under the NRH but have not been empirically examined. While there are studies examining the effects of arctic small mammals on soils (Stark and Grellmann 2002, Roy et al. 2020), these have not directly taken population phases into account or were too short-term to effectively examine the population cycle. Furthermore, the NRH was developed under historic, high density lemming populations, but as the system and population cycles have changed; it is unclear whether the NRH is still supported under contemporary, lower lemming density population cycles. Here we directly evaluate the NRH by examining changes in above- and below-ground ecosystem processes using simulated population cycles of brown lemmings (*Lemmus trimucronatus*) near Utqiagvik, Alaska, where the NRH was originally formed (Pitelka 1964). As arctic tundra is considered nutrient limited (Jonasson et al. 1999), any effect of lemmings on biogeochemical variables should readily be detectable. Our specific aims were to 1) determine if patterns of soil nutrient availability varied at different phases of the population cycle supporting the NRH, and 2) examine whether the original predictions of the NRH were still supported under contemporary population densities.

Materials and Methods

Study site

We conducted this study near Utqiagvik, Alaska (71.290°, -156.788°) in the summers of 2018-2020. Mean annual air temperature, soil temperature, precipitation are -11°C (NOAA 2020), 4°C (Hinkel et al. 2001), 107.3 cm (ACRC 2019), respectively. Experimental sites were located in high-centered polygon tundra dominated by graminoids, dwarf shrubs, mosses, and lichens (Johnson et al. 2011, Assmann et al. 2019). Site elevation was approximately 5 m. Soils at the experimental sites are Gelisols defined by their permafrost layer (Bockheim et al. 1999, USDA 1999). The mean maximum active layer of the region ranges from 17-101 cm (Drew et al. 1958, Nelson et al. 1998, Zhang and Stamnes 1998). The dominant small mammal herbivores are

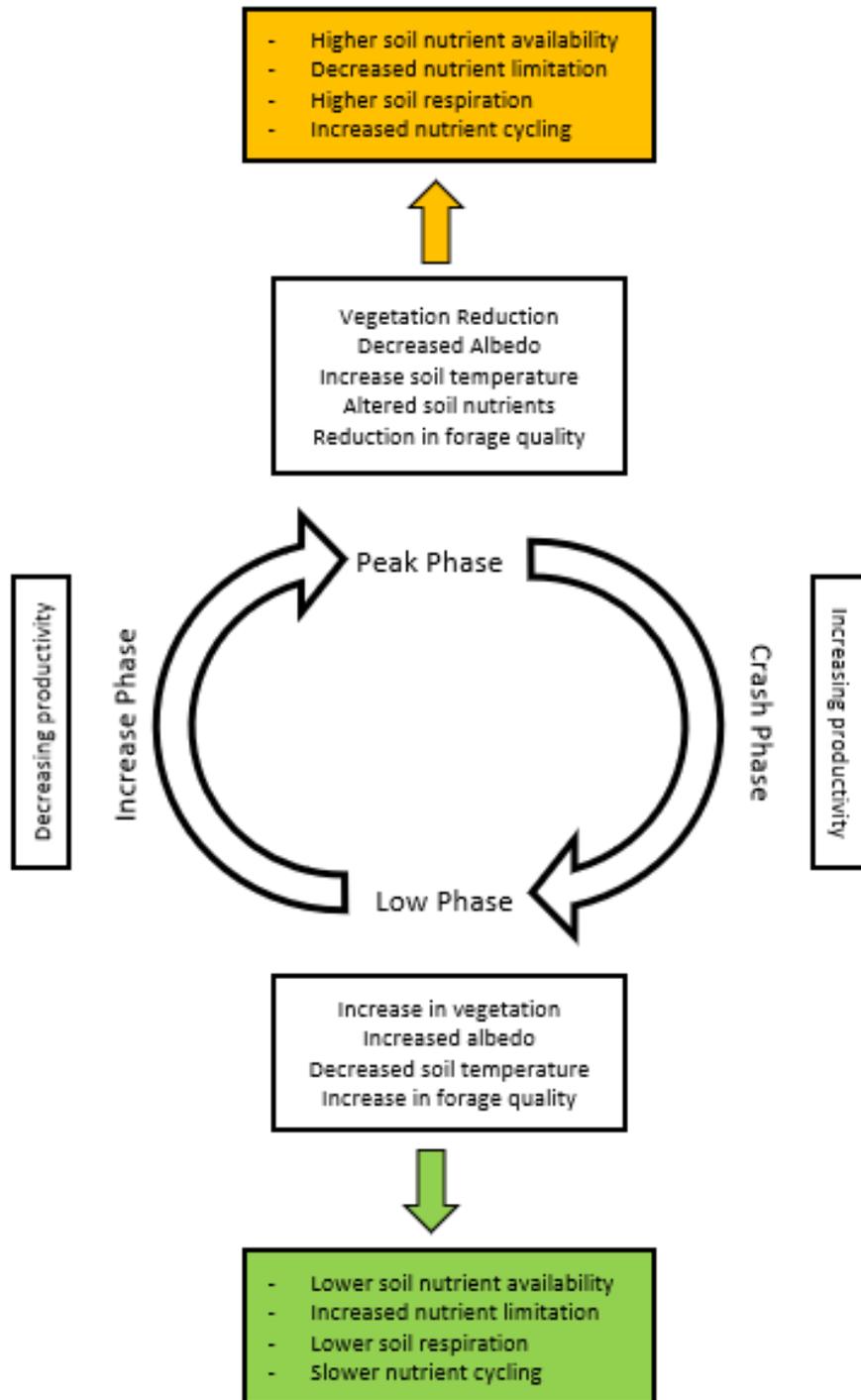


Figure 4.1: Conceptual model showing the effects of a small mammal population cycle on ecosystem processes and potential feedbacks on ecosystem function as predicted by the Nutrient Recovery Hypothesis (Pitelka 1964).

brown lemmings (*Lemmus trimucronatus*), with a mean summer abundance of 11, 30, and 0.66 individuals ha⁻¹ in 2018-2020, respectively, near our sites (Rowe and Steketee, unpublished data). Other small mammal species that occur at low abundance near our sites include collared lemmings (*Dicrostonyx groenlandicus*), Arctic ground squirrels (*Spermophilus parryii*), and Arctic hare (*Lepus arcticus*) (Batzli et al. 1980). The dominant forage species important for brown lemmings in the region include *Dupontia* spp., *Carex* spp., and *Eriophorum* spp., and mosses (Batzli and Pitelka 1983).

Experimental design

Experimental blocks of lemming fencing were established at three sites in 2018 near Utqiagvik, Alaska (Figure 4.2). Each fencing block consisted of four treatments representing different small mammal population scenarios (Figure 4.2):

1. Control (CT) – 8 x 8 m unfenced plot. This plot represented the ambient lemming population level.
2. Exclosure (EX) – 8 x 8 m fenced plot. This fence excluded all small mammal herbivores over the entirety of the experiment and represented an absence of lemmings from the landscape (low population phase)
3. Pulse (PU) – 20 x 20 m fenced enclosure. This fence was stocked with four lemmings for one summer (2018) and any remaining individuals were removed from the fence the following summer (2019) and subsequently the fence was treated as an exclosure, and represented a population peak (100 individuals ha⁻¹, Batzli et al. 1980) for one year, followed by a population crash for two years (2019-2020).
4. Press (PR) – 20 x 20 m enclosure fence. This fence was stocked and maintained with four lemmings for the entirety of the experiment (2018-2020) and represented an extended population peak.

Fences were monitored regularly to ensure the planned animal density was maintained. Each fence was constructed of 1.3 x 1.3 cm mesh, was approximately 2 m tall and had approximately 0.5 m of the fence buried into the soil to prevent lemmings from burrowing under the fences. Each treatment was subdivided into non-destructive and destructive (approximately ¼ of treatment plot) sampling areas. Due to persistent standing water in one of the exclosure sites, it was not sampled in 2019-2020.

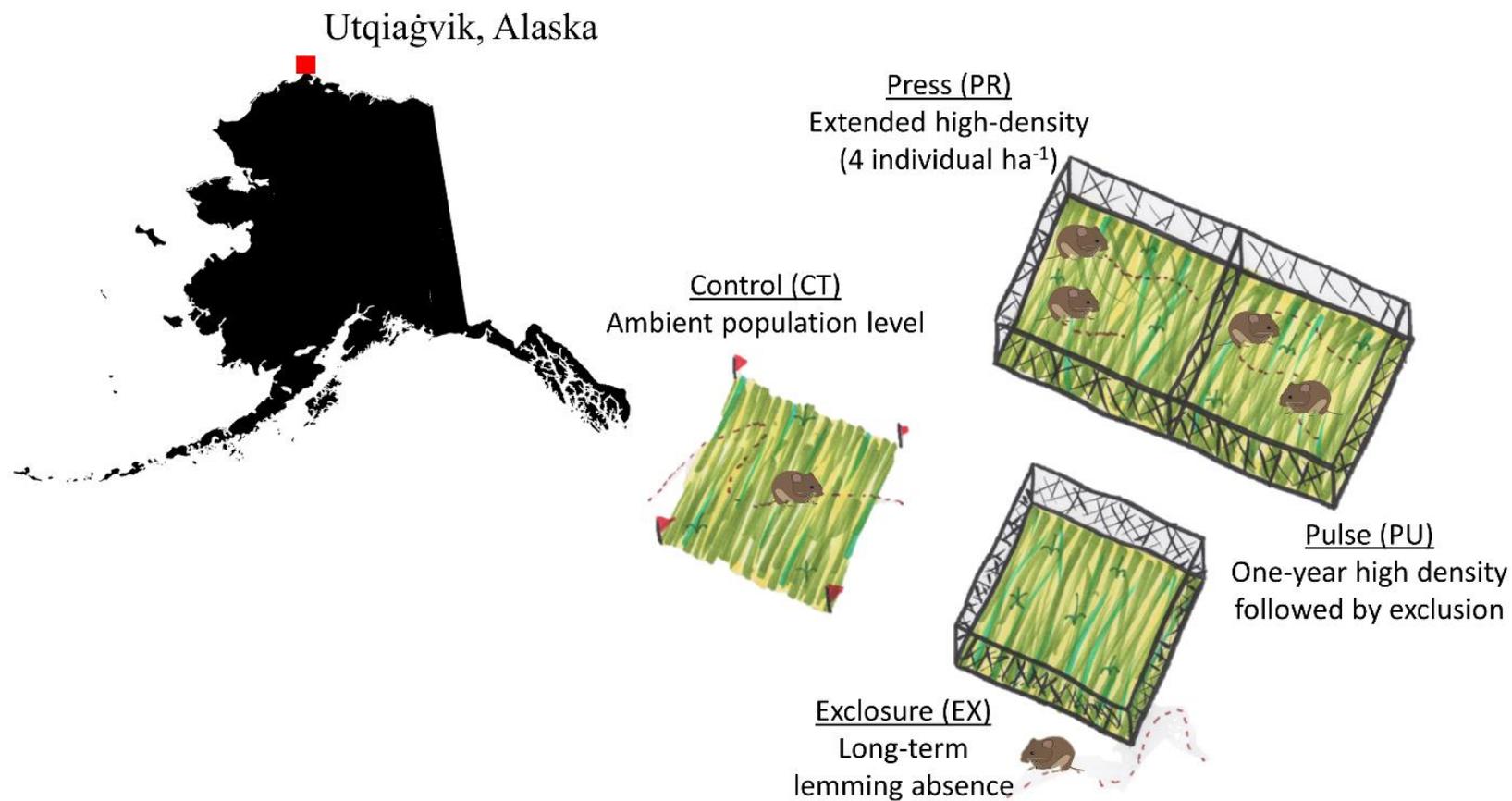


Figure 4.2: Overview of study area and experimental design located in arctic tundra near Utqiagvik, Alaska, USA. Fencing treatments include a control (CT, no fence), press (PR, stocked with four individuals each year), pulse (PU, stocked with four individuals for one year, followed by exclusion), and exclosure (EX, excluded individuals for entirety of experiment) fencing.

Vegetation sampling

In late July of 2018 and 2019, we used 1 × 1 m quadrats to quantify the percentage cover of vascular and nonvascular plants, bare ground, and plant litter in eight contiguous replicates within each experimental plot. Vascular plants were identified to species level and mosses and lichens were grouped across species. For analysis we determined proportional cover by summing cover of all plants and then calculating the relative abundance of each group to standardize across plots. Most analyses were conducted on plant growth forms (graminoids, evergreen shrubs, deciduous shrubs, forbs, lichens, mosses) rather than individual species. Due to Covid-19 sampling limitations, we did not collect vegetation data in 2020.

Spectral data

In July of each year, we used a RapidScan (Model CS-45, Holland Scientific) to calculate normalized difference vegetation indices (NDVI) within each cover quadrat. We collected eight measurements per plot, encompassing the entire quadrat. We then calculated mean NDVI per quadrat and fence each year. Due to malfunctioning equipment, measurements were not collected in 2020.

Soil temperature

Between summer 2018 and 2020, soil temperatures were measured every 4 hours in the destructive are of each plot using Thermocron iButtons (model DS1921G-F5, Maxim Integrated, San Jose, CA, USA). at the soil surface, 5 cm beneath the soil surface in the organic soil layer, and at the top of the mineral layer. We calculated mean daily temperatures for each soil depth within every treatment plot.

Soil nutrient pools and enzyme activity

We collected three randomly sampled ca. 10 x 10 cm blocks of soil to a depth of 5 cm using a serrated knife from the destructive sampling area within each treatment in early August of each year. For each soil sample, we dried a subsample of known volume (approximately 5 cm³) at 50 °C for 48 hours to assess bulk density and volumetric water content. Subsequently, within two days of collection, we homogenized the remainder of each soil sample by hand, removing all large roots (>1 mm diameter), and partitioned samples for analysis. Soil samples were kept cool and shipped fresh to the University of Texas at El Paso (UTEP), where they were either processed immediately (within 5 days of collection) or frozen at -80°C until analysis (enzyme samples only). In 2020, due to sampling and shipping limitations, we froze all soil samples prior

to shipment to UTEP. Once at UTEP, the 2020 samples were thawed, homogenized, and re-frozen until analysis.

We analyzed soil samples for total C and N; inorganic nutrients (NH_4^+ , NO_3^- , PO_4^{3-}); total extractable nutrients (extractable organic C (EOC), extractable total N (ETN)); microbial biomass C, N, P; and extracellular enzyme activity using the following methods.

We dried, ground, and processed soil subsamples for total C and N content using a dry combustion C and N analyzer (ElementarPyroCube®). To determine soil inorganic nutrients, we extracted subsamples (5 g) in 25 ml of 0.5 M K_2SO_4 for 2 hours, filtered through glass filter paper and analyzed extractant using colorimetric microplate assays (BioTEK Synergy HT microplate reader, Winooski, Vermont, USA). NH_4^+ was determined using a modified Berlethot assay (Rhine et al. 1998), NO_3^- using a modified Griess assay (Doane and Horwath 2003), and PO_4^{3-} using a malachite green assay (D'Angelo et al. 2001).

EOC and ETN were determined for the extracts described above using an extractable organic C/total extractable N (EOC/ETN) analyzer (Shimadzu Corporation, TOC-V Series CN analyzer). To determine microbial biomass C, N, and P, we used a direct chloroform-addition modification of the fumigation-extraction method (Brookes et al. 1985, Voroney et al. 2006), where 5 g of soil was incubated for 24 hours with 2 mL of ethanol-free chloroform, followed by extraction in 25 mL of 0.5 M K_2SO_4 and analysis of EOC/ETN or PO_4^{3-} as above. We calculated microbial biomass for C, N, and P (MBC, MBN, and MBP) by subtracting EOC, ETN, or PO_4^{3-} respectively of non-fumigated samples from that of fumigated samples. No correction factor was applied for incomplete CHCl_3 -release, or sorption of P because these values are not known for K_2SO_4 -extraction for this ecosystem. Microbial biomass C, N, and P were not calculated in 2020, because of the different soil handling procedures required during limited sampling that year.

Extracellular enzyme (exoenzyme) activity was assessed for 10 exoenzymes involved in the microbial acquisition of C, N, and P: C-acquiring enzymes (β -glucosidase, β -cellobiosidase, β -xylosidase, α -glucosidase), N-acquiring enzymes (N-acetyl-glycosaminidase (NAG), leucine amino peptidase (LAP)) and P-acquiring enzymes (phosphatase, phosphodiesterase), as well as the oxidative enzymes phenol oxidase and peroxidase. One g of soil was blended with a sodium acetate buffer to reflect natural soil conditions (pH = 5) and pipetted onto 96 well plates with eight replicates per soil. Substrate tagged with fluorescing 4-methylumbelliferone (MUB) or 7-amido-4-methyl coumarin (MC) (LAP only) was added to soil slurries. Samples were incubated

at 20°C and enzyme activity (fluorescence) measured every 30 minutes for 3.5 hours following methods adapted from Sayia-Cork et al. (2002) and McLaren et al. (2017b). For each substrate, we measured the background fluorescence of soils and substrate and the quenching of MUB or MC by soils and used standard curves of MUB or MC to calculate the rate of substrate hydrolyzed. Fluorescence was measured at 360 nm excitation and 460 nm emission using a BioTek Synergy HT microplate reader (BioTek Instruments Inc., Winooski, VT, USA). Oxidative enzyme analysis was performed using an L-3,4-dihydroxyphenylalanine (L-DOPA) substrate for phenol oxidase and peroxidase. Color absorbance was measured at 460 nm using the BioTek Synergy HT microplate reader after 24 hours of incubation at 6 °C.

N-mineralization rates

We examined how N mineralization rates were influenced by lemming treatments using an *in situ*, intact core mineralization method (DeMarco et al. 2011). In the fall of 2019, we installed one mineralization core within each fencing treatment. Soil cores were incubated *in situ* in butyrate plastic tubes (15cm depth, 4.8 cm diameter), containing the entire organic layer. A sample adjacent to each soil core was collected at the time of core installation to determine soil bulk density and initial N. Each tube contained three 30 g resin bags, made from mixed bed exchange resin bead (IONAC NM-60 H⁺/OH⁻ Form, JT Baker, Phillipsburg, NJ, USA); a single bag was placed each at the top of the soil core (to prevent inflow of N from above) and below the organic layer (to capture N leaking out of the core) followed by a second resin bag (to prevent inflow from below). When the organic soil layer was less than 10 cm depth, any empty space at the bottom of the tube was filled with the mineral layer below. Mineralization cores were incubated *in situ* for approximately one year, encased in a nylon stocking. Resin bags and soils were removed from each tube, homogenized, and frozen until analysis.

Soils and resin bags were analyzed for NH₄⁺ and NO₃⁻ following the same protocols described above. Net N-mineralization was calculated as the differences between DIN (NH₄⁺ + NO₃⁻) in the initial soil sample and DIN in the final soil core plus the DIN accumulated in the resin bag directly under the organic layer (DeMarco et al. 2011). Mineralization rates were calculated as net N-mineralization divided by the number of incubation days in the field.

Ecosystem respiration

Ecosystem respiration (RE) measurements were taken between 10 AM and 4 pm during July of 2018 and 2019 from each lemming treatment, only when plants were dry (e.g., no fog or dew). We measured RE using a Li-6400XT (IRGA, Li-Cor, Lincoln, NE) infrared gas analyzer operating a closed mode and connected to a polycarbonate, cylindrical chamber with a lid (height 41 cm, diameter 75.5 cm) covered with a blackout cloth to exclude sunlight (Min et al. 2021). To minimize air leakage between the chamber and outside-chamber conditions, we attached a plastic skirt to the bottom of the chamber and weighed down by a chain (Min et al. 2021). We measured changes in CO_2 concentrations, water vapor, and air temperature over a 40 second period at three subplots in each treatment. We collected data three times, in immediate succession, at each subplot and only measurements collected under stable environmental conditions for the duration of the sample period (40 seconds) were used for analysis. We calculated RE for each subplot using the following formula:

$$RE = (\rho * V * dC/dt) / A$$

Air density, ρ , is equal to $P/(RT)$ where P is pressure, R is the universal gas constant and T is temperature in K. V is the volume of the chamber, A is the surface area of the blackout cloth cover and dC/dt is the change in CO_2 concentration adjusted for water vapor. A negative RE value indicates a carbon flux from the atmosphere to the environment (Min et al. 2021).

Statistical analyses

We performed statistical analyses with the program R (R Core Team 2018) with a cutoff of $p < 0.05$ for inferring statistical significance.

To assess changes in plant communities, we used the package *vegan* (Oksanen et al. 2019) to calculate Shannon diversity indices for vascular plants in each treatment. Differences in diversity between treatments were examined using a 2-way ANOVA, with Shannon diversity indices as the response variable and treatment and year as the independent variables. To determine whether there was an effect of treatments on percentage cover of functional groups, we used a two-way ANOVA test with percent cover as our dependent variable and treatment and year as our independent variables.

To assess changes in NDVI we used a two-way ANOVA test with NDVI as the response variable and fence treatment and year as the independent variables.

To examine the influence of lemming treatments on soil temperatures, we used three-way ANOVAs. We used soil temperature as the dependent variable and treatment, year, and season as the independent variables. For soil temperature yearly analysis, we considered time since installation as a year (year 1 = July 2018 – July 2019 and year 2 = July 2019 – July 2020). For seasonal analysis, we compared the coldest months (winter: January and February) and the two warmest months (growing season: July and August). Each soil depth (surface, organic, mineral) was analyzed separately. Because fencing led to higher snow depth in PR, PU, and EX than CT, we excluded CT from the analysis. When data could not be normalized, Kruskal Wallis and Wilcoxon tests were used.

Differences in soil variables between treatments were determined using two-way ANOVA tests, with nutrient concentrations, microbial biomass, enzyme activity, N-mineralization rates ($\mu\text{g N m}^{-2} \text{ day}^{-1}$), *RE*, and thaw depth as response variables and fence type and year as independent variables, followed by Tukey's post hoc tests. When data could not be normalized, Kruskal Wallis and Wilcoxon tests were used.

Results

Vegetation cover

We did not observe differences in Shannon diversity indices by treatment ($p = 0.579$, $X^2 = 1.97$, $df = 3$) or by year ($p = 0.133$, $W = 84$). However, we did record changes in the cover of a few functional plant groups due to treatment (Table 4.1), but again, we did not observe differences between years (Table 4.1). Sedge cover differed by treatment (Table 4.1) because the press (PR) treatment had lower sedge cover than both the enclosure (EX, $p = 0.046$) and control (CT, $p = 0.058$, Figure 4.3). Additionally, forb cover (Table 4.1) trended lower in EX compared to PR ($p = 0.076$) and PU ($p = 0.066$, Figure 4.3).

NDVI

NDVI varied by year, with 2019 being higher than 2018, but we observed no difference by treatment (Supplemental Table 4.1). However, we did observe a non-significant pattern for higher NDVI values in treatments where animals are present (CT, PR, PU) than where animals were absent (EX, Supplemental Figure 4.1).

Table 4.1: Statistical impact of brown lemming (*Lemmus trimucronatus*) fencing treatments the relative percent cover (%) of different functional cover groups. Data were collected near Utqiagvik, Alaska, USA in 2018-2019.

Functional Group	Treatment			Year			Year x Treatment		
	stat	<i>p</i>	<i>df</i>	stat	<i>p</i>	<i>df</i>	stat	<i>p</i>	<i>df</i>
Grass	$F = 0.51$	0.685	3	$F = 1.04$	0.326	1	$F = 0.05$	0.986	3
Sedge	$F = 4.59$	0.02	3	$F = 2.95$	0.108	1	$F = 1.12$	0.375	3
Forb	$X^2 = 8.66$	0.034	3	$W = 58$	0.898	1			
Shrub	$X^2 = 2.69$	0.441	3	$W = 64$	0.844	1			
Lichen	$X^2 = 1.68$	0.642	3	$W = 64$	0.847	1			
Moss	$F = 1.36$	0.296	3	$F = 1.26$	0.28	1	$F = 0.99$	0.424	3
Litter	$F = 0.94$	0.449	3	$F = 0.636$	0.438	1	$F = 0.47$	0.707	3
Bare ground	$X = 1.56$	0.67	3	$W = 59.5$	0.97	1			

Table 4.2: Statistical results of brown lemming (*Lemmus trimucronatus*) fencing treatments effects on soil temperatures (°C) between fencing treatments (T), seasons (S), and sampling years (Y), at three soil depth (soil surface, organic layer (five cm beneath the soil surface), mineral layer (five cm under the beginning of the mineral soil layer)). Data were collected within fencing treatments located near Utqiagvik, Alaska, USA.

Depth	T x S		T x Y		S x Y		T x S x Y	
	Stat	<i>p</i>	Stat	<i>p</i>	Stat	<i>p</i>	Stat	<i>p</i>
Surface	$F_2 = 14.84$	<0.001	$F_2 = 2.10$	0.123	$F_1 = 4.78$	0.028	$F_2 = 7.35$	< 0.001
Organic	$F_2 = 8.56$	< 0.001	$F_2 = 18.31$	< 0.001	$F_1 = 0.19$	0.662	$F_2 = 0.69$	0.501
Mineral	$F_2 = 6.16$	0.002	$F_2 = 6.45$	0.002	$F_1 = 40.38$	<0.001	$F_2 = 2.18$	0.113

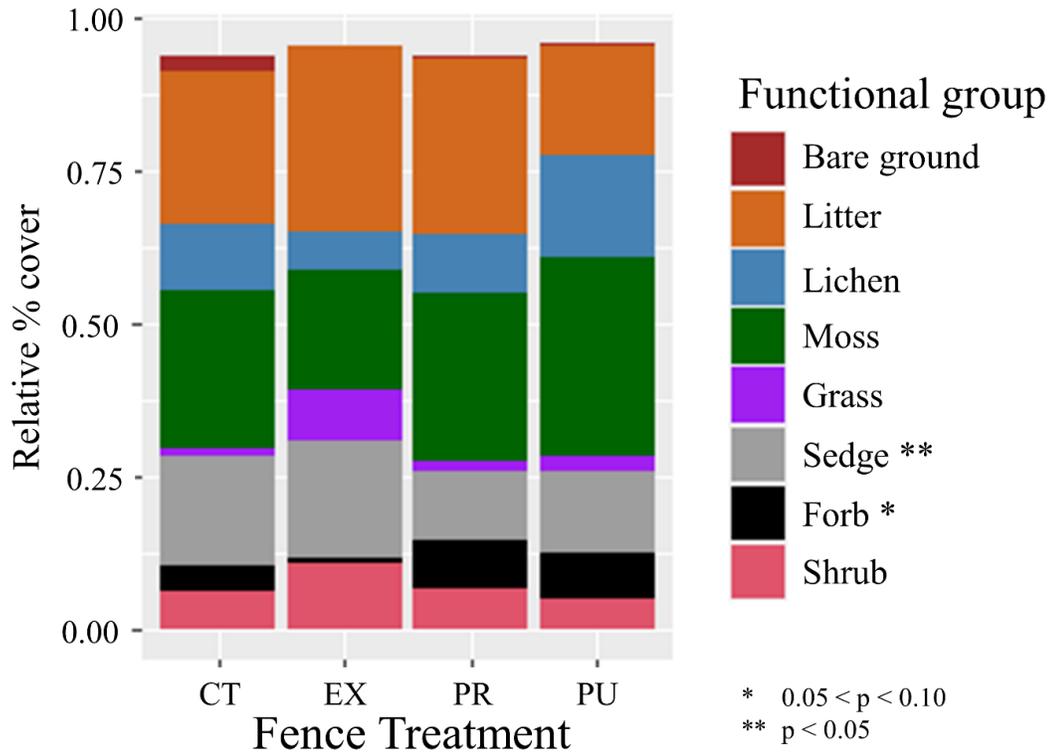


Figure 4.3: Stacked bar plot showing the mean relative percent (%) cover of different plant functional cover types within experimental fencing treatments (CT, EX, PR, PU) located at study sites near Utqiagvik, Alaska, USA. Data were collected in 2018 and 2019. Asterisks represent differences in cover between experimental treatments.

Soil temperatures

We observed effects of fencing treatments on soil temperatures at multiple soil depths. At the soil surface there was a significant Treatment \times Season \times Year interaction (Table 4.2) because in the second year of the study, surface soil temperatures were lower in the pulse fence (PU) than EX and PR during winter (Figure 4.4). In both the organic and mineral layers, we observed a Season \times Treatment interaction (Table 4.2), but no year effect. During the growing season, PU organic soil temperatures were higher than EX and PR ($p < 0.05$), and during winter PU trended lower than PR ($p < 0.100$, Figure 4.4). In the mineral layer, PR soil temperatures were higher than EX and PU during winter ($p < 0.05$), and PU trended higher than EX during the growing season ($p < 0.10$, Figure 4.4).

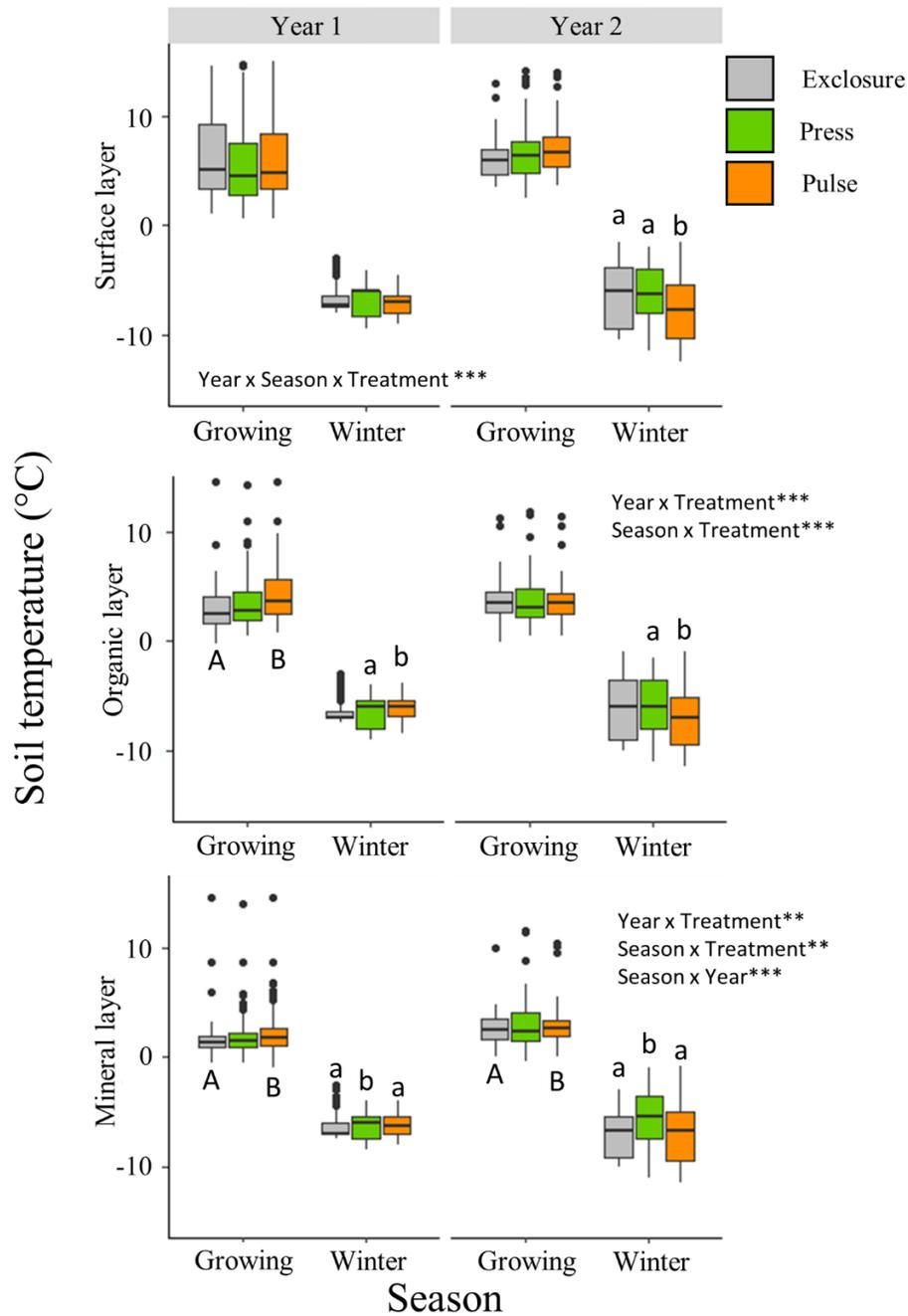


Figure 4.4: Boxplots showing differences in soil temperatures ($^{\circ}\text{C}$) between fencing treatments (EX, PR, PU), seasons (growing season, winter season), and sampling years (Year 1 = Summer 2018-Summer 2019; Year 2 = Summer 2019-Summer 2020), and soil depth (soil surface, organic layer (five cm beneath the soil surface), mineral layer (five cm under the beginning of the mineral soil layer)). Data were collected within fencing treatments located near Utqiagvik, Alaska, USA.

Thaw depth

We observed no difference in thaw depth between our treatments ($p = 0.237$, $F_3 = 1.56$), but did detect differences by year with no Year x Treatment interaction ($p = 0.864$, $F_{6,23} = 0.41$).

Soil nutrient pools

After three years of treatment, generally there were few significant differences in individual soil nutrient pools due to treatments. Microbial biomass carbon (MBC) was the only pool that showed a treatment effect ($p = 0.013$, $F = 4.942$, Table 4.3), with CT ($p = 0.030$) and PR ($p = 0.029$) having higher MBC concentrations than EX (Figure 4.5). We also observed a trend for lower C:N in EX compared to the PR treatment ($p = 0.071$, Supplemental Figure 4.2), but total C and total N did not vary by treatment (Table 4.3). While other variables did not vary by treatment, they did vary by year (Table 4.3).

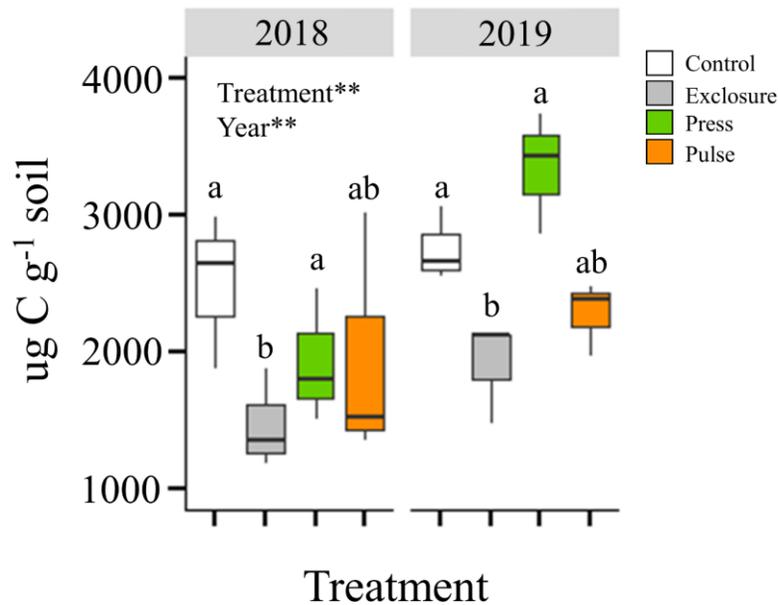


Figure 4.5: Box plots showing differences in microbial biomass carbon (MBC) in soils between fencing treatments (CT, EX, PR, PU) and sampling years (2018, 2019). Data were collected near Utqiagvik, Alaska, USA.

N-mineralization

While we observed no statistical differences in N-mineralization rates between our treatments ($p = 0.183$, $X^2 = 4.85$), we did observe a non-significant pattern ($p = 0.183$, $X^2 = 4.89$) for faster N-mineralization in our PR treatment compared to the CT and EX treatments (Supplemental Figure 4.3).

Table 4.3: Statistical results of brown lemming (*Lemmus trimucronatus*) fencing treatments across sampling years on total carbon and nitrogen (TC, TN), carbon:nitrogen ratios (C:N), inorganic nutrients (ammonium (NH₄⁺), nitrate (NO₃⁻), phosphate (PO₄³⁻)), extractable nutrients (extractable organic carbon (EOC), total extractable nitrogen (ETN), extractable inorganic nitrogen (EIN), extractable organic nitrogen (EON)), and microbial biomass nutrients (carbon (MBC), nitrogen, (MBN), phosphorus (MBP)) in soils collected within treatment plots near Utqiagvik, Alaska, USA. Data were collected in 2018-2020.

	Treatment			Year			Treatment x Year		
	Stat	<i>P</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>
TC	$X^2 = 4.82$	0.185	3	$X^2 = 4.54$	0.103	2			
TN	$X^2 = 0.35$	0.951	3	$X^2 = 4.48$	0.065	2			
CN	$X^2 = 8.90$	0.031	3	$X^2 = 3.90$	0.142	2			
NH ₄ ⁺	$F = 0.73$	0.547	3	$F = 14.96$	<0.001	2	$F = 0.44$	0.842	6
NO ₃ ⁻	$X^2 = 0.92$	0.82	3	$X^2 = 6.00$	0.05	2			
PO ₄ ³⁻	$F = 0.82$	0.5	3	$F = 1.02$	0.38	2	$F = 0.30$	0.93	
EOC	$F = 0.70$	0.563	3	$F = 1.42$	0.263	2	$F = 0.18$	0.98	6
ETN	$F = 0.81$	0.503	3	$F = 7.91$	0.002	2	$F = 0.69$	0.66	6
EIN	$F = 0.65$	0.591	3	$F = 14.65$	<0.001	2	$F = 0.46$	0.84	6
EON	$F = 0.66$	0.586	3	$F = 2.61$	0.095	2	$F = 0.51$	0.798	6
MBC	$F = 4.94$	0.013	3	$F = 8.87$	0.009	2	$F = 1.78$	0.192	6
MBN	$X^2 = 7.19$	0.066	3	$W = 39$	0.06	2			
MBP	$X^2 = 3.03$	0.387	3	$W = 43$	0.169	2			

Ecosystem respiration

We observed no difference in *RE* due to fencing treatments ($p = 0.780$, $F_3 = 0.36$) or year ($p = 0.525$, $F_1 = 0.42$).

Discussion

Our experimental study revealed a clear impact of lemmings on some ecosystem processes. In particular, their ability to reduce forage vegetation cover, increase soil temperatures, and alter soil microbial community size can influence ecosystem functioning. However, not all variables examined showed such clear effects, with most soil nutrient pools and thaw depth being unaffected during our study's time frame. This work highlights the importance of small mammal population cycles, their effects on arctic system ecology, and the continued monitoring of experiments to observe long-term effects.

Validity of NRH under contemporary conditions

The effects of contemporary small mammal population cycles on vegetation communities we observed provide partial support for the predictions made in the Nutrient Recovery Hypothesis (NRH). Our observation of decreased sedge and forb cover in plots with high lemming density is in line with predictions made by the NRH, and as these functional groups make up a large proportion of lemming diets (Batzli and Pitelka 1983) we reasonably assume that these groups would also decrease during periods of higher lemming density through selective grazing. Furthermore, while not significant, we saw a pattern for higher NDVI in the peak treatments compared to the low phase treatment, suggesting that lemmings may be altering productivity by potentially inducing compensatory growth (McNaughton 1979) or altering plant communities to have higher representations of more productive species (Johnson et al. 2011, Tuomi et al. 2019) when lemmings are present. Changes in plant production likely also represent changes in forage nutrient content due changes in vegetation community assemblage (Petit Bon et al. 2020). It is unclear whether the vegetation responses we observed were strong enough to fully support the NRH under contemporary population cycles, but our work and that of others do suggest that small mammals and their population dynamics can influence ecosystem processes.

Contrary to predictions made by NRH about nutrient availability, we found few effects of our lemming fencing treatments on soil biogeochemistry. We analyzed below-ground variables for the first time in an examination of the NRH, and only observed effects of lemming fencing treatment on microbial biomass (MBC), with lemming presence, where moderate (CT) and high

density (PR) lead to higher microbial biomass (MBC). Our results support similar findings of the effects of small mammals' ability to alter microbial community biomass (Stark and Grellmann 2002), activity (Manaeva et al. 2014, Stark and Vaisanen 2014), and assemblage (Kuznetsova et al. 2013, Su et al. 2020) in some systems, but not in others (Virtanen et al. 2008, Rinnan et al. 2009, Roy et al. 2020). It is possible that lemming presence did increase production of soil nutrients (N and P), but these nutrients may have been taken up by the increased plant productivity suggested the pattern of increased NDVI and changes in plant species composition we observed. Future examination of nutrient contents or biomass of plants growing in the fences may provide more information on the effects of our treatments on biogeochemical cycling. Interestingly, while we observed increases in the microbial community size, this increase did not translate into changes in ecosystem respiration (*RE*) in our treatments and suggests that our treatments did not affect C flux which has been documented in other studies (Lara et al. 2016, Min et al. 2021). While we did observe effects of population cycles on some below-ground factors, it is unclear whether the magnitude of the effects would be strong enough to influence other ecosystem properties as predicted by the NRH.

While the soil biogeochemical aspects of the NRH were not strongly supported, our temperature data do provide partial support the second tenet of the hypothesis, that exposed soils will experience increased soil temperatures and result in altered nutrient availability (Lara et al. 2016). We observed higher summer soil temperatures in our high-density treatments compared to low density exclosures, particularly in deeper soil layers. While similar changes in soil temperatures due to herbivores have been observed in other studies (Van der Wal et al. 2001), our lack of change in soil nutrient pools between treatments and years does not support that such changes in temperature alter nutrient availability. We have seen that specific lemming activities lead to higher soil temperatures and higher nutrient pools compared to control sites (see Chapter 3), but the effects of these localized activities may not be widespread enough to alter soil biogeochemistry at the scale of our plot or detectable with the random placement of soil sampling.

Though not tested here, the NRH also predicts that changes in vegetation should be a driver of lemming population cycles, but contemporary evidence does not support this prediction. Observed changes in population cycles near Utqiagvik (Ott and Currier 2012, Ott 2017) cannot be fully explained by population cycle-induced vegetation change. It has been > 10

years since the last lemming population peak (Ott 2017) and is likely that the vegetation would have recovered in that time to the point where a population peak should have occurred (as predicted by the NRH). Additionally, this refutation of the NRH may be supported by research suggesting that multifactorial effects, including climate and winter freeze-thaw cycles, play stronger roles regulating population cycles than the variables examined in the NRH (Ims et al. 2011, Cornulier et al. 2013, Krebs 2013b). However, an examination of lemming and other arvicoline cycles in additional locations may be able to provide for a more thorough examination of the NRH.

NRH and the future of tundra ecosystems

The responses of small mammals on tundra at Utqiagvik still support the prediction that small mammals can influence ecosystem functioning, even if the responses were weaker under a more contemporary, moderate population cycle peak (100 individuals ha⁻¹), compared to the high-density population peaks (150-225 individuals ha⁻¹) which the NRH was first developed under (Batzli et al. 1980). First, while the changes in plant community composition we observed were relatively small, they may still impact both carbon sequestration and nutrient cycling (Van Der Wal et al. 2007, Sjögersten et al. 2011). Herbivore-induced shifts toward slower-growing and less photosynthetically active species (e.g., evergreen shrubs) likely slows the rate of C sequestration within this system (Tuomi et al. 2019, Yläne and Stark 2019). Alternatively, increases in shrub and other species cover can alter the contributions of these species to the litter pool, resulting in altered decomposition and C-cycling rates (McLaren et al. 2017a, Tuomi et al. 2019). Second, even though our data did not support it, increases in soil temperatures during population peaks may lead to increased microbial activity and alteration of soil pool stoichiometry (Rinnan et al. 2007, Gu and Grogan 2020, Meng et al. 2020). Such effects at depth may lead to a loss of nutrients at lower soil depths and changes in C cycling (Mack et al. 2004). Third, the changes we observed in microbial biomass can lead to increased nutrient availability through increased decomposition (Allison et al. 2013). This may potentially have strong effects in arctic systems with high amounts of soil organic matter substrate (Ping et al. 2008). It is also worth noting that arctic tundra may be slow to respond to and recover from disturbance (Egelkraut et al. 2018), and effects of our treatments may be stronger and easier to detect in the future. The influence of small mammals on these vegetation and soils highlights the role these species play in regulating ecosystem processes.

If the NRH holds true, contemporary population cycles may strengthen the ability of the Arctic to act as a C-sink by keeping the system closer to the low-phase predictions of the NRH (Figure 4.6). With fewer animals during population peaks, thus decreasing the amount of vegetation impacted during the peak of the cycle, the NRH predicts that soil temperatures will remain cooler, thus reducing biogeochemical cycling (Ylänne and Stark 2019, Ylänne et al. 2020) and C flux from the soil to the atmosphere (Fang and Moncrieff 2001). While not observed in our study, other research has found that low-density small mammal populations tended to increase the amount of vegetation cover (Tuomi et al. 2019, Wei et al. 2020) compared to high-density populations. Although these studies (Tuomi et al. 2019, Wei et al. 2020) found no effects of low-density small mammal populations on soil biogeochemistry in arctic systems, increases in soil organic carbon under light and moderate grazing have been observed in other ecosystems (Jüdt 2020, Zhou et al. 2020). Additionally, intermediate amounts of herbivory may allow for increases in C-sequestration, via compensatory growth, but effect sizes vary by ecosystem (Forbes et al. 2019). Alternatively, slower nutrient cycling due to lower lemming density and associated vegetation effects may reduce the ability of tundra to sequester C due to N and P limitation (Tuomi et al. 2019, Ylänne and Stark 2019). If contemporary population cycles persist, all else being equal, we may expect long term changes in arctic biogeochemical cycling into the future.

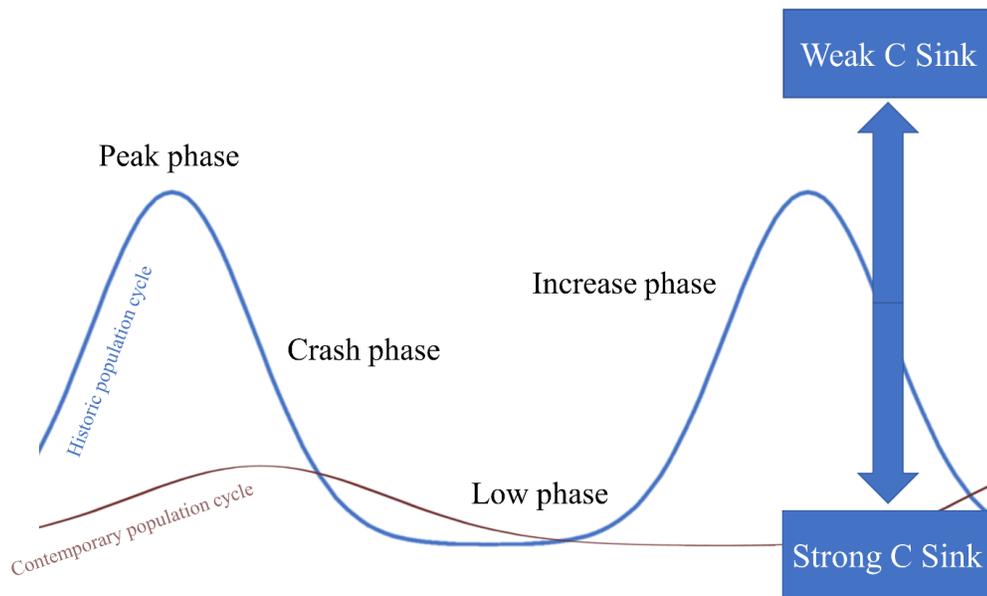


Figure 4.6: Conceptual model showing the potential effects of historic and contemporary lemming population cycles on tundra carbon source-sink dynamics.

As the effects we observed of our small mammal manipulations were not generally strong, it is unclear how the role of lemming population cycles will influence ecosystem functioning in the light of other changes co-occurring in the Arctic. Changes in the system such as permafrost collapse and arctic greening have been shown to influence C and N cycling (Mekonnen et al. 2018, Xu et al. 2020), and these changes may act in tandem with small mammal effects as recent work has also shown that the effects of herbivores and warming are strongest when they act in concert (Ylänne et al. 2020). It is likely that small mammal effects will interact with and feedback upon climate change effects to further alter ecosystem functioning in arctic systems. Furthermore, we must ask if the system has changed to the point where brown lemmings are not as important in impacting arctic ecosystems as they were previously. Here we focused on brown lemming population cycles, as this species was used in the creation of the original NRH, but research suggests that some species (e.g., tundra voles, *Microtus oeconomus*) may expand their range northward and may displace brown lemmings (Baltensperger and Huettmann 2015, Ehrich et al. 2020) and other research suggests that there may be a shift in species dominance (Krebs et al. 2019) due to climate change, and brown lemmings would be replaced as the most abundant small mammal species on the landscape. As different species interact with their habitats in different ways, changes in small mammal community composition and species dominance is likely to affect the role of small mammals in arctic C cycling in the future.

It is of note that our experiment near Utqiagvik occurred within an ecosystem that is grazed by other herbivore guilds. In particular, the system has seen an increase in the abundance of geese (Fox et al. 2005), which have the potential to greatly impact coastal tundra biogeochemical cycling and ecosystem function (Speed et al. 2010). As our control plots and fences did not exclude geese (Roy et al. unpublished data), it is possible that the effects we observed from small mammal herbivores were affected by the effects of these other important herbivore species. This may be supported by the fact that we observed generally higher goose activity in our control plots compared to our other treatments (CT = 1.08%, EX = 0.1%, PR = 0.5%, PU = 0.4%); however, there were no statistical differences in goose activity between treatments (Roy et al., unpublished data) and may suggest that goose impacts were uniform across our treatments. Additionally, the highest amount of goose activity occurred over approximately 1% of plot, which was less than that of small mammal activity (12.5%, Chapter 3)

and may suggest that our findings were mainly due to small mammal impacts on biogeochemical processes. A closer examination of the differential impacts of small mammals and geese where they co-occur may provide insights into how these guilds may alleviate or compound the effects of each in tundra systems.

Data Accessibility

Data from this project will be made available on the Arctic Data Center when this chapter is submitted for publication.

Author Contributions

A version of this chapter will be submitted for publication in a peer-reviewed journal, and will be co-authored by Austin Roy (AR), Elizabeth Min (EM), Natalie Boelman (NTB), Laura Gough (LG), Rebecca Rowe (RJR), Kevin Griffin (KLG), and Jennie McLaren (JRM). NTB, LG, KLG, RJR, and JRM co-conceived the larger study of which this specific study led by ANR is part of; all authors contributed to the ideas and designed the methodology; ANR collected and analyzed all datasets, except the *RE* data which was analyzed by EM; ANR and JRM interpreted the results; ANR led the writing of the manuscript. All authors contributed critically to this manuscript.

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Chapter 5: When top-down is also bottom-up: examining consumer-driven nutrient recycling in an arctic herbivore population

Abstract

While herbivore consumers represent both top-down and bottom-up forces in ecosystem regulation, the bottom-up roles of herbivores on primary productivity are often underappreciated. The consumer-driven nutrient recycling hypothesis (CNR) provides a framework for linking consumer populations and bottom-up regulation of ecosystem processes due to potential impacts of fecal nutrients on plant nutrient limitation. Here, we examine CNR by evaluating how changes in brown lemming density and foraging behavior during different phases of their population cycle influence nutrient availability in an arctic tundra ecosystem. Our specific aims were to test whether CNR was supported in arctic tundra and whether CNR can be used to understand tundra ecosystem function. To achieve this, we 1) examined if fecal nutrient content and ratios varied between different phases of the lemming population cycle, 2) determined whether fecal nutrients are affected by diet, 3) evaluated if changes in diet-caused changes in fecal quality influence plant nutrients, and 4) examined the decomposition and nutrient loss from feces. We found seasonal differences in fecal carbon (C) and phosphorus (P), with lower fecal C and P during late summer compared to mid-summer, but no differences in fecal N across seasons or changes in fecal nutrients across years. We also observed no differences in fecal nutrients of lemmings fed different diets, but plants grown in feces from an *Eriophorum* diet had greater biomass than that of plants grown with feces from a *Carex* diet. Feces persisted 1.5 - 4.4 years on the tundra and while C and N were retained within decomposing feces for several years, P was rapidly lost. Our data suggest tentative support for the CNR hypothesis in a tundra ecosystem; by providing limiting nutrients during the peak of the population cycle, fecal nutrients may control ecosystem function and explain how the system recovers from cyclical disturbance regimes. Due to slow fecal decomposition, nutrients supplied during a population cycle peak may provide legacy effects on ecosystem function across multiple years.

Introduction

While ecosystems have long been debated to be controlled more by top-down (i.e., consumption driven) or by bottom-up (i.e., resource driven) forces (Lindeman 1942, Hairston et al. 1960, Estes 1996), herbivore consumers may represent both forces in regulating ecosystems. The top-down roles of herbivores, such as in controlling vegetation through consumption and

corresponding effects on ecosystems, are well studied (e.g., (Min et al. 2021, Staver et al. 2021)). However, their bottom-up influences as consumers, through altering soil nutrient availability, are relatively underappreciated (although see (Turkington 2009) and Chapter 3) despite having potentially strong effects on ecosystem function. Through the production of nutrient-rich waste, including urine and feces, herbivores can alter nutrient supply and cycling with important feedbacks on ecosystem structure and processes (Van Der Wal et al. 2004, Barthelemy et al. 2019). An appreciation of the link between herbivore consumers and biogeochemical cycling will allow for a more complete understanding of how ecosystems function.

The Consumer-driven Nutrient Recycling hypothesis (CNR) provides a framework to examine how consumers may have bottom-up effects on autotrophic community assemblage and productivity (Elser and Urabe 1999). CNR consists of two rules (Sitters et al. 2017): the first assumes a relationship between forage stoichiometry (e.g., nitrogen (N):phosphorus (P) ratios) and consumer stoichiometry in predicting waste (e.g., feces and urine) stoichiometry; and the second assumes that waste stoichiometry will influence nutrient limitation of primary productivity (Sturner 1990, Elser and Urabe 1999). While originally described and thoroughly examined in aquatic systems (Sturner 1986;1990, Elser et al. 1998, Elser and Urabe 1999), there have been recent suggestions that this hypothesis may also apply to terrestrial systems (Sitters and Olde Venterink 2015, Sitters et al. 2017). Recent work by Daufresne (2021) has highlighted the differences in CNR between aquatic and terrestrial systems and argued that CNR would be most supported in terrestrial systems under a steady ecological state. However, due to natural variations in consumer populations (Batzli 1992, Krebs 2013b) and climate change-induced alterations to ecosystems (Walther 2010), many terrestrial ecosystems are likely not in a steady state and it remains to be determined whether CNR would also apply under non-steady-state ecological conditions.

Arctic tundra regions provide a unique opportunity to study CNR in a non-steady state system due to the combination of three main factors. The first is that the system receives pulses of disturbance and nutrient deposition because the dominant mammalian consumers, small mammals, exhibit population cycles (Krebs 2013b). For example, brown lemming (*Lemmus trimucronatus*) cycles can result in high density population cycle peaks (225 individuals ha⁻¹) every 3-5 years, followed by sparse animal abundance (0.02 individual ha⁻¹) during the low phase of the cycle (Batzli et al. 1980). Such large increases or decreases in animal abundance

result in large changes in the quantity of feces being produced and deposited on the landscape during different phases of the population cycle (Figure 5.1). Changes in animal density between population phases would also alter resource and forage availability, and as the Optimal Foraging Theory suggests (Pyke et al. 1977, Ostfeld 1982), lemming diets should change as resource availability changes with changes in animal density (Pyke et al. 1977, Batzli et al. 1980, Ostfeld 1982, Moen et al. 1993). These changes in diet may alter the stoichiometry of feces and urine (Figure 5.1) and allow for changes in fecal quality to occur concurrently with changes in fecal quantity (Figure 5.1). Changes in both the quantity and quality of feces during the different phases of the population cycle will likely impact nutrient availability for plant and microbial communities (Sitters et al. 2017, Sitters and Olde Venterink 2021b), with feedbacks on ecosystem productivity and decomposition.

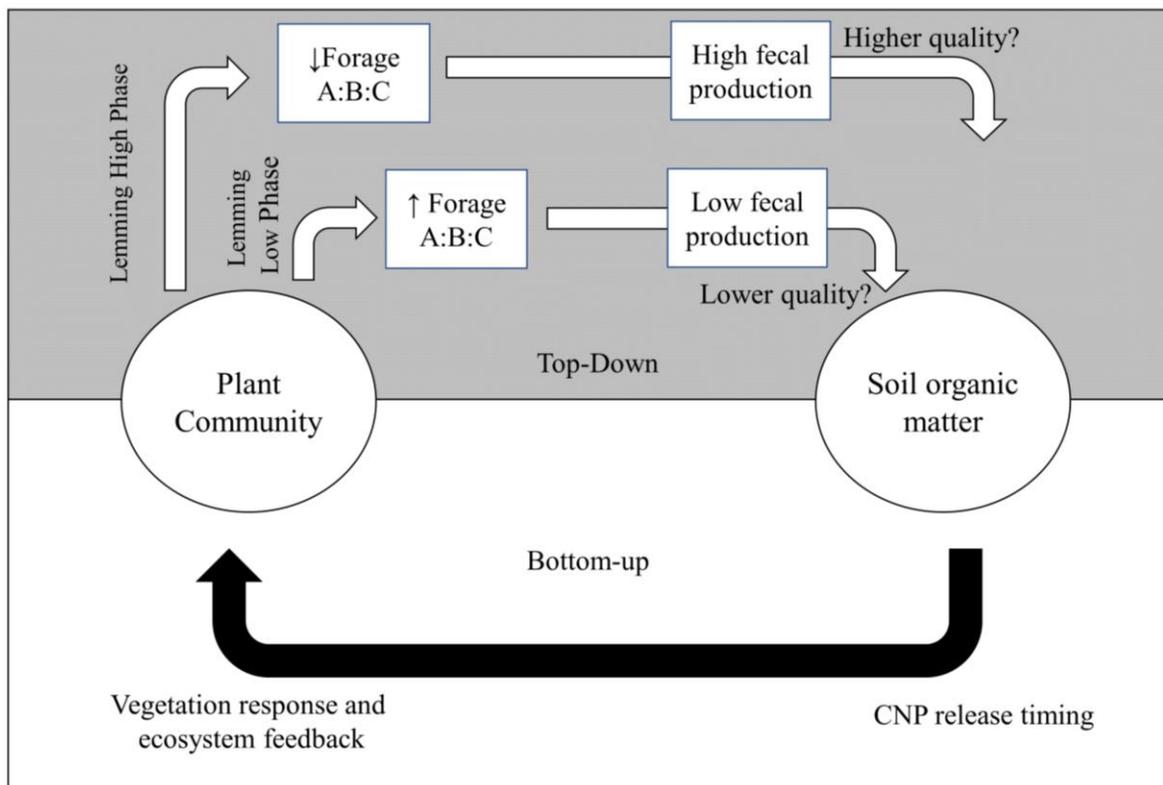


Figure 5.1: Conceptual diagram showing the interactions between the Consumer-driven nutrient recycling hypothesis (CNR) and brown lemming population cycles with potential effects on ecosystem function.

Secondly, the arctic tundra is an opportune ecosystem to study CNR because it is considered a strongly nutrient-limited ecosystem (Jonasson et al. 1999) and changes in nutrient inputs may alter the state of the system by changing ecosystem processes such as vegetation community dynamics and C-cycling (Boelman et al. 2003, Mack et al. 2004, Nemergut et al. 2008). Additionally, because many ecosystem processes, such as decomposition, are slow (Zhou et al. 2008), changes in fecal quantity and quality may have persistent effects on ecosystem function. Slow decomposition may allow feces to act as nutrient sources (Sitters and Olde Venterink 2021b) for multiple years, which may help explain how tundra systems recover from disturbances in the year following small mammal population peaks. Nutrient limitation and slow biogeochemical processes may allow for feces to have strong legacy effects that alter how the system functions over larger time scales.

The third reason CNR should be studied in arctic tundra is that tundra ecosystems exemplify systems undergoing novel changes within the ecosystem which may alter ecological function (Ims et al. 2008, McGuire et al. 2009, Box et al. 2019). Herbivore-driven changes in nutrient cycling will likely interact with concurrent changes in ecological conditions to affect ecosystem processes such as C cycling. It has already been observed that herbivore presence or absence can influence how arctic systems respond to global change (Johnson et al. 2011, Cahoon et al. 2012, Min et al. 2021), and changes in nutrient inputs via feces may provide controls of C-balance in tundra systems by altering primary productivity and ecosystem biogeochemical cycling (Daufresne 2021, Li et al. 2021). As arctic tundra holds a large amount of the world's soil carbon relative to its size (Ping et al. 2008), herbivore-induced changes in tundra C-cycling may have implications on global biogeochemical cycling.

Here we examine CNR in a tundra ecosystem that has lemmings as the dominant consumer, using both field and *ex situ* experiments. Specifically, we asked if the two rules of CNR (Rule 1: There is a relationship between forage and consumer stoichiometry in predicting waste stoichiometry. Rule 2: Waste stoichiometry will influence nutrient limitation for primary production (Sitters et al. 2017)) are supported in an arctic tundra ecosystem, and whether CNR can be used to better understand how small mammals influence ecosystem function over time. To answer these questions, our research aims were to:

1. Determine if fecal C, nitrogen (N), and phosphorus (P) concentrations and ratios shift between different phases of the lemming population cycle.

2. Evaluate if fecal C, N, and P change with changes in lemming diets.
3. Determine if changes in fecal nutrients due to diet can influence plant C, N, and P.
4. Examine the decomposition rate of lemming feces and the decay rates of C, N, and P from feces back to the environment.

Materials and Methods

Study Site

We conducted this study near Utqiagvik, Alaska (71.290°, -156.788°) in the summers of 2018-2020. The climate of the region is relatively dry with average annual rainfall and snowfall being approximately 11.5 and 95.8 cm yr⁻¹ respectively (ACRC 2019). Air temperatures of the region range from -20 °C to 47°C (mean annual air temperature = 11°C, NOAA 2020) and soil temperatures range from -26 °C to 11 °C (mean thaw soil temperature = 4 °C, Hinkel et al. 2001). Experimental sites were located in high-centered polygon tundra, where vegetation species vary between aquatic and semi-aquatic polygon troughs and edges, dominated by graminoids, through the relatively dry zone of polygon centers, dominated by dwarf shrubs, mosses, and lichens (Johnson et al. 2011, Assmann et al. 2019). Elevation of sites were approximately five m in elevation. The dominant small mammal herbivores were brown lemmings, with other small mammal species in the region including collared lemmings (*Dicrostonyx groenlandicus*), Arctic ground squirrels (*Spermophilus parryii*), and Arctic hare (*Lepus arcticus*, Batzli et al. 1980). Brown lemmings create latrines, areas where lemmings repeatedly defecate (Bee and Hall 1956). The dominant vegetation species important for brown lemmings include *Dupontia* spp., *Carex* spp., and *Eriophorum* spp., and mosses (Batzli and Pitelka 1983).

Experimental design

This study was composed of four parts including: analysis of feces from wild captured lemmings at different phases of the population cycle and analysis of seasonal changes in the nutrient content of the forage species of lemmings (Aim 1); analysis of feces from lemmings fed different diets (Aim 2); analysis of the effects of feces on vegetation in a greenhouse experiment and under *in situ* conditions (Aim 3); and a fecal decomposition experiment (Aim 4). All animal handling and husbandry activities were in accordance with Alaska Fish and Game (ADFG) trapping permits (18-081, 19-141, 20-143) and IACUC protocols through the University of New Hampshire (160101, 190101) and the University of Texas at El Paso (1384700).

Temporal fecal and vegetation nutrients (Aim 1)

Between 2018-2020, brown lemmings were live-trapped at three tundra sites as part of a demography study (Rowe and Steketee, unpublished data) using 3 x 3 x 3.5-inch Sherman live-traps (H. B. Sherman Traps, Tallahassee, FL) baited with peanut butter and bird seed. Lemmings were trapped over the course of five days in July and five days in August in 2018 and 2019 but only five days in August in 2020, due to coronavirus-induced fieldwork limitations. Animals were also haphazardly captured between the established trapping sessions as part of an effort to maintain animal densities within established lemming enclosures as part of a concurrent project (Boelman et al., unpublished data). The feces used in our study were restricted to those collected from animals captured outside of the enclosures. After animals were released, fresh feces were collected from traps within 24 hours and frozen. Samples were then shipped to the University of Texas at El Paso (UTEP) and analyzed for total carbon (C), nitrogen (N), and phosphorus (P) as below.

In 2019, ca. 3 g of fresh, non-senesced leaf tissue was collected from five individuals each of four plant species growing at tundra sites near Utqiagvik, Alaska, USA: *Carex aquatilis*, *Eriophorum angustifolium*, *Petasites frigidus*, and a moss species. These species were chosen due to their relatively high abundance in brown lemming diets (Batzli and Pitelka 1983). We were not able to identify the moss to species but collected moss material that looked morphometrically similar. Plant material was collected once during the early growing season (June) and once during the late growing season (August). Vegetation material was dried at 50 °C for 48 hours and shipped to UTEP for the analysis of total C, N, and P content (described below).

Diet shifts and fecal nutrients (Aim 2)

In 2019, we collected feces from captively held lemmings fed two diets to test how diet influences nutrient recycling. Ten captive brown lemmings were held at the Barrow Arctic Research Center located in Utqiagvik, Alaska. Lemmings were housed in individual wire-top cages (26.7 x 48.3 x 20.2 cm) and provided with alfalfa hay as bedding. Five lemmings were fed rodent chow (Rodent Food, Mulberry Lane Farm) and *C. aquatilis* for 48 hours and then rodent chow and *E. angustifolium* for 48 hours. We did not use other species of forage which are less preferred due to the risk morbidity and mortality (Jung and Batzli 1981, Batzli and Lesieutre 1991). Feces was collected from each cage after each 48-hour period. Once collected, half of the fecal samples were oven dried at 50 °C for 48 hours and the other half of the samples were

frozen at -20C for use in a greenhouse experiment (see below); all dried samples were then shipped to UTEP for total C, N, and P analysis (described below).

Effects of feces on vegetation (Aim 3)

To test effects of small mammal diet shifts on plant nutrient content through shifts in fecal nutrient content, we conducted a greenhouse experiment. Annual ryegrass (*Lolium multiflorum*) seeds (OrOlam, orolam.com) were grown hydroponically in a slurry made from feces of animals fed either a *C. aquatilis* or *E. angustifolium* diet (see above). *L. multiflorum* was used because of its germination success and growth rate and its use as model species in other nutrient studies (Sharma and Sahi 2005, Liu et al. 2017). To make the slurry, two grams of feces were shaken in one liter of DI water for five minutes. This solution was then added to 9 L of DI water and used to fill a 40 x 27 x 13 cm hydroponics grower kit (HYDDNIce Dydroponic Grower Kit). We sprouted ryegrass seeds in 3 x 3.3 x 4.5 cm foam sponges soaked in tap water, with one seed per sponge. Once sprouted, we transferred sponges with seeds (11 sponges per treatment) to the appropriate *C. aquatilis* or *E. angustifolium* hydroponics tank. Plants were grown in the hydroponics tanks for 27 days. After 14 days, we added an additional one-liter fecal slurry to each tank. After 27 days, we harvested the above-ground plant material and recorded the average dry mass of each treatment after drying at 50 °C for 48 hours. We then analyzed the plant material for total C, N, and P (see below).

In 2020, we also collected green plant material of *C. aquatilis* growing from immediately adjacent to latrine sites (within 5 cm) and from control sites (areas at least 1 m from a latrine and lacking any observable lemming disturbance) to determine effects of feces on *in situ* plant nutrient content. Immediately after collection, plant material was dried at 50 °C for 48 hours before shipping to UTEP for total C, N, and P content (see below).

Decomposition experiment (Aim 4)

We determined lemming feces decomposition rates and loss of fecal nutrients over time using a fecal decomposition bag experiment. Feces were collected from ten captively held lemmings (see above) and refrigerated daily over the course of seven days. The fecal samples were then mixed across days, partitioned into one-g replicates, and placed into mesh (5 x 5 cm) bags made from window screening, with six replicates saved as initial condition samples. Initial condition samples were oven dried at 50 °C for 48 hours prior to analysis for total C, N, and P (see below).

We installed sets of decomposition bags in stations located at the center and along the edge of seven high-centered polygons. We chose these microhabitats as they represented areas where decomposition was expected to be slowest and fastest, respectively, due to differences in soil moisture. Each station consisted of 16 decomposition bags: four bags collected at each of four collection time-replicates. Decomposition bags were collected at 4, 16, and 64 days after installation, and the fourth time-replicate was left *in situ* overwinter and collected at 401 days after installation. Immediately after collection, feces were dried at 50 °C for 48 hours and then the dry mass was recorded. All samples were then shipped to UTEP for total C, N, and P (see below).

Fecal and plant nutrient analysis

Dry fecal and plant materials were ground and analyzed for total C and N content using a dry combustion C and N analyzer (ElementarPyroCube ®). Total P content was determined after ashing samples at 500 C, digesting using 6M HCl, then analyzing PO₄³⁻ content using a malachite green assay (D'Angelo et al. 2001).

Statistical analysis

Data were managed in Microsoft Excel (Microsoft, Edmond, WA) and analyzed in Program R (R-Development Core Team, <http://www.r-project.org>). Values were determined as statistically significant at an alpha of 0.05 and $p < 0.05$.

Fecal nutrients and population cycle (Aim 1)

The nutrient concentrations of feces collected from seasonal and yearly live-trapping were compared between growing season (early = 1 July to 15 July, middle = 16 July to 31 July, late = 18 August to 27 August) and year (2018-2020) using a two-way ANOVA. We also compared plant nutrient concentrations between growing seasons using two-way ANOVAs with leaf C, N, and P variables as dependent variables and plant species and growing season (early, late) as the independent variables.

Diet shifts and nutrients (Aim 2)

We analyzed the effect of diet shifts on fecal nutrients by comparing the C, N, and P concentrations of lemmings fed two diets using Wilcoxon sign-ranked tests, where fecal C, N, and P were the dependent variables and diet type (*C. aquatilis* and *E. angustifolium*) as the independent variable.

Feces-vegetation effects (Aim 3)

We examined the impact of differences in feces due to diet on vegetation differences using student's t-tests, with either above-ground biomass or leaf C, N, and P from the greenhouse experiment as the dependent variable and lemming diet (*C. aquatilis* or *E. angustifolium*) as the independent variables. We also examined the impact of latrines on plant nutrients using student's t-tests, or Wilcoxon sign-ranked tests for non-normal data, with plant nutrient variables as the dependent variable and sample location (latrine or control) as the independent variable.

Fecal Decomposition (Aim 4)

Average decay rate, k , for each decomposition station was calculated based on an exponential model of decay: $X_t = X_0 e^{-kt}$, where X_t is the average fecal mass remaining at time t (days) from three litter bag replicates, X_0 is the initial fecal mass at time t_0 , and k is expressed day^{-1} and represents the instantaneous mass loss rate. The rate of nutrient loss from feces over time was calculated for C, N, and P using the same decay formula but using the mass of each nutrient in feces instead of total fecal mass. Additionally, we calculated time until full decay assuming full decay occurred at 0.01 g (mass and C), 0.001 g (N), and 0.0001 g (P). Decay rates for mass and nutrients were compared between polygon edge and center locations using a student's t-test.

Results

Fecal and vegetation nutrients across time (Aim 1)

Across the different phases of the population cycle (years and seasons), we analyzed 84 individual fecal samples for total % C and N, and 19 composited samples for total % P (Supplemental Table 5.1). We observed differences in fecal total % C and P of feces by growing season but not by year (Table 5.1). Total % C was lower in feces late in the growing season compared to the middle of the growing season ($p = 0.049$), and there was a trend for lower total % C in late growing season compared to early growing season ($p = 0.075$) with no difference between early and middle growing seasons (Figure 5.2a). Similarly, total % P was lower at the end of the growing season compared to the middle of the growing season ($p = 0.031$, Figure 5.2c), with no differences observed between these periods and the early growing season. We did not observe changes in total fecal % N over the course of the experiment (Fig 2b). Like total % C, N, and P, we observed no differences in nutrient ratios across years, and only differences in C:P across seasons (Table 5.1), with C:P being lower during the middle growing season compared to late growing season ($p = 0.019$, Figure 5.2e).

Table 5.1: Statistical differences in brown lemming (*Lemmus trimucronatus*) fecal nutrients (TC = total % carbon (C), TN = total % nitrogen (N), TP = total % phosphorus (P), C:N ratios, C:P ratios, N:P ratios) of lemming feces collected at study sites near Utqiagvik, Alaska, USA during early, middle, and late growing seasons of 2018-2020. ANOVA and Kruskal-Wallis summary results from comparisons of fecal nutrients between growing seasons and years.

	Year			Season			Year x Season		
	Stat	df	<i>p</i>	Stat	df	<i>p</i>	stat	df	<i>p</i>
TC	F = 2.40	2	0.109	F = 4.33	2	0.017	F = 2.23	2	0.115
TN	F = 0.47	2	0.630	F = 1.04	2	0.357	F = 4.23	2	0.018
TP	F = 0.39	2	0.683	F = 4.49	2	0.035	F = 1.90	2	0.193
C:N	F = 0.62	2	0.541	F = 0.48	2	0.622	F = 5.88	2	0.004
C:P	F = 0.23	2	0.801	F = 4.41	2	0.037	F = 1.27	2	0.316
N:P	X ² = 0.34	2	0.846	X ² = 4.51	2	0.105			

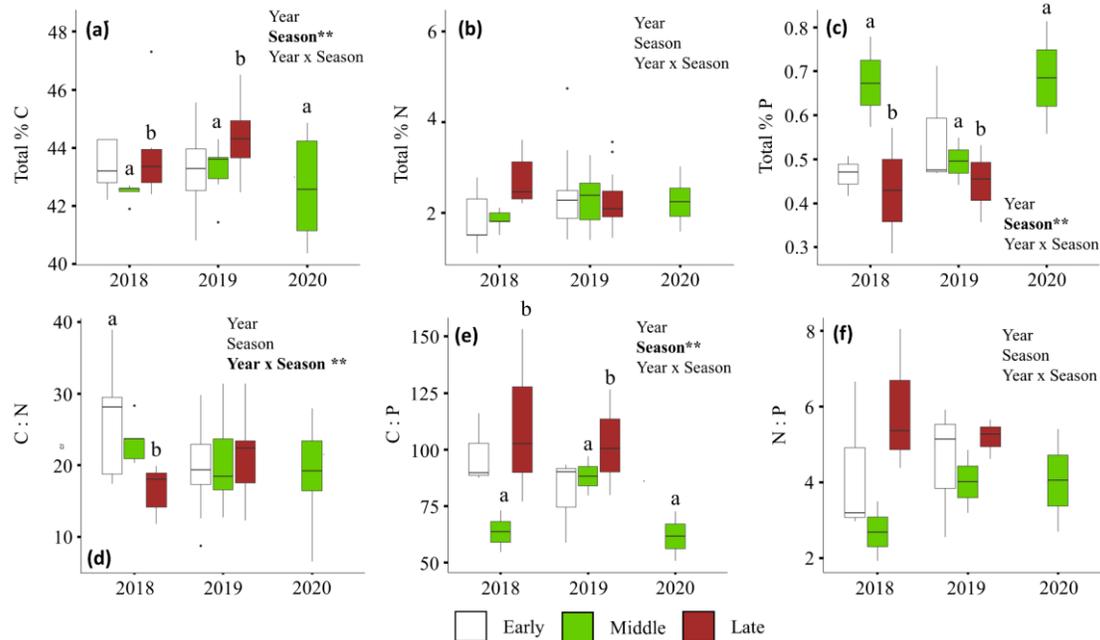


Figure 5.2: Box plots showing differences in total percent (%) carbon (C), total % nitrogen (N), total % phosphorus (P, and C, N, and P ratios of feces collected during different parts of the lemming population cycle (growing seasons (early, middle, late) and years). Samples were collected from live-trapped brown lemmings (*Lemmus trimucronatus*) near Utqiagvik, Alaska, USA during the summers of 2018-2020. Bolded text represents statistical differences. A single asterisk represents $0.10 > p > 0.05$ and a double asterisk represents $0.05 > p > 0.001$.

For plant tissues, we observed differences in C, N, and P concentrations between species, with few seasonal effects (Table 5.2). Total % C was lowest in *P. frigidus*, followed by moss, and *E. angustifolium* and *C. aquatilis*, while there was no difference between the latter two species ($p = 0.099$, Figure 5.3a). Total %N in moss was lower than *P. frigidus* ($p = 0.048$) and *C. aquatilis* ($p = 0.010$), but there were no other differences between species (Figure 5.3b). Total %P was lower in moss compared to *C. aquatilis* ($p = 0.004$), *E. angustifolium* ($p < 0.001$), and *P. frigidus*, while *C. aquatilis* had lower total % P than *P. frigidus* ($p = 0.002$) and *E. angustifolium* ($p = 0.001$, Figure 5.3c). The only seasonal change in plant nutrients we observed was with *P. frigidus*, with early season total % P being higher than later season total % P ($p < 0.001$, Figure 5.3c). Plant nutrient ratios followed similar patterns to total % C, N, P with differences between species, but few effects by season (Table 5.2), with only a potential trend for N:P being lower in plant tissues later in the growing season compared to early in the growing season ($p = 0.067$, Figure 5.3d-f).

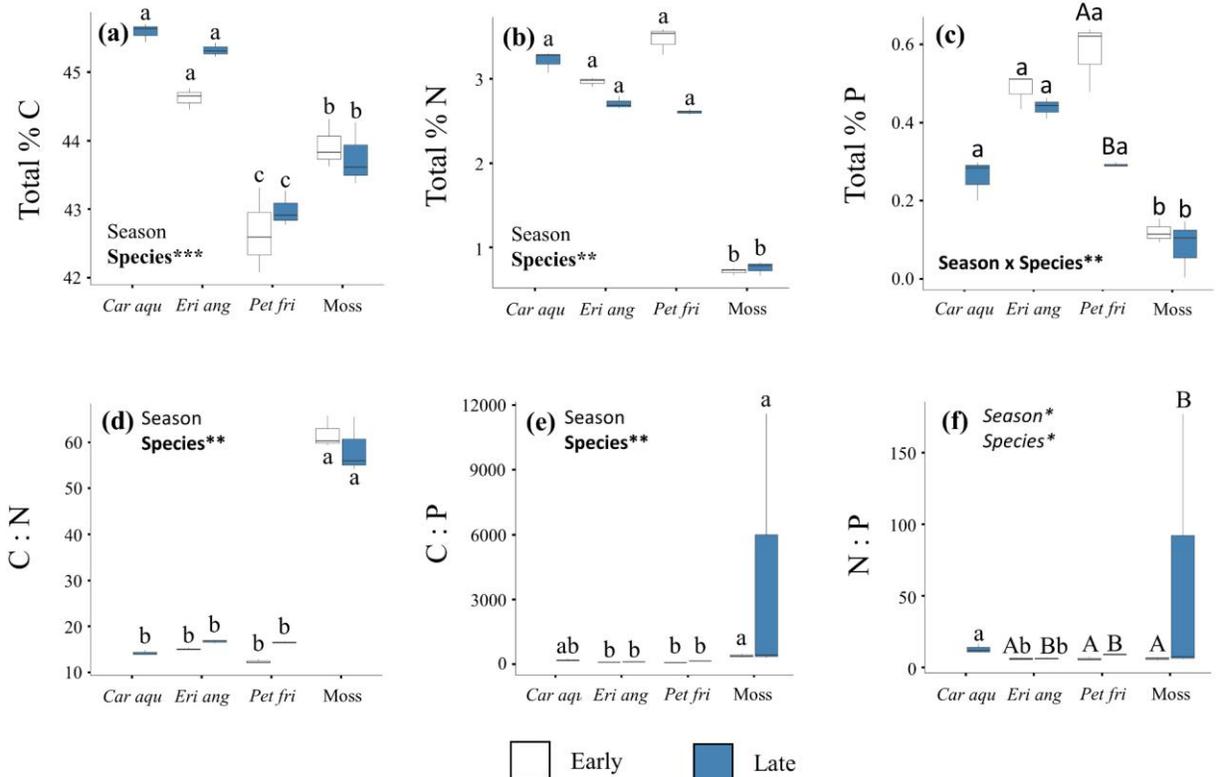


Figure 5.3: Box plots showing differences in total % C, total % N, total % P, and C, N, and P ratios between plant species collected at study sites near Utqiagvik, Alaska, USA during the early and late summer growing seasons of 2019. Bolded text represents statistical differences. A single asterisk represents $0.10 > p > 0.05$, a double asterisk represents $0.05 > p > 0.001$, and a triple asterisk represents $p < 0.001$. Lower case letters represent differences between species and uppercase letters represent differences between growing seasons.

Table 5.2: Statistical differences in plant species (*Carex aquatilis*, *Eriophorum angustifolium*, *Petasites frigidus*, moss species) nutrients (TC = total % carbon (C), TN = total % nitrogen (N), TP = total % phosphorus (P), C:N ratios, C:P ratios, N:P ratios) collected at study sites near Utqiagvik, Alaska, USA during early and late growing seasons of 2019. ANOVA and Kruskal-Wallis summary results from comparisons of leaf tissue nutrients between species and growing seasons.

	Species			Season			Species x Season		
	Stat	df	p	Stat	df	p	Stat	df	p
TC	F = 59.55	3	<0.001	F= 3.03	1	0.104	F = 2.38	2	0.129
TN	X² = 13.49	3	0.004	W = 65	1	0.464	-	-	-
TP	F = 59.14	3	<0.001	F = 24.51	1	<0.001	F = 10.87	2	0.001
CN	X² = 14.10	3	0.003	W = 65	1	0.464	-	-	-
CP	X² = 15.81	3	0.001	W = 76	1	0.129	-	-	-
NP	F = 2.865	3	0.074	F = 4.49	1	0.053	F = 1.02	2	0.358

Diet-feces effects (Aim 2)

We observed no differences in fecal C, N, P or their ratios in the feces of animals that were fed different plant diets (Supplemental Table 5.2).

Effects of feces on vegetation (Aim 3)

We found that plants grown in feces from lemmings fed a diet of *E. angustifolium* had greater above-ground biomass than plants grown in feces from lemmings fed a diet of *C. aquatilis* ($t = -2.69$, $p = 0.014$, $df = 18.96$, Figure 5.4e). While we observed changes in plant mass due to lemming fecal-diet, we did not observe changes in C or N concentration in plant tissues due to lemming fecal diet (Figure 5.4a-c, Supplemental Table 5.3).

Plants growing from near lemming latrine sites had no differences in leaf tissue nutrient contents or ratios compared to plants growing at control locations (Supplemental Table 5.4).

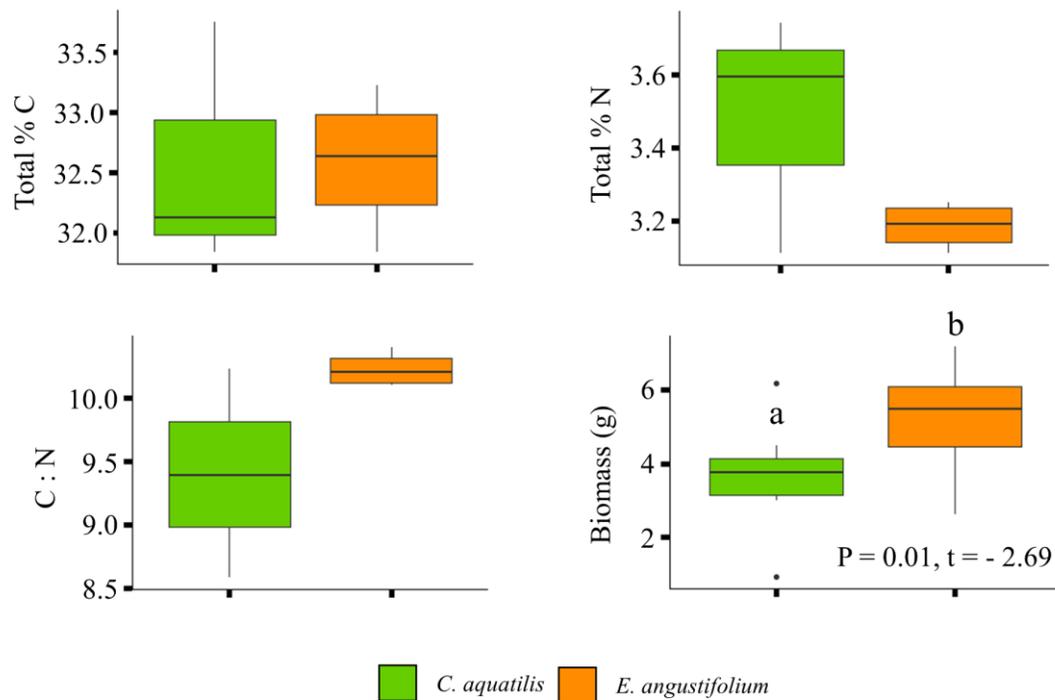


Figure 5.4: Box plots showing differences in total% C, total % N, total % P, and above-ground biomass of plants grown in feces from a *C. aquatilis* and a *E. angustifolium* diet. Data were collected from a greenhouse experiment conducted at the University of Texas at El Paso in 2021.

Feces Decomposition (Aim 4)

Lemming feces decomposed (k) faster along polygon edges than polygon centers ($p = 0.001$, $W = 0$, Figure 5.5a, Supplemental Table 5.5), with the time until full decay being $1.52 (\pm 0.20)$ years and $4.41 (\pm 0.00)$ years for polygon edges and centers, respectively (Table 5.3). Similarly, C loss ($W = 0$, $p = 0.001$) and N loss ($W = 0$, $p = 0.001$) from feces were fastest in polygon edges, but there was no difference in P loss between polygon locations ($W = 30$, $p = 0.535$, Figure 5.5b-d). Time until full decay of nutrients varied by nutrient (Table 5.3), with P decaying the fastest (7.35 ± 0.51 days) and C decaying the slowest (3.59 ± 0.44 years).

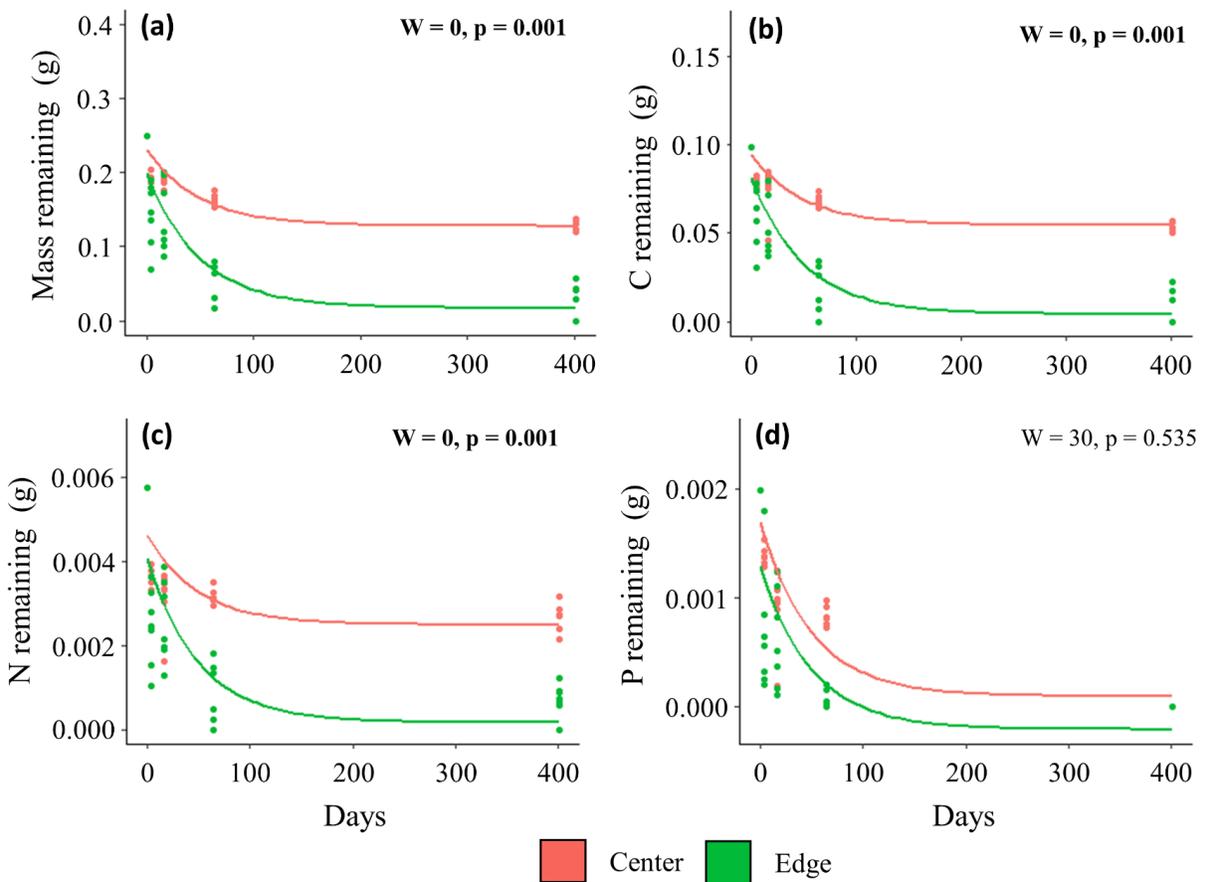


Figure 5.5: Dot plot showing differences in the amount fecal mass, carbon (C), nitrogen (N), and phosphorus remaining between feces decomposed at polygon centers and polygon edges during each sampling period (4, 16, 64, 401 days) of the fecal decomposition study. The trendlines represent an exponential rate of decay. The decomposition took place in polygonised tundra near Utqiagvik, Alaska, USA from summer 2019-2020.

Table 5.3: Mean and standard error (SE) of time until full decomposition or decay of feces (mass) and fecal nutrients (carbon (C), nitrogen (N), phosphorus (P)) in grams in either years or days (Time) for feces decomposed at high-centered polygon centers and edges, and the total between the two locations. Full decay was estimated to be 0.01 g for mass and C, 0.001 g for N, and 0.00001 for P.

Unit		Total		Center		Edge	
		Time	SE	Time	SE	Time	SE
Mass	Years	2.96	0.41	4.41	0	1.52	0.2
C	Years	2.27	0.43	3.59	0.45	0.96	0.19
N	Years	1.52	0.22	2.28	0.11	0.76	0.11
P	Days	7.35	0.51	6.94	0.55	7.76	0.87

Discussion

Validity of CNR in a tundra ecosystem

Our study provides one of the earliest direct examinations of the Consumer-driven Nutrient Recycling hypothesis (CNR) in a terrestrial system (Sitters et al. 2017, Daufresne 2021) and the first examining CNR using vertebrate herbivores in a tundra ecosystem. We found potential support for CNR in the tundra by examining the two rules of CNR and showing that changes in lemming diets may influence fecal nutrients and in turn plant productivity.

Our observation of changes in fecal nutrients over the course of the growing season provide tentative support for the first rule of CNR, that there is a relationship between forage and consumer stoichiometry in predicting waste stoichiometry. The increase in fecal C:P in the late compared to peak growing season may be related to a shift in diet (Batzli and Pitelka 1983), as predicted by the first rule of CNR. This is supported by the fact that we did not observe changes in the seasonal nutrient content of plant tissues, except for *P. frigidus* which is a less preferred forage species of lemmings (Batzli and Pitelka 1983), and suggests that changes in fecal C:P were due to a shift in diet and not a seasonal change in the C:P of forage species themselves. However, we cannot rule out that this shift in C:P may have also been due to seasonal changes in the physiological needs (Andrews 1968) or stressors of lemmings (Romero et al. 2008). Further, we did not observe differences in fecal stoichiometry when lemmings were fed two different diets, although differences in fecal CNP have been documented in other species due to shifting diets (e.g., Leslie and Starkey 1985). The lack of fecal nutrient change may have been because we supplementally fed lemmings with rodent chow which overrode the effects of the plant diet (Jørgensen et al. 2013). Additionally, it is possible that the species used in the diet experiment (*E. angustifolium* and *C. aquatilis*) are too similar in their CNP ratios and that they may not effect changes in fecal CNP. If animals had been fed plant species with larger CNP differences (e.g., *C. aquatilis* and *P. frigidus*), effects on fecal CNP may have been observable. More controlled experiments that combine larger changes in diet and temporal changes in herbivore stoichiometric requirements will allow for a more comprehensive understanding of how these variables interact to influence fecal CNP.

We also found support for the second rule of the CNR, which assumes that waste nutrient ratios will influence nutrient limitation of primary productivity. Previous studies have found positive effects of herbivore fecal additions on plant biomass (Barthelemy et al. 2018,

Barthelemy et al. 2019, Li et al. 2021), but this study is one of the first to consider different effects of feces from animals fed different diets. In our greenhouse study, we found that plants grown in feces from lemmings fed an *E. angustifolium* diet had greater above-ground biomass than plants grown in feces from a *C. aquatilis* diet. It is of note that we observed no differences in fecal C, N, or P due to diet, yet feces from lemmings fed different diets still changed plant productivity (biomass) and total amount of nutrients in individual plants (via changed biomass with no change in plant nutrient concentration) in different ways. It is possible that differences in plant productivity due to feces-diet treatments may have been due to differences in fecal micronutrients (e.g., sodium, potassium) between diet types which were not examined here. Furthermore, it is interesting that we found differences in plant biomass and nutrient content between diets under *ex situ* conditions, but no effects of feces on plant nutrients under *in situ* conditions (latrine sites), when other studies have found effects of feces on plant biomass *in situ* (e.g., Barthelemy et al. 2019). We did not test for differences in plant productivity during the *in situ* experiment, though, which may have helped to explain why we did not observe differences in leaf tissue nutrient ratios between latrine and control sites. The discrepancy between *ex situ* and *in situ* findings may have been due to additional factors such as rapid leaching of nutrients from latrines, environmental conditions around latrines and runways altering nutrient cycling (Bee and Hall 1956, Olofsson et al. 2004a), and interactive effects between fecal nutrients and plant responses to herbivory (Huitu et al. 2014, Barthelemy et al. 2019, Petit Bon et al. 2021).

While support for CNR in this study is somewhat limited, additional support for the hypothesis in the Arctic can be strengthened by examining other studies using vertebrate herbivores in arctic tundra. Links between small mammal presence and plant community productivity and vegetation community structure and soil nutrient concentrations have been observed in numerous tundra studies (e.g., Grellmann 2002, Stark and Grellmann 2002, Gough et al. 2012, Roy et al. 2020), including effects on specific plant species in work by Petit Bon (2020, 2021) which found that small mammal disturbance in winter enhanced the quality of individual forage species in summer. Within these studies, several have hypothesized a link between increases in biogeochemical availability of nutrients in the soil and fecal and urine nutrient inputs (e.g., Stark and Grellmann 2002, Petit Bon et al. 2020). Support for CNR can also be supplied by studies examining other herbivore guilds. The excrement of caribou and sheep have been shown to have strong effects of plant biomass and plant and soil nutrient concentrations (Barthelemy et

al. 2018, Barthelemy et al. 2019, Li et al. 2021), again providing additional support for Rule 2. As there is some support for Rule 2 (linking fecal nutrients to plant productivity and nutrient content) across arctic ecosystems and consumer types, additional studies explicitly examining CNR, and incorporating Rule 1 (linking animal diet to fecal stoichiometry) in particular, would elucidate the role of herbivores in altering arctic ecosystem function.

Potential legacy effects of CNR in tundra systems

CNR can have legacy effects on tundra ecosystems through multiple mechanisms. First, as we observed, alterations in lemming diets can change the ratio of nutrients returned to the environment via feces, with resulting effects on plant biomass and productivity. The relatively rapid changes in plant biomass due to feces from different lemming diets during our 27-day greenhouse experiment may show potential lasting effects on tundra systems by altering plant biomass and plant species dominance (Shaver et al. 2001). In a system with relatively slow plant species turnover (Callaghan and Emanuelsson 1985), changes in plant communities would likely also have long-term effects on biogeochemical cycling through alterations to litter quantity and quality and decomposition (Parker et al. 2018). Changes in vegetation community assemblage may also have longer-term consequences for tundra biogeochemical cycling and responses to climate change (Mack et al. 2004, Natali et al. 2012, Parker et al. 2021). However our findings may need to be qualified due to differences between our greenhouse experimental species and tundra vegetation (Callaghan and Emanuelsson 1985) and responses to nutrient availability (Shaver et al. 2001).

Secondly, the slow fecal decomposition and C and N leaching rates observed here and in other tundra studies (McKendrick et al. 1980) exemplify how feces can act as nutrient sources over long periods (1.5 – 4.4 years). As C and N availability determine the rates of multiple ecosystem processes (Weintraub and Schimel 2003, Chapin et al. 2002b, Peek and Forseth 2003, Sistla et al. 2012), the slow release of these nutrients under a traditional lemming population cycle (3-5) likely supports processes such as primary productivity between and across small mammal population peaks. Such persistent effects of feces may aid in maintaining long-term shifts in vegetation dynamics due to herbivory (Egelkraut et al. 2018, Barthelemy et al. 2019) or help explain how tundra systems respond to disturbance, such as changes in NDVI after a population peak (Olofsson et al. 2012, Chapter 4). The quick leaching of P from feces may also have legacy effects on ecosystems by increasing P availability after a population peak, also

resulting in increases in plant biomass (Boelman et al. 2003, McLaren and Buckeridge 2019). Such alterations in vegetation processes due to changes in the quantity of nutrients entering tundra systems via feces is likely to have impacts over long periods of time.

A critical question to ask is whether feces deposited during the high phase of the cycle may persist and overshadow the effects of low-phase feces? Stronger effects of diet on fecal stoichiometry would be expected under more drastic population cycling than what we observed in our study, but it is unclear how differences in fecal quantity and stoichiometry during the low phase of the population cycle may influence the ecosystem versus feces deposited during the peak of the population cycle. As lemmings can defecate up to their body mass each day in captivity (13-52 g of feces collected in a 12 hour period from lemmings weighing 51-84 g), the amount of feces deposited daily on the landscape between a population low phase and peak would be 1.1 g ha⁻¹ vs. 12,600 g ha⁻¹, respectively (assuming an average body mass of 56 g, Rowe and Steketee, unpublished data, and animal densities of 0.02 and 225 individuals ha⁻¹, Batzli et al. 1980). With the apparent long persistence of feces in the Arctic, the larger amounts of feces deposited during a population peak may drive ecosystem function more so than feces deposited during the low phases. However, feces from the low phase of the population may contain different nutrients or nutrient ratios that do not occur during the peak of the cycle, due to differences in the representation of forage items in diets, allowing for low-phase feces to also be important in influencing the ecosystem.

While the potential long-term effects of feces and CNR may be apparent, the larger effects of CNR on the landscape remain unclear. At a landscape scale, population cycles of small mammals are not always spatially synchronous (Krebs 2013a, Ehrich et al. 2020), which may make effects of feces patchy at the landscape level. At local scales, seasonal habitat-use by lemmings may change fecal nutrients throughout the season due to differences in dominant vegetation between microhabitats as well as the location where feces are deposited seasonally (e.g., polygon centers in winter vs. edges in summer, Batzli et al. 1983). At an even finer scale, the fate of nutrients once they leave feces and how far they disperse remains unknown, but other studies have shown that the area affected by animal waste may cover a 5x greater area than the actual excretion site (White et al. 2001). If similar spatial effects are possible in tundra systems, then latrines may have an effective area up to a 0.1 m². As latrines can be spaced closely together

(<1 m, Roy, personal observation), it is reasonable that during a population peak, latrines may affect large areas of the landscape.

CNR in a changing tundra system

The time frame of our experiment did not include a population peak, and we were unable to test how larger changes in animal density influence fecal CNP. However, small mammal population cycles may have become suppressed or disappeared in some areas of the Arctic (Ims et al. 2008), but not necessarily other locales (Ehrich et al. 2020), and hence our study gives us the ability to hypothesize about CNR under potential future conditions in the Arctic. If cycles have already become suppressed at Utqiagvik and animal density remains relatively constant across time, similar to the cycle observed in this study, there may no longer be density-dependent shifts in animal forage that result in changes in fecal stoichiometry. Additionally, without future large population peaks we may expect a decrease in nutrients returned via feces to occur overall due to lower population numbers and reduced fecal output and also less variability in fecal nutrients due to more stable population abundances.

Another potential change to small mammal population dynamics is a shift in the community composition and distribution of small mammals and other consumers in the Arctic. In some parts of the Arctic, previously sub-dominant species have become dominant or novel species have been documented (Krebs et al. 2019, Ehrich et al. 2020). As different rodent species have different physiological needs and foraging preferences (Batzli and Jung 1980, Batzli 1983, Batzli and Pitelka 1983), the feces produced by these species is likely to vary in the nutrient content released (Elser and Urabe 1999, Sitters and Olde Venterink 2021a). Such changes in nutrient recycling due to changes in herbivore assemblages has been seen in other studies (Elser et al. 1996, Elser and Urabe 1999, Sitters and Olde Venterink 2021a) and could also affect arctic ecosystem function.

Lastly, the arctic environment is changing simultaneously with changes in consumer communities. Potential environmental changes that might affect CNR include a warmer and wetter arctic (Bintanja and Selten 2014, Boisvert and Stroeve 2015) which will likely result in faster decomposition rates (Walse et al. 1998) resulting in quicker leaching of nutrients from feces and latrines. With decreases in the persistence of feces, the ability of feces to act as a nutrient source between population peaks may decrease, resulting in stronger feces-driven nutrient limitation in the Arctic between population peaks, although this may be overridden by

concurrent changes in other nutrient availability processes (e.g., increases in mineralization rates, Rustad et al. 2001). Additional environmental changes are likely to alter other ecosystem properties (e.g., plant community assemblage, Jeong et al. 2012, Lorant and Goetz 2012, Weber-Grullon et al. 2022) which will interact with both consumer biology and biogeochemical cycling (Yu et al. 2017), and more research is needed to understand the interconnections and feedbacks between all of the factors regulating biogeochemical cycling and ecosystem function in the Arctic

Conclusion

Exploring the links between fecal-plant stoichiometry and fecal quantity can help elucidate the controls of herbivores within tundra ecology and biogeochemical cycling. We found support for the hypothesis that lemmings may regulate tundra stoichiometry through our examination of the consumer-driven nutrient recycling hypothesis (CNR) in a tundra ecosystem. We found that changes in lemming diets can affect plant biomass, possibly through changes in fecal nutrients. These changes in lemming fecal nutrients can also have important effects on primary productivity and other ecosystem processes, leading to potential legacy implications, which help to regulate ecosystem function over decadal time scales. Changes in the herbivore population cycles, abundances, and community assemblage may interact with ongoing environmental changes in the Arctic to alter how vertebrate consumers interact with CNR and affect ecosystem function. While support for CNR was found in our study and tentative support has been pulled from other studies, more comprehensive examination of CNR across the arctic terrestrial systems and consumer groups is needed to better understand the links between arctic organisms and bottom-up regulation of arctic ecosystem function.

Data Accessibility

Data from this project will be made available on the Arctic Data Center when this chapter is submitted for publication.

Author Contributions

A version of this chapter will be submitted for publication in a peer-reviewed journal, and will be co-authored by Austin Roy (AR), Rebecca Rowe (RJR), and Jennie McLaren (JRM). AR and JRM co-conceived this specific study led by ANR is part of; all authors contributed to the ideas and designed the methodology; ANR collected and analyzed all datasets; ANR and JRM

interpreted the results; ANR led the writing of the manuscript. All authors contributed critically to this manuscript.

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Chapter 6: Conclusions

Summary of Research Findings

This research highlights the roles of small mammal herbivores in arctic biogeochemical cycling. While small mammal herbivores have previously been shown to have important impacts in multiple ecosystems, there has been a recent call to better understand their role specifically in arctic biogeochemical cycling, both now and into the future (Schmitz et al. 2014, Rastetter et al. 2022). To fill this research need, I answer some key questions which expand the understanding of small mammal influences on arctic biogeochemistry including how biogeochemical cycling is affected by small mammal herbivore presence, structure building behaviors, and population dynamics in the arctic tundra of northern Alaska. I achieved this by examining the multiple ways that voles and lemmings influence soils, plants, and ecosystem processes in four chapters.

In Chapter 2, I explored how 20+ years of herbivore exclusion influenced ecosystem processes within two tundra plant communities (moist acidic tussock (MAT) and dry heath (DH) tundra). Specifically, I examined the differential effects of the exclusion of two herbivore guilds (small mammal and large mammal) on plant communities and soil biogeochemical cycling. After 20+ years of herbivore exclusion, I found that herbivore exclusion impacted each tundra plant community differently, with herbivore absence increasing moss and decreasing evergreen shrub cover in the MAT, while herbivore absence had no effect on vegetation community in the DH. Herbivores had little effect on soil biogeochemical processes in either tundra type, except for greater phosphorus-acquiring enzyme activity in areas where small mammals were present in the DH. This work helps show that the roles of herbivores in biogeochemical cycling may be specific to the tundra ecosystem where they occur and that small and large mammalian herbivores interact with tundra ecosystems in unique ways. In particular, herbivores can help shape plant communities that result in changes in nutrient availability (e.g., P) in soils which has potential to lead to broader ecosystem impacts.

In Chapter 3, I explored how the structures built by small mammals can have bottom-up influences on ecosystem processes. My specific aims were to compare plant and soil nutrient pools located at or near four small mammal structure types, identify potential mechanisms driving the effects of structures on nutrient pools, examine the effects of structures across multiple tundra systems, and determine how structure effects may vary at different phases of small mammal population cycles. In general, I found that small mammal structures increased

nitrogen (N) availability in soils, with effects varying across tundra systems. Hay piles and carcasses were the least abundant structure types, but had influences on multiple C, N, and P pools. Whereas runways and latrines were the most abundant structures but increased fewer N and P pools. Each structure type was regulated by different mechanisms, with hay piles effects influenced by litter N-mineralization and the effects of other structure type were likely influenced by soil temperatures. Due to differences in the abundance and persistence of each structure type, small mammal structures have important spatiotemporal influences on ecosystem processes across tundra types. By influencing plant and soil nutrient availability, structures have bottom-up influences on ecosystem functioning, particularly when they are abundant during and after the peak of a population cycle.

In Chapter 4, I examined the importance of small mammal population cycles in understanding tundra ecosystem regulation by applying the Nutrient Recovery Hypothesis (NRH) to tundra mammal-plant-soil interactions. My goals were to determine if soil nutrient availability varied at different phases of the brown lemming population cycle and to examine whether the original predictions of the NRH are still supported when examining both above- and below-ground variables in a series of fences simulating a small mammal population cycle. I found moderate support of the NRH when examining above-ground variables, with a reduction in lemming forage species in the lemming population peak treatment, and also for soil temperatures, where summer soil temperatures were higher in the high-density treatments compared to the low phase treatments. Contrary to the NRH, however, I found few effects of the fencing treatments on soil biogeochemistry, with only microbial biomass carbon (C) being higher where lemmings were present. While effects were not as strong as predicted under the NRH, impacts of lemming population cycles may still have important implications for understanding how tundra ecosystems respond to disturbance.

In the last data chapter (Chapter 5), I examined how arctic herbivores can link top-down and bottom-up forces to impact tundra ecosystems during different phases of their population cycle using the Consumer-driven Nutrient Recycling hypothesis (CNR). I tested whether CNR was supported in an arctic tundra system and discussed whether it could be used to understand tundra ecosystem function. I achieved this by 1) examining the nutrient (C, N, P) concentrations of feces during different phases of the brown lemming population cycle, 2) determining if fecal C, N, and P change with diet, 3) determining if fecal C, N, and P influence plant biomass and

nutrient levels, and 4) examining fecal decomposition and the decay rates of nutrients from feces. I found support for CNR from variation in fecal C and P across the summer growing season, and the effects of lemming diet on plant biomass. Furthermore, I observed slow decomposition and C and N loss from feces, but relatively rapid P loss. The influence of small mammal feces on nutrient recycling further highlights the bottom-up influence of small mammals on tundra ecosystems. Changes in fecal nutrients due to diet and changes in both quantity and quality of feces during different phases of lemming population cycle, along with relatively long persistence of feces in tundra systems, may provide important legacy effects for ecosystem function over time.

Ongoing Changes in the Arctic and Future Research Needs

This work occurred under contemporary conditions (2017-2021), in the midst of ongoing ecological changes in the Arctic (Post et al. 2009). While this research provides an important snapshot into arctic ecosystem functioning, it is important to note that current conditions and effects may not be the same as those of the past and will likely be different from those in the future. To continue improving the understanding of the role of small mammals and improving predictions of the future of the Arctic, several key pieces of knowledge are needed.

First, a better understanding of the spatiotemporal impacts of small mammals, and in particular their structures, will improve the understanding of their role in influence ecosystems. As I described in Chapter 3, small mammal structures are important to regulating biogeochemical cycling at local scales, but it is unclear how far these impacts may reach. Studies examining the spatial impacts of structures on nutrient cycling will allow for more accurate scaling of biogeochemical impacts of small mammals from the site level to the landscape level. This could be assessed through some relatively simple experiments. First, to examine the local spatial impacts of structures on soil nutrient pools, soils could be sampled at expanding buffers around each structure (e.g., 5, 10, 30, 1000 cm from each structure). Once the spatial reach of structure effects is established, the data could then be used to scale up effects to higher spatial scales. This could be paired with counts of structures within a known area; so that if it is known that a hay pile affects a 0.5 m^2 area (for example), and there are $1000 \text{ hay piles ha}^{-1}$, then we might expect to see a 5% increase in N availability ha^{-1} due to hay piles. Additionally, understanding how long the influences of structures lasts is will improve the ability to examine the legacy level effects of small mammal structures. This could be accomplished by repeated

sampling at different structure types, both seasonally and yearly, to examine how structure effects change through time. As the impacts of small mammals may take time to accumulate, may be transient, and/or be persistent (Tilman 1988, Mallen-Cooper et al. 2019), long term monitoring of small mammal structures and continued monitoring of enclosure/exclosure experiments may elucidate how small mammal-induced effects change through time.

In addition to examining the spatiotemporal impact of small mammals, understanding the mechanisms behind their impacts will be useful to understanding how effects may change under future conditions. In Chapter 3, I found that small mammal structure effects on abiotic conditions are likely important to their influences on soil biogeochemistry, but there are likely additional mechanistic variables not explored in this dissertation that are important. Through identifying the mechanisms by which these structures, and small mammals in general, influence biogeochemical cycling, researchers can better predict how future environmental conditions (e.g., warming) may affect these mechanisms and alter small mammal impacts on arctic systems. Furthermore, the relative importance of individual structure types in affecting biogeochemical processes may change as well. For example, while nests are rarer on the landscape than runways (Figure 3.7), their influences on biogeochemical cycling may be less affected by warming arctic temperatures due to the insulating effects of nests on soils (Chapter 3). Because of this, nests may become relatively more important than other structures in maintaining current ecosystem function in the future. I suggest sampling additional structure site variables such as soil pH, soil compaction, soil moisture, soil respiration, soil temperature, hay pile composition and nutrient content. These variables could then be modelled with structure effects on soils for different structure types to determine which mechanisms are most important in predicting soil nutrient responses. In addition to environmental mechanisms, biological mechanisms influencing structure effects should also be considered. For example, information on the role of herbivore gut-derived enzymes in determining phosphorus availability (Böök and Saborowski 2020) would be advantageous given the influences I observed of feces on soil and plant nutrient concentrations. This could simply be done by collecting fresh feces or feces from latrine sites and analyzing the feces for various P-acquiring enzymes and comparing it with P concentrations in soils and plants to determine if these gut-derived enzymes are likely important to soil nutrient cycling. As it is likely that multiple mechanisms interact to determine nutrient cycling, researchers must first

identify which mechanisms best predict nutrient availability from each structure before they can begin examining how future changes may alter their effects.

This study focused on the effects of brown lemmings and tundra voles in high-centered polygonal tundra and moist acidic tussock tundra, respectively, but these tundra types are among several ecosystem types occurring in the Arctic. The examination of different arctic ecosystems and herbivore species will allow for a better synthesis of the research presented here and more importantly a better prediction of how the entirety of terrestrial arctic systems may change in the future. This is particularly important because the study of additional systems and species may provide insights into future shifts in herbivore communities. As stated earlier in this dissertation, small mammal population densities and community assemblage may shift due to climate change. As small mammal species use habitats differently and have different physiological needs and foraging preferences (Batzli and Jung 1980, Batzli 1983, Batzli and Pitelka 1983), they likely interact with ecosystems differently and alter biogeochemical cycling in different ways (as seen in Chapters 2 and 3). By understanding how species affect ecosystem functioning in their current range and habitats researchers may be able to predict how they will interact with ecosystems if species dominance shifts, or species expand their ranges into new habitats. This could be achieved through several experiments. First, a comparison of the effects of the structures from dominant (e.g., brown lemmings) and sub-dominant (e.g., collared lemmings) arctic small mammals could reveal insights on how the effects of structures may change in the densities of these species shift. Additionally, these data could be used to predict how soil nutrient availability may be altered as species' ranges shift and species move into novel habitats. Secondly, to understand physiological difference between species, researchers may synthesize published physiological and diet research (Batzli and Jung 1980, Batzli 1983, Batzli and Pitelka 1983) and/or analyze difference in fecal nutrients between species to better understand how nutrient recycling may be affected by changes in small mammal community assemblage.

I focus on the small mammal guild in this dissertation, but additional herbivore guilds should be examined as well. In particular, migratory species such as geese and caribou are experiencing shifts in their migration and abundances (Fox et al. 2005, Sharma et al. 2009). As these organisms have different ecological effects than small mammals (see Chapter 2) and the ability to transport nutrients between ecosystem types (Doughty et al. 2020, Daufresne 2021), they represent a pathway for potential changes in arctic ecology. The impacts of these different

guilds on arctic ecosystems have been studied previously (e.g., Wilson and L. Jefferies 1996, Egelkraut et al. 2018), but few attempts have been made to synthesize the effects of all arctic herbivores to understand ecosystem function. A more comprehensive approach examining the contributions to all herbivore species would allow for a greater understanding of the connections between species and the effects they have on terrestrial ecosystem function in the Arctic (Koltz et al. 20XX, in review).

Throughout this dissertation I have highlighted the importance of small mammals in arctic ecosystems, and it is worth discussing the conservation of small mammal herbivores for not only their intrinsic value but also the ecosystem services they provide. Ecosystem engineers and soil bioturbators are declining worldwide and loss of these species is likely to cause cascading effects on ecosystem function (Beca et al. 2021). Decreases in ecosystem functioning in arctic ecosystems may be expected if species' abundances decrease. As I describe in Chapter 4, due to general lower animal abundances compared to historic numbers, the role of small mammals in the tundra may be weakened. Additionally, a loss of population cycling may result in a loss of pulse dynamics and influxes of nutrients into the system which may lead to slower nutrient cycling and changes in ecosystem C storage and flux. A question that should be asked is whether there is anything that can be done to mitigate the effects of climate change on small mammal populations. Key to maintaining animal densities or restoring densities to historic numbers is a need for a better understanding of the drivers of small mammal population dynamics in the Arctic. Understanding why arctic small mammal populations fluctuate may allow for wildlife managers to manipulate habitats or conditions to promote small mammal abundance and maintain ecosystem function and services.

Conclusion

This research elucidates the impacts of small mammal herbivores in tundra ecosystems by highlighting the role they play in influencing biogeochemical cycling and regulation of tundra ecosystem processes. By controlling plant community composition (Chapter 2, 4) and nutrient concentrations in soils and plants (Chapters 2-5), small mammals help to regulate competition for resources among and between plants and soil microbes. These effects on resource limitation and competition can feedback to affect tundra ecosystem properties such as primary productivity and decomposition, with resulting effects on tundra C-cycling.

As arctic tundra holds a large portion of soil C, especially relative to its area (Ping et al. 2008), changes in tundra C-cycling can have implications for global C concerns. By linking the effects of small mammals on biogeochemical cycling at local scales, I have shown the importance they may have at higher or longer ecosystem scales. This dissertation contributes to a growing interest in linking organisms, communities, and ecosystems to create a better understanding of the natural world and aiding in predictions for how the natural world will continue to function into the future. In pursuit of this, the data and findings of this dissertation can be used to update ecosystem models involving arctic ecosystem function (e.g., Rastetter et al. 2022) and this research can be used to meet needs identified in the Arctic Research Plan (Aim 7: Advance an Integrated, Landscape-scale Understanding of Arctic Terrestrial and Freshwater Ecosystems and Potential for Future Change, IARPC 2016).

References

- Aguirre, D., A. E. Benhumea, and J. R. McLaren. 2021. Shrub encroachment affects tundra ecosystem properties through their living canopy rather than increased litter inputs. *Soil Biology and Biochemistry* 153:108121.
- Aho, K., N. Huntly, J. Moen, and T. Oksanen. 1998. Pikas (*Ochotona princeps*: Lagomorpha) as allogenic engineers in an alpine ecosystem. *Oecologia* 114:405-409.
- Alaska Climate Research Center [ACRC]. 2019. Climate Normal. in <http://akclimate.org/Climate/Normals>.
- Allison, S. D., Y. Lu, C. Weihe, M. L. Goulden, A. C. Martiny, K. K. Treseder, and J. B. H. Martiny. 2013. Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology* 94:714-725.
- Andreassen, H. P., J. Sundell, F. Ecke, S. Halle, M. Haapakoski, H. Henttonen, O. Huitu, J. Jacob, K. Johnsen, E. Koskela, J. J. Luque-Larena, N. Lecomte, H. Leirs, J. Mariën, M. Neby, O. Rätti, T. Sievert, G. R. Singleton, J. van Cann, B. Vanden Broecke, and H. Ylönen. 2020. Population cycles and outbreaks of small rodents: ten essential questions we still need to solve. *Oecologia* 195:601-622.
- Andrews, R. V. 1968. Daily and Seasonal variation in adrenal metabolism of the brown lemming. *Physiological Zoology* 41:86-94.
- Arens, S. J. T., P. F. Sullivan, and J. M. Welker. 2008. Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem. *Journal of Geophysical Research: Biogeosciences* 113: G03S09, doi:10.1029/2007JG000508.
- Assmann, J. J., I. H. Myers-Smith, A. B. Phillimore, A. D. Bjorkman, R. E. Ennos, J. S. Prevéy, G. H. R. Henry, N. M. Schmidt, and R. D. Hollister. 2019. Local snow melt and temperature—but not regional sea ice—explain variation in spring phenology in coastal Arctic tundra. *Global Change Biology* 25:2258-2274.
- Ayarbe, J. P., and T. L. Kieft. 2000. Mammal mounds stimulate microbial activity in a semiarid shrubland. *Ecology* 81:1150-1154.
- Bagchi, S., T. Namgail, and M. E. Ritchie. 2006. Small mammalian herbivores as mediators of plant community dynamics in the high-altitude arid rangelands of Trans-Himalaya. *Biological Conservation* 127:438-442.

- Bakker, E. S., H. Olf, M. Boekhoff, J. M. Gleichman, and F. Berendse. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138:91-101.
- Ballová, Z., L. Pekárik, V. Píš, and J. Šibík. 2019. How much do ecosystem engineers contribute to landscape evolution? A case study on Tatra marmots. *CATENA* 182:104121.
- Baltensperger, A. P., and F. Huettmann. 2015. Predicted shifts in small mammal distributions and biodiversity in the altered future environment of Alaska: an open access data and machine learning perspective. *PLOS ONE* 10:e0132054.
- Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258-2268.
- Barkley, S. A., G. O. Batzli, and B. D. Collier. 1980. Nutritional ecology of microtine rodents: a simulation model of mineral nutrition for brown lemmings. *Oikos* 34:103-114.
- Barthelemy, H., E. Dorrepaal, and J. Olofsson. 2019. Defoliation of a grass is mediated by the positive effect of dung deposition, moss removal and enhanced soil nutrient contents: results from a reindeer grazing simulation experiment. *Oikos* 128:1515-1524.
- Barthelemy, H., S. Stark, A. Michelsen, and J. Olofsson. 2018. Urine is an important nitrogen source for plants irrespective of vegetation composition in an Arctic tundra: insights from a ¹⁵N-enriched urea tracer experiment. *Journal of Ecology* 106:367-378.
- Bartlett, R. J., and D. S. Ross. 1988. Colorimetric determination of oxidizable carbon in acid soil solutions. *Soil Science Society of America Journal* 52:1191-1192.
- Batzli, G. O. 1978. The role of herbivores in mineral cycling. *Environmental Chemistry and Processes, Department of Energy Series* 45:95-112.
- _____. 1983. Responses of arctic rodent populations to nutritional factors. *Oikos* 40:396-406.
- _____. 1992. Dynamics of small mammal populations: a review. Pages 831-850 in D. R. McCullough, and R. H. Barrett, editors. *Wildlife 2001: Populations*. Springer Netherlands, Dordrecht.
- Batzli, G. O., and H. Henttonen. 1990. Demography and resource use by microtine rodents near Toolik Lake, Alaska, U.S.A. *Arctic and Alpine Research* 22:51-64.
- Batzli, G. O., and H. J. G. Jung. 1980. Nutritional ecology of microtine rodents – resource utilization near Atkasook, Alaska. *Arctic and Alpine Research* 12:483-499.

- Batzli, G. O., and C. Lesieutre. 1991. The influence of high quality food on habitat use by arctic microtine rodents. *Oikos* 60:299-306.
- Batzli, G. O., and F. A. Pitelka. 1983. Nutritional ecology of microtine rodents: food habits of lemmings near Barrow, Alaska. *Journal of Mammalogy* 64:648-655.
- Batzli, G. O., F. A. Pitelka, and G. N. Cameron. 1983. Habitat use by lemmings near Barrow, Alaska. *Holarctic Ecology* 6:255-262.
- Batzli, G. O., R. G. White, S. F. MacLean, F. A. Pitelka, and B. D. Collier. 1980. The herbivore-based trophic system. Pages 335-410 in J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell, editors. *An Arctic Ecosystem*. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA.
- Beca, G., L. E. Valentine, M. Galetti, and R. J. Hobbs. 2021. Ecosystem roles and conservation status of bioturbator mammals. *Mammal Review* 52:192-207.
- Bee, J. W., and E. R. Hall. 1956. *Mammals of northern Alaska on the arctic slope*. University of Kansas, Museum of Natural History.
- Beylich, A., H.-R. Oberholzer, S. Schrader, H. Höper, and B.-M. Wilke. 2010. Evaluation of soil compaction effects on soil biota and soil biological processes in soils. *Soil and Tillage Research* 109:133-143.
- Bintanja, R., and F. M. Selten. 2014. Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat. *Nature* 509:479-482.
- Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. *Ecological Applications* 8:469-479.
- Bockheim, J. G., L. R. Everett, K. M. Hinkel, F. E. Nelson, and J. Brown. 1999. Soil organic carbon storage and distribution in arctic tundra, Barrow, Alaska. *Soil Science Society of America Journal* 63:934-940.
- Boelman, N. T., M. Stieglitz, H. M. Rueth, M. Sommerkorn, K. L. Griffin, G. R. Shaver, and J. A. Gamon. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia* 135:414-421.
- Boisvert, L. N., and J. C. Stroeve. 2015. The Arctic is becoming warmer and wetter as revealed by the Atmospheric Infrared Sounder. *Geophysical Research Letters* 42:4439-4446.
- Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, L. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, Y. M. Buckley, M. Cadotte, C. Chu, E. E. Cleland, M. J. Crawley, P. Daleo,

- E. I. Damschen, K. F. Davies, N. M. DeCrappeo, G. Du, J. Firn, Y. Hautier, R. W. Heckman, A. Hector, J. HilleRisLambers, O. Iribarne, J. A. Klein, J. M. H. Knops, K. J. La Pierre, A. D. B. Leakey, W. Li, A. S. MacDougall, R. L. McCulley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, B. Mortensen, L. R. O'Halloran, J. L. Orrock, J. Pascual, S. M. Prober, D. A. Pyke, A. C. Risch, M. Schuetz, M. D. Smith, C. J. Stevens, L. L. Sullivan, R. J. Williams, P. D. Wragg, J. P. Wright, and L. H. Yang. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508:517.
- Box, J. E., W. T. Colgan, T. R. Christensen, N. M. Schmidt, M. Lund, F.-J. W. Parmentier, R. Brown, U. S. Bhatt, E. S. Euskirchen, V. E. Romanovsky, J. E. Walsh, J. E. Overland, M. Wang, R. W. Corell, W. N. Meier, B. Wouters, S. Mernild, J. Mård, J. Pawlak, and M. S. Olsen. 2019. Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters* 14:045010.
- Brookes, P. C., A. Landman, G. Pruden, and D. S. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biogeochemistry* 17:837-842.
- Bueno, C. G., S. N. Williamson, I. C. Barrio, Á. Helgadóttir, and D. S. HiK. 2016. Moss mediates the influence of shrub species on soil properties and processes in alpine tundra. *PLOS ONE* 11:e0164143.
- Burda, H., R. Šumbera, and S. Begall. 2007. Microclimate in Burrows of Subterranean Rodents — Revisited. Pages 21-33 in S. Begall, H. Burda, S. E. Schleich, editors. *Subterranean Rodents*. Springer, Berlin, Heidelberg.
- Böök, I. M., and R. Saborowski. 2020. Extracellular phosphoesterases of invertebrate origin: underrated actors in phosphorus recycling? *Marine Biology* 167:47.
- Cahoon, S. M. P., P. F. Sullivan, E. Post, and J. M. Welker. 2012. Large herbivores limit CO₂ uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology* 18:469-479.
- Callaghan, T. V., and U. Emanuelsson. 1985. Population structure and processes of tundra plants and vegetation. Pages 399-439 in J. White, editor. *The Population Structure of Vegetation*. Springer Netherlands, Dordrecht.
- Canals, R.-M., and M.-T. Sebastià. 2000. Soil nutrient fluxes and vegetation changes on molehills. *Journal of Vegetation Science* 11:23-30.

- Cao, G., Y. Tang, W. Mo, Y. Wang, Y. Li, and X. Zhao. 2004. Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. *Soil Biology and Biochemistry* 36:237-243.
- Chapin, F. S., and R. A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64:376-391.
- Chapin, F. S., P. A. Matson, and H. A. Mooney. 2002a. Carbon input to terrestrial ecosystems. Pages 97-122 in F. S. Chapin, P. A. Matson, and H. A. Mooney, editors. *Principles of Terrestrial Ecosystem Ecology*. Springer New York, New York, NY.
- _____. 2002b. Terrestrial plant nutrient use. Pages 176-196 in F. S. Chapin, P. A. Matson, and H. A. Mooney, editors. *Principles of Terrestrial Ecosystem Ecology*. Springer New York, New York, NY.
- Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76:694-711.
- Chapin, S. F., D. A. Johnson, and J. D. McKendrick. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. *Journal of Ecology* 68:189-209.
- Chew, R. M. 1974. Consumers as regulators of ecosystems: an alternative to energetics. *Ohio Journal of Science* 74:359-370.
- Clark, J. E., E. C. Hellgren, J. L. Parsons, E. E. Jorgensen, D. M. Engle, and D. M. Leslie. 2005. Nitrogen outputs from fecal and urine deposition of small mammals: implications for nitrogen cycling. *Oecologia* 144:447-455.
- Clark, K. L., L. C. Branch, J. L. Kierro, and D. Villareal. 2016. Burrowing herbivores alter soil carbon and nitrogen dynamics in a semi-arid ecosystem, Argentina. *Soil Biology & Biochemistry* 103:253-261.
- Cohen, J., J. A. Screen, J. C. Furtado, M. Barlow, D. Whittleston, D. Coumou, J. Francis, K. Dethloff, D. Entekhabi, J. Overland, and J. Jones. 2014. Recent arctic amplification and extreme mid-latitude weather. *Nature Geoscience* 7:627-637.
- Collett, R. 1895. *Myodes lemmus*, its habits and migrations in Norway. *Christiana, Videnskabs-Selskabs Forhandling* 3:1-62.

- Coppedge, B. R., S. D. Fuhlendorf, D. M. Engle, B. J. Carter, and J. H. Shaw. 1999. Grassland soil depressions: relict bison wallows or inherent landscape heterogeneity? *The American Midland Naturalist* 142:382-392.
- Cornelissen, J. H. C., P. M. Van Bodegom, R. Aerts, T. V. Callaghan, R. S. P. Van Logtestijn, J. Alatalo, F. Stuart Chapin, R. Gerdol, J. Gudmundsson, D. Gwynn-Jones, A. E. Hartley, D. S. Hik, A. Hofgaard, I. S. Jónsdóttir, S. Karlsson, J. A. Klein, J. Laundre, B. Magnusson, A. Michelsen, U. Molau, V. G. Onipchenko, H. M. Quested, S. M. Sandvik, I. K. Schmidt, G. R. Shaver, B. Solheim, N. A. Soudzilovskaia, A. Stenström, A. Tolvanen, Ø. Totland, N. Wada, J. M. Welker, X. Zhao, and M. O. L. Team. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters* 10:619-627.
- Cornulier, T., N. G. Yoccoz, V. Bretagnolle, J. E. Brommer, A. Butet, F. Eecke, D. A. Elston, E. Framstad, H. Henttonen, B. Hornfeldt, O. Huitu, C. Imholt, R. A. Ims, J. Jacob, B. Jedrzejewska, A. Millon, S. J. Petty, H. Pietiainen, E. Tkadlec, K. Zub, and X. Lambin. 2013. Europe-wide dampening of population cycles in keystone herbivores. *Science* 340:63-66.
- Coulloudon, B., K. Eshelman, J. Gianola, N. Habich, L. Hughes, C. Johnson, M. Pellant, P. Podborny, A. Rasmussen, and B. Robles. 1999. Sampling vegetation attributes, technical reference 1734-4. Bureau of Land Management, Denver, Colorado.
- Couñteaux, M.-M., P. Bottner, and B. Berg. 1995. Litter decomposition, climate and litter quality. *Trends in Ecology & Evolution* 10:63-66.
- Culbertson, A. E. 1946. Observations on the natural history of the Fresno kangaroo rat. *Journal of Mammalogy* 27:189-203.
- Cumming, D. H. M., and G. S. Cumming. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* 134:560-568.
- D'Angelo, E., J. Crutchfield, and M. Vandivere. 2001. Rapid, sensitive, microscale determination of phosphate in water and soil. *Journal of Environmental Quality* 30:2206-2209.
- Daufresne, T. 2021. A consumer-driven recycling theory for the impact of large herbivores on terrestrial ecosystem stoichiometry. *Ecology Letters* 24:2598-2610.

- Davidson, A. D., J. K. Detling, and J. H. Brown. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment* 10:477-486.
- Davidson, A. D., E. A. Hunter, J. Erz, D. C. Lightfoot, A. M. McCarthy, J. K. Mueller, and K. T. Shoemaker. 2018. Reintroducing a keystone burrowing rodent to restore an arid North American grassland: challenges and successes. *Restoration Ecology* 26:909-920.
- Davidson, E. A., S. E. Trumbore, and R. Amundson. 2000. Soil warming and organic carbon content. *Nature* 408:789-790.
- DeMarco, J., M. C. Mack, and M. S. Bret-Harte. 2011. The effects of snow, soil microenvironment, and soil organic matter quality on N availability in three Alaskan arctic plant communities. *Ecosystems* 14:804-817.
- Detling, J. K., and E. L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia* 57:65-71.
- Doane, T. A., and W. R. Horwath. 2003. Spectrophotometric determination of nitrate with a single reagent. *Analytical Letters* 36:2713-2722.
- Doughty, C., A. Abraham, and J. Roman. 2020. The sixth R: Revitalizing the natural phosphorus pump. *EcoEvoRxiv*. March 18. doi:10.32942/osf.io/45cnu.
- Drew, J. V., J. C. F. Tedrow, R. E. Shanks, and J. J. Koranda. 1958. Rate and depth of thaw in Arctic soils. *Eos Transactions: American Geophysical Union* 39:697-701.
- Edwards, K. A., and R. L. Jefferies. 2013. Inter-annual and seasonal dynamics of soil microbial biomass and nutrients in wet and dry low-Arctic sedge meadows. *Soil Biology and Biochemistry* 57:83-90.
- Egelkraut, D., K.-Å. Aronsson, A. Allard, M. Åkerholm, S. Stark, and J. Olofsson. 2018. Multiple feedbacks contribute to a centennial legacy of reindeer on tundra vegetation. *Ecosystems* 21:1545-1563.
- Egelkraut, D., H. Barthelemy, and J. Olofsson. 2020. Reindeer trampling promotes vegetation changes in tundra heathlands: Results from a simulation experiment. *Journal of Vegetation Science* 31:476-486.
- Ehrich, D., N. M. Schmidt, G. Gauthier, R. Alisauskas, A. Angerbjörn, K. Clark, F. Ecke, N. E. Eide, E. Framstad, J. Frandsen, A. Franke, O. Gilg, M.-A. Giroux, H. Henttonen, B. Hörnfeldt, R. A. Ims, G. D. Kataev, S. P. Kharitonov, S. T. Killengreen, C. J. Krebs, R. B.

- Lanctot, N. Lecomte, I. E. Menyushina, D. W. Morris, G. Morrisson, L. Oksanen, T. Oksanen, J. Olofsson, I. G. Pokrovsky, I. Y. Popov, D. Reid, J. D. Roth, S. T. Saalfeld, G. Samelius, B. Sittler, S. M. Sleptsov, P. A. Smith, A. A. Sokolov, N. A. Sokolova, M. Y. Soloviev, and D. V. Solovyeva. 2020. Documenting lemming population change in the Arctic: Can we detect trends? *Ambio* 49:786-800.
- Eldridge, D. J., T. B. Koen, A. Killgore, N. Huang, and W. G. Whitford. 2012. Animal foraging as a mechanism for sediment movement and soil nutrient development: evidence from the semi-arid Australian woodlands and the Chihuahuan Desert. *Geomorphology* 157-158:131-141.
- Eldridge, D. J., and C. A. Myers. 2001. The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. *Journal of Arid Environments* 47:325-337.
- Elias, S. A. 2019. Mammals of the high arctic. In Reference Module in Earth Systems and Environmental Sciences. Elsevier.
- Elser, J. J., T. H. Chrzanowski, R. W. Sterner, and K. H. Mills. 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian Shield. *Ecosystems* 1: 120-136.
- Elser, J. J., D. Dobberfuhl, N. A. Mackay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry: towards a unified view of cellular and ecosystem processes. *Bioscience* 46:674-684.
- Elser, J. J., and J. Urabe. 1999. The stoichiometry of consumer-driven nutrient cycling: theory, observations, and consequences. *Ecology* 80:735-751.
- Elton, C. S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. *Journal of Experimental Biology* 2:119-163.
- Environmental Data Center Team. 2017. Meteorological monitoring program at Toolik, Alaska. in, Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775.
- Estes, J. A. 1996. Predators and ecosystem management. *Wildlife Society Bulletin (1973-2006)* 24:390-396.

- Fafard, P., J. Roth, and J. Markham. 2019. Nutrient deposition on Arctic fox dens creates atypical tundra plant assemblages at the edge of the Arctic. *Journal of Vegetation Science* 31:173-179.
- Falk, J. M., N. M. Schmidt, T. R. Christensen, and L. Ström. 2015. Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. *Environmental Research Letters* 10:045001.
- Fang, C., and J. B. Moncrieff. 2001. The dependence of soil CO₂ efflux on temperature. *Soil Biology and Biochemistry* 33:155-165.
- Fontaine, S., S. Barot, P. Barré, N. Bdioui, B. Mary, and C. Rumpel. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450:277.
- Fonte, S. J., and T. D. Schowalter. 2004. Decomposition of greenfall vs. senescent foliage in a tropical forest ecosystem in Puerto Rico. *Biotropica* 36:474-482.
- Forbes, E. S., J. H. Cushman, D. E. Burkepile, T. P. Young, M. Klope, and H. S. Young. 2019. Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology* 33:1597-1610.
- Fox, A. D., J. Madsen, H. Boyd, E. Kuijken, D. W. Norriss, I. M. Tombre, and D. A. Stroud. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Global Change Biology* 11:881-893.
- Gornall, J. L., S. J. Woodin, I. S. Jónsdóttir, and R. van der Wal. 2011. Balancing positive and negative plant interactions: how mosses structure vascular plant communities. *Oecologia* 166:769-782.
- Gough, L., and D. R. Johnson. 2017. Mammalian herbivory exacerbates plant community responses to long-term increased soil nutrients in two Alaskan tundra plant communities. *Arctic Science* 4:153-166.
- Gough, L., J. C. Moore, G. R. Shaver, R. T. Simpson, and D. R. Johnson. 2012. Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. *Ecology* 93:1683-1694.
- Gough, L., E. A. Ramsey, and D. R. Johnson. 2007. Plant-herbivore interactions in Alaskan arctic tundra change with soil nutrient availability. *Oikos* 116:407-418.

- Gough, L., K. Shrestha, D. R. Johnson, and B. Moon. 2008. Long-term mammalian herbivory and nutrient addition alter lichen community structure in Alaskan dry heath tundra. *Arctic Antarctic and Alpine Research* 40:65-73.
- Gough, L., P. A. Wookey, and G. R. Shaver. 2002. Dry heath arctic tundra responses to long-term nutrient and light manipulation. *Arctic, Antarctic, and Alpine Research* 34:211-218.
- Grant, W. 1974. The functional role of small mammals in grassland ecosystems. Colorado State University, Fort Collins, CO.
- Grellmann, D. 2002. Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos* 98:190-204.
- Gu, Q., and P. Grogan. 2020. Nutrient availability measurement techniques in arctic tundra soils: *in situ* ion exchange membranes compared to direct extraction. *Plant and Soil* 454: 359-378. 10.1007/s11104-020-04658-2.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *The American Naturalist* 94:421-425.
- Hansell, M. H. 1993. The ecological impact of animal nests and burrows. *Functional Ecology* 7:5-12.
- Hinkel, K. M., F. Paetzold, F. E. Nelson, and J. G. Bockheim. 2001. Patterns of soil temperature and moisture in the active layer and upper permafrost at Barrow, Alaska: 1993–1999. *Global and Planetary Change* 29:293-309.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *The Journal of Wildlife Management* 60:695-713.
- Hobbs, N. T., and K. R. Searle. 2005. A reanalysis of the body mass scaling of trampling by large herbivores. *Oecologia* 145:462-464.
- Hogan, E. J., G. Minnullina, L. J. Sheppard, I. D. Leith, and P. D. Crittenden. 2010. Response of phosphomonoesterase activity in the lichen *Cladonia portentosa* to nitrogen and phosphorus enrichment in a field manipulation experiment. *New Phytologist* 186:926-933.
- Holland, J. N., W. Cheng, and D. A. Crossley. 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. *Oecologia* 107:87-94.
- Holmgren, M., C.-Y. Lin, J. E. Murillo, A. Nieuwenhuis, J. Penninkhof, N. Sanders, T. van Bart, H. van Veen, H. Vasander, M. E. Vollebregt, and J. Limpens. 2015. Positive shrub–tree

- interactions facilitate woody encroachment in boreal peatlands. *Journal of Ecology* 103:58-66.
- Hope, A. G. 2019. Arctic Tundra Mammals. Pages 256-373 in M. Goldstein, D. Della Salla, editors. Reference Module in Earth Systems and Environmental Sciences. Elsevier. 10.1016/B978-0-12-409548-9.11770-1.
- Howe, H. F., and J. S. Brown. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80:1776-1781.
- Huitu, O., K. M. Forbes, M. Helander, R. Julkunen-Tiitto, X. Lambin, K. Saikkonen, P. Stuart, S. Sulkama, and S. Hartley. 2014. Silicon, endophytes and secondary metabolites as grass defenses against mammalian herbivores. *Frontiers in Plant Science* 5:478.
- Hull Sieg, C. 1987. Small mammals: pests or vital components of the ecosystem. *Great Plains Wildlife Damage Control Workshop Proceedings* 97:88-92.
- Ims, R. A., J.-A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. *Trends in Ecology & Evolution* 23:79-86.
- Ims, R. A., N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. *Proceedings of the National Academy of Sciences USA* 108:1970-1974.
- Interagency Arctic Research Policy Committee [IARPC]. 2016. Arctic research plan FY2017-2021. National Science and Technology Council.
- Jefferies, R. L., D. R. Klein, and G. R. Shaver. 1994. Vertebrate herbivores and the northern plant-communities-reciprocal influences and responses. *Oikos* 71:193-206.
- Jeong, J.-H., J.-S. Kug, B.-M. Kim, S.-K. Min, H. W. Linderholm, C.-H. Ho, D. Rayner, D. Chen, and S.-Y. Jun. 2012. Greening in the circumpolar high-latitude may amplify warming in the growing season. *Climate Dynamics* 38:1421-1431.
- Johnson, D. R., M. J. Lara, G. R. Shaver, G. O. Batzli, J. D. Shaw, and C. E. Tweedie. 2011a. Exclusion of brown lemmings reduces vascular plant cover and biomass in Arctic coastal tundra: resampling of a 50+ year herbivore exclosure experiment near Barrow, Alaska. *Environmental Research Letters* 6:045507.
- Joly, K., R. R. Jandt, and D. R. Klein. 2009. Decrease of lichens in arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. *Polar Research* 28:433-442.

- Jonasson, S., A. Michelsen, and I. K. Schmidt. 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. *Applied Soil Ecology* 11:135-146.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- Jung, H.-J. G., and G. O. Batzli. 1981. Nutritional ecology of microtine rodents: effects of plant extracts on the growth of arctic microtines. *Journal of Mammalogy* 62:286-292.
- Jørgensen, H., T. Prapasongsa, V. T. K. Vu, and H. D. Poulsen. 2013. Models to quantify excretion of dry matter, nitrogen, phosphorus and carbon in growing pigs fed regional diets. *Journal of Animal Science and Biotechnology* 4:42.
- Jüdt, A. K. 2020. The associations between grazing, soil N: P stoichiometry and carbon pools in Hluhluwe-iMfolozi Park.
- Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Ostbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, T. Solhøy, and N. C. Stenseth. 2008. Linking climate change to lemming cycles. *Nature* 456:93-97.
- Kielland, K., J. P. Bryant, and R. W. Ruess. 2006. Mammalian herbivory, ecosystem engineering, and ecological cascades in Alaskan boreal forests. Pages 211-226 in M. W. O. F. S. Chapin, K. van Cleve, L. A., and D. V. Viereck, editors. *Alaska's changing boreal forest*. Oxford University Press, New York, USA.
- Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs* 3:3-78.
- Koltz, A., L. Gough, and J. McLaren. 20XX. Herbivores in arctic ecosystems: effects of climate change and implications for carbon and nutrient cycling. In Review
- Krebs, C. 2013a. Spatial dynamics of populations. Pages 98-112 in C. Krebs, editor. *Population Fluctuations in Rodents*. The University of Chicago Press, Chicago, IL, USA.
- Krebs, C. J. 2013b. *Population fluctuations in rodents*. University of Chicago Press, Chicago, Illinois.
- Krebs, C., R. Boonstra, B. Scott Gilbert, A. J. Kenney, and S. Boutin. 2019. Impact of climate change on the small mammal community of the Yukon boreal forest. *Integrative Zoology* 14:528-541.

- Kuznetsova, T. A., M. Kam, I. S. Khokhlova, N. V. Kostina, T. G. Dobrovolskaya, M. M. Umarov, A. A. Degen, G. I. Shenbrot, and B. R. Krasnov. 2013. Desert gerbils affect bacterial composition of soil. *Microbial Ecology* 66:940-949.
- Lajtha, K., C. T. Driscoll, W. M. Jarrell, and E. T. Elliot. 1999. Soil phosphorus: characterization and total element analysis. Pages 115-142 in G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, editors. *Stand Soil Methods for Long-term Ecological Research*. Oxford University Press, New York.
- Lara, M., S. Villarreal, D. Johnson, R. Hollister, P. Webber, and C. Tweedie. 2012. Estimated change in tundra ecosystem function near Barrow, Alaska between 1972 and 2010. *Environmental Research Letters* 7:15507-15510.
- Lara, M. J., D. R. Johnson, C. Andresen, R. D. Hollister, and C. E. Tweedie. 2016. Peak season carbon exchange shifts from a sink to a source following 50+ years of herbivore exclusion in an Arctic tundra ecosystem. *Journal of Ecology* 105:122-131.
- Laundre, J. W. 1993. Effects of small mammal burrows on water infiltration in a cool desert environment. *Oecologia* 94:43-48.
- Legagneux, P., G. Gauthier, D. Berteaux, J. Bêty, M. C. Cadieux, F. Bilodeau, E. Bolduc, L. McKinnon, A. Tarroux, J. F. Therrien, L. Morissette, and C. J. Krebs. 2012. Disentangling trophic relationships in a high arctic tundra ecosystem through food web modeling. *Ecology* 93:1707-1716.
- Leslie, D. M., and E. E. Starkey. 1985. Fecal indices to dietary quality of cervids in old-growth forests. *The Journal of Wildlife Management* 49:142-146.
- Li, L., J. Zhang, X. Z. He, and F. Hou. 2021. Different effects of sheep excrement type and supply level on plant and soil C:N:P stoichiometry in a typical steppe on the loess plateau. *Plant and Soil* 462:45-58.
- Li, X., Q. Huang, X. Mi, Y. Bai, M. Zhang, and X. Li. 2018. Grazing every month minimizes size but boosts photosynthesis in *Stipa grandis* in the steppe of Inner Mongolia, China. *Journal of Arid Land* 10:601-611.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399-417.
- Liu, M., Y. Li, Y. Che, S. Deng, and Y. Xiao. 2017. Effects of different fertilizers on growth and nutrient uptake of *Lolium multiflorum* grown in Cd-contaminated soils. *Environmental Science and Pollution Research* 24:23363-23370.

- Loranty, M. M., and S. J. Goetz. 2012. Shrub expansion and climate feedbacks in Arctic tundra. *Environmental Research Letters* 7:011005.
- Louw, M. A., N. S. Hausmann, and P. C. le Roux. 2019. Testing for consistency in the impacts of a burrowing ecosystem engineer on soil and vegetation characteristics across biomes. *Scientific Reports* 9:19355.
- Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431:440-443.
- Maguire, A. J., and R. J. Rowe. 2017. Home range and habitat affinity of the singing vole on the North Slope of Alaska. *Arctic, Antarctic, and Alpine Research* 49:243-257.
- Makkonen, S., R. S. K. Hurri, and M. Hyvärinen. 2007. Differential responses of lichen symbionts to enhanced nitrogen and phosphorus availability: an experiment with *Cladina stellaris*. *Annals of Botany* 99:877-884.
- Mallen-Cooper, M., S. Nakagawa, and D. J. Eldridge. 2019. Global meta-analysis of soil-disturbing vertebrates reveals strong effects on ecosystem patterns and processes. *Global Ecology and Biogeography* 28:661-679.
- Manaeva, E. S., N. O. Lomovtseva, N. V. Kostina, M. V. Gorlenko, and M. M. Umarov. 2014. Biological activity of soils in the settlements of southern (*Microtus rossiaemeridionalis*) and bank (*Clethrionomys glareolus*) voles. *Biology Bulletin* 41:80-88.
- Mayengo, G., A. K. Piel, and A. C. Treydte. 2020. The importance of nutrient hotspots for grazing ungulates in a Miombo ecosystem, Tanzania. *PLOS ONE* 15:e0230192.
- McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. Guo, D. J. Hayes, M. Heimann, T. D. Lorenson, R. W. Macdonald, and N. Roulet. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* 79:523-555.
- McKendrick, J. D., G. O. Batzli, K. R. Everett, and J. C. Swanson. 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arctic and Alpine Research* 12:565-578.
- McLaren, J. R., and K. M. Buckeridge. 2019. Decoupled above- and belowground responses to multi-decadal nitrogen and phosphorus amendments in two tundra ecosystems. *Ecosphere* 10:e02735.

- McLaren, J. R., K. M. Buckeridge, M. J. van de Weg, G. R. Shaver, J. P. Schimel, and L. Gough. 2017a. Shrub encroachment in Arctic tundra: *Betula nana* effects on above- and belowground litter decomposition. *Ecology* 98:1361-1376.
- McLaren, J. R., A. Darrouzet-Nardi, M. N. Weintraub, and L. Gough. 2017b. Seasonal patterns of nitrogen availability in moist acidic tundra. *Arctic Science* 4:98-109.
- McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *The American Naturalist* 113:691-703.
- Mekonnen, Z. A., W. J. Riley, and R. F. Grant. 2018. 21st century tundra shrubification could enhance net carbon uptake of North America Arctic tundra under an RCP8.5 climate trajectory. *Environmental Research Letters* 13:054029.
- Meng, C., D. Tian, H. Zeng, Z. Li, H. Y. H. Chen, and S. Niu. 2020. Global meta-analysis on the responses of soil extracellular enzyme activities to warming. *Science of The Total Environment* 705:135992.
- Metcalfe, D. B., and J. Olofsson. 2015. Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO₂ exchange during the peak of the growing season. *Oikos* 124:1632-1638.
- Min, E., M. E. Wilcots, S. Naeem, L. Gough, J. R. McLaren, R. J. Rowe, E. B. Rastetter, N. T. Boelman, and K. L. Griffin. 2021. Herbivore absence can shift dry heath tundra from carbon source to sink during peak growing season. *Environmental Research Letters* 16:024027.
- Moen, J., P. A. Lundberg, and L. Oksanen. 1993. Lemming grazing on snowbed vegetation during a population peak, Northern Norway. *Arctic and Alpine Research* 25:130-135.
- Moen, J., and L. Oksanen. 1998. Long-term exclusion of folivorous mammals in two arctic-alpine plant communities: a test of the hypothesis of exploitation ecosystems. *Oikos* 82:333-346.
- Moorhead, L. C., L. Souza, C. W. Habeck, R. L. Lindroth, and A. T. Classen. 2017. Small mammal activity alters plant community composition and microbial activity in an old-field ecosystem. *Ecosphere* 8:e01777.
- Morrison, P., and W. Galster. 1975. Patterns of hibernation in the arctic ground squirrel. *Canadian Journal of Zoology* 53:1345-1355.

- Mosbacher, J. B., A. Michelsen, M. Stelvig, H. Hjermstad-Sollerud, and N. M. Schmidt. 2018. Muskoxen modify plant abundance, phenology, and nitrogen dynamics in a high arctic fen. *Ecosystems* 22:1095-1107.
- Mossman, A. S. 1955. Light penetration in relation to small mammal abundance. *Journal of Mammalogy* 36:564-566.
- Mullen, D. A., and F. A. Pitelka. 1972. Efficiency of winter scavengers in the Arctic. *Arctic* 25:225-231.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, U. Sass-Klaassen, and S. Weijers. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6:045509.
- Myers-Smith, I. H., J. T. Kerby, G. K. Phoenix, J. W. Bjerke, H. E. Epstein, J. J. Assmann, C. John, L. Andreu-Hayles, S. Angers-Blondin, P. S. A. Beck, L. T. Berner, U. S. Bhatt, A. D. Bjorkman, D. Blok, A. Bryn, C. T. Christiansen, J. H. C. Cornelissen, A. M. Cunliffe, S. C. Elmendorf, B. C. Forbes, S. J. Goetz, R. D. Hollister, R. de Jong, M. M. Lorant, M. Macias-Fauria, K. Maseyk, S. Normand, J. Olofsson, T. C. Parker, F.-J. W. Parmentier, E. Post, G. Schaepman-Strub, F. Stordal, P. F. Sullivan, H. J. D. Thomas, H. Tømmervik, R. Treharne, C. E. Tweedie, D. A. Walker, M. Wilmking, and S. Wipf. 2020. Complexity revealed in the greening of the Arctic. *Nature Climate Change* 10:106-117.
- Natali, S. M., E. A. G. Schuur, and R. L. Rubin. 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology* 100:488-498.
- National Oceanic and Atmospheric Administration [NOAA]. 2020. Global Monitoring Laboratory. Barrow Atmospheric Baseline Observatory, United States.
- Nelson, F. E., S. I. Outcalt, J. Brown, N. I. Shiklomanov, and K. M. Hinkel. 1998. Spatial and temporal attributes of the active-layer thickness record, Barrow, Alaska, U.S.A. *PERMAFROST - Seventh International Conference (Proceedings)* 55:797-802.
- Nemergut, D. R., A. R. Townsend, S. R. Sattin, K. R. Freeman, N. Fierer, J. C. Neff, W. D. Bowman, C. W. Schadt, M. N. Weintraub, and S. K. Schmidt. 2008. The effects of chronic nitrogen fertilization on alpine tundra soil microbial communities: implications for carbon and nitrogen cycling. *Environmental Microbiology* 10:3093-3105.

- Oechel, W. C., S. J. Hastings, G. Vourlitis, M. Jenkins, G. Riechers, and N. Grulke. 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* 361:520-523.
- Oelbermann, M., M. English, and S. L. Schiff. 2008. Evaluating carbon dynamics and microbial activity in arctic soils under warmer temperatures. *Canadian Journal of Soil Science* 88:31-44.
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlenn, P. R. Minchin, R. B. O'hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. *vegan: Community Ecology Package*. R package version 2.5-5.
- Olofsson, J., P. E. Hulme, L. Oksanen, and O. Suominen. 2004a. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* 106:324-334.
- Olofsson, J., H. Kitti, P. Rautiainen, S. Stark, and L. Oksanen. 2001. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography* 24:13-24.
- Olofsson, J., J. Moen, and L. Oksanen. 2002. Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. *Oikos* 96:265-272.
- Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15:2681-2693.
- Olofsson, J., S. Stark, and L. Oksanen. 2004b. Reindeer influence on ecosystem processes in the tundra. *Oikos* 105:386-396.
- Olofsson, J., H. Tommervik, and T. V. Callaghan. 2012. Vole and lemming activity observed from space. *Nature Climate Change* 2:880-883.
- Ostfeld, R. S. 1982. Foraging strategies and prey switching in the California sea otter. *Oecologia* 53:170-178.
- Ott, K. 2017. Personal correspondence.
- Ott, K. O., and K. D. Currier. 2012. Monitoring lemming abundance and distribution near Barrow, Alaska, 2012. U.S. Fish & Wildlife Service, Fairbanks Fish and Wildlife Field Office, Fairbanks, Alaska. Technical Report.

- Ouellet, J.-P., S. Boutin, and D. C. Heard. 1994. Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. *Canadian Journal of Zoology* 72:1426-1435.
- Pajunen, A., R. Virtanen, and H. Roininen. 2008. The effects of reindeer grazing on the composition and species richness of vegetation in forest–tundra ecotone. *Polar Biology* 31:1233-1244.
- Pang, X. P., and Z. G. Guo. 2017. Plateau pika disturbances alter plant productivity and soil nutrients in alpine meadows of the Qinghai-Tibetan Plateau, China. *The Rangeland Journal* 39:133-144.
- Parker, T. C., J. Sanderman, R. D. Holden, G. Blume-Werry, S. Sjögersten, D. Large, M. Castro-Díaz, L. E. Street, J.-A. Subke, and P. A. Wookey. 2018. Exploring drivers of litter decomposition in a greening Arctic: results from a transplant experiment across a treeline. *Ecology* 99:2284-2294.
- Parker, T. C., A. M. Thurston, K. Raundrup, J.-A. Subke, P. A. Wookey, and I. P. Hartley. 2021. Shrub expansion in the Arctic may induce large-scale carbon losses due to changes in plant-soil interactions. *Plant and Soil* 463:643-651.
- Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467-480.
- Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:690-705.
- Peek, M. S., and I. N. Forseth. 2003. Enhancement of photosynthesis and growth of an aridland perennial in response to soil nitrogen pulses generated by mule deer. *Environmental and Experimental Botany* 49:169-180.
- Petit Bon, M., K. Gunnarsdotter Inga, I. S. Jónsdóttir, T. A. Utsi, E. M. Soininen, and K. A. Bråthen. 2020. Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities. *Oikos* 129:1229-1242.
- Petit Bon, M., K. G. Inga, T. A. Utsi, I. S. Jónsdóttir, and K. A. Bråthen. 2021. Forage quality in tundra grasslands under herbivory: Silicon-based defenses, nutrients and their ratios in grasses. *Journal of Ecology* 110:129-143.
- Ping, C.-L., G. J. Michaelson, M. T. Jorgenson, J. M. Kimble, H. Epstein, V. E. Romanovsky, and D. A. Walker. 2008. High stocks of soil organic carbon in the North American Arctic region. *Nature Geoscience* 1:615-619.

- Pitelka, F. A. 1964. The nutrient-recovery hypothesis for arctic microtine cycles. I. Introduction. Pages 55-56 in D. J. Crisp, editor. *Grazing in Terrestrial and Marine Environments*. Blackwell Scientific Publications, Oxford.
- Pitelka, F. A., and G. O. Batzli. 2018. Demography and condition of brown lemmings (*Lemmus trimucronatus*) during cyclic density fluctuations near Barrow, Alaska. *Annales Zoologici Fennici* 55:187-237.
- Post, E., C. Forchhammer Mads, M. S. Bret-Harte, V. Callaghan Terry, R. Christensen Torben, B. Elberling, D. Fox Anthony, O. Gilg, S. Hik David, T. Høye Toke, A. Ims Rolf, E. Jeppesen, R. Klein David, J. Madsen, A. D. McGuire, S. Rysgaard, E. Schindler Daniel, I. Stirling, P. Tamstorf Mikkel, J. C. Tyler Nicholas, R. van der Wal, J. Welker, A. Wookey Philip, M. Schmidt Niels, and P. Aastrup. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355-1358.
- Post, E., C. Pedersen, C. Wilmers Christopher, and C. Forchhammer Mads. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proceedings of the Royal Society B: Biological Sciences* 275:2005-2013.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* 52:137-154.
- Quay, W. B. 1951. Observations of mammals of the Seward Peninsula, Alaska. *Journal of Mammalogy* 32:88-99.
- R Core Team. 2018. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Racine, C. H., L. A. Johnson, and L. A. Viereck. 1987. Patterns of vegetation recovery after tundra fires in northwestern Alaska, USA. *Arctic and Alpine Research* 19:461-469.
- Rastetter, E. B., K. L. Griffin, R. J. Rowe, L. Gough, J. R. McLaren, and N. T. Boelman. 2022. Model responses to CO₂ and warming are underestimated without explicit representation of Arctic small-mammal grazing. *Ecological Applications* 32:e02478.
- Rhine, E. D., R. L. Mulvaney, E. J. Pratt, and G. K. Sims. 1998. Improving the Berthelot reaction for determining ammonium in soil extracts and water. *Soil Science Society of American Journal* 62:473-480.

- Rinnan, R., A. Michelsen, E. BÅÅTh, and S. Jonasson. 2007. Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. *Global Change Biology* 13:28-39.
- Rinnan, R., S. Stark, and A. Tolvanen. 2009. Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. *Journal of Ecology* 97:788-800.
- Romero, L. M., C. J. Meister, N. E. Cyr, G. J. Kenagy, and J. C. Wingfield. 2008. Seasonal glucocorticoid responses to capture in wild free-living mammals. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 294:R614-R622.
- Roper, T. J., N. C. Bennett, L. Conratt, and A. J. Molteno. 2001. Environmental conditions in burrows of two species of African mole-rat, *Georhynchus capensis* and *Cryptomys damarensis*. *Journal of Zoology* 254:101-107.
- Ross, B. E., A. W. Reed, R. L. Rehmeier, G. A. Kaufman, and D. W. Kaufman. 2007. Effects of prairie vole runways on tallgrass prairie. *Transactions of the Kansas Academy of Science (1903-)* 110:100-106.
- Roy, A., M. Suchocki, L. Gough, and J. R. McLaren. 2020. Above- and belowground responses to long-term herbivore exclusion. *Arctic, Antarctic, and Alpine Research* 52:109-119.
- Ruser, R., H. Flessa, R. Russow, G. Schmidt, F. Buegger, and J. C. Munch. 2006. Emission of N₂O, N₂ and CO₂ from soil fertilized with nitrate: effect of compaction, soil moisture and rewetting. *Soil Biology and Biochemistry* 38:263-274.
- Rustad, L., J. Campbell, G. Marion, R. Norby, M. Mitchell, A. Hartley, J. Cornelissen, J. Gurevitch, and N. Gcte. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543-562.
- Rydgren, K., R. H. Økland, F. X. Picó, and H. d. Kroon. 2007. Moss species benefits from breakdown of cyclic rodent dynamics in boreal forests. *Ecology* 88:2320-2329.
- Sayia-Cork, K. R., R. L. Sinsabaugh, and D. R. Zak. 2002. The effects of long term nitrogen deposition on extracellular enzyme activity in an *Acer saccharum* forest soil. *Soil Biology & Biochemistry* 34:1309-1315.
- Schimel, J. P., and F. S. Chapin. 1996. Tundra plant uptake of amino acid and NH₄⁺ nitrogen in situ: plants complete well for amino acid N. *Ecology* 77:2142-2147.

- Schmidt, N. M., R. A. Ims, T. T. Hoye, O. Gilg, L. H. Hansen, J. Hansen, M. Lund, E. Fuglei, M. C. Forchhammer, and B. Sittler. 2012. Response of an arctic predator guild to collapsing lemming cycles. *Proceedings of the Royal Society B* 279:4417-4422.
- Schmitz, O. J., P. A. Raymond, J. A. Estes, W. A. Kurz, G. W. Holtgrieve, M. E. Ritchie, D. E. Schindler, A. C. Spivak, R. W. Wilson, M. A. Bradford, V. Christensen, L. Deegan, V. Smetacek, M. J. Vanni, and C. C. Wilmers. 2014. Animating the carbon cycle. *Ecosystems* 17:344-359.
- Schrama, M., P. Heijning, J. P. Bakker, H. J. van Wijnen, M. P. Berg, and H. Olf. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia* 172:231-243.
- Sharma, N. C., and S. V. Sahi. 2005. Characterization of phosphate accumulation in *Lolium multiflorum* for remediation of phosphorus-enriched soils. *Environmental Science & Technology* 39:5475-5480.
- Sharma, S., S. Couturier, and S. D. CÔTÉ. 2009. Impacts of climate change on the seasonal distribution of migratory caribou. *Global Change Biology* 15:2549-2562.
- Shaver, G. R., M. S. Bret-Harte, M. H. Jones, J. Johnstone, L. Gough, J. Laundre, and F. S. Chapin. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* 82:3163-3181.
- Shaver, G. R., J. A. Laundre, M. S. Bret-Harte, F. S. Chapin, J. A. Mercado-Diaz, A. E. Giblin, L. Gough, W. A. Gould, S. E. Hobbie, G. W. Kling, M. C. Mack, J. C. Moore, K. J. Nadelhoffer, E. B. Rastetter, and J. P. Schimel. 2014. Terrestrial ecosystems at Toolik Lake, Alaska. Pages 90-142 in J. E. Hobbie, and G. W. Kling, editors. *Alaska's Changing Arctic*. Oxford University Press, New York.
- Siewert, M. B., and J. Olofsson. 2021. UAV reveals substantial but heterogeneous effects of herbivores on Arctic vegetation. *Scientific Reports* 11:19468.
- Sistla, S. A., S. Asao, and J. P. Schimel. 2012. Detecting microbial N-limitation in tussock tundra soil: implications for arctic soil organic carbon cycling. *Soil Biology and Biochemistry* 55:78-84.
- Sitters, J., E. S. Bakker, M. P. Veldhuis, G. F. Veen, H. Olde Venterink, and M. J. Vanni. 2017. The stoichiometry of nutrient release by terrestrial herbivores and its ecosystem consequences. *Frontiers in Earth Science* 5:32. 10.3389/feart.2017.00032.

- Sitters, J., M. Cherif, D. Egelkraut, R. Giesler, and J. Olofsson. 2019. Long-term heavy reindeer grazing promotes plant phosphorus limitation in arctic tundra. *Functional Ecology* 33:1233-1242.
- Sitters, J., and H. Olde Venterink. 2015. The need for a novel integrative theory on feedbacks between herbivores, plants and soil nutrient cycling. *Plant and Soil* 396:421-426.
- _____. 2021a. Herbivore dung stoichiometry drives competition between savanna trees and grasses. *Journal of Ecology* 109:2095-2106.
- _____. 2021b. Stoichiometric impact of herbivore dung versus urine on soils and plants. *Plant and Soil* 462:59-65.
- Sjögersten, S., R. van der Wal, M. J. J. E. Loonen, and S. J. Woodin. 2011. Recovery of ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry* 106:357-370.
- Sjögersten, S., R. van der Wal, and S. J. Woodin. 2008. Habitat type determines herbivory controls over CO₂ fluxes in a warmer arctic. *Ecology* 89:2103-2116.
- Speed, J. D. M., S. J. Woodin, H. Tommervik, and R. van der Wal. 2010. Extrapolating herbivore-induced carbon loss across and arctic landscape. *Polar Biology* 33:789-797.
- Stark, S., D. Egelkraut, K.-Å. Aronsson, and J. Olofsson. 2019. Contrasting vegetation states do not diverge in soil organic matter storage: evidence from historical sites in tundra. *Ecology* 7:1-14:e02731.
- Stark, S., and D. Grellmann. 2002. Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. *Ecology* 83:2736-2744.
- Stark, S., R. Strömmer, and J. Tuomi. 2002. Reindeer grazing and soil microbial processes in two suboceanic and two subcontinental tundra heaths. *Oikos* 97:69-78.
- Stark, S., and M. Vaisanen. 2014. Insensitivity of soil microbial activity to temporal variation in soil N in subarctic tundra: evidence from responses to large migratory grazers. *Ecosystems* 17:906-917.
- Staver, A. C., J. O. Abraham, G. P. Hempson, A. T. Karp, and J. T. Faith. 2021. The past, present, and future of herbivore impacts on savanna vegetation. *Journal of Ecology* 109:2804-2822.
- Sterner, R. W. 1986. Herbivore's direct and indirect effects on algal populations. *Science* 231:605-607.

- _____. 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena. *The American Naturalist* 136:209-229.
- Su, J., W. Ji, H. Li, T. Yao, J. Wang, and Z. Nan. 2020. Zokor disturbances indicated positive soil microbial responses with carbon cycle and mineral encrustation in alpine grassland. *Ecological Engineering* 144:105702.
- Tang, Z., Y. Zhang, N. Cong, M. Wimberly, L. Wang, K. Huang, J. Li, J. Zu, Y. Zhu, and N. Chen. 2019. Spatial pattern of pika holes and their effects on vegetation coverage on the Tibetan Plateau: An analysis using unmanned aerial vehicle imagery. *Ecological Indicators* 107:105551.
- Taylor, W. P. 1935. Some Animal Relations to Soils. *Ecology* 16:127-136.
- Tikhomirov, B. A. 1959. Relationship of the animal world and the plant cover of the tundra. Botanical Institute, Academy of Sciences of the U.S.S.R.:83.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ.
- Tolvanen, A., J. M. Alatalo, and G. H. R. Henry. 2002. Resource allocation patterns in a forb and a sedge in two arctic environments—short-term response to herbivory. *Nordic Journal of Botany* 22:741-747.
- Tuomi, M., S. Stark, K. S. Hoset, M. Väisänen, L. Oksanen, F. J. A. Murguzur, H. Tuomisto, J. Dahlgren, and K. A. Bråthen. 2019. Herbivore effects on ecosystem process rates in a low-productive system. *Ecosystems* 22:827-843.
- Turkington, R. 2009. Top-down and bottom-up forces in mammalian herbivore – vegetation systems: an essay review. *Botany* 87:723-739.
- United States Department of Agriculture [USDA]. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. 2nd edition. United States Department of Agriculture, National Resources Conservation Science.
- Van Der Wal, R., R. D. Bardgett, K. A. Harrison, and A. Stien. 2004. Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. *Ecography* 27:242-252.
- Van Der Wal, R., S. SjöGersten, S. J. Woodin, E. J. Cooper, I. S. JÓNsdÓttir, D. Kuijper, T. A. D. Fox, and A. D. Huiskes. 2007. Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Global Change Biology* 13:539-545.

- Van der Wal, R., S. M. J. van Lieshout, and M. J. J. E. Loonen. 2001. Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biology* 24:29-32.
- van Klink, R., M. Schrama, S. Nolte, J. P. Bakker, M. F. WallisDeVries, and M. P. Berg. 2015. Defoliation and soil compaction jointly drive large-herbivore grazing effects on plants and soil arthropods on clay soil. *Ecosystems* 18:671-685.
- van Wijk, M. T., M. Williams, and G. R. Shaver. 2005. Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia* 142:421-427.
- Veldhuis, M. P., M. I. Gommers, H. Olf, and M. P. Berg. 2018. Spatial redistribution of nutrients by large herbivores and dung beetles in a savanna ecosystem. *Journal of Ecology* 106:422-433.
- Virtanen, R., J. Salminen, and R. Strömmer. 2008. Soil and decomposer responses to grazing exclusion are weak in mountain snow-beds. *Acta Oecologica* 33:207-212.
- Voroney, R. P., P. C. Brooks, and R. P. Beyaert. 2006. Soil microbial biomass C, N, P, and S. in M. R. Carter, and E. G. Gregorich, editors. *Soil Sampling and Methods of Analysis*. Lewis, Boca Raton.
- Väisänen, M., H. Yläne, E. Kaarlejärvi, S. Sjögersten, J. Olofsson, N. Crout, and S. Stark. 2014. Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change* 4:384-388.
- Walker, D. A., J. G. Bockheim, F. S. Chapin III, W. Eugster, F. E. Nelson, and C. L. Ping. 2001. Calcium-rich tundra, wildlife, and the “Mammoth Steppe”. *Quaternary Science Reviews* 20:149-163.
- Walse, C., B. Berg, and H. Sverdrup. 1998. Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity. *Environmental Reviews* 6:25-40.
- Walsh, N. E., T. R. McCabe, J. M. Welker, and A. N. Parsons. 1997. Experimental manipulations of snow-depth: effects on nutrient content of caribou forage. *Global Change Biology* 3:158-164.
- Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2019-2024.

- Wang, C., G. Wang, P. Wu, R. Rafique, H. Zi, X. Li, and Y. Luo. 2017. Effects of ant mounds on the plant and soil microbial community in an alpine meadow of Qinghai–Tibet Plateau. *Land Degradation & Development* 28:1538-1548.
- Wardle, D. A., K. I. Bonner, and G. M. Barker. 2002. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology* 16:585-595.
- Warne, R. 2014. The micro and macro of nutrients across biological scales. *Integrative and Comparative Biology* 54:864-872.
- Weber-Grullon, L., L. Gherardi, W. A. Rutherford, S. R. Archer, and O. E. Sala. 2022. Woody-plant encroachment: precipitation, herbivory and grass-competition interact to affect shrub recruitment. *Ecological Applications* :e2536.
- Wei, W. R., J. D. He, and Q. Y. Zheng. 2020. Plateau pikas (*Ochotona curzoniae*) at low densities have no destructive effect on winter pasture in alpine meadows. *The Rangeland Journal* 42:55-61.
- Weintraub, M. N., and J. P. Schimel. 2003. Interactions between carbon and nitrogen mineralization and soil organic matter chemistry in arctic tundra soils. *Ecosystems* 6:0129-0143.
- _____. 2005. Nitrogen Cycling and the Spread of Shrubs Control Changes in the Carbon Balance of Arctic Tundra Ecosystems. *BioScience* 55:408-415.
- White, S. L., R. E. Sheffield, S. P. Washburn, L. D. King, and J. T. Green Jr. 2001. Spatial and time distribution of dairy cattle excreta in an intensive pasture system. *Journal of Environmental Quality* 30:2180-2187.
- Whitford, W. G., and F. R. Kay. 1999. Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* 41:203-230.
- Whitford, W. G., and Y. Steinberger. 2010. Pack rats (*Neotoma* spp.): keystone ecological engineers? *Journal of Arid Environments* 74:1450-1455.
- Wilson, D., and R. L. Jefferies. 1996. Nitrogen mineralization, plant growth and goose herbivory in an arctic coastal ecosystem. *Journal of Ecology* 84:841-851.
- Woods, C. A., and D. K. Boraker. 1975. *Octodon degus*. *Mammalian Species*:1-5.
- Wookey, P. A., R. Aerts, R. D. Bardgett, F. Baptist, Brathen, Kari Anne, J. H. C. Cornelissen, L. Gough, I. P. Hartley, D. W. Hopkins, S. Lavorel, and G. R. Shaver. 2009. Ecosystem

- feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology* 15:1153-1172.
- Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape level. *Oecologia* 132:96-101.
- Xu, S., J. Sardans, J. Zhang, and J. Peñuelas. 2020. Variations in foliar carbon:nitrogen and nitrogen:phosphorus ratios under global change: a meta-analysis of experimental field studies. *Scientific Reports* 10:12156.
- Ylänne, H., S. Stark, and A. Tolvanen. 2015. Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: evidence from 19 years of warming and simulated herbivory in subarctic tundra. *Global Change Biology* 21:3696-3711.
- Ylänne, H., E. Kaarlejärvi, M. Väisänen, M. K. Männistö, S. H. K. Ahonen, J. Olofsson, and S. Stark. 2020. Removal of grazers alters the response of tundra soil carbon to warming and enhanced nitrogen availability. *Ecological Monographs* 90:e01396.
- Ylänne, H., and S. Stark. 2019. Distinguishing rapid and slow C cycling feedbacks to grazing in sub-arctic tundra. *Ecosystems* 22:1145-1159.
- Yu, Q., H. Epstein, R. Engstrom, and D. Walker. 2017. Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory. *Global Change Biology* 23:3895-3907.
- Zamin, T. J., and P. Grogan. 2013. Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. *Journal of Ecology* 101:671-683.
- Zhang, T., and K. Stamnes. 1998. Impact of climatic factors on the active layer and permafrost at Barrow, Alaska. *Permafrost & Periglacial Processes* 9:229-246.
- Zhou, G., D. Zhang, Y. Luo, and D. Hui. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *Journal of Plant Ecology* 1:85-93.
- Zhou, G., L. Zhou, and X. Zhou. 2020. Effects of grazing intensity on belowground carbon and nitrogen cycling. in V. M. Kindomihou, editor. *Grasses and Grassland Aspects*. IntechOpen.

Supplemental Tables

Supplemental Table 2.1. Mean (standard error) total % carbon (%C), total nitrogen (%N), carbon:nitrogen (C:N), inorganic nutrient concentrations (NH_4^+ , NO_3^- , PO_4^{3-}), extractable organic nutrients (EOC, ETN, EOP), and microbial biomass CNP (MBC, MBN, MBP) in soil collected from the upper organic layer of control (CT) plots in dry heath (DH, n = 3) and moist acidic tundra (MAT, n = 4) in the Summer of 2017.

Variable	Units	MAT	DH
% C	%	5.39 (0.44)	2.66 (0.31)
% N	%	0.88 (0.07)	0.73 (0.08)
C:N	Ratio	6.25 (0.54)	3.64 (0.06)
NH_4	ug $\text{NH}_4\text{-N g}^{-1}$ soil	12.65 (4.04)	6.58 (0.97)
NO_3	ug $\text{NO}_3\text{-N g}^{-1}$ soil	1.79 (1.27)	0.01 (0.01)
PO_4	ug $\text{PO}_4\text{-P g}^{-1}$ soil	68.28 (14.63)	0.51 (1.89)
EOC	ug C g^{-1} soil	2512.00 (409.53)	158.46 (24.18)
ETN	ug N g^{-1} soil	219.74 (35.49)	51.56 (7.34)
EOP	ug P g^{-1} soil	95.47 (21.31)	0.82 (0.37)
MBC	ug C g^{-1} soil	950.50 (242.04)	759.96 (103.50)
MBN	ug N g^{-1} soil	126.49 (26.92)	167.73 (23.80)
MBP	ug P g^{-1} soil	164.36 (24.51)	12.93 (3.78)

Supplemental Table 2.2. The impact of herbivores on soil variables after 20 years of exclusion. ANOVA and Kruskal-Wallis summary results from comparisons of soil variables between exclosures at dry heath (DH, n = 3) and moist acidic tundra (MAT, n = 4). Most variables were analyzed using non-parametric tests and there was no interaction (Exclosure x Depth) analysis (Exclosure x Depth), except for TN ($F_2 = 0.43$, $p = 0.658$) and C:N ($F_2 = 0.001$, $p = 0.994$)

	Dry Heath			Moist Acidic Tussock					
	Fence			Fence			Depth		
	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>
% C	$F = 0.39$	0.69	2,6	$W = 78.00$	0.76	1	$X^2 = 15.54$	<0.01	2
% N	$F = 0.36$	0.71	2,6	$F = 0.68$	0.42	1,6	$F = 31.12$	<0.01	3,8
C:N	$F = 0.20$	0.82	2,6	$F = 0.25$	0.62	1,6	$F = 0.65$	< 0.01	3,8
NH ₄	$F = 0.16$	0.86	2,6	$W = 75.50$	0.86	1	$X^2 = 4.57$	0.10	2
NO ₃	$X^2 = 2.00$	0.37	2	$W = 68.00$	0.83	1	$X^2 = 0.42$	0.81	2
PO ₄	$X^2 = 0.80$	0.67	2	$W = 85.00$	0.47	1	$X^2 = 17.27$	< 0.01	2
EOC	$F = 0.53$	0.61	2,6	$W = 89.00$	0.35	1	$X^2 = 16.21$	<0.01	2
ETN	$F = 0.36$	0.71	2,6	$W = 69.00$	0.89	1	$X^2 = 16.21$	<0.01	2
EOP	$X^2 = 0.83$	0.66	2	$W = 79.00$	0.71	1	$X^2 = 14.74$	<0.01	2
MBC	$X^2 = 0.62$	0.73	2	$W = 64.00$	0.30	1	$X^2 = 11.90$	<0.01	2
MBN	$X^2 = 0.80$	0.67	2	$W = 79.00$	0.44	1	$X^2 = 11.74$	<0.01	2
MBP	$X^2 = 0.36$	0.84	2	$W = 66.00$	0.75	1	$X^2 = 14.53$	<0.01	2

Supplemental Table 2.3. The impact of herbivores on enzyme activity after 20 years of exclusion. ANOVA and Kruskal-Wallis summary results from comparisons between enclosure type in dry heath (DH, n = 3) and moist acidic tundra (MAT, n = 4). The only enzymes for which we could run parametric statistics (and thus test interactions between Fence and Depth) were Phosphodiesterase ($F_2 = 0.05$, $p = 0.952$) and α -glucosidase ($F_2 = 0.41$, $p = 0.678$), NAG ($F_2 = 0.24$, $p = 0.786$), and peroxidase ($F_2 = 0.16$, $p = 0.857$).

	Dry Heath			Moist Acidic Tussock					
	<u>Fence</u>			<u>Fence</u>			<u>Depth</u>		
	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>
Phosphatase	$F = 2.80$	0.14	2,6	$W = 75.50$	0.89	1	$X^2 = 15.44$	<0.01	2
Phosphodiesterase	$F = 8.66$	0.02	2,6	$F = 2.67$	0.12	1,6	$F = 27.82$	<0.01	3,8
β -glucosidase	$X^2 = 1.87$	0.39	2	$W = 51.00$	0.86	1	$X^2 = 13.51$	<0.01	2
β -cellobiosidase	$X^2 = 0.69$	0.71	2	$W = 31.00$	0.28	1	$X^2 = 10.02$	<0.01	2
β -xylosidase	$F = 0.45$	0.66	2,6	$W = 60.00$	0.74	1	$X^2 = 14.01$	<0.01	2
α -glucosidase	$X^2 = 3.52$	0.17	2	$F = 3.44$	0.10	1,6	$F = 15.36$	<0.01	3,8
LAP	$X^2 = 0.62$	0.73	2	$W = 81.00$	0.38	1	$X^2 = 14.23$	<0.01	2
NAG	$F = 1.25$	0.35	2,6	$F = 0.42$	0.53	1,6	$F = 4.43$	0.03	3,8
Phenol oxidase	$F = 0.31$	0.75	2,6	$W = 88.00$	0.38	1	$X^2 = 0.41$	0.82	2
Peroxidase	$F = 0.35$	0.49	2,6	$F = 0.47$	0.37	1,6	$F = 1.90$	0.18	2

Supplemental Table 3.1: Mean (standard error) of total percent % carbon (TC), total % nitrogen (TN), total % phosphorus (TP), C:N ratio, C:P ratio, N:P ratio, inorganic nutrient (NH_4^+ , NO_3^- , PO_4^{3-}) concentrations, extractable organic nutrients (EOC, ETN, EIN), and microbial biomass CNP (MBC, MBN, MBP) in soils collected beneath lemming structures (CON = control, HAY = hay pile, LAT = latrine, RUN = runway, BUR = burrow) sites near Utqiagvik (2018), Toolik (2018), and Nome (2019), Alaska, USA.

	Barrow					Toolik				Nome	
	CON	HAY	LAT	RUN	BUR	CON	HAY	LAT	RUN	CON	HAY
TC	32.77 (2.32)	37.61 (1.78)	30.27 (3.02)	38.46 (1.33)	34.97 (2.14)	40.60 (0.66)	41.70 (0.99)	42.42 (0.90)	38.67 (1.11)	43.74 (0.56)	43.74 (0.40)
TN	1.77 (0.16)	2.28 (0.11)	1.61 (0.14)	2.03 (0.10)	1.75 (0.10)	1.02 (0.07)	1.05 (0.07)	1.28 (0.16)	1.10 (0.10)	1.04 (0.07)	1.09 (0.07)
TP	0.26 (0.05)	0.46 (0.10)	0.29 (0.07)	0.37 (0.07)	0.16 (0.02)	0.08 (0.01)	0.09 (0.01)	0.14 (0.03)	0.10 (0.01)	0.09 (0.01)	0.09 (0.01)
CN	19.16 (0.86)	16.60 (0.45)	18.66 (0.64)	19.27 (0.68)	20.08 (0.82)	42.46 (3.30)	43.53 (4.60)	36.43 (4.63)	38.80 (3.63)	46.52 (5.22)	42.88 (3.27)
CP	190.26 (27.02)	145.49 (23.70)	177.96 (29.16)	186.56 (32.00)	251.02 (20.96)	622.54 (80.28)	553.28 (72.81)	482.84 (170.27)	427.22 (39.93)	618.43 (116.11)	551.44 (50.17)
NP	10.58 (1.54)	8.67 (1.33)	9.80 (1.60)	9.98 (1.74)	12.42 (0.95)	14.35 (0.92)	12.60 (0.83)	11.98 (2.67)	11.42 (1.03)	12.53 (0.71)	12.88 (0.55)
NH_4^+	9.72 (2.32)	38.76 (8.20)	11.05 (2.29)	15.53 (3.39)	25.04 (5.69)	25.61 (5.07)	30.94 (6.41)	60.65 (16.64)	50.44 (17.42)	3.24 (1.18)	2.64 (1.18)
NO_3^-	0 (0)	0.63 (0.44)	0.18 (0.15)	0 (0)	2.07 (1.84)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
PO_4^{3-}	0.76 (0.34)	1.71 (0.66)	0.79 (0.29)	0.76 (0.33)	1.44 (0.56)	4.64 (1.33)	6.83 (2.27)	26.58 (10.84)	3.82 (0.69)	0.18 (0.18)	1.52 (1.52)
EOC	395.34 (53.53)	646.17 (54.97)	478.85 (48.76)	640.80 (51.40)	561.82 (63.22)	742.65 (145.88)	795.93 (110.80)	1889.72 (479.05)	875.16 (133.54)	907.66 (51.36)	1000.53 (80.12)
ETN	43.52 (7.14)	96.12 (13.46)	53.75 (6.84)	70.79 (8.15)	76.33 (8.73)	67.55 (14.75)	80.36 (13.23)	200.78 (55.94)	107.15 (19.85)	57.94 (6.08)	61.55 (7.42)
EIN	9.72 (2.32)	39.39 (8.37)	11.23 (2.28)	15.53 (3.38)	27.11 (6.19)	25.61 (5.07)	30.94 (6.41)	60.65 (16.64)	50.44 (17.42)	3.24 (1.18)	2.64 (1.18)
EON	33.79 (5.12)	56.73 (8.15)	42.53 (5.07)	55.26 (6.74)	49.22 (6.98)	41.94 (10.35)	49.43 (8.18)	140.13 (40.33)	56.71 (10.47)	54.71 (5.67)	58.91 (7.41)
MBC	3627.26 (709.63)	4972.88 (912.10)	4138.43 (1175.26)	4970.51 (766.19)	2821.69 (507.31)	3032.63 (447.40)	3120.74 (333.71)	4730.92 (544.00)	4310.36 (363.87)	3693.77 (504.99)	3902.26 (359.03)
MBN	378.08 (87.01)	820.38 (168.23)	595.61 (196.61)	647.53 (120.74)	484.14 (96.84)	342.03 (45.14)	377.78 (35.18)	570.19 (78.58)	526.41 (56.35)	346.23 (47.46)	402.07 (43.35)
MBP	26.26 (11.60)	32.96 (12.96)	35.32 (19.15)	26.79 (12.87)	56.80 (23.52)	148.30 (13.70)	149.15 (13.78)	193.60 (45.60)	130.81 (21.17)	45.55 (14.56)	26.70 (8.84)

Supplemental Table 3.2: Statistical impact of small mammal structures on potential exoenzyme activity in soils collected beneath small mammal structures and control sites at study sites near Utqiagvik and Toolik, Alaska, USA in 2018. ANOVA and Kruskal-Wallis summary results from comparisons of potential exoenzyme activity between small mammal structure types and study regions.

	Structure			Region			Activity X Region		
	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>
β-glucosidase	$X^2 = 6.94$	0.074	3	$W = 1215$	0.063	1	-----	-----	-----
β-cellobiosidase	$X^2 = 6.48$	0.091	3	$W = 1475$	0.747	1	-----	-----	-----
β-xylosidase	$X^2 = 7.44$	0.059	3	$W = 1826$	0.080	1	-----	-----	-----
α-glucosidase	$X^2 = 2.23$	0.526	3	$W = 769$	0.007	1	-----	-----	-----
LAP	$X^2 = 2.86$	0.414	3	$W = 770$	0.018	1	-----	-----	-----
NAG	$F = 0.87$	0.460	3	$F = 74.50$	<0.001	1	$F = 0.34$	0.798	3, 103
Phosphatase	$F = 0.72$	0.544	3	$F = 61.40$	<0.001	1	$F = 0.43$	0.734	3, 103
Phosphodiesterase	$F = 0.65$	0.583	3	$F = 28.77$	<0.001	1	$F = 1.12$	0.345	3, 103
Phenol oxidase	$F = 1.64$	0.185	3	$F = 1.07$	0.304	1	$F = 5.84$	0.001	3, 103
Peroxidase	$X^2 = 2.53$	0.470	3	$W = 2797$	<0.001	1	-----	-----	-----

Supplemental Table 3.3: Mean (standard error) of total percent % carbon (TC), total % nitrogen (TN), total % phosphorus (TP), C:N ratio, C:P ratio, N:P ratio, inorganic nutrient (NH₄⁺, NO₃⁻, PO₄³⁻) concentrations, extractable organic nutrients (EOC, ETN, EIN), and microbial biomass CNP (MBC, MBN, MBP) in soils collected beneath lemming structures (CON = control, HAY = hay pile, LAT = latrine, RUN = runway, BUR = burrow) sites near Utqiagvik, Alaska, USA in 2018. ANOVA and Kruskal-Wallis summary results from comparisons of soil variables between small mammal structure types.

	Structure Type					Statistics		
	CON	HAY	LAT	RUN	BUR	Stat	<i>p</i>	<i>df</i>
TC	32.77 (2.32)	37.61 (1.78)	30.27 (3.02)	38.46 (1.33)	34.97 (2.14)	<i>F</i> = 2.40	0.059	4
TN	1.77 (0.16)	2.28 (0.11)	1.61 (0.14)	2.03 (0.10)	1.75 (0.10)	<i>X</i> ² = 16.56	0.002	4
TP	0.26 (0.05)	0.46 (0.10)	0.29 (0.07)	0.37 (0.07)	0.16 (0.02)	<i>X</i> ² = 13.261	0.010	4
CN	19.16 (0.86)	16.60 (0.45)	18.66 (0.64)	19.27 (0.68)	20.08 (0.82)	<i>X</i> ² = 13.42	0.009	4
CP	190.26 (27.02)	145.49 (23.70)	177.96 (29.16)	186.56 (32.00)	251.02 (20.96)	<i>X</i> ² = 9.21	0.056	4
NP	10.58 (1.54)	8.67 (1.33)	9.80 (1.60)	9.98 (1.74)	12.42 (0.95)	<i>X</i> ² = 2.63	0.622	4
NH ₄ ⁺	9.72 (2.32)	38.76 (8.20)	11.05 (2.29)	15.53 (3.39)	25.04 (5.69)	<i>F</i> = 8.81	<0.001	4
NO ₃ ⁻	0 (0)	0.63 (0.44)	0.18 (0.15)	0 (0)	2.07 (1.84)	<i>X</i> ² = 4.30	0.367	4
PO ₄ ³⁻	0.76 (0.34)	1.71 (0.66)	0.79 (0.29)	0.76 (0.33)	1.44 (0.56)	<i>X</i> ² = 4.00	0.635	4
EOC	395.34 (53.53)	646.17 (54.97)	478.85 (48.76)	640.80 (51.40)	561.82 (63.22)	<i>F</i> = 3.90	0.006	4
ETN	43.52 (7.14)	96.12 (13.46)	53.75 (6.84)	70.79 (8.15)	76.33 (8.73)	<i>F</i> = 5.44	0.001	4
EIN	9.72 (2.32)	39.39 (8.37)	11.23 (2.28)	15.53 (3.38)	27.11 (6.19)	<i>F</i> = 5.03	<0.001	4
EON	33.79 (5.12)	56.73 (8.15)	42.53 (5.07)	55.26 (6.74)	49.22 (6.98)	<i>F</i> = 2.13	0.086	4
MBC	3627.26 (709.63)	4972.88 (912.10)	4138.43 (1175.26)	4970.51 (766.19)	2821.69 (507.31)	<i>F</i> = 1.79	0.141	4
MBN	378.08 (87.01)	820.38 (168.23)	595.61 (196.61)	647.53 (120.74)	484.14 (96.84)	<i>F</i> = 2.03	0.099	4
MBP	26.26 (11.60)	32.96 (12.96)	35.32 (19.15)	26.79 (12.87)	56.80 (23.52)	<i>X</i> ² = 3.26	0.515	4

Supplemental Table 3.4: Mean (standard error) of total percent % carbon (TC), total % nitrogen (TN), total % phosphorus (TP), C:N ratio, C:P ratio, N:P ratio, inorganic nutrient (NH_4^+ , NO_3^- , PO_4^{3-}) concentrations, extractable organic nutrients (EOC, ETN, EIN), and microbial biomass CNP (MBC, MBN, MBP) in soils collected beneath control (CT) and lemming carcass (CAR) sites near Utqiagvik, Alaska, USA in 2019. Wilcox signed-ranked test results from comparisons of soil variables between CT and CAR sites.

	Structure type		Statistics	
	CT	CAR	W	P
TC	41.56 (1.29)	42.88 (0.43)	11	0.393
TN	1.43 (0.20)	1.47 (0.15)	7	1.000
TP	0.13 (0.02)	0.16 (0.02)	12	0.250
CN	30.71 (5.81)	31.01 (4.63)	9	0.786
CP	335.43 (50.61)	301.48 (67.96)	4	0.393
NP	11.73 (2.80)	9.41 (0.69)	6	0.786
NH_4^+	5.08 (2.18)	4082.12 (573.94)	15	0.036
NO_3^-	1.77 (1.45)	1.04 (0.31)	8	1.000
PO_4^{3-}	0 (0)	16.90 (11.51)	15	0.032
EOC	385.32 (19.75)	995.28 (101.40)	15	0.036
ETN	52.74 (17.06)	4377.08 (576.58)	15	0.036
EIN	6.85 (2.29)	4083.16 (573.75)	15	0.036
EON	45.89 (14.88)	293.93 (198.58)	11	0.393
MBC	1526.28 (57.92)	2177.23 (342.02)	12	0.250
MBN	884.65 (682.05)	135.65 (122.94)	2	0.127
MBP	3.30 (1.91)	46.06 (17.53)	12	0.250

Supplemental Table 3.5: Statistical impact of small mammal hay piles on soil variables collected in soils collected beneath hay piles and control sites at study sites near Utqiagvik (2018), Toolik (2018), and Nome (2019) Alaska, USA. ANOVA and Kruskal-Wallis summary results from comparisons of soil variables between small hay piles, control sites, and study regions.

	Structure			Region			Activity X Region		
	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>
TC	$W = 1148$	0.277	1	$X^2 = 11.53$	<0.001	2	-----	-----	-----
TN	$W = 1161$	0.233	1	$X^2 = 36.72$	<0.001	2	-----	-----	-----
TP	$W = 1064$	0.548	1	$X^2 = 51.45$	<0.001	2	-----	-----	-----
CN	$W = 927$	0.495	1	$X^2 = 77.20$	<0.001	2	-----	-----	-----
CP	$W = 929$	0.621	1	$X^2 = 64.84$	<0.001	2	-----	-----	-----
NP	$W = 871$	0.333	1	$X^2 = 2.56$	0.11	2	-----	-----	-----
NH ₄ ⁺	$F = 4.71$	0.032	1	$F = 66.81$	<0.001	2	$F = 6.70$	0.002	2, 84
NO ₃ ⁻	$W = 989$	0.551	1	$X^2 = 2.09$	0.351	2	-----	-----	-----
PO ₄ ³⁻	$F = 2.24$	0.139	1	$F = 26.64$	<0.001	2	$F = 0.14$	0.873	2, 84
EOC	$F = 3.25$	0.075	1	$F = 11.70$	<0.001	2	$F = 0.68$	0.512	2, 84
ETN	$F = 8.67$	0.004	1	$F = 0.05$	0.95	2	$F = 1.98$	0.145	2, 84
EIN	$W = 1236.5$	0.071	1	$X^2 = 45.24$	<0.001	2	-----	-----	-----
EON	$F = 3.39$	0.069	1	$F = 1.46$	0.239	2	$F = 0.85$	0.432	2, 84
MBC	$F = 1.47$	0.229	1	$F = 2.06$	0.134	2	$F = 0.69$	0.506	2, 82
MBN	$F = 6.72$	0.011	1	$F = 1.79$	0.174	2	$F = 0.66$	0.519	2, 82
MBP	$W = 962$	0.967	1	$X^2 = 43.77$	<0.001	2	-----	-----	-----

Supplemental Table 3.6: Statistical impact of small mammal hay pile on potential exoenzyme activity in soils collected beneath hay piles and control sites at study sites near Utqiagvik (2018), Toolik (2018), and Nome (2019) Alaska, USA. ANOVA and Kruskal-Wallis summary results from comparisons of soil variables between small hay piles, control sites, and study regions.

	Structure			Region			Activity X Region		
	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>	Stat	<i>p</i>	<i>df</i>
β-glucosidase	<i>F</i> = 13.22	<0.001	1	<i>F</i> = 72.26	<0.001	2	<i>F</i> = 0.83	0.441	2, 81
β-cellobiosidase	<i>F</i> = 8.33	0.005	1	<i>F</i> = 70.30	<0.001	2	<i>F</i> = 0.69	0.505	2, 83
β-xylosidase	<i>W</i> = 744	0.044	1	<i>X</i> ² = 59.20	<0.001	2	-----	-----	-----
α-glucosidase	<i>F</i> = 0.56	0.458	1	<i>F</i> = 30.29	<0.001	2	<i>F</i> = 0.11	0.896	2, 70
LAP	<i>W</i> = 493	0.81	1	<i>X</i> ² = 46.89	<0.001	2	-----	-----	-----
NAG	<i>F</i> = 8.96	0.004	1	<i>F</i> = 59.26	<0.001	2	<i>F</i> = 0.34	0.714	2, 83
Phosphatase	<i>F</i> = 0.01	0.932	1	<i>F</i> = 30.84	<0.001	2	<i>F</i> = 1.32	0.272	2, 83
Phosphodiesterase	<i>W</i> = 915	0.543	1	<i>X</i> ² = 48.74	<0.001	2	-----	-----	-----
Phenol oxidase	<i>W</i> = 1041	0.68	1	<i>X</i> ² = 4.93	0.085	2	-----	-----	-----
Peroxidase	<i>W</i> = 1039	0.692	1	<i>X</i> ² = 52.56	<0.001	2	-----	-----	-----

Supplemental Table 3.7: Mean (standard error) of nitrogen mineralization rates (Nmin) from mineralization tubes containing three litter types (hayed, preferred, and non-preferred) and control tubes (no litter) installed at Toolik and Nome, Alaska, USA. summary results from comparisons of Nmin between litter types and study region.

Site	Litter type				Statistics			
	Control	Hayed	Preferred	Non-preferred	ANOVA	<i>F</i>	<i>p</i>	<i>df</i>
Pooled Sites	317.26 (53.30)	2072.78 (400.58)	440.70 (136.41)	151.10 (67.80)	Litter type	10.53	<0.001	3
Toolik	277.41 (17.02)	2202.16 (576.81)	451.80 (202.41)	175.76 (113.26)	Region	0.16	0.688	1
Nome	357.11 (82.08)	2143.41 (600.83)	429.60 (199.07)	126.44 (82.90)	Litter x Region	0.09	0.966	3, 42

Supplemental Table 3.8: Mean (standard error) of total percent % carbon (TC), total % nitrogen (TN), total % phosphorus (TP), C:N ratios, C:P ratios, and N:P ratios of *Carex aquatilis* leaf tissue from plants growing in or adjacent to control sites (CON) and lemming structures (HAY = hay pile, LAT = latrine, RUN = runway, and BUR = burrow) collected beneath lemming structures (CON = control, HAY = hay pile, LAT = latrine, RUN = runway, BUR = burrow) sites near Utqiagvik, Alaska, USA in 2020. ANOVA summary results from comparisons of leaf nutrient variables between small mammal structure types.

	Structure type					Statistics	
	CON	HAY	LAT	RUN	BUR	F-score	P
TC	45.49 (0.13)	44.41 (0.37)	45.18 (0.23)	45.69 (0.14)	45.61 (0.15)	5.67	0.003
TN	2.63 (0.16)	3.20 (0.30)	2.91 (0.15)	2.99 (0.13)	3.10 (0.15)	1.36	0.28
TP	0.23 (0.01)	0.41 (0.03)	0.25 (0.01)	0.25 (0.00)	0.24 (0.03)	10.37	<0.001
CN	17.60 (1.11)	14.52 (1.78)	15.68 (0.83)	15.39 (0.63)	14.88 (0.73)	1.19	0.346
CP	199.01 (10.55)	108.59 (7.83)	182.99 (9.66)	181.37 (2.19)	203.89 (27.35)	5.92	0.003
NP	11.37 (0.40)	8.50 (0.53)	11.73 (0.62)	11.85 (0.44)	13.63 (1.65)	3.86	0.019

Supplemental Table 4.1: Statistical results of brown lemming (*Lemmus trimucronatus*) fencing treatments on NDVI. Data were collected during July of 2018-2019.

Treatment		Year		Treatment x Year	
Stat	<i>p</i>	Stat	<i>p</i>	Stat	<i>p</i>
$F_3 = 2.10$	0.143	$F_1 = 9.69$	0.007	$F_3 = 0.12$	0.946

Supplemental Table 5.1. Sample sizes (n) of brown lemming (*Lemmus trimucronatus*) feces analyzed for fecal nutrients (TC = total % carbon (C), TN = total % nitrogen (N), TP = total % phosphorus (P)) across years and growing seasons. TC and TN samples were from individual lemmings, while TP samples were composited to achieve the minimum mass needed for analysis.

Year	Season	n	
		TC & TN	TP
2018	Early	5	3
	Middle	5	3
	Late	10	3
2019	Early	31	3
	Middle	6	2
	Late	19	3
2020	Early	0	0
	Middle	8	2
	Late	0	0

Supplemental Table 5.2: Statistical effects of brown lemming (*Lemmus trimucronatus*) diet on fecal nutrients (TC = total % carbon (C), TN = total % nitrogen (N), TP = total % phosphorus (P), C:N ratios, C:P ratios, N:P ratios). Lemmings were fed either *Carex aquatilis* or *Eriophorum angustifolium* for a minimum of two days before fecal collection for analysis. Wilcox signed-rank test results from comparisons of fecal nutrients between diet.

	<i>W</i>	<i>p</i>
TC	7	0.310
TN	16	0.548
TP	8	0.421
CN	14	0.841
CP	8	0.421
NP	9	0.548

Supplemental Table 5.3. Statistical effects of brown lemming (*Lemmus trimucronatus*) latrines on plant (*C. aquatilis*) tissue nutrients (TC = total % carbon (C), TN = total % nitrogen (N), TP = total % phosphorus (P), C:N ratios, C:P ratios, N:P ratios). Plant leaf tissue was collected at latrine sites in 2020 from study sites near Utqiagvik, Alaska, USA.

Sample	Variable	Stat	<i>p</i>
Plant	TC	<i>W</i> = 16	0.548
	TN	<i>W</i> = 7	0.310
	TP	<i>W</i> = 10	0.691
	CN	<i>W</i> = 18	0.310
	CP	<i>W</i> = 17	0.421
	NP	<i>W</i> = 12	1.000

Supplemental Table 5.4. Statistical effects of brown lemming (*Lemmus trimucronatus*) feces from animals fed two diets on plant biomass (mass) and leaf tissue nutrient content (TC = total % carbon (C), TN = total % nitrogen (N), TP = total % phosphorus (P), C:N ratios, C:P ratios, N:P ratios). Lemmings were fed either *Carex aquatilis* or *Eriophorum angustifolium* for a minimum of two days before fecal collection for analysis. Wilcox signed-rank and student t-test results from comparisons.

	Stat	<i>p</i>
Mass	$t = -2.69$	0.014
TC	$W = 5$	0.857
TN	$W = 9$	0.400
CN	$W = 10$	0.229

Supplemental Table 5.5. Mean and standard error (SE) of decomposition rates or decay rates (k) of feces (mass) and fecal nutrients (carbon (C), nitrogen (N), phosphorus (P)) in g day^{-1} for feces decomposed at high-centered polygon centers and edges, and the total between the two locations.

	Total		Center		Edge	
	k	SE	k	SE	k	SE
Mass	0.0049	0.0015	0.002	0	0.0079	0.0019
C	0.0069	0.0025	0.0019	0.0001	0.0119	0.0031
N	0.0056	0.0019	0.0021	0.0001	0.009	0.0024
P	0.7564	0.0402	0.7863	0.0347	0.7265	0.0463

Supplemental Figures

LIST OF SUPPLEMENTAL FIGURES

Supplemental Figure 2.1: Boxplots showing the impact of herbivores on total carbon and nitrogen, and C:N ratios in soils collected in July 2017 from an herbivore enclosure experiment (CT = control (no herbivores excluded), SF = Small Fence (large and small herbivores excluded), LF = Large Fence (large herbivores only excluded)) in dry heath (DH, n = 3) and moist acidic tussock (MAT, n = 4) tundra at the Arctic-LTER located at Toolik Lake, AK.

Supplemental Figure 2.2: Boxplots showing the impact of herbivores on inorganic nutrient concentrations (NH_4^+ , NO_3^- , PO_4^{3-}) in soils collected from the upper organic layers from an herbivore enclosure experiment (CT = control (no herbivores excluded), SF = Small Fence (large and small herbivores excluded), LF = Large Fence (large herbivores only excluded)) in dry heath (DH, n = 3) and moist acidic tussock (MAT, n = 4) tundra at the Arctic-LTER located at Toolik Lake, AK.

Supplemental Figure 2.3: Boxplots showing the impact of herbivores on extractable organic nutrients (EOC, ETN, EOP) and microbial biomass CNP concentrations (MBC, MBN, MBP), and activity of three CNP enzymes in soils collected in July 2017 from an herbivore enclosure experiment (CT = control (no herbivores excluded), SF = Small Fence (large and small herbivores excluded), LF = Large Fence (large herbivores only excluded)) in moist acidic tussock (MAT, n = 4) tundra at the Arctic-LTER located at Toolik Lake, AK.

Supplemental Figure 2.4: Boxplots showing the impact of herbivores on potential microbial exoenzyme activity in soils collected in July 2017 from an herbivore enclosure experiment (CT = control (no herbivores excluded), SF = Small Fence (large and small herbivores excluded), LF = Large Fence (large herbivores only excluded)) in dry heath (DH, n = 3) tundra at the Arctic-LTER located at Toolik Lake, AK.

Supplemental Figure 2.5: Boxplots showing the impact of herbivores on potential microbial exoenzyme activity in soils collected in July 2017 from an herbivore enclosure experiment (CT = control (no herbivores excluded), SF = Small Fence (large and small herbivores excluded), LF = Large Fence (large herbivores only excluded)) in moist acidic tussock (MAT, n = 4) tundra at the Arctic-LTER located at Toolik Lake, AK.

Supplemental Figure 2.6: Boxplots showing the impact of herbivores on inorganic nutrient (NH_4 , NO_3 , PO_4), extractable organic nutrient (EOC, ETN, EOP), and microbial biomass CNP (MBC, MBN, MBP) concentrations in soils from the upper organic, lower organic, and mineral layers of soil collected in July 2017 from an herbivore exclosure experiment (CT = control (no herbivores excluded), SF = Small Fence (large and small herbivores excluded), LF = Large Fence (large herbivores only excluded)) in moist acidic tundra (MAT, $n = 4$) at the Arctic-LTER located at Toolik Lake, AK.

Supplemental Figure 2.7: Boxplots showing the impact of herbivores on potential microbial exoenzyme activity in soils from the upper organic, lower organic, and mineral layers of soils collected in July 2017 from an herbivore exclosure experiment (CT = control (no herbivores excluded), SF = Small Fence (large and small herbivores excluded), LF = Large Fence (large herbivores only excluded)) in moist acidic tundra (MAT, $n = 4$) at the Arctic-LTER located at Toolik Lake, AK.

Supplemental Figure 3.1: Boxplots showing the relative impacts of small mammal structures (CON = control, HAY = hay pile, RUN = runway, LAT = latrine) on (a) Total percent (%) carbon (C), (b) Total % nitrogen (N), (c) Total % phosphorus (P), (d) C:N ratios, (e) C:P ratios, and (f) N:P ratios in soils collected in 2018 from beneath small mammal structures at study sites near Utqiagvik and Toolik, Alaska, USA.

Supplemental Figure 3.2: Boxplots showing the relative impacts of small mammal hay piles (HAY) compared to control sites (CON) on (a) Total percent (%) carbon (C), (b) Total % nitrogen (N), (c) Total % phosphorus (P), (d) C:N ratios, (e) C:P ratios, and (f) N:P ratios in soils collected from beneath small mammal structures at study sites near Utqiagvik (2018), Toolik (2018), and Nome (2019), Alaska, USA. Uppercase letters represent differences between study regions.

Supplemental Figure 3.3: Boxplots showing the relative impacts of small mammal structures (CON = control, HAY = hay pile, RUN = runway, LAT = latrine) on nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}) concentrations in soils collected from beneath small mammal structures at study sites near Utqiagvik (2018), Toolik (2018), and Nome (2019), Alaska, USA. Uppercase letters represent differences between study regions and lowercase letters represent differences between structure types.

Supplemental Figure 3.4: Boxplots showing the relative impacts of small mammal structures (CON = control, HAY = hay pile, RUN = runway, LAT = latrine) on extractable organic carbon (EOC), extractable total nitrogen (ETN), and extractable inorganic nitrogen (EIN) concentrations in soils collected from beneath small mammal structures at study sites near Utqiagvik (2018), Toolik (2018), and Nome (2019), Alaska, USA. Uppercase letters represent differences between study regions and lowercase letters represent differences between structure types.

Supplemental Figure 3.5: Boxplots showing the relative impacts of small mammal structures (CON = control, HAY = hay pile, RUN = runway, LAT = latrine) on microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and microbial biomass phosphorus (MBP) concentrations in soils collected from beneath small mammal structures at study sites near Utqiagvik (2018), Toolik (2018), and Nome (2019), Alaska, USA. Uppercase letters represent differences between study regions and lowercase letters represent differences between structure types.

Supplemental Figure 3.6: Boxplots showing the relative impacts of small mammal structures (CON = control, HAY = hay pile, RUN = runway, LAT = latrine) on potential exoenzyme activity in soils collected from beneath small mammal structures collected in 2018 at study sites near Utqiagvik and Toolik, Alaska, USA. Uppercase letters represent differences between study regions and lowercase letters represent differences between structure types.

Supplemental Figure 3.7: Boxplots showing the relative impacts of small mammal hay piles (HAY) compared to control sites (CON) on potential exoenzyme activity in soils collected from beneath small mammal structures at study sites near Utqiagvik (2018), Toolik (2018), and Nome (2019), Alaska, USA. Uppercase letters represent differences between study regions and lowercase letters represent differences between structure types.

Supplemental Figure 3.8: Boxplots showing the relative impacts of lemming carcasses (CAR) compared to control sites (CT) on (a) Total percent (%) carbon (C), (b) Total % nitrogen (N), (c) Total % phosphorus (P), (d) C:N ratios, (e) C:P ratios, and (f) N:P ratios in soils collected in 2019 at study sites near Utqiagvik, Alaska, USA. Lowercase letters represent differences between treatments.

Supplemental Figure 3.9: Boxplots showing the relative impacts of small mammal structures (CON = control, HAY = hay pile, RUN = runway, LAT = latrine, BUR = burrow) on (a)

Total percent (%) carbon (C), (b) Total % nitrogen (N), (c) Total % phosphorus (P), (d) C:N ratios, (e) C:P ratios, and (f) N:P ratios in soils collected in 2018 from beneath small mammal structures at study sites near Utqiagvik, Alaska, USA. Lowercase letters represent differences between structure types.

Supplemental Figure 3.10: Boxplots showing the relative impacts of small mammal structures (CON/CT = control, HAY = hay pile, RUN = runway, LAT = latrine, BUR = burrow, CAR = carcass) on nitrate (NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}) concentrations in soils collected from beneath small mammal structures at study sites near Utqiagvik, Alaska, USA in 2018 (structures) and 2019 (carcass study). Lowercase letters represent differences between structure types.

Supplemental Figure 3.11: Boxplots showing the relative impacts of small mammal structures (CON/CT = control, HAY = hay pile, RUN = runway, LAT = latrine, BUR = burrow, CAR = carcass) on extractable organic carbon (EOC), extractable total nitrogen (ETN), and extractable inorganic nitrogen (EIN) concentrations in soils collected from beneath small mammal structures at study sites near Utqiagvik, Alaska, USA in 2018 (structure study) and 2019 (carcass study). Lowercase letters represent differences between structure types.

Supplemental Figure 3.12: Boxplots showing the relative impacts of small mammal structures (CON/CT = control, HAY = hay pile, RUN = runway, LAT = latrine, BUR = burrow, CAR = carcass) on microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) concentrations in soils collected from beneath small mammal structures at study sites near Utqiagvik, Alaska, USA in 2018 (structure study) and 2019 (carcass study). Lowercase letters represent differences between structure types.

Supplemental Figure 3.13: Stacked bar plot showing the mean percent (%) cover of different functional cover types collected at small mammal structure sites (CON = control, HAY = hay pile, RUN = runway, LAT = latrine, BUR = burrow) located at study sites near Utqiagvik, Alaska, USA in 2018.

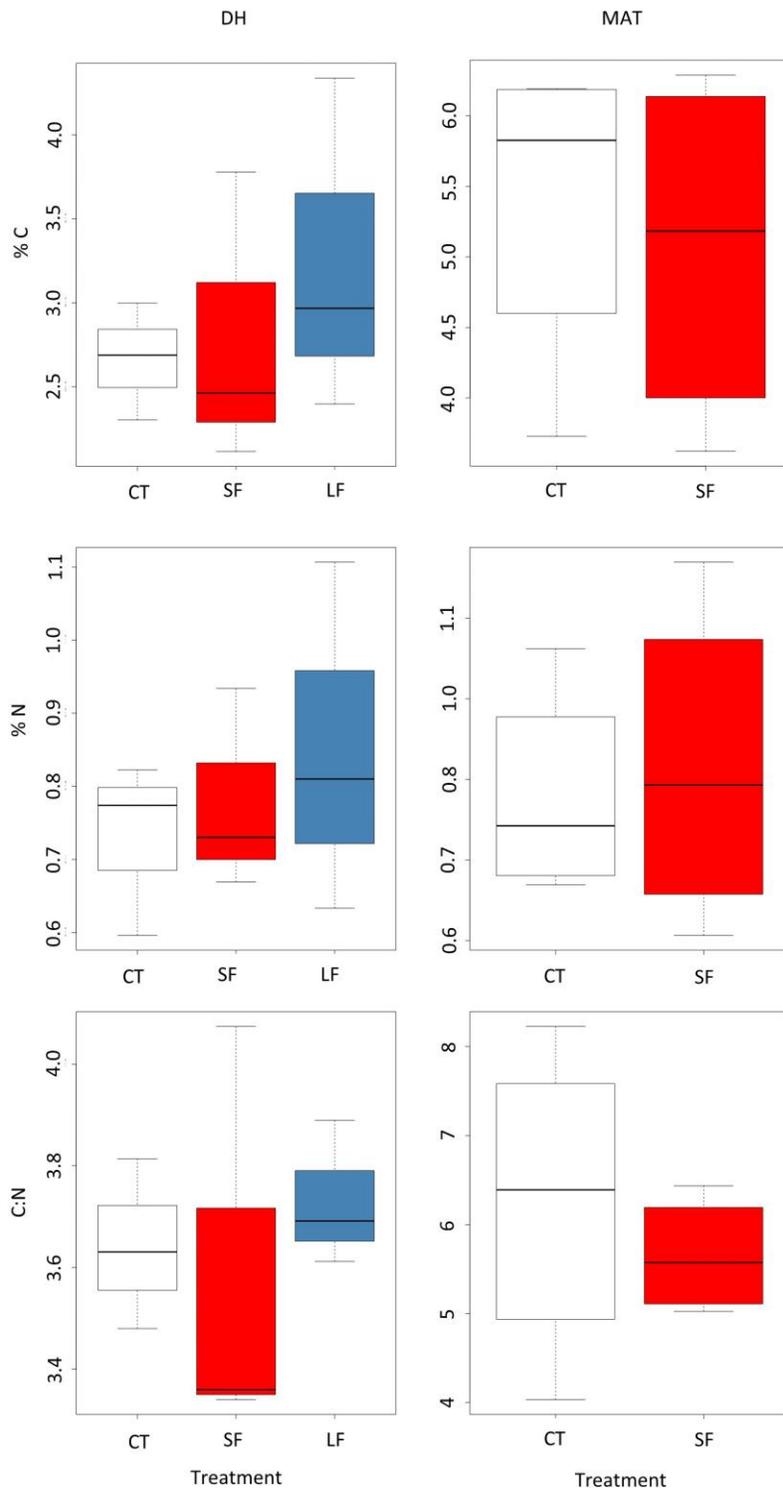
Supplemental Figure 4.1: Boxplots showing the relative impacts of brown lemming (*Lemmus trimucronatus*) fencing treatments on NDVI. Data were collected during July of 2018-2019 near Utqiagvik, Alaska, USA.

Supplemental Figure 4.2: Boxplots showing total percent (%) carbon (TC), total % nitrogen (TN), and carbon:nitrogen ratios (C:N) in soils collected within brown lemming (*Lemmus*

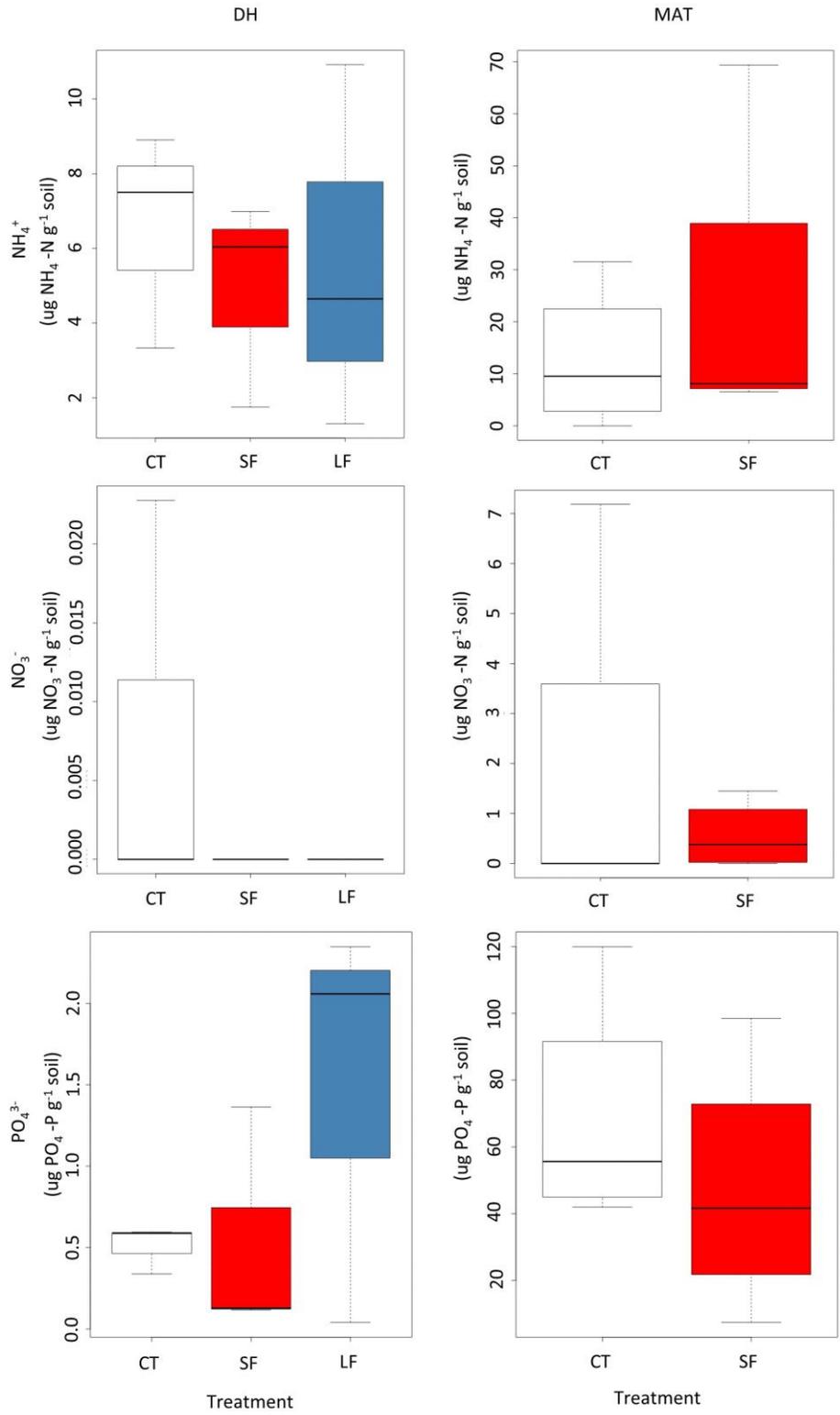
trimucronatus) fencing treatments. Data were collected during the summer of 2018-2020 near Utqiagvik, Alaska, USA.

Supplemental Figure 4.3: Boxplots showing nitrogen mineralization rates from an intact mineralization core experiment installed within brown lemming (*Lemmus trimucronatus*) fencing treatments in 2019 and collected in 2020 near Utqiagvik, Alaska, USA.

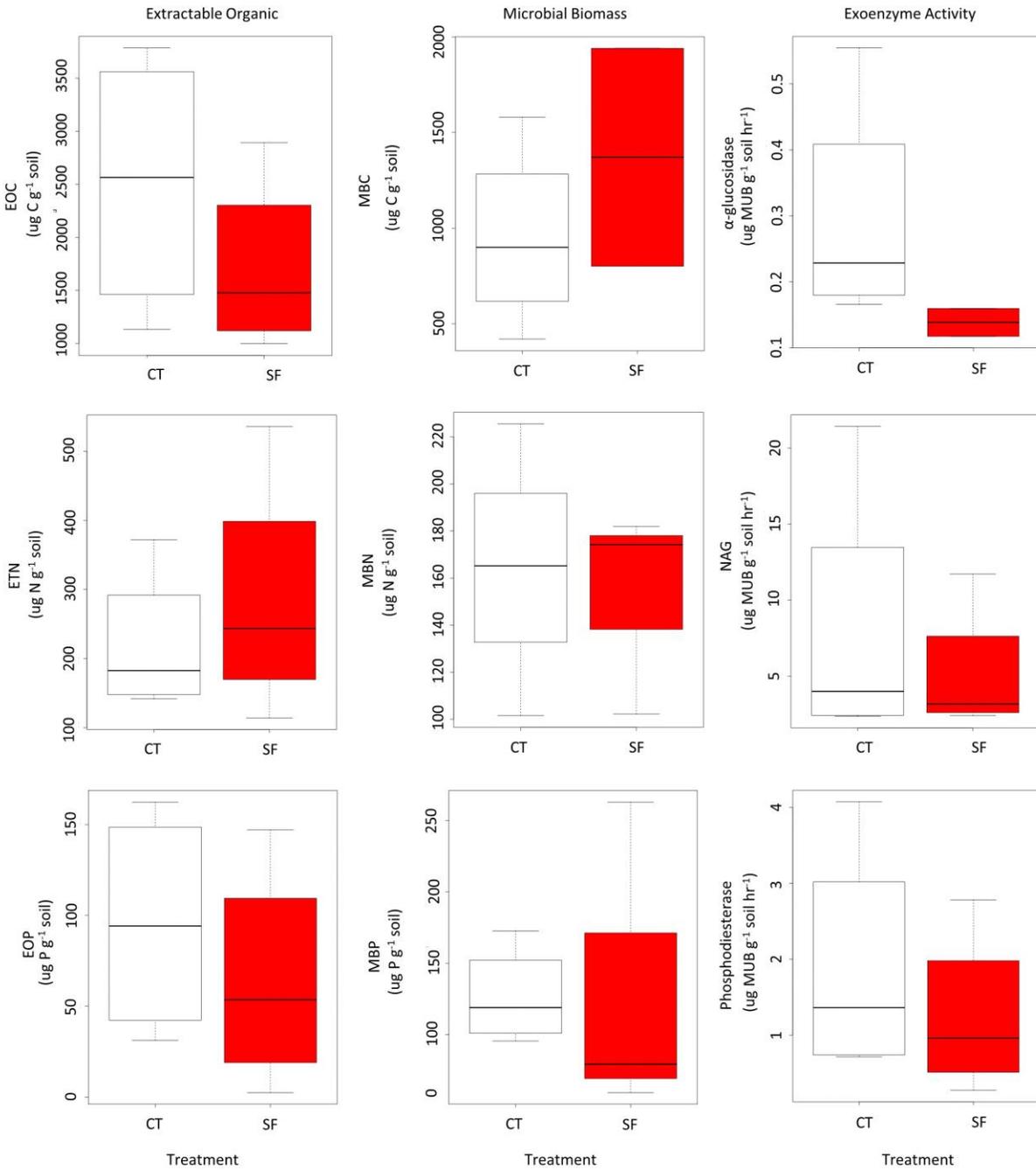
Supplemental Figure 2.1



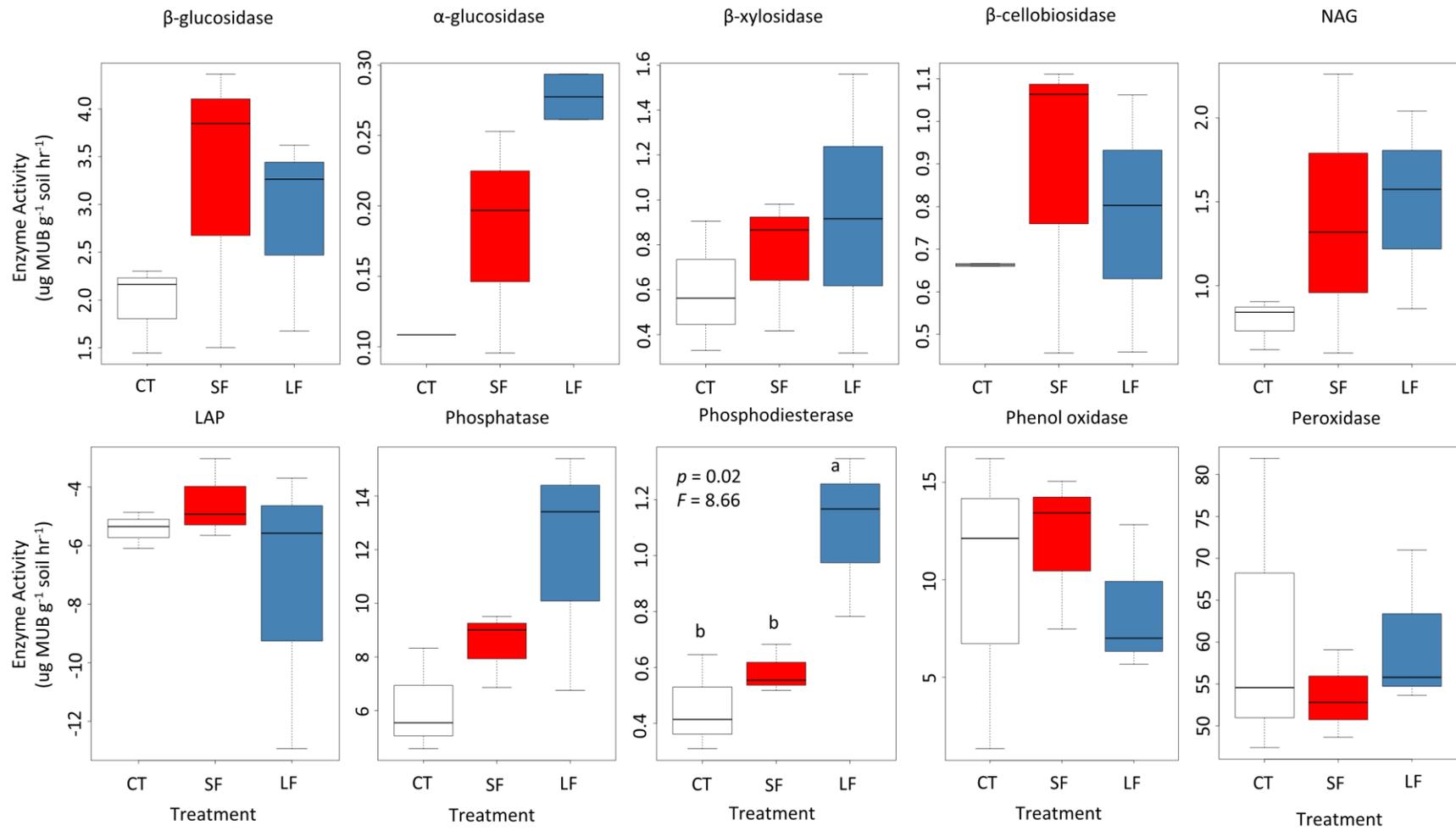
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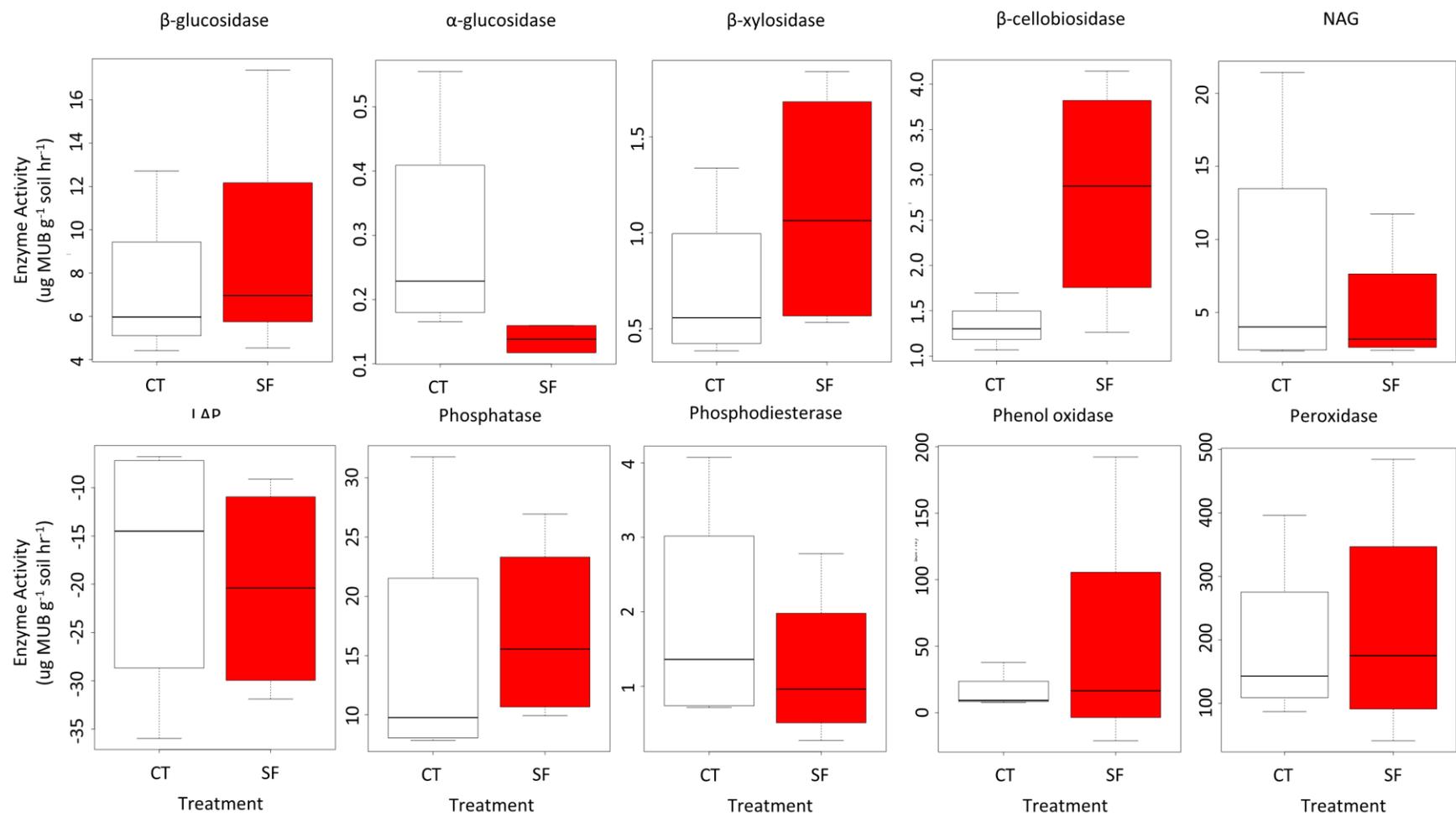
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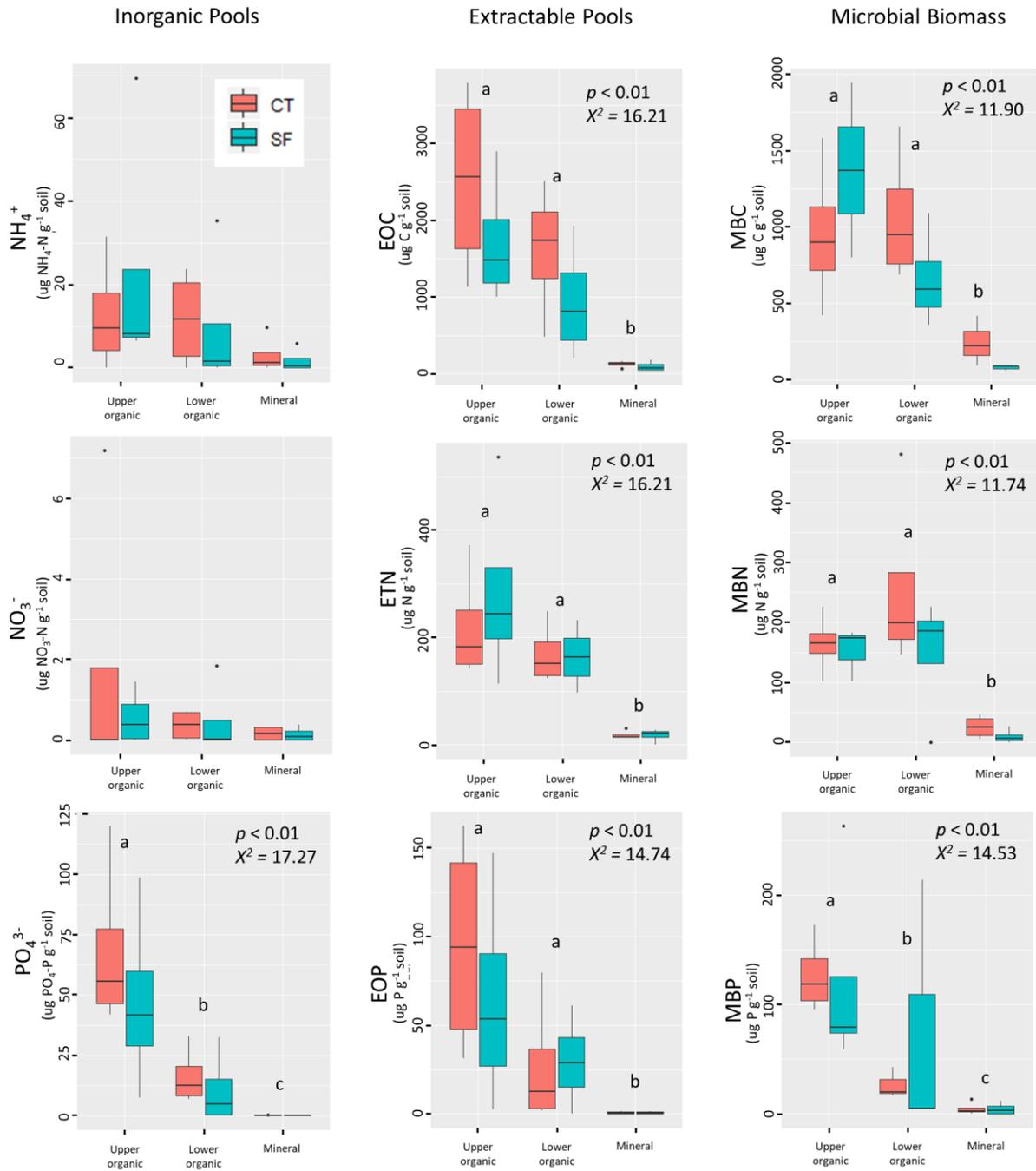
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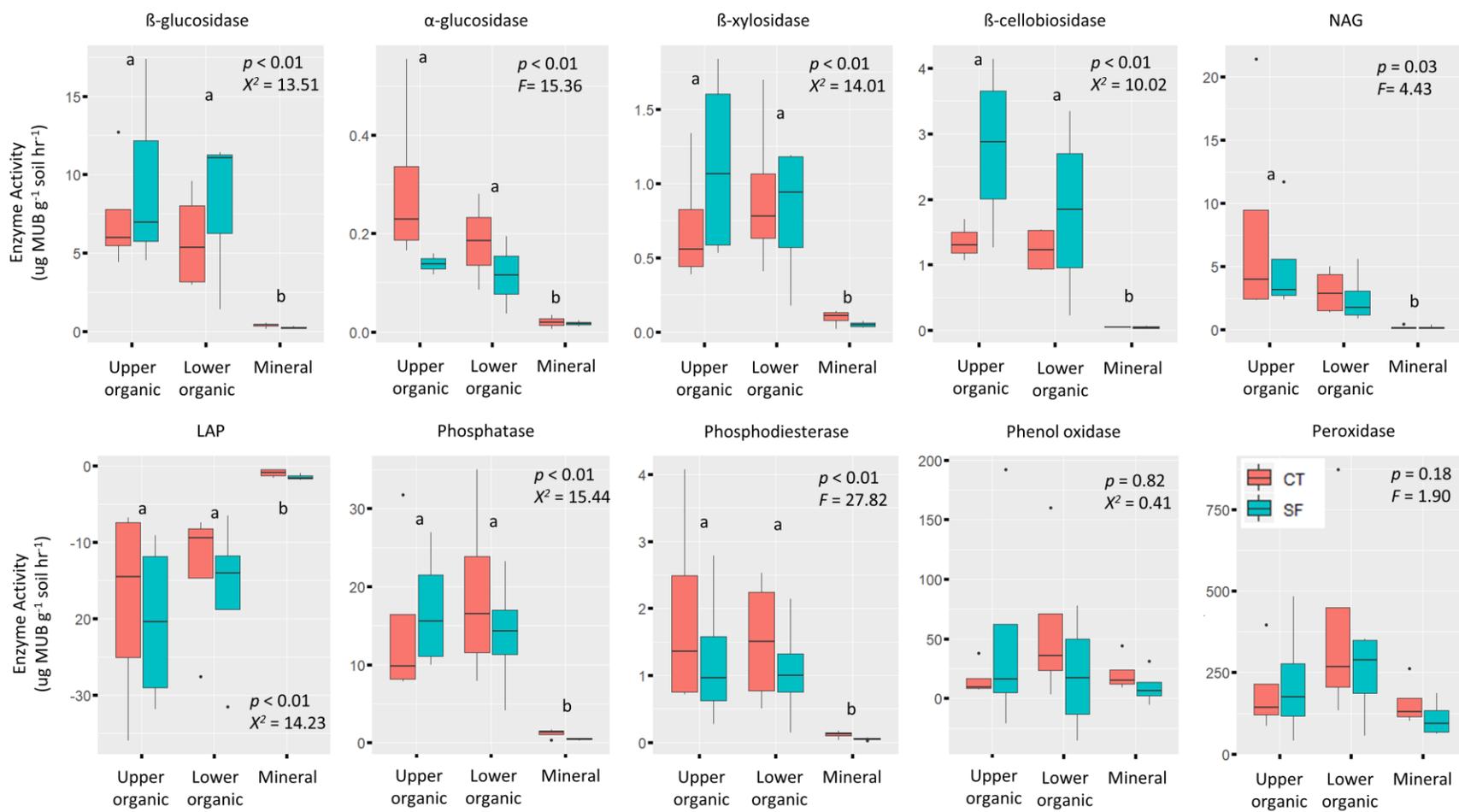
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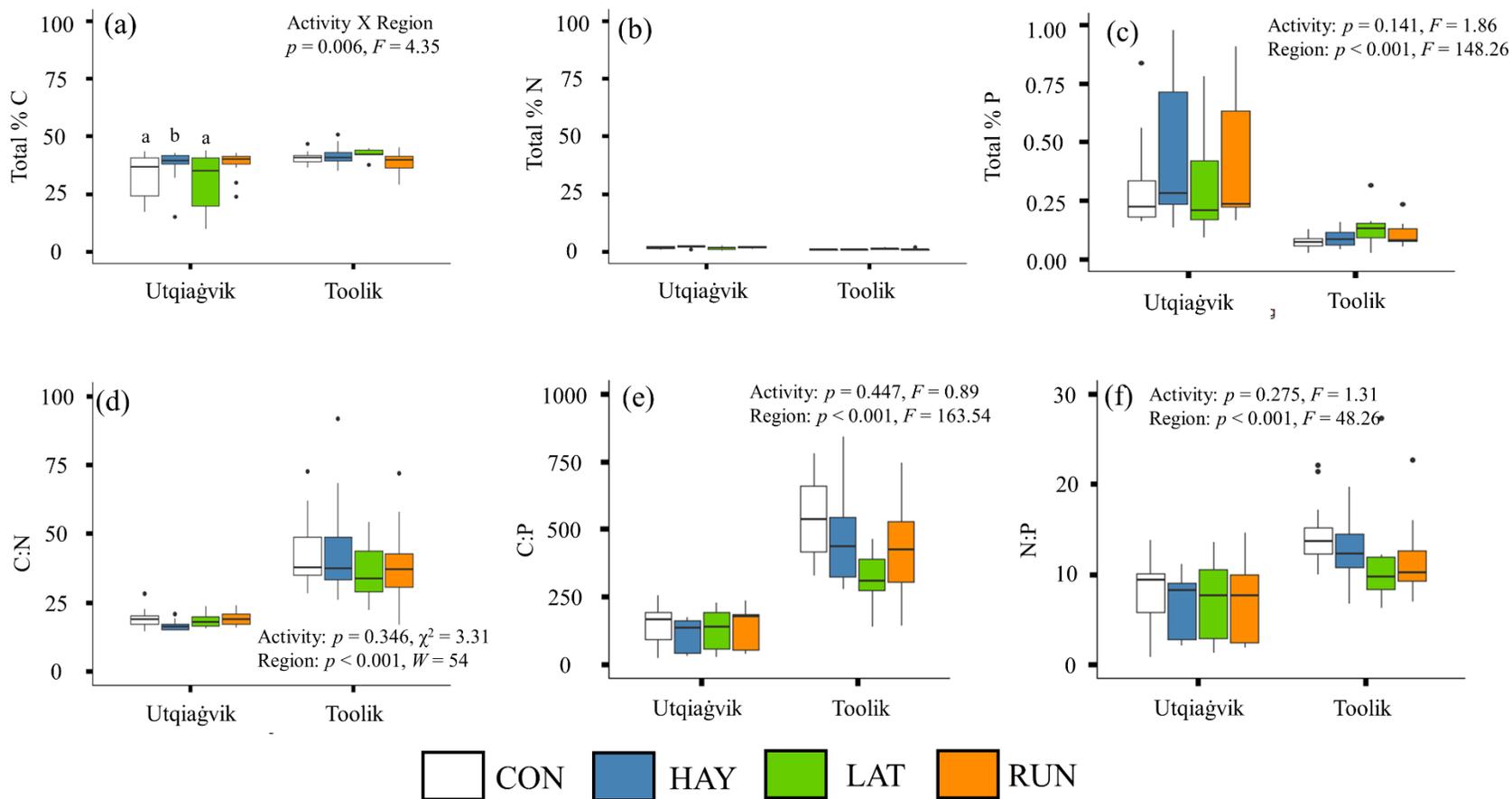
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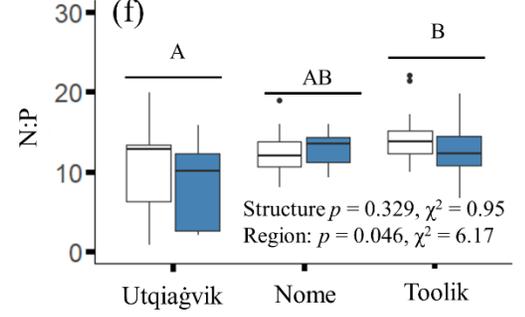
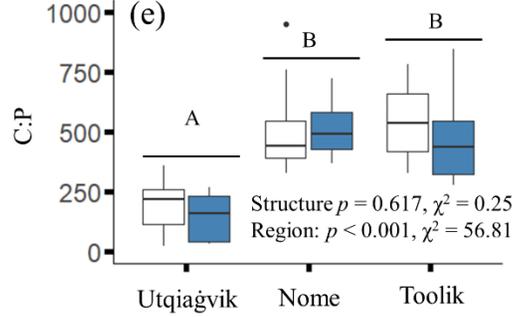
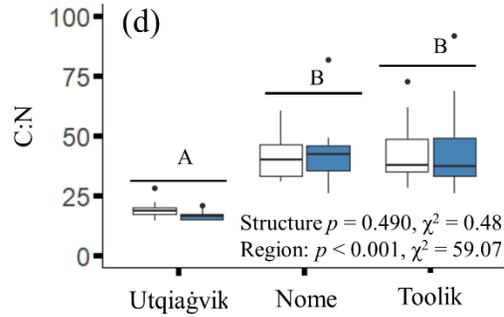
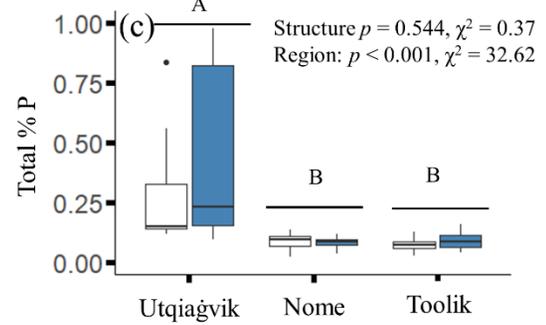
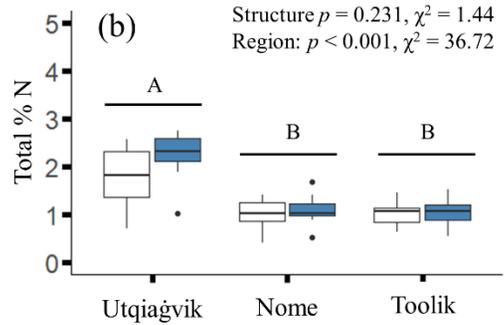
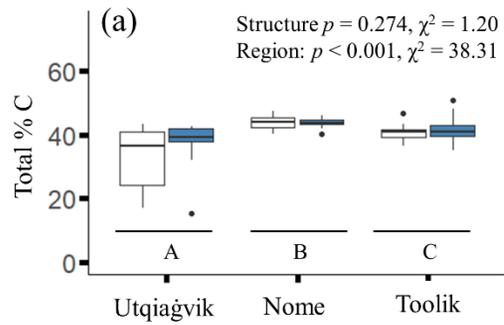
Supplemental Figure 2.7



Supplemental Figure 3.1

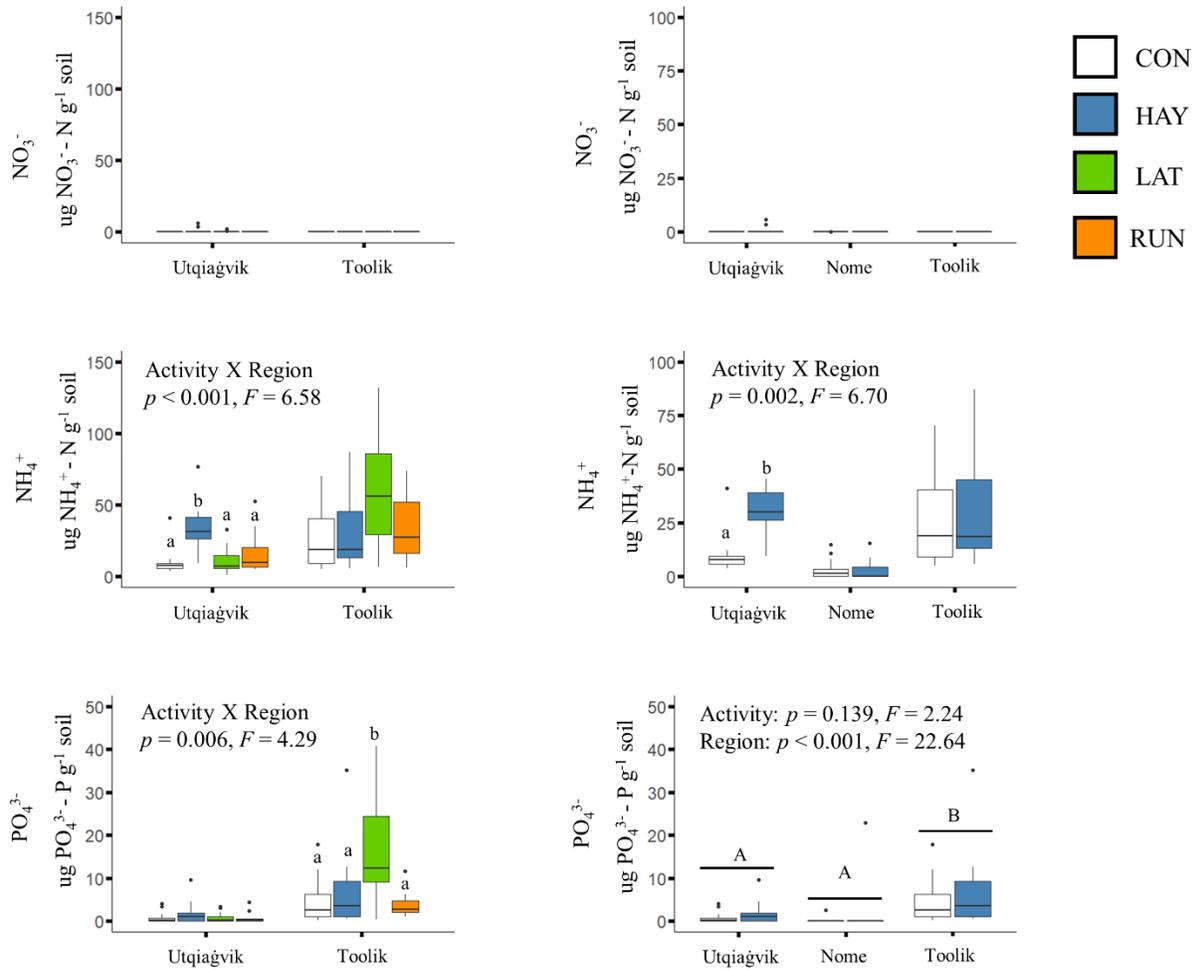


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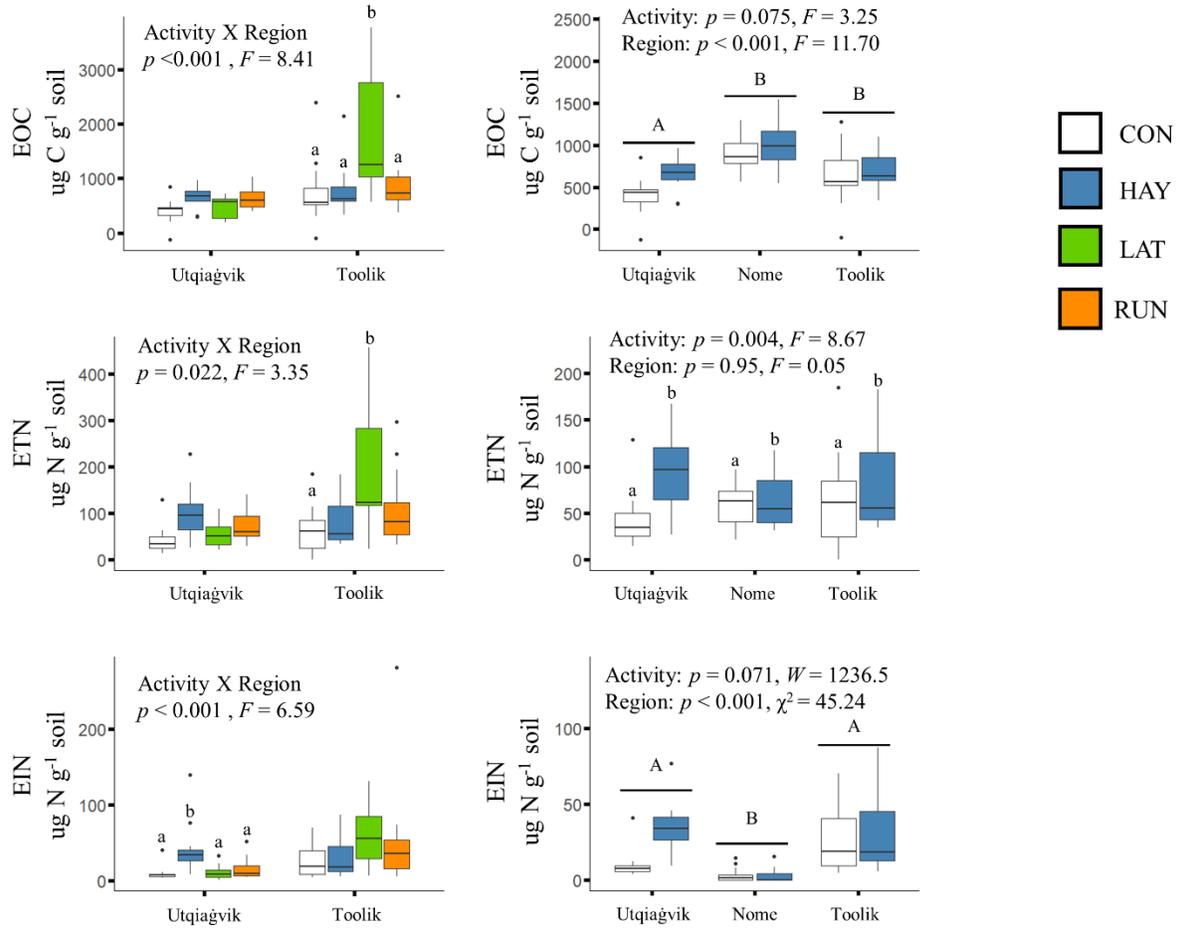


□ CON ■ HAY

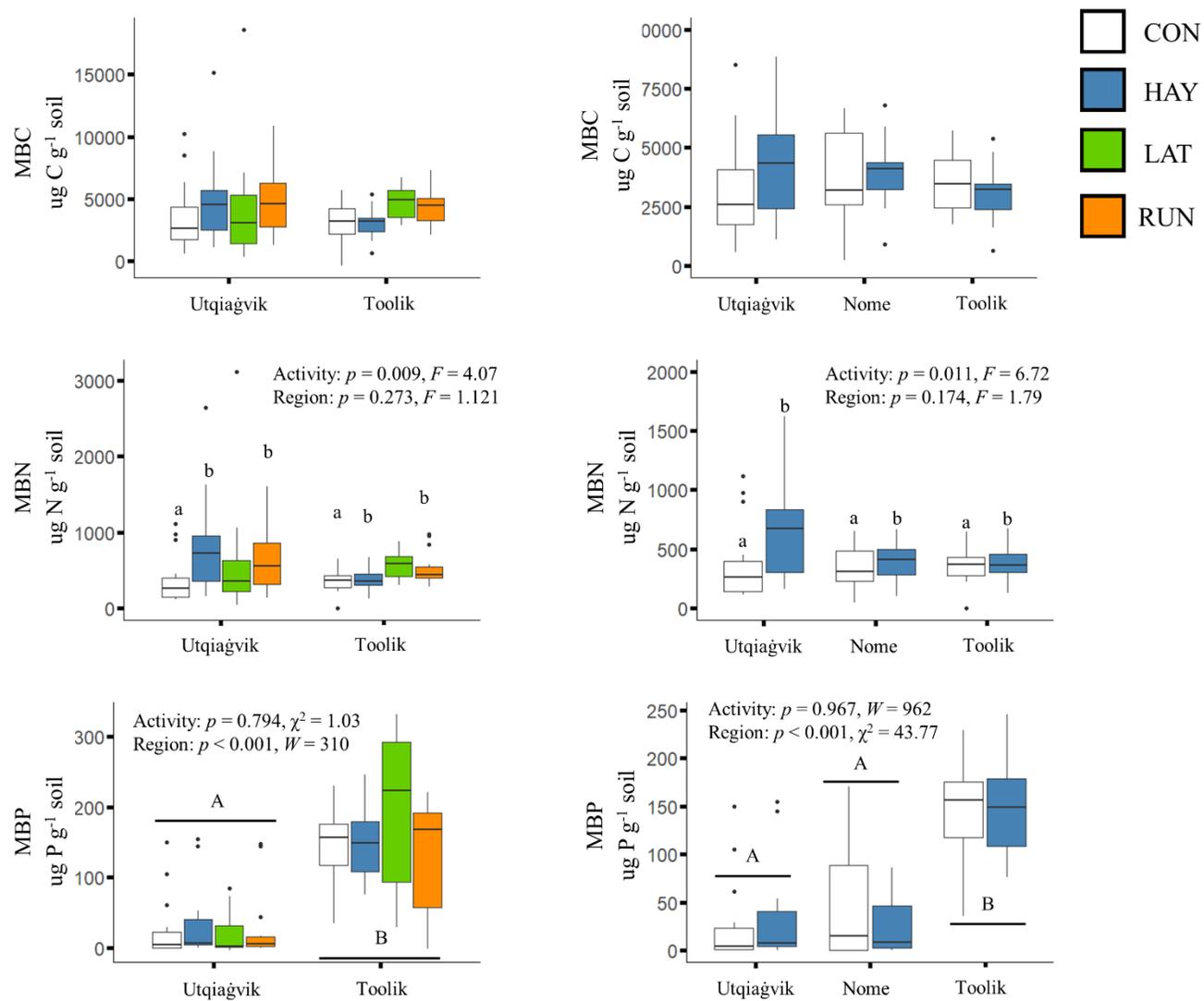
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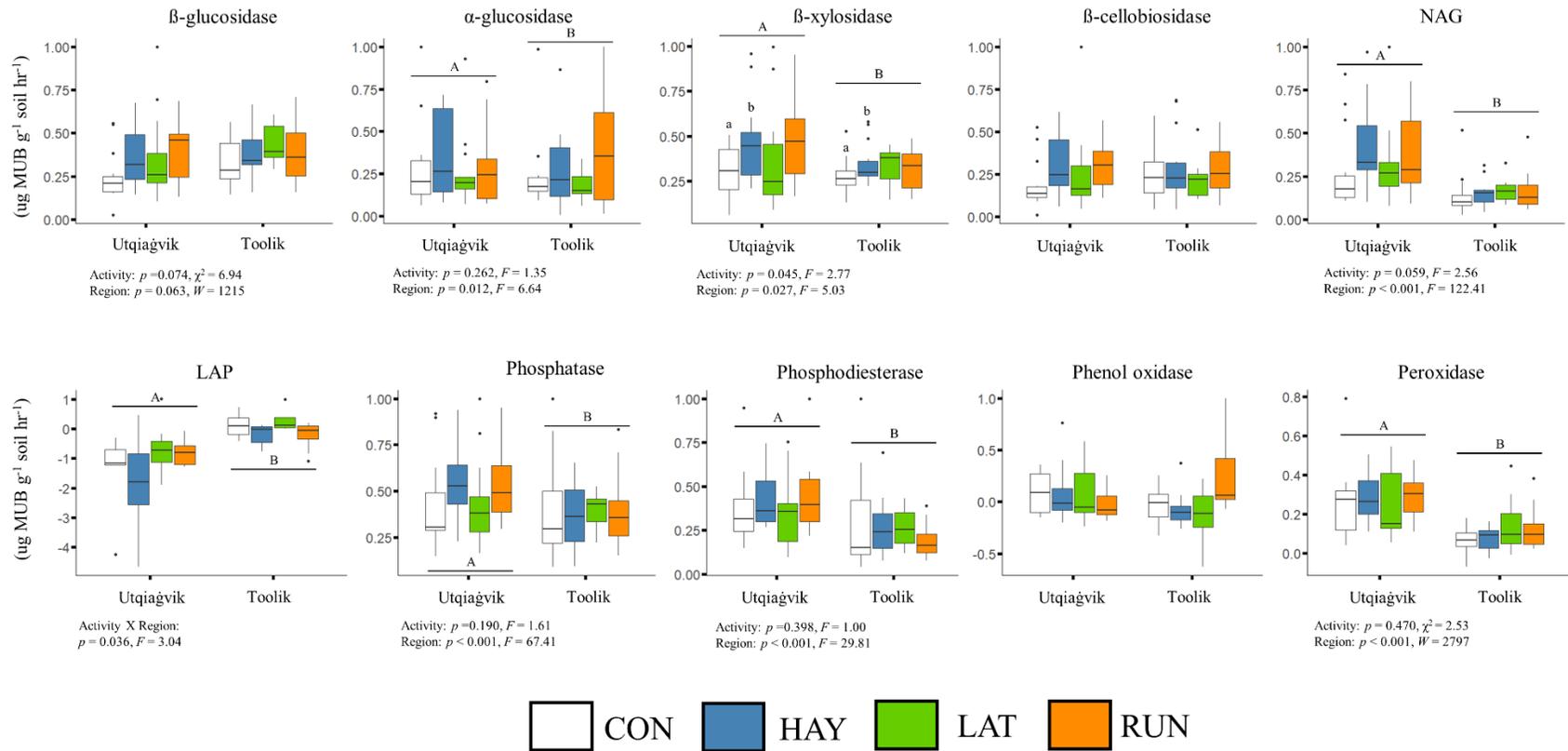
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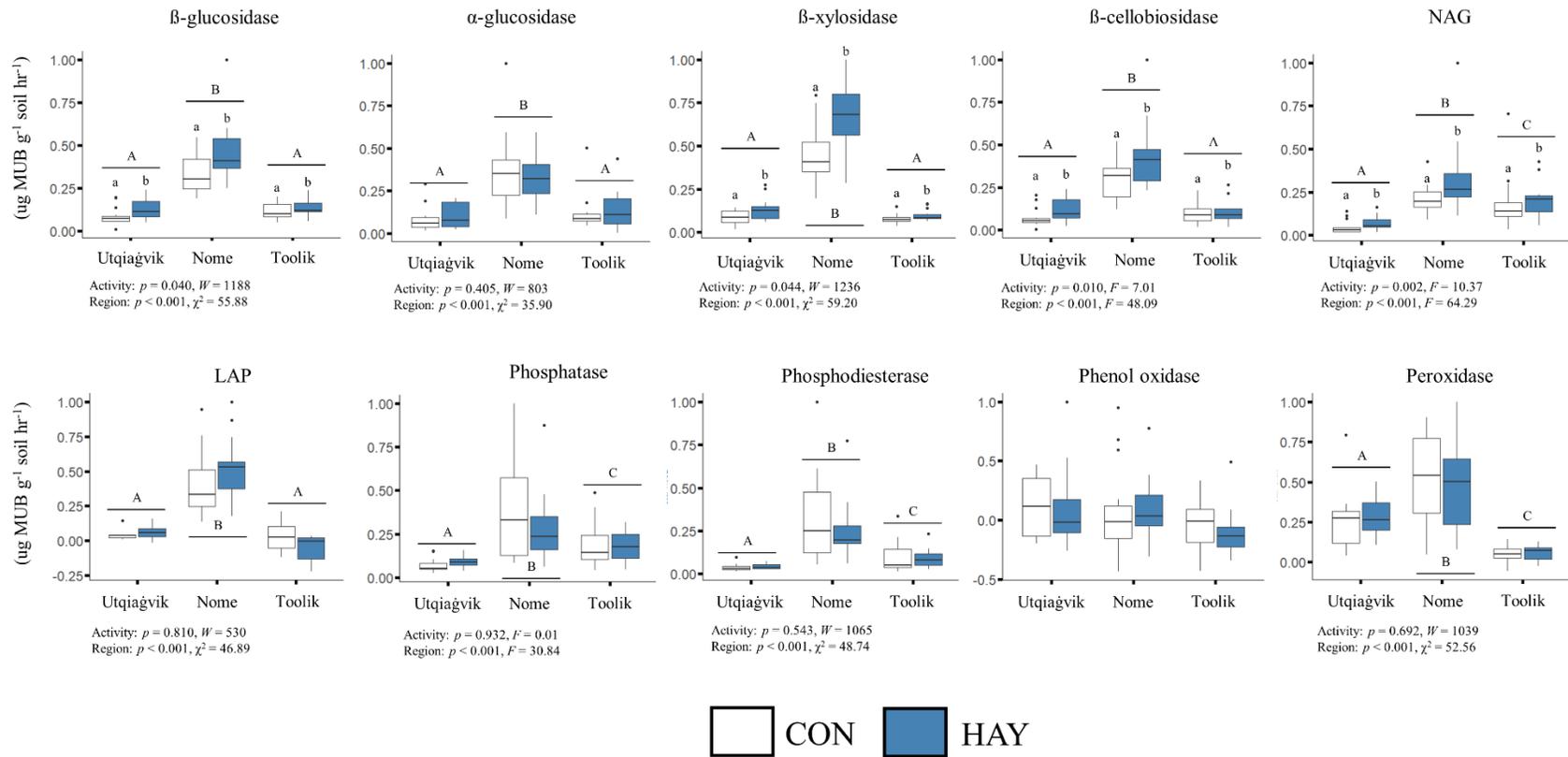
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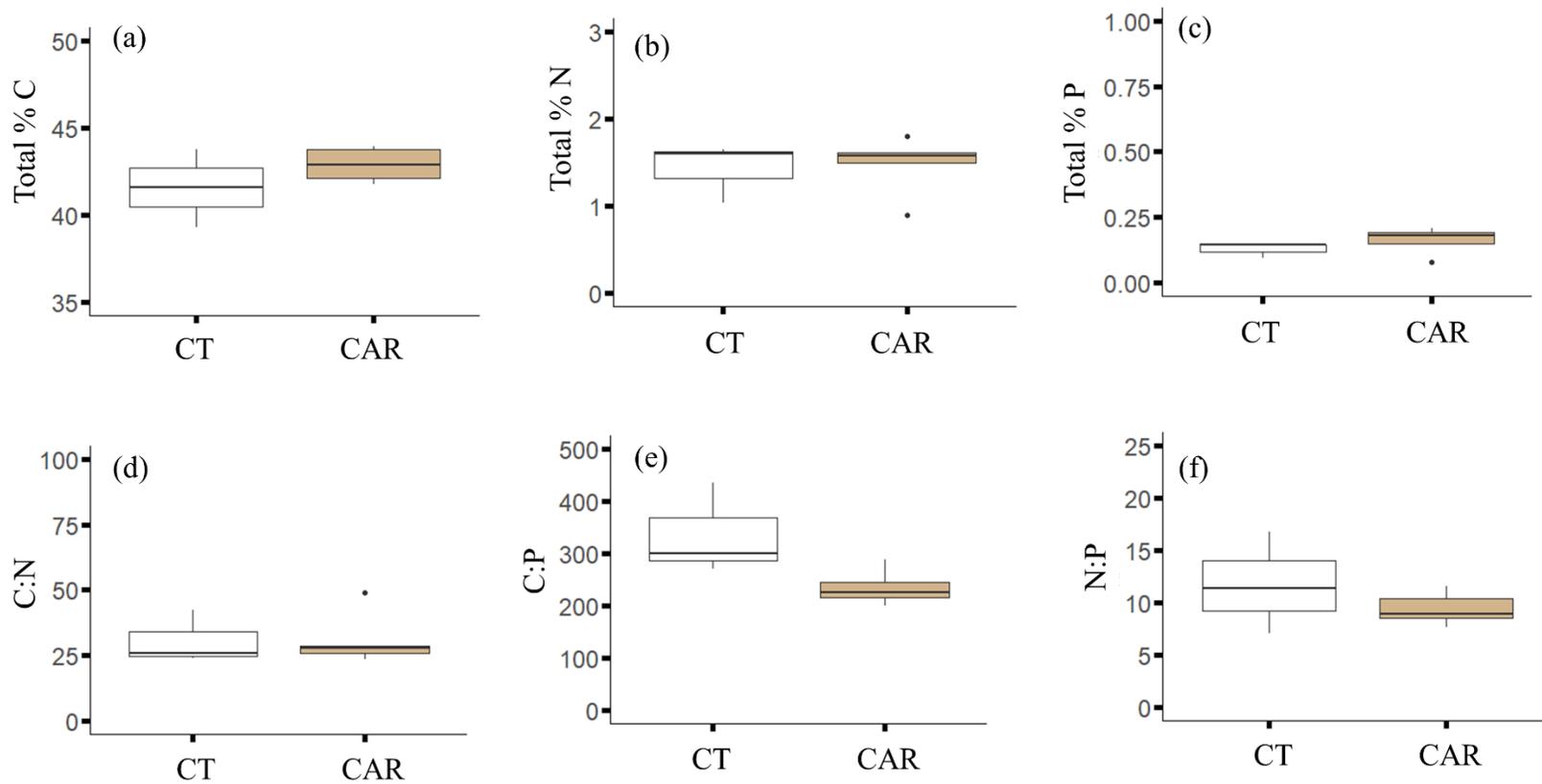
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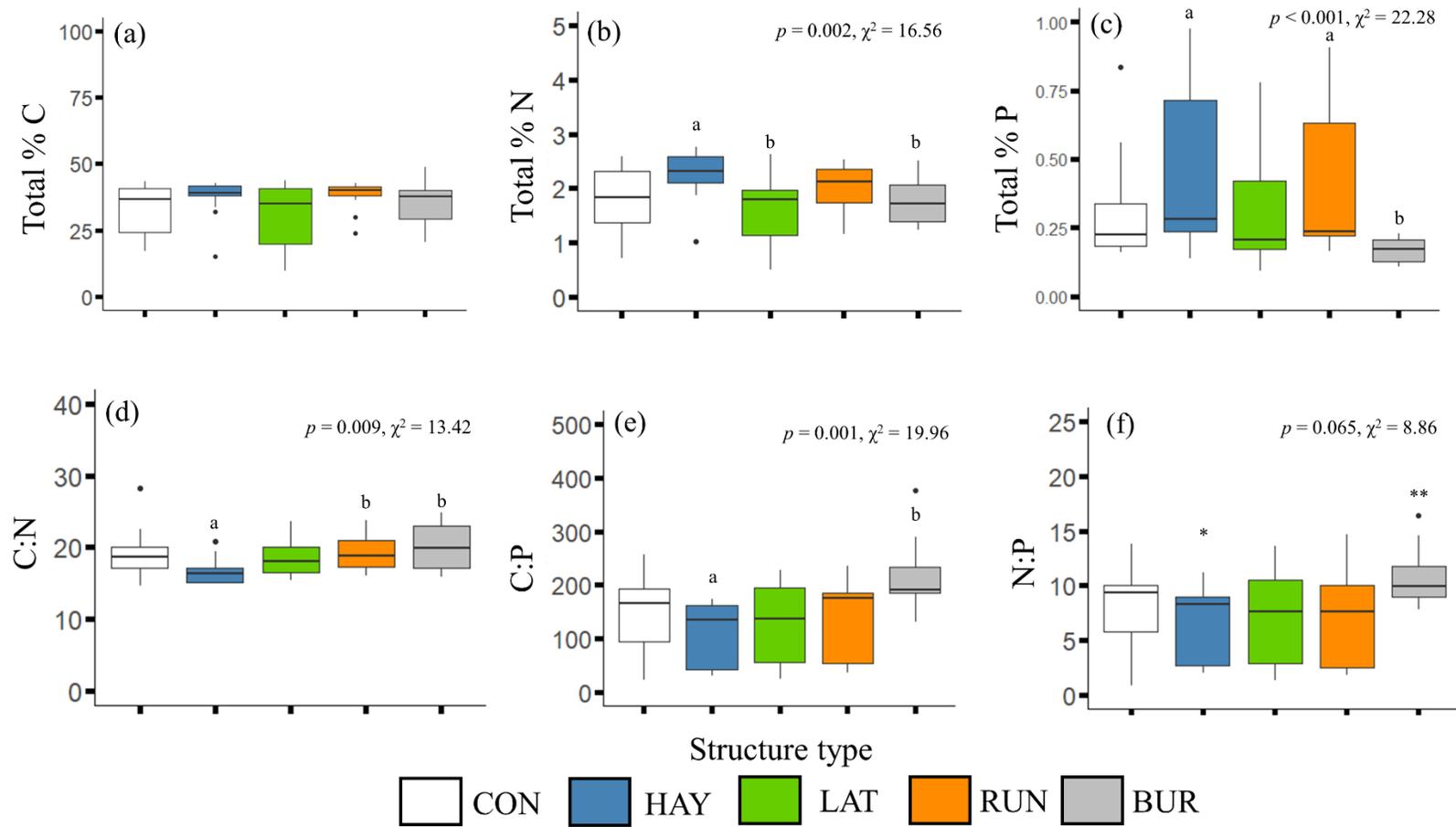
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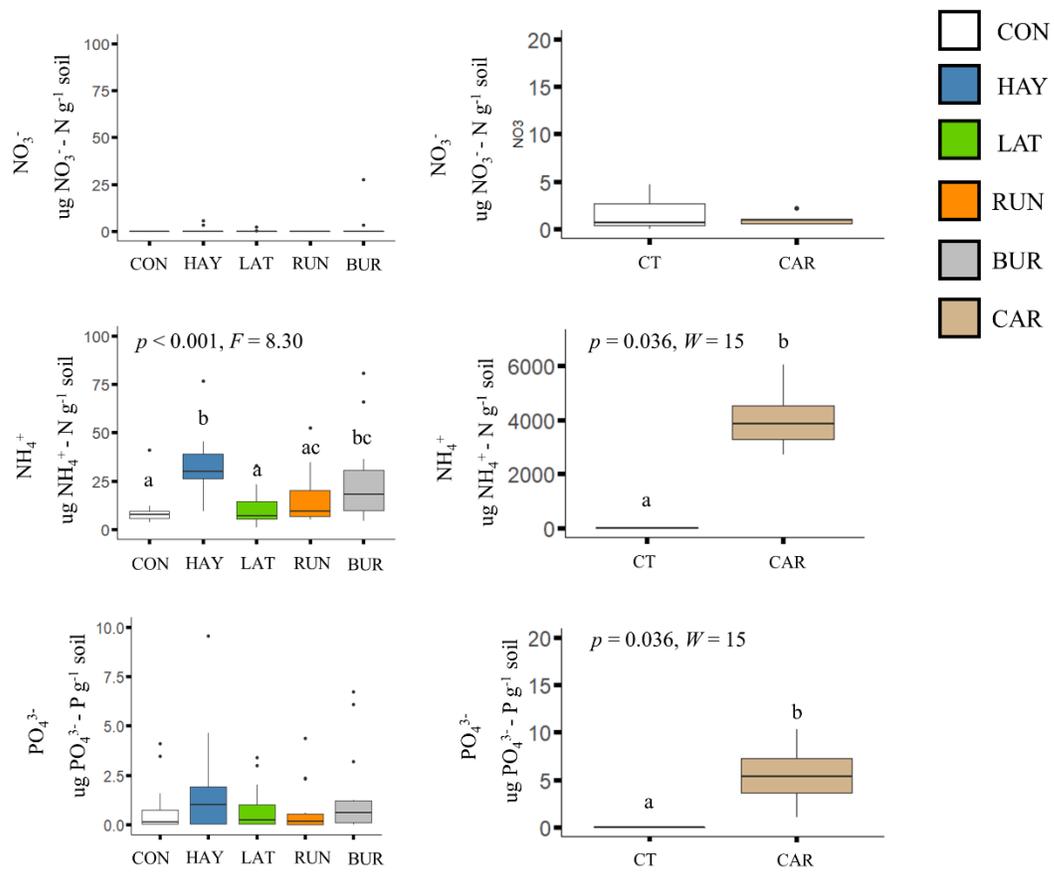
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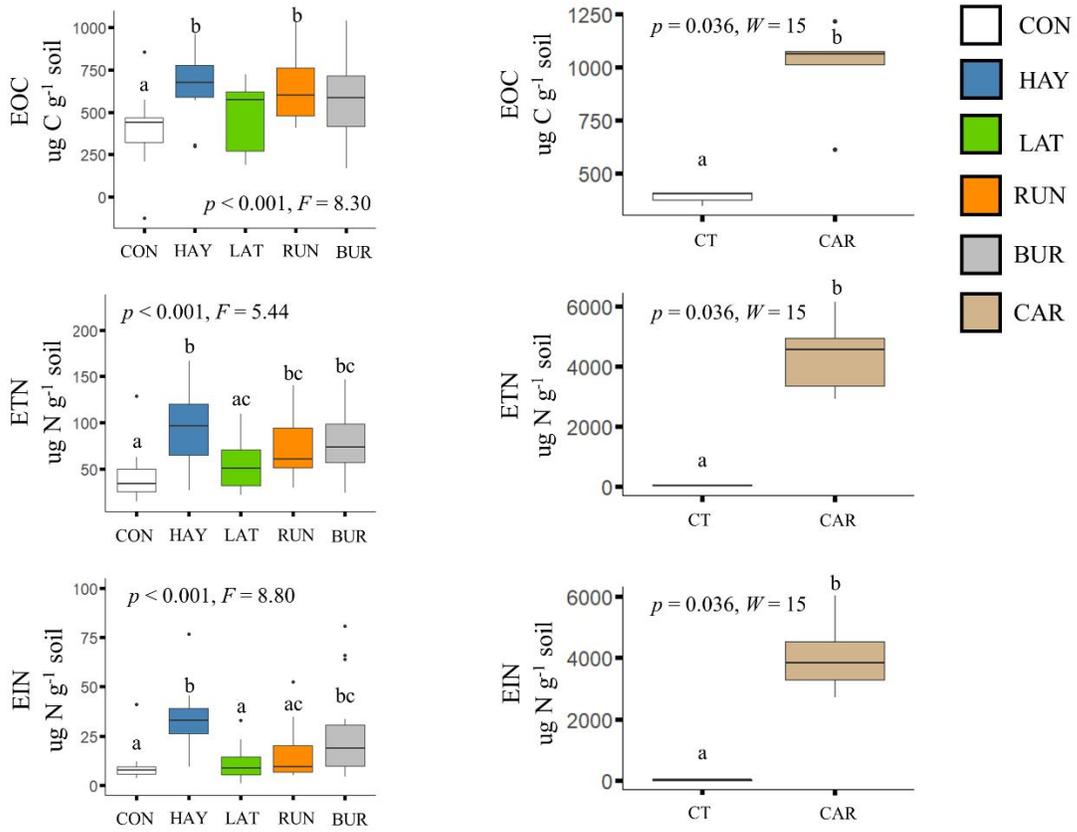
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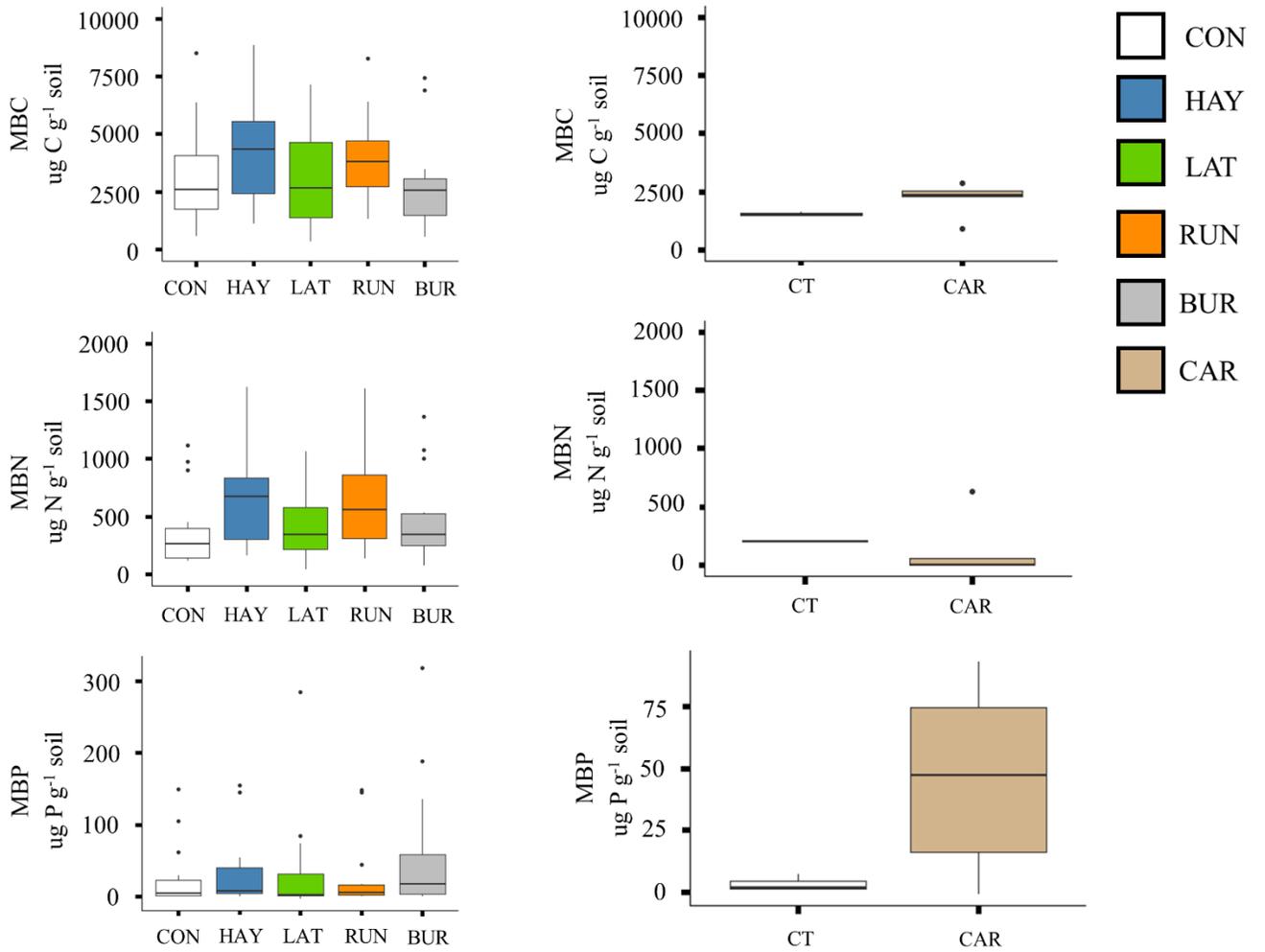
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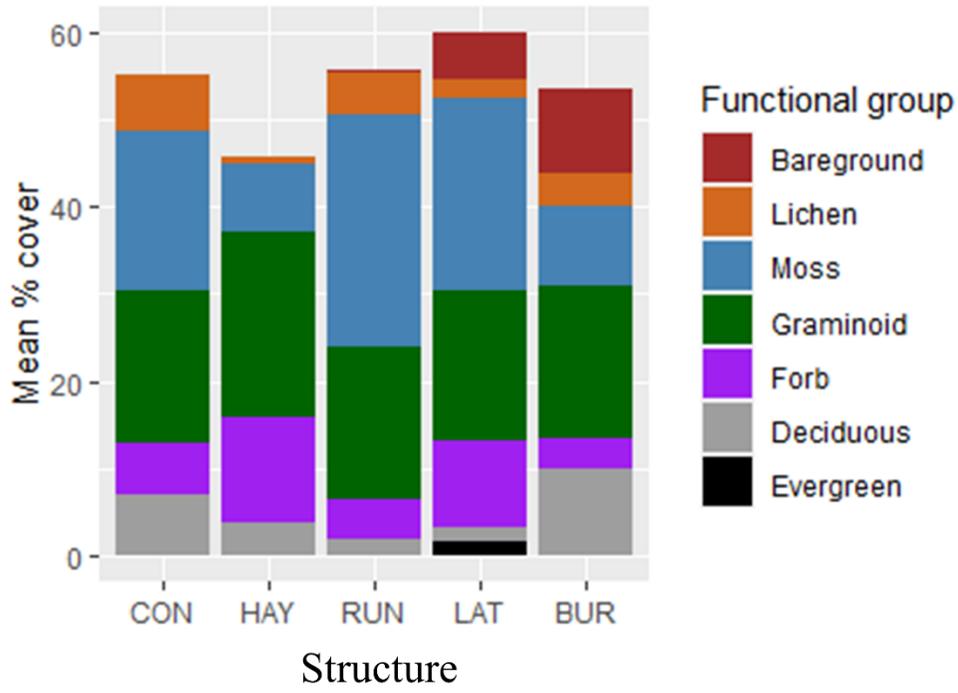
Supplemental Figure 3.11



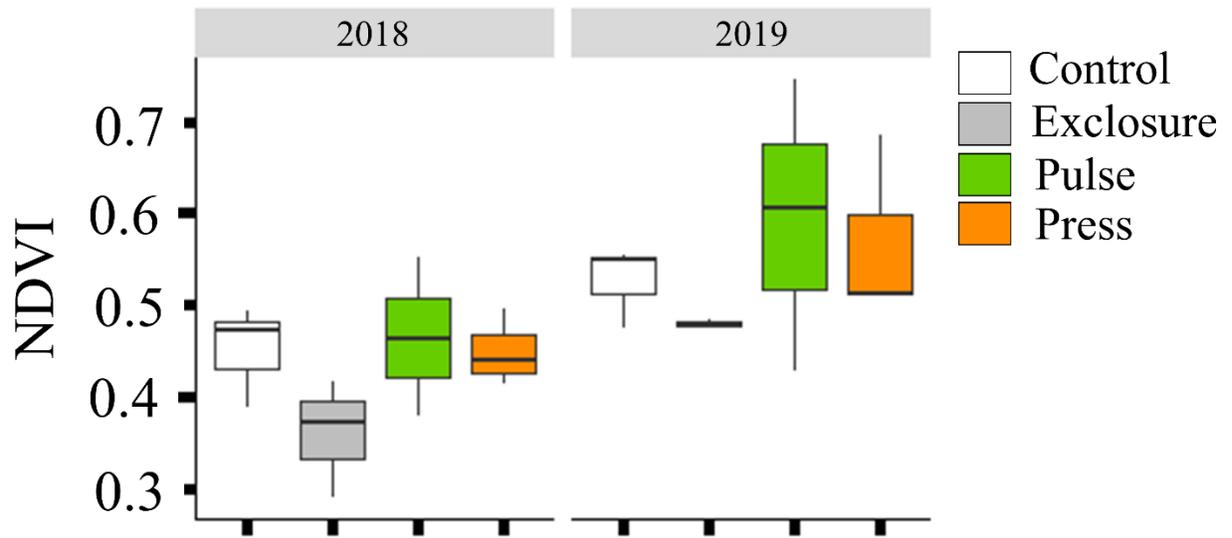
Supplemental Figure 3.12



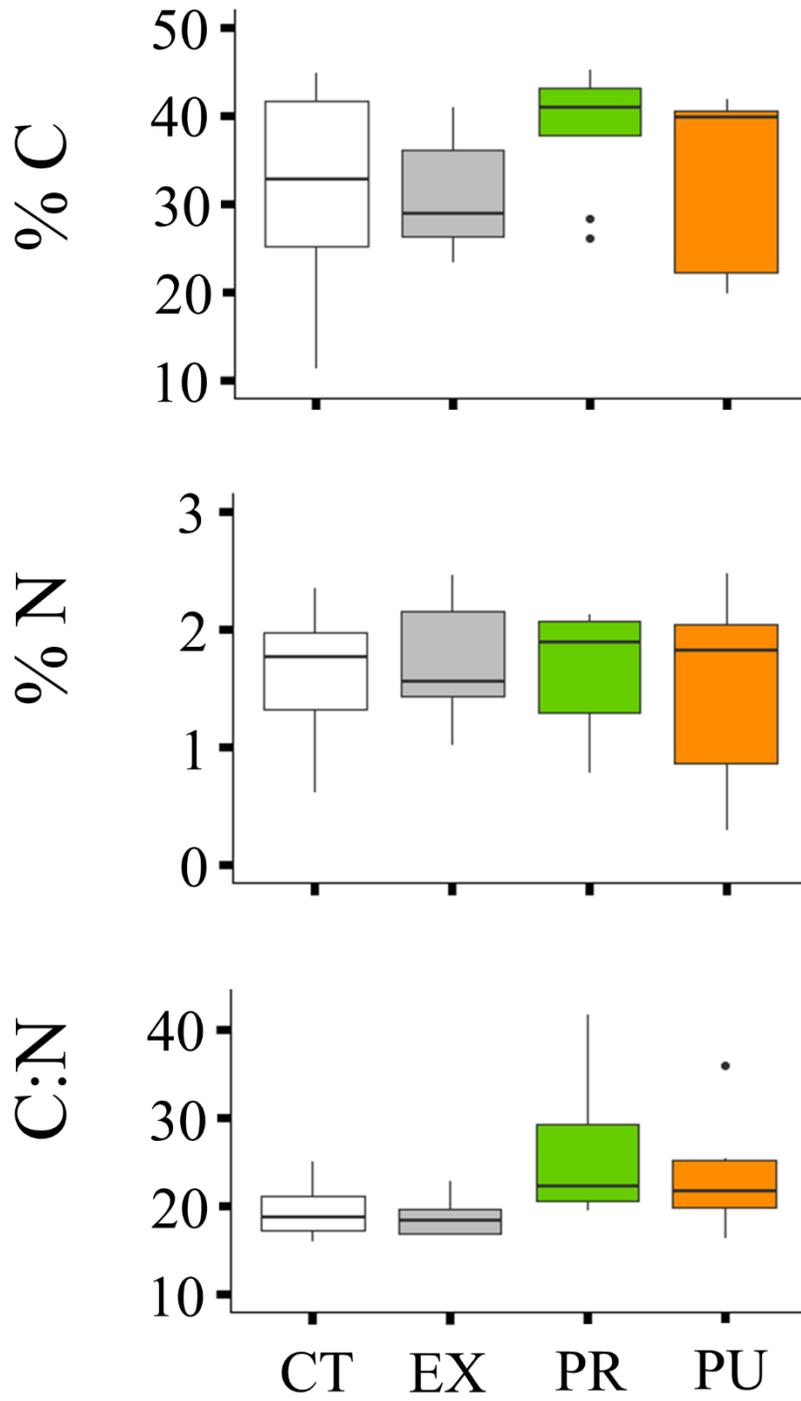
Supplemental Figure 3.13



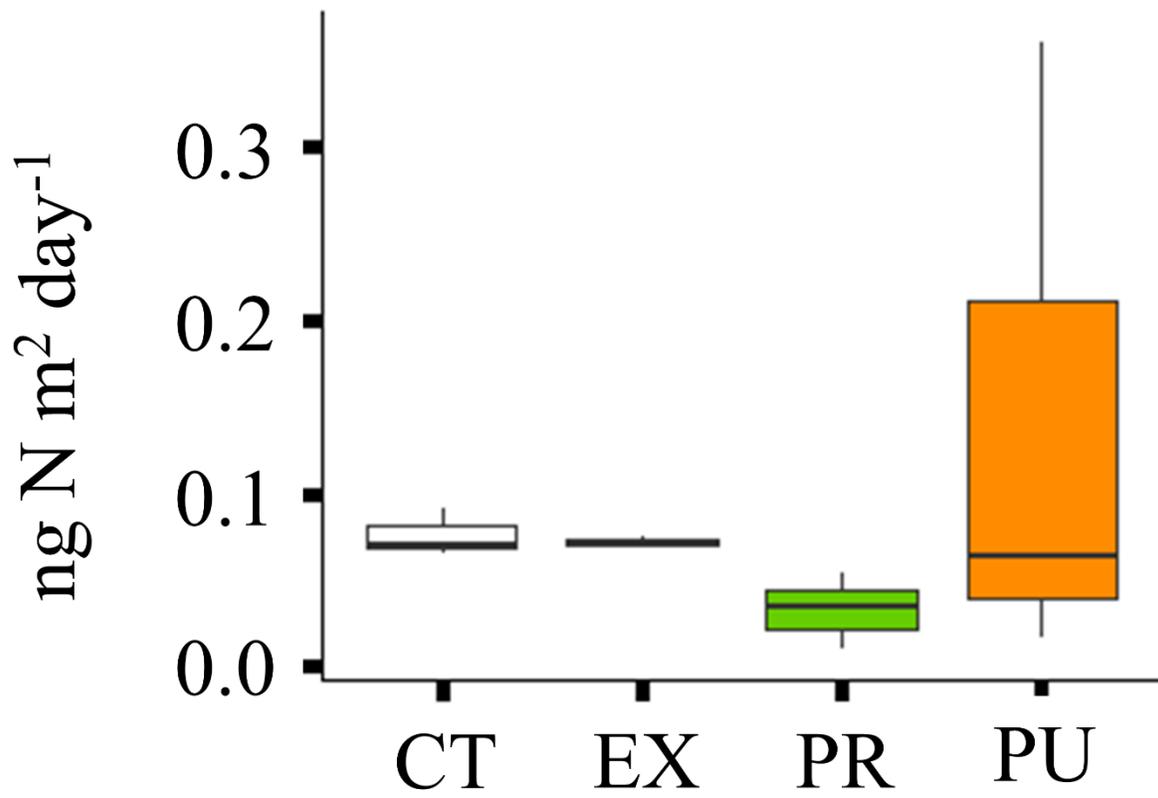
Supplemental Figure 4.1



Supplemental Figure 4.2



Supplemental Figure 4.3



Vita

Austin Roy received a B.S. in Wildlife (emphasis in Management and Conservation) from Humboldt State University in 2012. Before coming to the University of Texas at El Paso (UTEP), Austin worked for several wildlife research and management groups including the California Department of Fish & Wildlife, University of California, Davis, and the U.S. Forest Service – Pacific Southwest Research Station. While at UTEP, Austin was a Graduate Research Assistant under Dr. Jennie McLaren and served as a Graduate Teaching Assistant for the following courses: Organismal Biology, Ecology, Plant Ecology. Austin has published research examining small mammal ecology in *Arctic; Antarctic, and Alpine Research; Western Wildlife; Vector Borne and Zoonotic Diseases; PLoS ONE; Journal of Wildlife Diseases; and Journal of Medical Entomology*. Furthermore, Austin has presented his research at several professional and academic conferences, including *The Wildlife Society, 50th Annual Arctic Workshop, Texas Society of Mammalogists (TSM), Ecological Society of America, Ukpeagvik Inupiat Corporation Science Division, The Western Section of The Wildlife Society, Explorit Science Series*; and has won an award for Best Graduate Student Poster at TSM. Austin was also a co-founder and served as Treasurer for the Biology, Environmental, and Engineering Graduate Student Group (BEE) at the University of Texas at El Paso, whose goal is to engage with and advocate for graduate students.

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