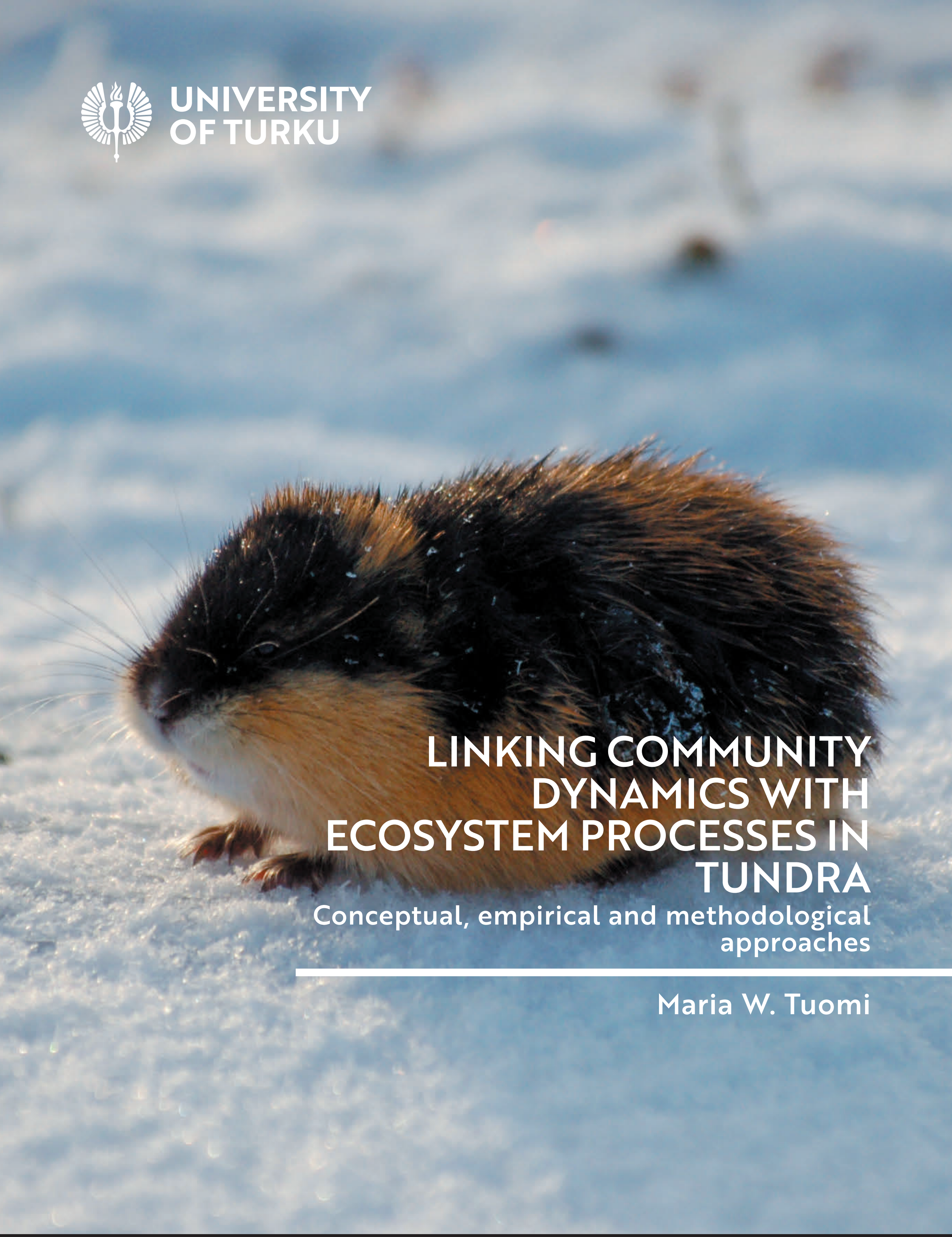

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LINKING COMMUNITY DYNAMICS WITH ECOSYSTEM PROCESSES IN TUNDRA

Conceptual, empirical and methodological approaches

Maria W. Tuomi

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University of Turku

Faculty of Science and Engineering
Department of Biology
Section of Ecology
Doctoral Programme in Biology, Geography and Geology (BGG)

Supervised by

Prof. Kari Anne Bråthen
The Arctic University of Norway

Prof. Hanna Tuomisto
University of Turku

Prof. emeritus Lauri Oksanen
The Arctic University of Norway
University of Turku

Reviewed by

Prof. Riikka Rinnan
University of Copenhagen

Prof. Kari Klanderud
Norwegian University of Life Sciences

Opponent

Prof., Philip Wookey
University of Stirling

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To all who feel like giving up: Don’t

Äpille, joka opetti lapselle metsän saloja

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Faculty of Science and Engineering
Department of Biology
Section of Ecology
MARIA W. TUOMI: Linking community dynamics with ecosystem processes in tundra – Conceptual, empirical and methodological approaches
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ABSTRACT

In low-productive tundra systems, both small and large herbivores exert strong control over plant biomass and community composition. They may also modulate ecosystem process rates, including availability and cycling of nutrients and soil decomposition rates. However, evidence from different tundra systems is highly idiosyncratic, with reports of both deceleration and acceleration of ecosystem process rates in response to herbivore presence. Acceleration of process rates contradicts dynamics predicted by prevailing theories of herbivore-plant-soil interactions, which assume primacy of selective foraging and defection/urination in driving ecosystem process rates. In many tundra systems, such assumptions should therefore be re-evaluated. In my thesis, I used empirical (Chapters I and II) and conceptual (Chapters II and IV) approaches to address this research gap. I studied the effects of prominent activities small rodents and large ungulates - non-selective dwarf-shrub decimation and trampling, respectively - which up until now have barely been addressed in tundra. The dearth of research on spatially explicit interlinkages between small rodents, plants and soil may partially result from a lack of cost-efficient methods to estimate in situ rodent abundances. Therefore, I developed a novel method to study small rodent populations (Chapter III) that could augment current methods and allow addressing small rodent-plant-soil dynamics with small spatial grain and large extent.

I provided both observational and experimental evidence that small rodents decimate poorly palatable dwarf-shrubs during their population peaks. An exceptionally strong vole and lemming peak resulted in severe plant decimation across a productivity gradient, as temporarily relaxed top-down control of predators allowed for strong herbivore-plant interactions in the productive tundra-forest ecotone (Chapter I). I showed, for the first time, that such decimation of dominant dwarf-shrubs can promote higher ecosystem process rates, indicated by increased community-level plant N content, increased soil inorganic N content and increased litter decomposition rates (Chapter II).

In Chapter III, I assessed the ability of a near-infrared reflectance spectroscopy (NIRS) -based method to identify individual rodent fecal pellets to species. The model predictions were highly accurate especially with feces exposed to ambient weather. Moreover, I showed that a model based on feces from two regions predicted accurately samples from both regions, indicating feasibility of inter-regional or circumpolar calibrations.

Ungulate trampling may contribute to tundra state-shifts towards accelerated process rates, yet little empirical knowledge and no conceptual synthesis exists of trampling effects on tundra soils. In Chapter IV, I review original papers on trampling effects on tundra soil structure, biota, microclimate and biogeochemistry, and present a conceptual model on ungulate trampling effects on tundra soils. Trampling may drive changes in process rates by e.g. compacting soil, altering soil fauna and microbiota, and by modulating plant-soil feedbacks. In tundra, trampling may accelerate process rates especially by reducing insulating bryophyte cover, which increases soil temperatures and promotes temperature-limited microbial activity and decomposition.

I conclude that Arctic herbivores are likely to alter ecosystem process rates through both trophic and non-trophic activities, the latter being overlooked in prominent theories. Especially non-trophic or non-selective activities may be key to accelerated process rates. A realistic view on herbivore effect on tundra ecosystem function now and under a warming climate needs to build on a better understanding of small rodent and ungulate effects on soil, as well as an explicit consideration of all salient herbivore activities and their multiple roles.

KEYWORDS: reindeer, small rodents, NIRS, mineralization, trampling, non-trophic interactions, high population density

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TIIVISTELMÄ

Pienet ja suuret kasvinsyöjät kontrolloivat voimakkaasti kasvillisuuden biomassaa ja yhteisörakennetta perustuotannoltaan alhaisissa tundraekosysteemeissä. Kasvinsyöjät vaikuttavat myös ekosysteemiprosesseihin ja niiden nopeuteen, kuten ravinteiden saatavuuteen ja kiertoon sekä orgaanisen aineksen hajotustoimintaan maaperässä. Tutkimustulokset tundralta viittaavat siihen, että kasvinsyöjät voivat sekä nopeuttaa että hidastaa ekosysteemiprosesseja; prosessien nopeutuminen on kuitenkin ristiriidassa vallitsevien, kasvinsyöjien kasvillisuus- ja ekosysteemivaikutuksia käsittelevien teorioiden kanssa. Prosessien hidastumista ennustavien teorioiden taustalla on oletus siitä, että valikoiva ravinnonkäyttö ja ulosteet/virtsa ovat kasvinsyöjien vaikutuksia välittävistä mekanismeista voimakkaimmat. Monilla tundra-alueilla nämä taustaoletukset on kuitenkin syytä kyseenalaistaa. Väitöskirjassani keskityin tähän tutkimusaukkoon käyttäen empiirisiä (luvut I ja II) ja käsitteellisiä (luvut II ja IV) lähestymistapoja. Tutkin sekä pienjyrsijöiden ei-valikoivan varpujen katkomisen että suurten laiduntajien tallauksen (ns. ei-trofinen mekanismi) kasvillisuus- ja ekosysteemivaikutuksia, joita on tätä ennen tutkittu tundralla vain vähän. Kehitin lisäksi uuden, kustannustehokkaan menetelmän pienjyrsijäpopulaatioiden tutkimukseen (luku III): menetalmä voi mahdollistaa pienjyrsijöiden, kasvillisuuden ja maaperän *in situ* vuorovaikutusten tutkimisen ja parantaa jyrsijäpopulaatioiden seurannan maantieteellistä kattavuutta ja tarkkuutta.

Väitöskirjani havainnollinen ja kokeellinen aineisto osoitti että pienjyrsijät katkovat ravintona heikkolaatuisia tai syömäkelvottomia varpuja populaatiohuippujensa aikana. Harvinaisen voimakas myyrä- ja sopulihuippu johti näiden varpujen hävitykseen maisematasolla ja halki tuottavuusgradientin, sillä petojen heikko ja viivästynyt saalistusvaste mahdollisti kasvinsyöjien voimakkaan vaikutuksen kasvillisuuteen myös tuottavassa puurajan ekotonissa (luku I). Osoitin ensimmäistä kertaa että tällainen dominanttien varpujen hävittäminen voi nopeuttaa ekosysteemiprosesseja, ts. johtaa kasviyhteisön korkeampaan typen pitoisuuteen, maaperän korkeampaan epäorgaanisen typen pitoisuuteen ja kohonneeseen karikkeen mikrobihengitykseen (luku II).

Luvussa III osoitin että NIR-spektroskopian (NIRS) avulla pienjyrsijöiden yksittäiset papanat voi tunnistaa suvun ja lajin tarkkuudella. Kehittämäni malli tunnisti erityisen hyvin papanat, joita oli kokeellisesti altistettu sääoloille: tämä viittaa menetelmän soveltuvan maastosta kerättyihin papanoihin. Lisäksi osoitin että eri alueilta kerättyihin papanoihin perustuva malli tunnistaa papanat molemmilta alueilta: laajan alueellisen tai sirkumpolaarisen mallin kehittäminen voi siis olla mahdollista.

Laiduntajien tallaus voi aiheuttaa ekosysteemitilan muutoksia ja ekosysteemiprosessien nopeutumista tundralla, mutta aiheesta on vain vähän empiiristä tietoa eikä yhtään käsitteellistä synteesiä. Luvussa IV tein kirjallisuuskatsauksen tallauksen vaikutuksista tundran maaperän rakenteeseen, eliöstöön, mikroilmastoon ja biogeokemiaan ja kehitin käsitemallin laiduntajien tallauksen maaperävaikutuksista. Tallaus voi vaikuttaa ekosysteemiprosesseihin tiivistämällä maata, muuttamalla maaperäeliöstön yhteisöjä ja muokkaamalla kasvi-maaperävuorovaikutuksia. Tallaus voi nopeuttaa ekosysteemiprosesseja etenkin ohentamalla eristävän sammalkerroksen paksuutta, mikä voi nostaa maaperän lämpötilaa ja johtaa lämpötilarajoitteisen mikrobitoiminnan nopeutumiseen.

Johtopäätöksenäni esitän että arktiset kasvinsyöjät voivat muokata ekosysteemiprosesseja paitsi valikoivan ravinnonkäytön ja ulosteiden/virtsan kautta, myös tutkimieni ei-valikoivien ja ei-trofisten mekanismien välityksellä. Tällaiset ei-trofiset tai ei-valikoivat mekanismit voivat olennaisesti vaikuttaa ekosysteemiprosessien nopeutumisen taustalla. Realistisen kuvan kasvinsyöjien vaikutuksesta tundran ekosysteemien toimintaan – nyt ja lämpenevässä ilmastossa – on siksi huomioitava myös ei-trofiset ja ei-valikoivat mekanismit, ja tunnistettava kasvinsyöjien moninaiset roolit osana tundran ekosysteemejä.

ASIASANAT: poro, pienjyrsijät, NIRS, mineralisaatio, tallaus, ei-trofiset vuorovaikutukset, korkea populaatiotiheys

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List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

- I Hoset KS, Ruffino L, **Tuomi M**, Oksanen T, Oksanen L, Mäkynen A, Johansen B, Moe T: Changes in the Spatial Configuration and Strength of Trophic Control Across a Productivity Gradient During a Massive Rodent Outbreak. *Ecosystems.* 2017; 20(8): 1421-1435.
- II **Tuomi M**, Stark S, Hoset KS, Väisänen M, Oksanen L, Murguzur FJA, Tuomisto H, Dahlgren J, Bråthen KA: Herbivore Effects on Ecosystem Process Rates in a Low-Productive System. *Ecosystems*. 2019; 22(4): 827-843.
- III **Tuomi M**, Murguzur FJA, Hoset KS, Soininen EM, Vesterinen E, Utsi TAa, Kaino S, Bråthen KA: Novel frontier in wildlife monitoring: identification of small rodent species from faecal pellets using Near-Infrared Reflectance Spectroscopy (NIRS). *Manuscript*.
- IV **Tuomi M***, Väisänen M*, Ylänne H, Brearley FQ, Barrio IC, Bråthen KA, Eischeid I, Forbes BC, Jónsdóttir IS, Kolstad AL, Macek P, Petit Bon M, Speed JDM, Stark S, Svavarsdóttir K, Thórsson J, Bueno CG: Stomping in silence: about time to consider ungulate trampling effects on tundra soils. *Manuscript*.

*equal contribution

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1 Introduction

Arctic tundra ecosystems cover the circumpolar areas between the boreal forests and the Arctic Ocean, and comprise ca. 5% of the world's terrestrial biomes. Tundra is characterized by low temperatures and resource availability, which constrains both primary production and microbial decomposition (Chapin et al., 1996; Schimel et al., 1996), leading to low rates of element cycling and vast below-ground carbon pools (Davidson and Janssens, 2006; Weintraub and Schimel, 2003). Alongside strong abiotic constraints on plant growth, also resident forage-limited herbivores control vegetation biomass and modulate species composition and ecosystem processes (Aunapuu et al., 2008; Bernes et al., 2015; Olofsson et al., 2004a).

An abundance of past theoretical and conceptual work (Augustine and McNaughton, 1998; Pastor and Naiman, 1996; Schmitz, 2008) has dealt with herbivore modulation of ecosystem processes, specifically herbivore-plant and herbivore-plant-soil interactions in low-productive tundra systems, yet many idiosyncratic effects of herbivores on plants and soil remain unexplained (Bernes et al., 2015; Stark et al., 2015). While in low-productive systems mammalian herbivores are generally expected to slow down nutrient cycling (Bardgett and Wardle, 2003; Sitters and Andriuzzi, 2019), studies across the circumpolar tundra frequently report opposite effects (Olofsson et al., 2001, 2004a; van der Wal, 2006). In my PhD thesis, I focus on the frequently observed strong interactions between herbivores and poorly palatable plants that dominate many arctic vegetation communities (Chapin et al., 1996; Walker et al., 1994), and these dynamics' consequences for ecosystem function. Specifically, I ask how different activities of dominant arctic herbivores can affect ecosystem processes by providing conceptual (Chapters II and IV), empirical (Chapters I-II) and methodological (Chapter III) insights.

In the thesis, I use acceleration vs. deceleration of ecosystem process rates (cf. Bardgett and Wardle, 2003), including changes in primary production, soil nutrient pools and rates of nutrient turnover and microbial activity, as the main theoretical context for developing the conceptual understanding of herbivore modulation of plant-soil feedbacks and interactions. I will at times reference stoichiometric theory in discussing my findings, as stoichiometric mismatches explain both herbivore foraging choices (Simpson et al., 2010), as well as herbivore effects on element cycling (Cherif and Loreau, 2013); however, as I have not explicitly measured C:N/P ratios, the stoichiometric inference is limited. While the herbivore-plant-soil interactions could also be framed in the context of successional change (Bardgett and Wardle, 2003; Pastor and Naiman, 1996), a recent revision of the successional theory suggests that understanding of the complex role of herbivores modulating successional drivers is still only emerging (Meiners et al., 2015; Pulsford et al., 2016). Even so, without direct interpretation of the work within successional theory, I will explore how herbivores alter site conditions and plant performance, i.e. two of three major drivers of vegetation community change over time (Meiners et al., 2015).

Despite the obvious interlinked nature between trophic regulation of herbivore populations and plant-soil interactions, the co-consideration of above-ground trophic dynamics and herbivore control of plant-soil interactions is still rather uncommon (Ims et al., 2013). The current work is one contribution to address this gap, and to explain some major discrepancies between prevailing theories and empirically observed dynamics in low-productive tundra systems. In order to do this, I adopt a further theoretical, and functional, context, as I in particular consider the non-selective and non-trophic activities of herbivores (Kéfi et al., 2012; Sitters and Andriuzzi, 2019), and juxtapose those dynamics with previously reported effects of selective foraging and excretion, which are far more extensively covered in literature (Augustine and McNaughton, 1998; Bakker et al., 2004; Bardgett and Wardle, 2003).

1.1 Setting the stage: strong herbivore effects on vegetation in Fennoscandian tundra

Many arctic above-ground trophic webs are characterized by low numbers of dominant species and feature high-amplitude cyclic and chaotic population fluctuations of predators and herbivores (Ims and Fuglei, 2005; Reid et al., 2013). Especially reindeer and small rodents, focal herbivores of the thesis (Fig. 1), are considered keystone herbivores, as they control plant biomass and support avian and mammalian predators (Forbes and Kumpula, 2009; Ims and Fuglei, 2005). Empirical and conceptual work over the past decades has focused on determining drivers of cyclic and chaotic fluctuations of uniform guilds of vertebrate herbivores and their predators, and their interactions with aboveground vegetation. Hairston et al. (1960), in their Green World Hypothesis (GWH), proposed that herbivores would generally decimate green plant biomass if it was not for predators keeping herbivore populations in check. The strong herbivore-plant interactions implied in the GWH have been questioned, as in many systems constitutive or induced plant defenses may severely constrain the ability of herbivores to limit plant biomass (Polis and Strong, 1996). Inspired by observations from sub-arctic tundra, GWH was later developed in the context of primary productivity gradients and the endotherm trophic guilds. Put simply, the Exploitation Ecosystem Hypothesis (EEH) by Oksanen et al. (1981) proposes that in those low-productive systems which lack substantial predator subsidies (e.g. marine resources; Legagneux et al., 2012), primary productivity will not sustain sufficient numbers of herbivores to maintain an abundant specialist predator guild. Hence, these systems are inherently characterized by strong and fluctuating herbivore-plant interactions, where increasing productivity will translate to increasing herbivore biomass, plant biomass remaining constant. With increasing primary productivity, the biomass of herbivores will eventually cross a threshold to support abundant resident predators able to control herbivore numbers, which in turn will initiate a trophic cascade and dynamics concordant with the GWH, where plants are released from herbivore control (Aunapuu et al., 2008).

The EEH has strong empirical support in low-productive tundra ecosystems in e.g. sub-arctic Fennoscandia (Aunapuu et al., 2008; Dahlgren et al., 2009a), where 3-5 year vole cycles and ca. 10 year lemming fluctuations across the forest-tundra ecotone display a change from predator to prey dynamics with increasing primary productivity (Ekerholm et al., 2001). In addition to small rodents, also wild reindeer populations exhibit 50 year density fluctuations driven by forage availability (Reid et al., 2013), and conform largely to two-trophic level dynamics of EEH (Newton et al., 2014; Oksanen and Oksanen, 2000). Hence, unproductive tundra landscapes are often characterized by strong herbivore control of above-ground plant biomass, exerted e.g. during population peak phases when herbivores are prone to over-exploit especially critical winter forage resources.

1.2 Herbivore foraging in tundra

The potential of herbivores to deplete or control plant communities in two-trophic level systems, e.g. in many low-productive tundra systems, has been a subject of a multi-decadal debate (see e.g. Schmitz, 2008). Predominantly, these dynamics have been interpreted through constitutive or induced anti-herbivore defences and nutritional or stoichiometric constraints of herbivore foraging (Elser et al., 2000; Simpson et al., 2010). In N-limited tundra systems, carbon-based secondary metabolites are by far most common, and especially phenolics and stilbenes are present in high concentrations in leaves of dominant evergreen dwarf shrubs (Herms and Mattson, 1992; Stamp, 2003). In addition, high and continuous grazing pressure may induce silica-based defences in graminoids (Massey et al., 2008), yet recent evidence has questioned the prevalence of induced Si-based defences in tundra plants grazed by small rodents (Soininen et al., 2013a).

From the herbivore side, plants represent forage sources of varying quality and availability (Schmitz, 2008). Discarding a simplistic view of defended and non-defended plants, palatability is likely relative and determined jointly by the dietary quality (incl. secondary metabolites) of the plant, herbivore stoichiometric needs and the alternative forage present in the foraging patch (Elser et al., 2000; Schmitz, 2008; Simpson et al., 2010). Stoichiometric theory indicates that herbivores should aim to optimize their forage intake to match their element ratio, i.e. C:N and C:P, needs. In practice this means selective feeding on plants with low C:N ratio, high protein and low phenolic content, such as forbs and deciduous leaves (Cornelissen et al., 2004; Elser et al., 2000). However, diet quality is a relative concept, as for instance arctic lemmings have evolved to survive on relatively high C:N/P forage (Oksanen et al., 2008), while also reindeer and caribou survive winter on cryptogams (Danell et al., 1994). Recent research in arctic small rodent forage selection has revealed that voles and lemmings are generalists (at least during summer) with clear species-specific forage preferences, yet a flexible food selection (Soininen et al., 2013b, 2013c). Voles and lemmings tend to select for palatable species according to their abundance, and use what is available also when forced during population peaks into secondary habitats with poor quality forage (Soininen et al., 2013b, 2013c).

Alas, palatability is not the only consideration for foraging herbivores. In tundra, forage availability can be affected by abiotic conditions preventing access to, or limiting time to forage on a given resource (Korslund and Steen, 2006; Schmitz, 2008). Seasonal variation in forage availability is the most prominent example of this, as during winter only lower quality food is available and makes up higher proportions of diet (Shipley et al., 2009); meeting nutritional needs during winter may therefore require increased mobility (Simpson et al., 2010). Additionally, fear of predation and subsequent predator avoidance behaviours can alter foraging behaviour and in extreme cases lead to trophic cascades (Schmitz et al., 2004).

From the plant side, herbivores can remove and damage plant tissues, leading to mortality or reduced growth and reproductive success of individual plants, which may alter plant interspecific positive and negative interactions (Augustine and McNaughton, 1998; Lortie et al., 2004). Plant resistance to herbivory has been long conceptualized as (partial) trade-offs between tolerance and avoidance of herbivory (Briske, 1996). Plants with high tolerance to herbivory display physiological and morphological traits that allow for rapid regrowth after defoliation and damage (Briske, 1996; Strauss and Agrawal, 1999). In turn, avoidance strategies involve both chemical and mechanical defences (see above). In addition to levels of defence chemicals, also plant nutrient content may either increase or decrease in response to herbivory (Bardgett and Wardle, 2003; Strauss and Agrawal, 1999), where increased N levels generally link with grazing tolerance. In tundra, responses vary, but studies have reported mainly decreasing nutrient levels or no responses (Eckstein et al., 1999; Stark and Grellmann, 2002).

1.3 Herbivore modulation of plant-soil interactions

Herbivore-plant interactions play out in complex ecosystems, where strong effects of herbivores on plants are mediated via the soil system. Put in another way, herbivores are likely to not only modulate plant communities, but the function of the entire ecosystem owing to strong interlinkages between plants, soil biota and biogeochemical cycling (Sitters and Andriuzzi, 2019). By inducing changes in plant community composition or plant chemistry, and by returning digested plant biomass as dung and urine (Fig. 1; see below), herbivores alter the chemical composition and decomposability of litter entering the soil system (Augustine and Frank, 2001; Bakker et al., 2009; Barthelemy et al., 2015). Increased or decreased rates of litter decomposition control rates and time lags with which nutrients, especially N and P, become available for microbes and plants (Hobbie, 2015). Hence, plant community-level leaf chemistry (sensu Garnier et al., 2004) is tightly coupled with decomposition, mineralization and immobilization rates (Cherif and Loreau, 2013; Cornelissen et al., 2004; Hobbie, 2015). Long-term litter feedbacks have therefore been long considered as prime drivers of accelerated or decelerated nutrient turnover (Bardgett and Wardle, 2003; Pastor and Naiman, 1996).

In addition, plant functional composition affects soil decomposer and fauna community composition, including e.g. symbiotic microbes, root herbivores and pathogens, with cascading effects on soil biotic processes governing decomposition, soil nutrient availability, and carbon dynamics (Sitters and Andriuzzi, 2019). For instance, graminoid-dominated plant communities are linked with lower fungi:bacteria ratio than dwarf-shrub heaths (Egelkraut et al., 2018; Stark et al., 2012). Plant-soil feedbacks (PSFs) encompass complex interactions between plants and soil biota, which may promote species dominance and invasion (positive PSFs), or species replacement and turnover/coexistence (negative PSFs) (Bauer et al., 2015). However, herbivore effects may either modulate or even outweigh effects of PSFs (Heinze and Joshi, 2018): in tundra, herbivores appear to exert stronger control on locally stable graminoid-dominated communities via modulating abiotic soil conditions, and less via biotic PSFs (Egelkraut et al., 2018). Changes in plant community composition and damages to plants may also directly alter root exudation (i.e. inputs of labile C to soil microbes; Hafner et al., 2012), soil aggregate formation and moisture (Six et al., 2004). In addition, any herbivore-induced direct changes in soil physical and microclimatic structure, i.e. niche of soil biota, could also alter soil biological processes and biologically governed soil characteristics (Schrama et al., 2013a), and feed back to plant communities via changed PSFs.

1.4 Herbivore modulation of ecosystem process rates

Plant and soil biota responses arise not only from differential susceptibility and tolerance of species to negative effects of herbivores, but also from differential ability of plants to exploit ameliorating resource or growth conditions (Lortie et al., 2004). The plant economics spectrum (Freschet et al., 2012; Reich, 2014), is a salient paradigm for understanding herbivore-plant-soil interactions, as it summarizes long-established links between plant responses to abiotic and biotic environment and their effects on soil processes. Put simply, eco-evolutionary trade-offs in plant resource acquisition and retention manifest as sets of co-varying traits, whole-plant or leaf trait syndromes, along a gradient of fast vs. slow resource economy (Freschet et al., 2012; Reich, 2014). These syndromes link traits impacting on soil processes and decomposition (Chapters II and IV), e.g. quality and quantity of litter with traits affecting plant palatability to herbivores (Chapters I and II) and susceptibility to mechanical disturbance (Chapter IV) (Bardgett and Wardle, 2003; Briske, 1996; Cornelissen et al., 2004). In practice, slow plants have tissues of low decomposability and palatability, due to a high lignin and phenolic metabolite content (Fig. 1; Cornelissen et al., 2004). They generally correspond to late-successional competitors, often associated with positive plant-soil feedbacks that promote conspecifics over other species (Bauer et al., 2015). Slow plants are not favoured food and may be consumed only under extreme food limitation (Jefferies et al., 1994), and their ability to tolerate damage and regrow after tissue removal is low. Conversely, fast plants have a low C:N ratio, higher palatability, protected meristems and ability to regrow fast after disturbance (Fig. 1; Cornelissen et al., 2004). In tundra, different growth forms and especially few dominant species differ substantially in terms of their effects on ecosystem processes (Wookey et al., 2009). As noted by Chapin (1997), a change in abundance of such highly influential species "must affect ecosystem functioning". Changes in abundance and dominance of especially *Empetrum nigrum* spp. *hermaphroditum* (hereafter *Empetrum*) may be critical for low-productive tundra areas, due to its strong niche construction ability (Bråthen and Ravolainen, 2015; Chapters I and II) and potential legacy effects (Dorrepaal et al., 2007).

Seminal conceptual models of herbivore-plant-soil interactions predict that in low-productive or late-successional systems, low-intensity, selective herbivory of low C:N plants leads to declines in palatable plant species, and to competitive release of unpalatable ones (Bardgett and Wardle, 2003; Pastor and Naiman, 1996). This induces a long-term stabilizing feedback, whereby litter of slow species retards nutrient cycling and ecosystem process rates, further favouring slow species (Fig. 1; Bardgett and Wardle, 2003). In such systems, inputs of urine and dung may act to ameliorate conditions locally (Fig. 1), yet have little overall effect given low densities of resident herbivores (Bardgett and Wardle, 2003). The grazing optimization hypothesis (de Mazancourt et al., 1998) proposed that moderate levels of herbivory can increase primary productivity, e.g. by increasing nutrient turnover rates via nutritional processes; but only in systems where nutrient availability is high enough. In contrast, high levels of herbivory would lead to decimation of palatable biomass and reduced ecosystem process rates. Joint analysis of grazing optimization and plant species replacement have often considered only increasing abundance of slow species with selective grazing (de Mazancourt and Loreau, 2000).

These conceptualizations have been found to be applicable across e.g. boreal systems especially with ungulate browsers (Sitters and Andriuzzi, 2019), but in the context of tundra their predictions are frequently not met (Bernes et al., 2015; Olofsson et al., 2004a). In the present work, I highlight one systemic and one functional aspect that may contribute to this idiosyncrasy. First, while the model of Bardgett & Wardle (2003) incorporates variation in ecosystem nutrient status, it implicitly assumes herbivore population fluctuations to conform to those of tri-trophic systems. Following the logic of EEH, tundra systems are inherently low-productive systems, yet with periodically high densities of herbivores, owing to cyclic small rodent density peaks or reindeer migrations or other seasonal, herding-associated spatial aggregation. Second, these models tend to assume that selective herbivory is the most prominent herbivore activity in low-productive systems to modulate plant communities and ecosystem processes (Bardgett and Wardle, 2003; de Mazancourt and Loreau, 2000; Pastor and Naiman, 1996). However, both nutrient returns via the dietary pathway and non-trophic effects of herbivores (Fig. 1) can be strong drivers of vegetation and ecosystem processes and outweigh the effects of selective herbivory (Sitters and Andriuzzi, 2019), even in nutrient-limited and low-productive tundra (Barthelemy et al., 2015; van der Wal, 2006).

1.5 Making sense of idiosyncratic herbivory effects on ecosystem processes in tundra

> "All theories and models contain simplifying assumptions so as to focus other characteristics of the system. The problem with many assumptions is that they are unstated, even subconscious. Making such assumptions explicit sometimes may change the focus of the theory" – Scheiner & Willig (2011)

> "We propose that a variety of possible mechanisms is responsible for the idiosyncratic nature of herbivore effects on soil biota and ecosystem function; positive, negative, or neutral effects of herbivory are possible depending upon the balance of these different mechanisms." – Bardgett & Wardle (2003)

Empirical evidence from tundra systems indicates that herbivores frequently act to decrease abundance of slow species, and increase the abundance of faster ones. Long-term exclosure experiments reveal that small rodents have substantial effects on most plant growth forms, and that absence of small rodents consistently leads to proliferation of poorly palatable, slow species (Johnson et al., 2011; Olofsson et al., 2014). For instance, 10 to 20 years of vole and lemming exclusion led to increased dominance of evergreen dwarf-shrubs in the Fennoscandian sub-arctic (Olofsson et al., 2014) while in Alaska, 50 years of lemming exclusion resulted in near disappearance of vascular plants and dominance of mosses and lichens (Johnson et al., 2011). Such negative effects on slow, low-quality forage plants are clearly linked with cyclic small rodent population outbreaks, and especially their activities during winter, when they can decimate dwarf-shrubs across landscape scales (Olofsson et al., 2012). Reindeer effects on vegetation and ecosystem process rates are variable and dependent on e.g. herbivore density, seasonality and local site characteristics (Bernes et al., 2015; Sundqvist et al., 2019). Conforming to predictions of Bardgett and Wardle (2003), reindeer have been found to decrease ecosystem process rates across landscape scales by reducing the abundance of especially legumes (Bråthen et al., 2007). However, reindeer have also been found to increase the abundance of fast species (Olofsson et al., 2001; Ricca et al., 2016) and rates of element cycling (Egelkraut et al., 2018; Stark et al., 2002; Ylänne et al., 2018). At high densities, reindeer have been proposed to locally drive ecosystem state shifts from slow cryptogam dominated systems to fast graminoid-dominated ones (van der Wal, 2006). A recent large-scale experimental study revealed that long-term reindeer exclusion increases the abundancies of especially lichens and deciduous shrubs, and increases soil mineral N availability (Sundqvist et al., 2019). Indeed, both reindeer and small rodents may suppress shrub growth and counteract shrub expansion in a warming tundra (Kaarlejärvi et al., 2015). For instance, reindeer at densities of ca. 5 animals / km2 can keep tall shrubs in a “browse trap”, i.e. maintain a grassland state, while small rodents may also induce substantial mortality of small shrub shoots (Bråthen et al., 2017; Ravolainen et al., 2014). In addition, via controlling shrub-litter-soil N feedbacks (Buckeridge et al., 2010), herbivore suppression of shrub growth may modulate how tundra process rates and carbon dynamics respond to warming temperatures.

Indeed, the apparent mismatches between predicted decelerated process rates in tundra and idiosyncratic empirical evidence indicates that other forms of interaction than selective foraging and defecation, i.e. nutritional processes (sensu Cherif and Loreau, 2013), may be prominent. While biomass returns via the digestive pathway act to promote faster process rates and could even counteract effects of selective feeding on nutrient cycling and plant productivity, reindeer feces and urine alone have been found insufficient to drive a shift towards fast process rates (Barthelemy et al., 2018). Moreover, plant responses under simulations of nutritional processes (biomass removal and fertilization) deviate from responses observed with presence of herbivores (cf. Falk et al., 2014, 2015). Fecal/urine nutrient additions hardly explain why non-palatable plants frequently exhibit the strongest, and rapid, negative responses to herbivores (cf. Aerts, 2010; Olofsson et al., 2014). Hence, in the context of arctic community dynamics and ecosystem processes, empirical evidence prompts a need to question the assumptions that palatability always matters for herbivore-plant interactions, that selective foraging and nutritional processes dominate plant-herbivore interactions, and more broadly, that dominant forms of interactions between herbivores, plants and soil in two-trophic level systems can be predicted based on three-trophic level systems dynamics (cf. Sitters and Andriuzzi, 2019).

Recent conceptual work has begun to highlight the importance and omnipresence of non-trophic effects of herbivores (Andriuzzi and Wall, 2017; Howison et al., 2017; Kéfi et al., 2012), and both small rodents and large ungulates seem to affect vegetation and ecosystem processes via non-trophic activities (Barthelemy et al., 2018; Pascual et al., 2017). For instance, while generally herbivores have been estimated to consume 10% of plant primary productivity, which has been attributed to predator control of herbivore consumption, stoichiometric constraints or lack of access (e.g. Pastor and Naiman, 1996; Polis and Strong, 1996); however, the percentage of plant biomass damaged or removed by arctic herbivores can be as high as 90% (Heggenes et al., 2017; Olofsson et al., 2012), irrespective of their quality and palatability (Dahlgren et al., 2009a). A key behaviour of cyclic small rodents seems to be the tendency to decimate woody dwarf shrubs during winter (Fig. 1), but the spatial distribution of such damages along environmental gradients is seldom recorded on the ground (Chapter I). Owing to the strong effects that dwarf-shrubs have on litter decomposability and plant growth, their decimation could be expected to alter soil processes (Chapter II). Strikingly, despite these well-recorded impacts on vegetation, small rodent effects on soil processes and plant-soil interactions (Fig. 1) have only barely been studied in the Arctic (Stark and Grellmann, 2002; Virtanen et al., 2008) or elsewhere (Sirotnak and Huntly, 2000).

Strong negative effects on slow non-palatable plants appear to be linked also with high ungulate densities, for example along separation fences or in milking grounds (Egelkraut et al., 2018), and past theoretical and empirical research on ungulate effects on vegetation composition and soil has been heavily focused on nutritional processes (Augustine and Frank, 2001). While trampling (Fig. 1) has been recognized as a third key driver of ecosystem function (Bardgett and Wardle, 2003), it has largely been overlooked, despite the fact that trampling acts constantly, and randomly, on both plants and soil (Sitters and Andriuzzi, 2019). However, recent research from temperate systems indicates that trampling may even outweigh nutritional processes in driving nutrient mineralization rates (Schrama et al., 2013b).

In Northern Fennoscandian tundra and pastoral boreal systems, large ungulate trampling reduces strongly ground lichen cover (Heggenes et al., 2017), and dwarf-shrubs and cryptogams and erect forbs have been proposed as especially vulnerable growth forms to trampling (Egelkraut et al., 2017; Lezama and Paruelo, 2016). In contrast, especially tussock forming graminoids may be highly tolerant of trampling and able to colonize trampled sites (Chapin and Shaver, 1981; Kevan et al., 1995).

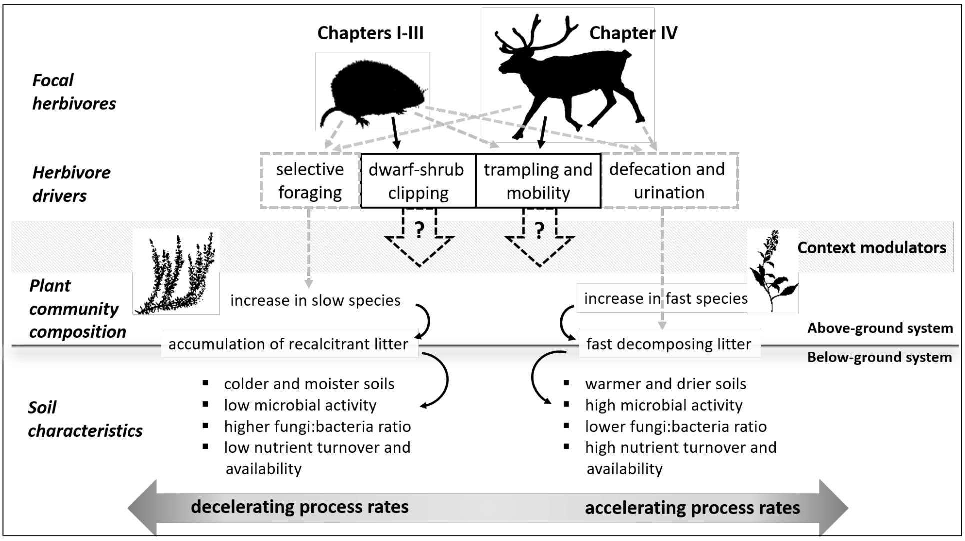

Figure 1. Illustration of herbivore-plant-soil interactions leading to accelerated vs. decelerated ecosystem process rates in low-productive tundra. Grey dashed boxes and arrows indicate herbivore drivers and effects on vegetation and soil, respectively that have been covered in previous literature. Black boxes indicate potential herbivore drivers that are not known and focal to empirical and conceptual work in Chapters I, II and IV. Context modulators include the abiotic and biotic environment, e.g. depletable soil resources, which can also be altered by herbivores. Methodological study in Chapter III focuses on small rodents.

Direct effects of trampling are likely to alter soil processes via altered root function and morphology, PSFs and long-term litter feedbacks, as described above. However, trampling may also have strong effects on soil characteristics that are not mediated via plant compositional change (Howison et al., 2017; Schrama et al., 2013b). Across different biomes, large ungulate trampling has been found to promote/retard N mineralization and cycling through compaction (Schrama et al., 2013b), lead to alternate stable states through reductions in bioturbating soil fauna and promotion of grazing lawns (Howison et al., 2017) and reduce soil microbial activity especially in harsh climates (Andriuzzi and Wall, 2017). In tundra, trampling by abundant large herbivores could be expected to have similarly strong effects on soils, although responses of cold tundra soils with high organic matter content and prevalence of cryogenic processes may differ from those found in mineral soils of temperate grasslands (Howison et al., 2017). However, in stark contrast to the known profound effects of arctic herbivores on plants and soil in general, no synthesis or conceptual understanding of trampling effects on tundra soils exist to date.

1.6 Studying small rodent populations and their effects on ecosystem processes

The ability to address complex herbivore-plant-soil dynamics across heterogeneous tundra landscapes hinges on the availability of data with sufficient spatial extent and grain, and temporal coverage. Methodological restrictions may constrain especially research on highly variable dynamics of elusive small rodents (Engeman and Whisson, 2006; Green et al., 2013) and consequently their impacts on vegetation and soils in landscape scales. These shortcomings are typically associated with high effort and costs of data collection, small spatial and/or temporal coverage or inability to distinguish between species in multispecies communities (Engeman and Whisson, 2006; Heisler et al., 2016; Villette et al., 2016). Small rodent monitoring and density censuses currently rely on density estimation based on capture-mark-recapture methods (CMR) or various indices of occurrence, occupancy or abundance (Engeman and Whisson, 2006; Fauteux et al., 2018), but are fraught with shortcomings. While providing rather reliable estimates of small rodent density, live-trapping is often extremely laboursome, covering only relatively small areas during short periods of time. In addition, some species are less likely to go into traps, e.g. the Norwegian lemming is known for its “trap shyness”, potentially leading to biased estimates especially during population lows (Jolly and Dickson, 1983). Various abundance indices include snap, hair or camera traps, tracking tunnels and counts of burrows, winter nests or other signs of activity such as runways (Engeman and Whisson, 2006; Fauteux et al., 2018) or feces (Green et al., 2013; Karels et al., 2004; Kohn and Wayne, 1997). Snap-trapping based indices have been widely used in long-term monitoring designs but come with ethical concerns. Tracking tunnels may become swamped with small mustelid tracks during peak years (Ruffino et al., 2015). Camera traps may provide a novel avenue to monitor rodent activity especially during winter (Soininen et al., 2015a), but are ill suited for landscape-scale monitoring due to high costs. Counts of burrows, winter nests, runaways and feces may provide accurate abundance estimates at low cost and large spatial scales, but they often fail to assign observations to species.

Even so, feces counts have a potential to circumvent most of the aforementioned issues, if combined with low-cost and high through-output analytical methods capable of determining species identity, as well as other demographic or physiological parameters. Feces are chemically and structurally complex organic material, who carry a large amount of information about e.g. animal diet, body condition and demography (Kohn and Wayne, 1997). Near Infrared Reflectance Spectroscopy (NIRS) is a non-destructive, fast and cheap analytical method, where scanning of the samples takes only seconds and no other pre-treatment than drying and homogenizing is typically needed (Foley et al., 1998). NIRS has been used in ecological and agricultural studies to determine a wide range of constituents with a distinct chemical imprint from different types of samples, including for instance soil chemistry and decomposer biota (Rinnan and Rinnan, 2007), species composition of honey (Escuredo et al., 2015), species identity of Amazonian seedlings and Drosophila (Aw and Ballard, 2019; Lang et al., 2015) as well as N, P and Si content of plant tissues (Murguzur et al., 2019). NIRS analysis of fecal samples (fNIRS) has been successfully used to identify species and/or sex of deer (Tolleson et al., 2005), captive giant pandas (Wiedower et al., 2012), leopards (Johnson-Ulrich et al., 2013) as well as dietary quality of various herbivores(e.g. Villamuelas et al., 2017).Up until now, fNIRS calibrations of small rodent feces for taxonomic identification have not been developed, although they could provide a powerful tool to aid monitoring small rodent populations (Chapter III).

As all previous fNIRS calibration models have been based on small sample sizes or animals with homogenous diet (Tolleson et al., 2005; Wiedower et al., 2012), it is unclear how well fNIRS would perform with fecal samples collected from heterogeneous tundra landscapes, where rodent individuals from a multispecies community show marked variation in their diet, body condition and age. Moreover, to be applicable for monitoring, fNIRS calibrations should not be adversely affected by exposure to field conditions, including leaching and irradiation, which may affect fecal element and hormonal metabolite concentrations (Jenks et al., 1990; Kamler et al., 2003). Finally, NIRS models are by default tied to those populations where their calibration data originates from. However, recent research indicates that combining samples from multiple sites or years with varying conditions may yield “global” NIRS calibrations, with ability to predict samples from other populations (Murguzur et al., 2019; Tolleson et al., 2005). A test of fNIRS for small rodent monitoring should thus incorporate existing environmental variability that may affect species imprint in fecal spectra, evaluate susceptibility of prediction accuracy to exposure as well as assess the ability of calibrations to predict samples from other regions.

1.7 Aims of the thesis

The overall aim of the thesis is to shed light on herbivore-plant-soil dynamics by considering herbivore roles other than selective feeding and excretion. I build on the premise of tight and complex coupling of community processes and ecosystem processes, mediated by shifts in resident plant species with contrasting traits (Chapin

III, 1997). In Chapters I and II, I study how peak small rodent densities affect especially dominant slow dwarf shrubs, and if voles affect plant-soil interactions. The goal of Chapter III is to contribute to development of analytical methods capable to address complex small rodent-plant-soil dynamics outlined in the thesis. In Chapters II and IV, my aim is to conceptualize mechanisms that would produce "idiosyncratic" herbivore effects on plant-soil interactions and soil processes, specifically outlining complex or multiple ecological roles of both small and large ungulate herbivores.

I addressed the following core research questions.

1) During a massive outbreak, do small rodents display runaway herbivory to affect and decimate dwarf-shrub communities in landscape scale and across a productivity gradient? (Chapter I)

2) How do cyclic small rodents alter plant community composition, soil nutrient content and microbial activity? Does the decimation of dwarf shrubs, caused by cyclic small rodent populations, promote or decelerate ecosystem process rates? (Chapter II)

3) How accurately is fNIRS able to predict species identity of five subarctic small rodents? Can it act as a novel tool to improve large-scale and high intensity sampling of small herbivore abundance and study of herbivore-plant-soil interactions (Chapter III)?

4) What changes does large ungulate trampling induce in tundra soil structure, biota, microclimate or biogeochemical processes? In light of the current empirical body of knowledge, is trampling likely to affect, accelerate or decelerate, ecosystem process rates in tundra? (Chapter IV)

2 Materials and Methods

2.1 The Arctic tundra

In the Circumpolar Arctic Vegetation Map (CAVM; Walker et al., 2005) the Arctic tundra proper has been divided into High Arctic and Low Arctic zones following large-scale, latitudinal bioclimatic patterns. Longitudinal variation in lowland vegetation structure further yields a divide into five distinct vegetation sub-zones, two in the High Arctic and three in the Low Arctic (Walker et al., 2005). South from the Low Arctic, sub-arctic tundra ecosystems span north from the edges of boreal timberline and merge with the southern border of the Low Arctic (Walker et al. 2005). Data for Chapters I-III has been collected in the Fennoscandian sub-arctic tundra, with Chapter III including also rodent individuals from Fennoscandian Low-Arctic. Chapter IV encompasses the entire circumpolar tundra areas, both Arctic and Antarctic.

High Arctic systems are characterized by highly discontinuous vegetation cover and only a few species of arctic specialist herbivores, most notably brown (*Lemmus* sp.) and collared lemmings (*Dicrostonyx* sp.) (Reid et al., 2013). Low Arctic ecosystems cover a wide productivity range with comparatively higher mean temperatures, and vegetation types from low-productive dwarf-shrub tundra and erect shrub (up to 2m) dominated habitats (Ims et al., 2013; Walker et al., 2005). Owing to higher productivity at lower latitudes, Low Arctic systems have higher diversity and more complex food webs, including numerous herbivores and predators with arctic and boreal distributions (Barrio et al., 2016; Reid et al., 2013), and promoting co-occurrence of bottom-up and top-down trophic regulation (Ims et al., 2013).

The Fennoscandian tundra ecosystems belong to the Sub-Arctic zone (Chapters I-IV) with the exception of northernmost parts of the (Low Arctic) Varanger peninsula (Chapter III), and also species with primarily boreal distribution are present (Barrio et al., 2016; Reid et al., 2013). Despite the sub-arctic position, the vast continental sub-arctic tundra areas are characterized by low levels of primary productivity and generally correspond reasonably well to southern Low Arctic dwarf-shrub vegetation (Virtanen et al., 2016; Walker et al., 2005). The extensively studied Fennoscandian sub-arctic tundra systems provide important insights into

Low Arctic ecosystem dynamics in general and forest-tundra ecotone dynamics in particular.

2.2 Main study species and interactions

The focal herbivores of the thesis are small rodents, i.e. lemmings and voles (Chapters I-III) and large ungulates (Chapter IV). Small rodents (Chapters I-III) are a key functional group in tundra (Ims and Fuglei, 2005), and hence their dynamics are widely monitored across the circumpolar ecosystems (e.g. Ehrich et al., 2019). Four small rodent species co-occur across the Fennoscandian tundra: Norwegian lemming (*Lemmus lemmus*; hereafter lemming), grey-sided vole (*Myodes rufocanus*), red vole (*Myodes rutilus*), root vole (*Microtus oeconomus*), with the boreal field vole (*Microtus agrestis*) occupying forest-tundra ecotones in the sub-arctic. Lemmings, famous for their high-amplitude outbreaks, and exhibiting ca. 10yr pseudo-cycles in Fennoscandian tundra, have seen dampening and partial disappearance of population peaks between late 80s and early 2000s owing to changing winter climate (Ehrich et al., 2019). As arctic specialists, lemmings prefer highland tundra areas, and their winter survival, reproduction and population growth are contingent on good snow cover. They also migrate between overwintering snowbed areas and more productive lowland habitats during summer (Ekerholm et al., 2001). *Myodes* and *Microtus* vole dynamics follow a regular 4-5 year cycle, with grey-sided voles being the dominant species across Fennoscandian tundra and displaying highest amplitude cycles (Ekerholm et al., 2001). Sympatric voles and lemmings have species-specific differences in diet preference. Grey-sided voles feed on deciduous dwarf-shrubs and forbs, while lemmings feed on graminoids during summer and on mosses (especially small *Dicranum* spp.) during winter (Soininen et al., 2013b, 2013d). In lemmings, large digestive tracts relative to body mass may indicate an evolutionary adaption to survive on poorly palatable forage (Oksanen et al., 2008); however a potential for high N content in mosses is linked with abundance of nitrogen fixing bacteria (Chapin and Bledsoe, 1992). Especially voles tend to consume resources based on their availability, and with large intra-specific variation in diet choices if forced to secondary habitats (Soininen et al., 2013b).

Reindeer and caribou (*Rangifer tarandus* ssp.) and musk ox (*Ovibos moschatus*) are the two large ungulate herbivores with an arctic distribution to survive the late Pleistocene megafauna extinctions 15 - 10 000 years ago (Chapter IV; Olofsson and Post, 2018). Wild and semi-domesticated reindeer are by far the most abundant large herbivores in the circumpolar tundra and in Fennoscandia (Forbes and Kumpula, 2009; Olofsson and Post, 2018). Reindeer are generalists with a seasonally changing diet. They feed on N-rich herbaceous plants during summer, prefer mushrooms during autumn, and survive on high-energy but nutrient-poor ground and arboreal lichens during winter (Danell et al., 1994; Nieminen and Heiskari, 1989). Following seasonally changing and spatially segregated resource pools, reindeer and caribou exhibit seasonal migrations. In Fennoscandia, these occur between coastal, productive summer pastures, and continental lichen-rich winter pastures (Forbes and Kumpula, 2009). Migrations and seasonal occupancy patterns are modified in large parts of Fennoscandia and especially inside Finland due to state and herding district borders. In Fennoscandia, declines in large apex predators and herding practices have resulted in a situation where humans are the major top-down force governing reindeer densities, movements, and subsequently their ecosystem effects (Forbes and Kumpula, 2009; Tuomi and Ravolainen, 2016). Within pasture scales, reindeer movement patterns and habitat selection are affected by plant species composition, plant phenology, as well as disturbance by parasitic insects and humans (Iversen et al., 2014; Tuomi and Ravolainen, 2016; Vistnes and Nellemann, 2007).

Plant productivity and vegetation community composition are primary governed by abiotic conditions in tundra. Owing to strong gradients and variation of moisture, snow, irradiation, cryogenic disturbance and soil nutrients, regional and local scale turnover in species assemblages is especially pronounced in many tundra systems (Oksanen and Virtanen, 1995). In addition, horizontal (competition, facilitation) and vertical (top-down) interactions structure the species composition of most tundra plant communities (Olofsson et al., 2014; le Roux et al., 2013). In Northern Fennoscandia, common tundra community types include barren ridges, nutrient-poor and -rich snow-beds that transition to dry-to-moist dwarf-shrub heaths or meadows, various types of bogs and peatlands, and willow-scrublands along creeks and rivers (Oksanen and Virtanen, 1995).

Dominant plant species in low-productive Fennoscandian tundra systems are deciduous and evergreen dwarf shrubs with varying palatability and grazing tolerance (Table 1). *Empetrum nigrum* ssp. *hermaphroditum* is a dominant evergreen ericoid dwarf shrub that forms dense clonal mats in dry and nutrient-poor tundra habitats. *Empetrum* litter has strong phytotoxic and allelopathic properties, as it induces seedling mortality and reduces growth of other species (Dorrepaal et al., 2007; Nilsson, 1994). This is due to high constitutive concentrations of carbon-based secondary metabolites, especially stilbenes (incl. batatasins) present in the leaves, while these compounds are not present in stems (Lavola et al., 2017; Väisänen et al., 2013). These metabolites also act as anti-herbivore defence through reduced palatability (Cornelissen et al., 2004), constitute an important abiotic stress response (Lavola et al., 2017; Väisänen et al., 2013), and they may decelerate soil nutrient cycling (Tybirk et al., 2000).

Deciduous *Vaccinium myrtillus* has been considered a key species for herbivore-plant interactions in low-productive tundra, as it is palatable and preferred forage of the grey-sided vole (Dahlgren et al., 2007). It has a moderate regrowth ability and tolerance to herbivory (Dahlgren et al., 2007; Strengbom et al., 2003), and the litter of *V. myrtillus* has only a limited potential to inhibit germination of seedlings, owing to high solubility and decomposability of phytotoxic compounds (Jäderlund et al., 1996). *V. myrtillus* is indicative of moderate snow cover and moisture, and is absent from dry ridges. Trait syndromes of focal plant species and growth forms (especially six dominant species considered in Chapter II) are described in Table 1.

Table 1. Summary of key functional attributes of dominant plant growth forms and species in low-productive tundra habitats. Dominant plant species in Chapter II differ in their palatability (based on dietary preferences), plant litter decomposability and plant growth rates (based on specific leaf area, SLA and leaf dry matter content, LDMC), which are major indicators of plant impacts on ecosystem process rates. Plant responses to selective vole grazing (i.e. removal of palatable plants) and to non-selective damage targeting also poorly palatable plants are presented as the change in relative abundance in the plant community. References for the specific plant characteristics are noted in superscript. (Adapted from Chapter II)

growth form	**relative growth rate^{1}**	**species**	**palatability^{2,3,}**	**decomposability^{4}**	**response to selective grazing^{5}**	**response to damage^{6}**
woody evergreen	low	*E. nigrum*	very low	very poor	increase	strong decrease
		V. vitis-idaea	low	very poor	increase	decrease
woody deciduous	Intermediate	*B. nana*	moderate	poor	increase/neutral	decrease
		V. myrtillus	high	fair	decrease	decrease
small forb	high	*R. chamaemorus**	high	good	decrease	increase
		C.suecica	high	very good	decrease	increase
graminoid	high	*sedges*	high	very good	decrease	increase
		grasses	high to low	very good to fair	decrease/neutral	Increase

1 Kleyer and others (2008)
2 Dahlgren and others (2009) and Cornelissen and others (2004).
3 Soininen and others (2013).
4 Cornelissen and others (2004).
5 Olofsson and others (2004a) and Dahlgren and others (2009).
6 Hoset and others (2017)
* woody stem

2.3 Study sites

Field sampling for Chapters I-III was conducted in Finnmark County, Northern Norway. I collected data for Chapter I from West-Finnmark, Joatka research area (JRA; 69°45′N, 23°55′E, 380–670 m a.s.l.) and for Chapter II from the islands on adjacent Lake Iešjávri 10 km south from JRA (69°45’N, 24°30’E). In Chapter IV, I used rodents trapped at JRA and in Skirvinjárga (77°86’N, 05°86’E), a coastal tundra area 50km north from JRA, as well as in three river catchments in Northeast-Finnmark (Ifjord 70°N, 27°E, Komagdalen and Vestre-Jakobselva 70-71°N, 28-31°E) – for these sites, detailed descriptions are given in Ruffino et al. (2015) and Ravolainen et al. (2014).

The Joatka Research Area (Chapter I) spans across three sub-areas with markedly different levels of primary productivity: the low-productive Highland dominated by low-stature dwarf-shrub tundra, the productive south-facing Slope featuring lush mountain-birch woodland and tall willow thickets, and the moderately productive Lowland, featuring mosaic vegetation of low-productive lichen heaths, open and willow mires and low-productive birch woodlands. Lake Iešjávri (Chapter II) is a 68.16 km2 lake located in the Lowland, where remote small islands have been assigned to experimental food-web manipulations. The convex islands' vegetation is zonal with willow thickets and wet meadows at the shoreline, transitioning into hummock bog habitats, and with the dry mid ridges dominated by dry dwarf-shrub heaths. The hummock bog is the focal habitat in Chapter II, as it is a favoured habitat for grey-sided voles in the mainland tundra and is subject to especially high vole densities (Ekerholm et al., 2001).

2.4 Chapter I: Spatiotemporal variation in tri-trophic interactions during a rodent outbreak

Chapter I focused on determining how small rodent abundances and their top-down control by predators vary across productivity gradient at JRA during a massive rodent outbreak 2010-2012, and how these dynamics affect slow-growing dwarf-shrubs and cryptogams. This was achieved by combining observational data on avian and mammalian predators, abundance data on rodent populations as well as measures of vegetation responses to rodent grazing, derived from both observational and experimental designs. Details on predator data and results are presented in Chapter I. An index of rodent abundance was obtained using small-quadrant method (SQM; Myllymäki et al., 1971), where 3 snap-traps were placed around each of the four corners of a ca. 15x15m trapping quadrant. At JRA, 77 quadrants have been placed along an 8km transect line running across Highland (á 25), Slope (á 10) and Lowland (á 42), stratified to represent the 11 major vegetation types of the landscape. The trapping at JRA has been conducted twice a year since 1986, each spring after snowmelt and in the autumn before snowfall. The traps were kept active for 48h and checked once a day. All trapped individuals were weighed and their species and gender recorded in the field, after which they were stored in the freezer (as subset of these animals were later used in Chapter III).

Rodent effects on vegetation biomass and cover were measured by four complementary means. First, visible destruction of dwarf-shrubs and cryptogams was estimated in rodent trapping quadrants in July 2012, where the length of patches with >50% visible vegetation destruction (clipped shoots and debris) as well as the total length of vegetated habitat along a diagonal line in each quadrant were measured. These data yielded a quadrant-specific index of destruction. Second, in summer 2011, 80 *V. myrtillus* shoots were marked with freeze clips in each trapping quadrant, and visible rodent-induced damage and mortality was recorded in summer 2012. Using the numbers of survived, dead and damaged shoots provided a quadrant-specific bilberry damage index, indicative of herbivory on a palatable dwarf shrub and preferred winter forage of the grey-sided vole. Third, a modified point frequency method (Jonasson, 1988) was used to compare and monitor vegetation cover in a paired exclosure and open control design. Four paired plots (50 x 50 cm) were erected and sampled in each sub-area in autumn 2010 and revisited during peak growing season in 2011 and 2012. Finally, in 2012 after measuring the vegetation cover, the vascular and cryptogam biomass in the original paired plots and additional three open plots around the fenced plot was sampled. Extra open plots were assigned objectively according to cardinal directions, and included to account for the spatial variation in rodent grazing impacts. After harvesting, biomass was dried and weighed to yield separate biomass measures for cryptogams and vascular plants.

Variation in rodent abundance index (total number of trapped individuals per quadrant) was analysed using generalized linear model with a quasi-Poisson error distribution, including year, season, sub-area and their second-degree interactions as explanatory variables. Variation in rodent summer and winter population growth rates were analysed using sub-area, season, year and their interactions as explanatory variables in a linear regression with normally distributed errors. Generalized linear models with quasi-binomial errors were then used to test, in separate models, how vegetation destruction index and *V. myrtillus* damage index varied with explanatory variables including sub-area, rodent abundance and their interaction. To analyse change in vegetation cover from 2010 to 2012 with rodent density, generalized mixed models with Poisson-distributed errors and plot ID as the random factor were applied. Point frequency scores were used as the response variable, while explanatory variables included sub-area, treatment, year and their interactions. Tukey’s post hoc tests was performed to test differences in responses between open and fenced plots between 2011 and 2012 in each sub-area. Variation in total vegetation biomass between fenced and open plots and in different sub-areas was analysed using linear mixed effects model, with plot ID as the random factor and treatment and sub-area as explanatory factors. Here, too, effects of interest were further tested with Tukey post hoc test.

2.5 Chapter II: Small rodent effects on ecosystem process rates

In Chapter II, I examined the effects of cyclic grey-sided vole populations on vegetation composition, plant N content as well as soil inorganic nutrient content and soil and litter microbial activity. I used data from a 10-year island experiment at Lake Iešjávri, where transplanted soil and vegetation blocks (hereafter transplants, 70 x 70 cm, depth >30 cm) were subjected to either high or low vole density from 2000 to 2011. Three randomly assigned islands were kept vole-free by trapping (hereafter low-density islands), while voles were introduced to four islands to mimic cyclic dynamics observed in the mainland (high-density islands). Peak densities on the experimental islands were higher compared to the large island with tri-trophic dynamics, where the transplanted blocks were excavated from. Thus, the experiment was designed to test for community changes from three-trophic system to two-trophic systems, or to one-trophic systems. In 2000, eight visually similar transplants were excavated from the large island, and transplanted on peat ridges of the hummock bog habitat on each of the experimental islands. Vole densities were monitored by summer-time live-trapping on the high-density islands, yielding vole density estimates per hectare covering the experiment duration.

Vegetation in the transplants was sampled at the start of the experiment in 2000, and again in 2010-2011 using a point intercept frequency method with 100 pins in a 50 x 50cm plot (Bråthen and Hagberg, 2004). I included measurements from both 2010 and 2011, as the rodent outbreak recorded at JRA (see Chapter I) resulted in lemmings swimming into the experimental islands, potentially modifying the herbivory treatment. These longitudinal transplant data allowed for an unequivocal evaluation of vole effects on vegetation community composition over three cycles. In addition to the transplanted plots, the entire small islands had been subjected to vastly differing density regimes. I wanted to access this spatially more robust data, and to assess how vegetation responses vary between microhabitats with different moisture and snow conditions. Hence, in 2013 I sampled paired transects running along the entire length of the hummock bog habitat (20-38 m) on each experimental island, with one transect placed on top of the ridge and one in the adjacent depression. I sampled plots every two meters, using a 9-pin point intercept frequency method in a 40 x 40 cm plot. Then, I used weighted linear regressions to calibrate point frequency scores against harvested biomass (Bråthen and Hagberg, 2004), and calculated estimated biomasses for all species separately. To this end, I harvested biomass of approximately half of the transplant plots in 2011, separated biomass to species as well as leaves and stems of woody dwarf-shrubs, and dried samples for 24h in 50°C before weighing. I focused the statistical analysis on biomass estimates of six most dominant plant species, including two each of evergreen and deciduous dwarf shrubs and small forbs (Table 1). These species made up >93-95% of transplant and >80% of transect vegetation. Furthermore, I used the logarithm of an evergreen dwarf shrub: forb ratio (EHr) as the central variable in both characterizing how vegetation responded to vole density and in explaining observed variation in soil characteristics (see below). Evergreen dwarf shrubs and forbs represent opposite ends of the resource economics spectrum in the study system and their abundance ratio correlated well with the first principal component axis of plant community composition in both transplants and transects (for details of the PCA and results, see Chapter II).

In order to link contrasting vole density regimes with variation in ecosystem process rates, I first analyzed the green tissue N content (% dry weight) of the six dominant species using NIRS (hereafter species-N). I used a subset of the dried transplant biomass samples (n = 96 distributed among species and islands), and the N contents were estimated based on an arctic-alpine calibration model (Murguzur et al., 2019). In addition, I used species-N to calculate community-weighted (cf. Garnier et al., 2004) green tissue N content for all transect and transplant plots (hereafter community-N). For this, species-N values were averaged within species, i.e. across islands and grazing treatments, resulting in a conservative community trait value that reflects only changes in vegetation composition, and not individual trait plasticity. Second, I sampled eight soil cores with an ø3cm core from inside each transplant in 2012. Samples included topsoil (0-5 cm) and bottom soil (from 5cm depth to mineral soil or max. 30 cm depth). I recorded the sample depth, separated and pooled depth fractions to form two composite samples per plot, and stored samples in freezer. After thawing, litter and roots were separated and soils were homogenized. I analyzed soil NH_4-N and PO_4-P content with standard extraction and colorimetric methods. Microbial respiration (used here as a proxy for microbial activity) in litter and soil were analyzed by incubating samples (1 g organic matter) in +9 degrees and field moisture, and measuring CO2 twice during 92h.

I used linear mixed effects models from the package nlme (Pinheiro and Bates, 2009; Pinheiro et al., 2016) with island as the random intercept to analyze the responses of six dominant species, EHr and community-N, each in separate models, to contrasting vole density regimes in transect plots. The full model included interactive fixed effects of vole density (low vs. high) and micro-topography (ridge vs. depression). I compared the resulting models using differences in small-sample corrected AIC values (ΔAICc). As no single model appeared superior, I applied model averaging on the entire candidate model set (Burnham and Anderson, 2002) using package MuMIn (Barton, 2016). With transplant plots, I first analyzed the interactive fixed effects of year (2000, 2010 and 2011) and vole density on the six dominant species, EHr and the community-N. Here, the random structure included year as a random slope, and island as the random intercept. Second, I analyzed species-N of the six dominant species, soil and litter microbial respiration as well as soil ln(NH_4-N) and PO_4-P with linear mixed models, using island as the random intercept. For species-N, the fixed term consisted of vole density. For soil and litter variables, the fixed term included interactive effects of vole density and continuous EHr values. I used model selection based on ΔAICc to indicate best model, indicative of the explanatory power of rodent density versus a key aspect of plant functional composition. Finally, I analyzed if variation in soil ln(NH_4-N) was explained by community-N as model fixed term, and with island as the random intercept.

2.6 Chapter III: Small rodent species identification using fNIRS

In Chapter III I used near-infrared reflectance spectroscopy (NIRS) to develop a novel method for small rodent genus and species identification from fecal pellets. In short, NIRS is an analytical method that estimates levels of qualitative or quantitative constituents from organic and inorganic samples, based on a known correlation between NIR-spectra and the constituent in question. NIRS analytics involves thus first a calibration modeling stage, after which the obtained calibrations can be used to predict new samples. When a sample is irradiated with wavelengths in the NIR-range (ca. 700-2500 nm), C-H, N-H, O-H, C-O and S-H bonds in the sample vibrate at bond-characteristic frequencies – wavelengths matching that frequency are absorbed, while others are reflected back to the NIR-spectrophotometer and measured (Cen and He, 2007; Foley et al., 1998; Pasquini, 2003). The resulting absorbance and reflectance spectra are highly complex due to overlapping overtones and overtone combinations (Cen and He, 2007), but they can be used to infer a vast array of chemically distinct features (Foley et al., 1998). Owing to this complexity, chemometric models are used to link scanned NIR-spectra with known levels of constituents of interest, be it quantitative (e.g. tissue N concentrations) or qualitative ones (e.g. species identity) (Pasquini, 2003).

However, there are restrictions for using NIRS calibrations to predict new samples. Most notably, a distinct feature of the complex NIR-spectra is the difficulty to assign any specific wavelengths or bands as responsible for a specific constituent; instead, each constituent manifests as multiple bands, and absorbance at each wavelength is affected by multiple vibrational bonds (e.g. Foley et al., 1998). Hence, NIRS calibrations are traditionally not considered reliable for predicting samples from populations outside the population used for calibration, as the relationship between the measured constituent and the NIR-spectra may differ in an unknown way. However, including high degrees of variation, e.g. samples from multiple populations, in the calibration samples can increase the model's ability to detect the constituent-specific signal (and not population-specific confounding signals) and result in a highly robust model applicable across populations (Murguzur et al., 2019).

In Chapter III, I set out to develop fecal-NIRS calibrations to separate between five rodent species: the Norwegian lemming, grey-sided vole, red vole, root vole and field vole. I utilized pellets from rodent individuals trapped as part of long-term rodent population monitoring at JRA and Skirvinjárga (hereafter West-Finnmark or WF) and Northeast-Finnmark (East-Finnmark or EF). Rodent individuals were dissected, their species identity verified from molar markers whenever necessary (all *Microtus* individuals) and reproductive status and body mass were recorded. Fecal pellets from each West-Finnmark individual were divided into two parallel samples (A and B samples) and placed in Eppendorf-tubes. After extraction, "A" samples were dried and scanned. "B" samples were subjected to a six-week exposure treatment in Tromsø, Norway during autumn, where pellets were kept at ground level in open frames and subjected to rain, sun and freezing. Each frame contained pellets of one species only, and every week 25 samples from each frame were taken for drying and scanning. To evaluate if NIR-spectra and prediction accuracy of species identity were affected by diet composition, 385 A samples were DNA-metabarcoded after NIRS-scanning adopting similar methods as used by Soininen (2015b) (for detailed methods, see Chapter III). Read counts were converted to relative read abundances (Deagle et al., 2018) for further analysis and data were pooled to family level. East-Finnmark samples were scanned directly after drying, and they were used to determine if calibrations could be applied across regions.

I used multivariate adaptive regression splines from R package earth (MARS; Friedman, 1991; Milborrow, 2014), alone and within flexible discriminant analysis (FDA, package mda; Hastie et al., 1994, 2015), to build calibration models for taxon identification. I adopted a repeated double Monte Carlo cross-validation strategy (Filzmoser et al., 2009; Xu et al., 2004), where the entire dataset was randomly split to a joint model selection and validation dataset (hereafter calibration set) and a model evaluation set (hereafter test set) 600 times, and separate calibration models were run on each data split. This gave a robust result of model overall performance, and indicated how much model performance depended on data allocation to calibration and test sets. For each model, I thus obtained mean and standard deviation of model misclassification rates and species-level prediction accuracies. I also extracted individual sample prediction accuracy IPA, calculated as the averaged classification success (0 = incorrect, 1 = correct) across all model iterations, which was later used to infer if misclassification was linked with exposure treatment or diet composition.

I built four FDA/MARS models to address three broad questions. First, to assess if fNIRS was able to accurately predict species identities, I built the calibration with intestinal and exposed samples from West-Finnmark samples. Then, to assess how exposure treatment affected prediction accuracy, I built a calibration model with only exposed samples, and compared species prediction accuracies to the model including also intestinal samples. In addition, I used Bayesian beta regressions from package rstanarm (Muth et al., 2018) to analyse the effects of exposure on IPA. Third, I studied the link between NIR-spectra and diet composition by using Mantel and Procrustes tests from package vegan (Oksanen et al., 2018) to assess similarity of diet composition and NIR-spectra of the same individuals. I built a calibration model with intestinal (West-Finnmark) samples only, and extracted IPA values for samples used in DNA-metabarcoding. I then used latent variable modelling (unconstrained ordination) from package HMSC (Blanchet, 2013) to model diet composition of rodent individuals, and explored if misclassified individuals (with low IPA) were also those whose diets were deviant from their conspecifics. Fourth, I tested the ability of calibrations based on one region, i.e West- vs. East-Finnmark, to predict samples from another, and the ability of a calibration models including samples from both sites, to predict test set samples from both sites.

2.7 Chapter IV: Ungulate trampling effects on tundra soils

After exploring the effects of small rodents on plant growth forms and soil characteristics in the first two chapters, in Chapter IV I asked how trampling by large ungulate herbivores affects tundra soils, and subsequently ecosystem processes. Based on theoretical and empirical work across temperate and cold biomes, I outlined a conceptual model of trampling effects on tundra soil characteristics, with four plausible mechanistic pathways (“effect pathways”). I reviewed literature reporting empirical data on trampling effects on soil variables in Arctic and Antarctic tundra areas (north of 60N and south of 60S, respectively). I used search strings “trampling OR trample AND subarctic OR arctic OR tundra OR polar” for Scopus and ISI Web or knowledge, and did supplementary searches in Google Scholar (including an additional search string “vehicle OR rut AND soil AND arctic OR subarctic OR tundra OR polar”). Papers were included if they fulfilled the geographic criteria and the following: they reported a response of one or more soil characteristics, and included a “trampling agent” (reindeer, musk ox, simulation of ungulate trampling, human, all-terrain vehicle) in the design or inference. These steps yielded a total of 28 papers. From each included study, I extracted qualitative (positive, neutral, negative) responses of soil characteristics (linked with soil structure, biota, microclimate and biogeochemistry), the trampling agent, site climatic characteristics and location data. If studies included measurements from multiple distinct sites, these were recorded as independent observations. Due to the scarcity of papers and few observations per majority of the variables, combined with inconsistencies in analytical methods (e.g. different ways to measure root responses or ecosystem C exchange), only qualitative analysis was warranted. After retrieving the data, I juxtaposed the review results with the conceptual model to identify prevalent effects of trampling specifically in tundra.

3 Results and Discussion

3.1 Small rodent peaks decimate dwarf-shrubs in tundra

In Chapters I and II, I reported small rodent population peak effects on dominant slow dwarf shrubs: in Chapter I during one peak but in a landscape scale, across a productivity gradient and in Chapter II, over three consecutive cycles in small islands. I found strong negative effects of small rodents on woody dwarf-shrubs, including *Empetrum*, several *Vaccinium* species and *Betula nana*, irrespective of their apparent differences in palatability. These results are in line with previous empirical findings from Fennoscandian tundra (Kaarlejärvi et al., 2015; Olofsson et al., 2004b, 2014), but contrast dynamics predicted based on selective feeding of palatable forage. To my knowledge, no previous work has linked these strong herbivore peak-density effects on dominant slow plants that characterize many low-productive tundra systems, to changes in soil characteristics and ecosystem process rates.

The rodent peak in 2010-2011 was of the highest amplitude in four decades, and it impacted vegetation across much of northern Fennoscandia (Olofsson et al., 2012). At JRA, the predation rates were not able to increase fast enough to limit populations even in the usually three-trophic level system, resulting in runaway herbivory in dwarf-shrub heaths across the landscape. This may have been a result of apparent mutualism between voles and lemmings, which together swamped the predator response. In addition, the lemming peak developed over two consecutive summers, as opposed to the more common one-year peak typical of resource-limited consumers (Ekerholm et al., 2001; Oksanen et al., 1981), which likely intensified the herbivory pressure on vegetation.

Results of Chapter I show that the decimation of dwarf-shrubs percolated across a landscape with profoundly different levels of primary productivity, which indicated a temporal weakening of trophic control of herbivores also in productive habitats. Based on my and the team's observations, vast majority of dwarf-shrub biomass decimated during the peak did not translate to herbivore biomass, but was left

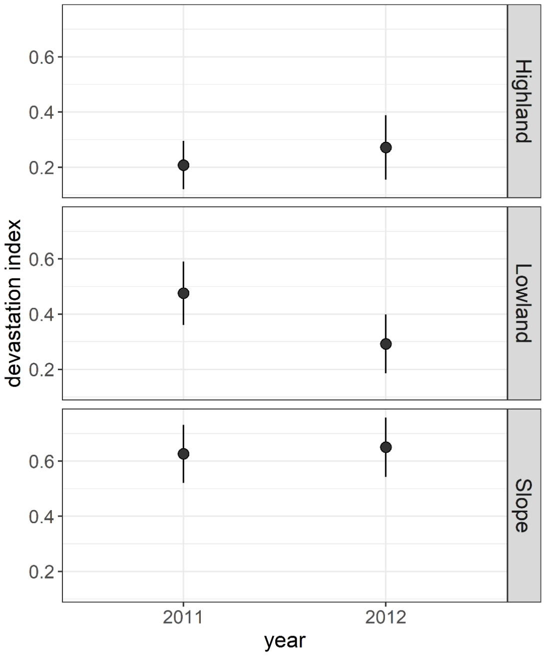

Figure 2. Vegetation devastation index (>50% of vegetation removed or damaged) recorded in the three different landscape areas at Joatka Research Area during both 2011 and 2012 growing season.

unconsumed. Decimation of both palatable and unpalatable dwarf shrubs was strongest in the Slope, and weaker in the Lowland and Highland, which directly contrasted predictions based on EEH (Fig. 2). Surprisingly, autumn 2011 vole density appeared to explain variation in decimation intensity differently in the productive and unproductive landscape areas. With low-to-moderate rodent densities, decimation was much stronger in the productive Slope than in Lowland and Highland. This result may be explained by a number of phenomena, yet first prompting the question of how well the autumn densities correlate with realized herbivory pressure. As cyclic populations peak during summer (Ekerholm et al., 2001), autumn trapping in the Slope may have captured populations already in decline phase, given spatial asynchrony in peak timing. Predators could have suppressed the rodent densities during summer in the Slope, whereas joint food limitation and spill-over predation would maybe manifest later in the low-productive two-level systems of Highland and Lowland. If so, major devastation in the Slope should have been induced already during the 2010-2011 winter. This interpretation is supported by the distribution of 2011 vs. 2012 damage data (Fig. 2), as major devastation in the Slope appears to have been induced already during the 2010-2011 winter. In contrast, the rodent devastation increased in Lowland also during the winter 2011 (Fig. 2).

Plant abundance, measured as cover, was reduced most during winter 2010-2011, i.e. before population peak in summer 2011. The result is likely explained by the seasonal variation in green biomass and plant regrowth. As the population peaked during the following summer, rodents were feeding on mainly herbaceous plants and green plant tissues, able to regenerate and regrow. Come winter and plant senescence, the high density populations collapsed rapidly. After the wintertime collapse, plants may have recovered during the spring and summer 2012 before plant censuses were conducted (Dahlgren et al., 2009b).

Results from the 11-year island experiment (Chapter II) corroborated the observation of slow plant species suffering the most under high-amplitude cyclic vole populations. In addition, I observed a shift in plant composition towards forb-dominance over the course of multiple population peaks. This shift resulted from joint declines of evergreen dwarf shrubs as well as concomitant increases of small forbs observed already after the first vole peak in 2003 (Dahlgren et al., 2009a), and was evident in both dry and wet microhabitats. Conversely, vegetation changes in the absence of voles were indicative of successional changes and resource competition, as especially *Empetrum* abundance increased and that of forb *Rubus chamaemorus* decreased. Vegetation censuses spanning entire habitats on the experimental island also illustrated high spatial variability in vegetation responses between micro-habitats of contrasting edaphic conditions. In each microhabitat, I observed strongest negative effects for the most abundant dwarf shrubs, i.e. evergreen in dry and deciduous in moist microhabitats. These results indicate that herbivores are likely to impact dwarf-shrubs according to their abundance, and can hence modulate small-scale variation in vegetation composition and abundance, contrasting previous work (le Roux et al., 2013).

My results also lend support to findings of Kaarlejärvi et al. (2015), pointing towards a strong potential of small rodents to control dwarf-shrub growth and state-shift in warming climate. However, my results also suggest that the interaction between vole dwarf-shrub decimation and potential for shrub expansion may be habitat specific. Vole-induced mortality of deciduous dwarf-shrubs is a key dynamics controlling tundra state shift with warming climate (Christie et al., 2015; Ravolainen et al., 2014). Yet, if *Empetrum* is decimated and its niche constructing effects were relaxed, this could provide a window of opportunity for competing deciduous dwarf-shrubs and herbaceous plants to increase in abundance (Bråthen et al., 2018), and this could subject the community to state transitions (Bråthen et al., 2017, 2018). Hence, more research across moisture and productivity gradients is needed to determine if vole dwarf-shrub clipping is exclusively an ecosystem service (preventing shrubification), or whether it could also be a disservice (releasing shrubification from *Empetrum* control); and how these small-scale dynamics translate to landscape-scale responses to the warming climate (Graae et al., 2018).

3.2 Small rodent peaks affect ecosystem process rates in low-productive tundra

Only a couple of studies have addressed the effects of small rodents on soil processes in tundra (Stark and Grellmann, 2002; Virtanen et al., 2008) or elsewhere (Sirotnak and Huntly, 2000), highlighting a substantial knowledge gap in tundra ecosystem dynamics. In Chapter II, I addressed this gap and studied how cyclic vole populations and vole-induced decimation of dwarf-shrubs affects ecosystem process rates. First, I studied how plant nutrient levels differed between dominant plant species and if they responded to herbivory at species and community levels. I found clear interspecific differences in tissue N content: surprisingly, N content was highest in the annually senescing tissues of deciduous shrubs. While small forbs had higher N content than evergreen dwarf shrubs, this difference was small, which may be explained by inclusion of forb stems with higher C:N ratio in the analysis. These interspecific differences contrasted the generally observed pattern of forbs having highest N content, followed by deciduous and evergreen dwarf shrubs (Reich et al., 2007). Importantly, the results indicate that the relatively "faster" forb species in dry hummock-bog tundra communities are still quite "slow".

Contrasting previous reports of negative or no small-rodent effects on plant N levels (Laine and Henttonen, 1987; Strengbom et al., 2003), I observed clear trends towards increased N content with high rodent density. Given the long duration of the experiment, this response may link with the increased soil N availability under high vole density (see below) and could point towards a form of positive feedback between herbivores, forage quality and soil N availability (Hobbie, 2015). Community- N combined the mean interspecific differences in nutrient content with the vole-induced shifts in plant community composition and plant community biomass. Hence, the increase in evergreen dwarf shrub biomass and dominance in low-density islands, together with the reduced abundance of forbs, led to decreases in community-N indicative of decelerating process rates and advancing succession in the absence of herbivores (Bardgett and Wardle, 2003). In contrast, in high-density islands community-N did not change over the course of 11 years, owing to the decrease in total biomass in the transplant plots, even with a strong shift towards forb-dominance. Importantly, the community-N in transplant plots correlated well with topsoil NH_4-N content, indicating that high vole densities promoted higher nutrient levels in both plant tissues and soil. Owing to the long duration of the experiment, it is impossible to say what mechanisms can have contributed to the vole-promoted community-level N and the co-varying soil NH_4-N content (Hobbie, 2015), highlighting a need for further research. Habitat-wide transect data revealed higher community-N on the ridges under high vole density. In depressions, voles did not increase the community N despite shifts in EHr, as dominant deciduous dwarf-shrubs with high leaf-N content were strongly reduced with vole density. This finding is important also in the context of warming climate, as decimation and strong browsing and clipping of deciduous dwarf shrubs, in habitats where they dominate, may in fact reduce the community-level N stored in plant above-ground tissues. Vole herbivory could thus act as a further mechanism to prevent an accelerating litter-soil feedback caused by enhanced shrub growth in warmer climate (Buckeridge et al., 2010).

Previous studies on small rodent effects on soil nutrient turnover and microbial activity in tundra have reported retarding (Stark and Grellmann, 2002) or positive yet statistically non-significant responses, linked with high small-scale variability in soil characteristics (Virtanen et al., 2008). Both of these studies are conducted in primarily lemming habitats without abundant dwarf-shrubs, and may therefore fail to recognize the effects of vole (or combined vole and lemming) peaks. My findings represent therefore the first evidence that high-density vole populations, and associated shift in plant community composition translated to increased ecosystem process rates: an increased NH_4-N content in topsoil and bottom soil, increased PO_4-P content in bottom soil, and higher microbial activity rates in litter (Chapter II). The increased soil inorganic nutrient levels may have emerged through joint effects of herbivore inputs of easily decomposable litter (Bakker et al., 2004) and a rapid compensatory increase in plant N content following herbivory, combined with repeated decimation of slow dwarf shrubs (Dahlgren et al., 2009a). These initial effects may have allowed for the observed species replacement, adding a longer-term feedback mechanism for nutrient cycling through changed litter quality and quantity (Bakker et al., 2009; Hobbie, 2015).

Counter to my prior expectations and dynamics that could be expected under a reduced slow:fast plant ratio and increased soil inorganic N content, soil microbial respiration did not respond to vole density treatments. This finding adds to a body of empirical evidence of partially decoupled aboveground and belowground dynamics and idiosyncratic soil responses to herbivory in tundra (Ricca et al., 2016; Stark et al., 2008, 2015). Owing to the complexity of aboveground-belowground linkages (Hobbie, 2015; van der Putten et al., 2013), possible explanations abound. For instance, soil microbial activity may be limited by labile C rather than inorganic N availability (Cherif and Loreau, 2013), which could link with decreased total vascular plant biomass under high vole density on the transplant plots. Alternatively, soil microbial activity may be constrained by large amounts of recalcitrant SOM, irrespective of N availability (cf. Craine et al., 2015), which could link with strong allelopathic legacy effects of *Empetrum* litter. It is also possible that explanations to unresponsive microbial activity rest in biotic or chemical soil variables not measured in the transplant experiment. For instance, I did not measure soil organic N content; yet, dissolved organic N may constitute a large part of total soil N pool in cold ecosystems (Schimel and Bennett, 2004).

3.3 Small rodent peaks – implications for ecosystem processes in tundra

Based on the results of Chapters I and II, small rodent-induced periodic decimation of slow species across landscape scales and associated potential to accelerate ecosystem process rates are omnipresent low-productive tundra systems. While high reindeer densities are linked with persistent shifts in vegetation composition and ecosystem state (Egelkraut et al., 2018; Ricca et al., 2016), it is unclear to what extent small rodents in fact modulate plant-soil interactions and ecosystem function of the tundra. Based on my findings in Chapter II, rodent-induced increases in process rates do not represent a change in stable ecosystem state, i.e. decreased dwarf-shrub dominance is likely maintained by recurring herbivory, and not by plant-soil feedbacks (cf. Egelkraut et al., 2018; Stark and Väisänen, 2014).

Below, I can only hypothesize whether small rodents could drive long-term increases or decreases in ecosystem process rates, and over which spatial scales could such effects take place. I propose that accelerating shifts in vegetation composition or process rates could be contingent on, among others, the following factors: first, the resilience of the dwarf-shrub dominance; second, the strength of feedback between feeding patch quality (i.e. amount of available forage) and rodent habitat choice (see Fig. 6 in Chapter II); and third, the long-term change in nutrient levels of the system.

First, occurrence of shifts in plant community composition of low-productive tundra dominated by *Empetrum* and other dwarf-shrubs is contingent on their ability to withstand severe disturbance events, during which up to 90-100% of their biomass is removed locally (Chapter I; Aerts, 2010). This resilience is likely modulated by a complex set of biotic and abiotic drivers, including dominant vegetation, frequency and type of herbivore effects, resource availability and the pool of species able to colonize after disturbance. Slow species' dominance, especially of *Empetrum*, can be highly resilient in dwarf-shrub tundra owing to legacy effects mediated by leaf litter (Dorrepaal et al., 2007; González et al., 2015), which affect interspecific plant performance and seedling germination, as well as litter decomposability and microbial activity (Dorrepaal et al., 2007; González et al., 2015). In the Iešjávri experiment (Chapter II), *Empetrum* abundance declined and resident forb abundance increased rapidly after only one peak (Dahlgren et al., 2009a). However, studies of reindeer-induced grass-state transitions indicate that repeated and high-density herbivore presence is likely needed for long-term shifts to occur (Egelkraut et al., 2018; Ricca et al., 2016). Past research indicates that *Empetrum* litter's ability to suppress growth and prevent establishment of other species may last for years (Aerts, 2010; Dorrepaal et al., 2007), and that this effect increases with the amount of litter (Dorrepaal et al., 2007). Devastation of dwarf-shrubs during small rodent outbreaks induces a rapid, high volume input of *Empertum* and other shrub litter, with potentially strong stabilizing feedback to *Empetrum* dominance and maintaining the status quo in plant community composition (Aerts, 2010). Experimental evidence on *Empetrum* recovery and replacement post-disturbance indicates however, that N and feces deposition may counteract the phytotoxic effects and promote establishment of forbs (Aerts, 2010; Bråthen et al., 2010), indicating that nutrient content and increased pH may ameliorate conditions. Alternatively, nutrient inputs may also be rapidly utilized by *Empetrum* to its benefit (Aerts, 2010). In summary, changes in the abundance of *Empetrum* as a niche constructor and functionally distinctive species (Bråthen and Ravolainen, 2015; Chapin III, 1997) are a likely central driver of ecosystem process responses to cyclic rodent populations, as well as resilience of tundra ecosystems in general (Bråthen et al., 2018).

Depending on site characteristics, weakening of *Empetrum* dominance may require repeated damage. The results from Iešjávri represent dynamics in a closed island system, where the increase in process rates was a result of high densities over multiple consecutive rodent peaks. Spatial-temporal variation in rodent densities and small-scale habitat choice would likely co-determine if sufficiently high rodent densities occur from one peak to another. In practice, if rodents were to increase the quality of the feeding patch by promoting faster and more palatable species, this should increase the density of rodents using that patch. As a result, a reinforcing feedback could stabilize the local patch in a state of higher average herbivore density and higher process rates (see e.g. Howison et al., 2017). Currently, research on such feedbacks and their potential to promote spatial heterogeneity in tundra is lacking. Long-term responses of vegetation and process rates to herbivory may indeed vary with spatial scale, with herbivory increasing within-landscape heterogeneity (Ricca et al., 2016). In sub-arctic islands with introduced reindeer/caribou, Ricca et al (2016) found accelerating responses in plant community but not in nutrient turnover at the island scale; however, at local scale intense herbivory reduced biomass of fast species. Apparently, scale-dependent dynamics may operate the other way around in mainland tundra systems, where herbivores may decelerate process rates over landscape scales (Bråthen et al., 2007), but increase them locally (Olofsson et al., 2004a). Spatially more detailed data on rodent habitat use during both winter and summer would allow linking variation in rodent habitat selection with resident vegetation; and conversely allow asking how rodent abundance affects local soil characteristics and ecosystem processes across tundra landscapes (see Chapter III).

Finally, ecosystem process rate responses are ultimately contingent on system nutrient status and inputs and outputs of limiting depletable resources (de Mazancourt and Loreau, 2000). Hence, while the compositional shift observed in Chapter II indicates changed aboveground-belowground dynamics, the long-term implications may prove different. Indeed, while initial and mid-term response to high herbivore density may be increased abundance of herbaceous species, nutrient turnover and primary production, ecosystem process rates and productivity may stay constant over long-term (e.g. 100yr) irrespective of the plant composition shift in closed island systems (Ricca et al., 2016). Therefore, persistent increases in ecosystem productivity could be brought about by either increased nutrient inputs to the system or reduced nutrient losses from it. For instance, herbivory may modulate inputs by either increasing (Sirotnak and Huntly, 2000) or decreasing abundance of highly palatable legumes (Bråthen et al., 2007). N-fixing bacteria living inside mosses can contribute a majority of N inputs in tundra (Chapin and Bledsoe, 1992), and hence strong reductions of mosses under small rodent and reindeer herbivory and trampling (Chapter IV; Virtanen et al., 2008; van der Wal et al., 2001) may translate to reduced N flow to the system, even if thinner moss carpet may lead to increased N mineralization rates over short term (Chapter IV).

In addition, spatial flows of elements between meta-communities (Leibold et al., 2004) may alter nutrient inputs and outputs and contribute to long-term productivity shifts. For instance, migrating reindeer have been proposed to decelerate ecosystem process rates in Highland at JRA by removing nutrients from the system (Stark and Grellmann, 2002). Similarly, migrating lemmings could, during their seasonal movement between overwintering and summer habitats as well as during outbreak migrations, redistribute nutrients across landscapes. For instance, one could expect a net nutrient input to snow-bed systems at JRA during the 2010-201 peak, as majority of population growth occurs during summer in the Slope, while population crashes occur during winter in Highland, and lemmings prefer to overwinter in snow-beds (Chapter I). The effects and importance of such spatial redistribution of nutrients and carbon for ecosystem processes have been speculated but, to my knowledge, not studied in tundra.

3.4 Novel method for small rodent monitoring and research

Fecal pellet counts and subsequent analysis of fecal chemical composition stand to provide spatially explicit data on links between herbivore abundance, their forage and resident plant and soil communities, and hence address many of the open questions presented in the context of Chapters I and II. In Chapter III, I explored the ability of NIRS to predict species identity from rodent feces, and thereby develop novel methodology to support more cost-efficient small rodent monitoring. If successful, future development of fNIRS calibrations could include not only improved taxonomic and demographic variables, but also dietary quality and plant secondary metabolites such as batatasin III present in *Empetrum* leaves (Steyaert et al., 2012; Tolleson, 2010).

In Chapter III, I present fNIRS calibrations with good to excellent accuracy for genus and species level identification of sub-arctic small rodents (Table 2). Genus-level predictions were most accurate, which mirrors the phylogenetic divergence of *Lemmus*, *Myodes* and *Microtus* at tribal level (Buzan et al., 2008). Also for species the prediction accuracy appeared to vary with the phylogenetic distance (Buzan et al., 2008; Cook et al., 2004; Kohli et al., 2014). *Lemmus*, with only one species, was predicted with ca. 97-98% accuracy, *Myodes* with ca 68% accuracy and *Microtus* with ca 95% accuracy. Within *Myodes*, prediction accuracy remained high (Table 2), but identification of *Microtus* species proved more difficult, when intestinal samples were included in the calibration data (Table 2). However, exposure of feces to ambient weather conditions increased the model prediction accuracy especially for Microtus species (Table 2). This result suggests that the fNIRS calibration is readily suitable for analysing feces collected from the field around JRA (with up to 6 week intervals). The result also indicates that some volatile or easily leaching compounds present in intestinal samples may mask the species-specific signal detected by the calibration algorithm.

Table 2. Species-specific prediction accuracies of fNIRS calibrations based on 600 model Monte Carlo cross-validation iterations for three different model types.

	fNIRS ability to predict species	**Effect of exposure**	**Regional specificity/generality of calibrations**			
	Data used in calibration modeling					
	intestinal and exposed WF samples	exposed WF samples	West-Finnmark samples	East-Finnmark samples	Joint WF and EF samples	Joint WF and EF samples
	Data used in independent test set, prediction accuracies (%)					
species	intestinal and exposed samples	exposed samples	East-Finnmark samples	West-Finnmark samples	East-Finnmark samples	West-Finnmark samples
L. lemmus	96.1% ± 3.18%	98.4% ± 2.79%	NA	NA	NA	NA
My. rufocanus	95.4% ± 4.02%	96.5 ± 3.76%	27.1% ± 15.6	89.7% ± 12.8%	85.3% ± 18.5%	96.7% ± 3.25%
My. rutilus	91.6% ± 9.20%	NA	NA	NA	NA	NA
Mi. oeconomus	68.8% ± 10.7%	85.4% ± 11.2%	99.4% ± 2.70%	47.9% ± 20.2%	93.9% ± 13.2%	94.6% ± 5.02%
Mi. agrestis	75.1% ± 9.85%	91.4% ± 8.25%	NA	NA	NA	NA

This result may indeed mirror the relatively recent radiation within *Microtus* (Barbosa et al., 2018) compared to *Myodes* (Cook et al., 2004; Kohli et al., 2014), but the fecal properties contributing to the high misclassification rate of intestinal samples remains unclear. The result may indicate that these species show similarities in e.g. volatile hormonal metabolites, which would be removed by exposure to ambient weather (Abáigar et al., 2010; Mesa-Cruz et al., 2014). In contrast, variation in diet does not appear to explain misclassifications of individuals within species. NIR-spectra and diet composition of individual samples showed only weak correlation based on both Mantel test ($r = 0.153$, $p < 0.001$) and Procrustes test (m12-squared = 0.932 correlation = 0.261, $p < 0.001$), and this interpretation was also supported by visual examination of Hmsc latent variables plot. While the diet analysis indicates that the species-specific signal is not a result of diet variation within JRA, diet differences may be a factor contributing to poor generalizability of calibration models between regions (Table 2; see below), if diets between populations differ markedly.

I also found that fNIRS calibrations have a potential to predict species identity of samples from different regions (Table 2). Calibration models built on West- or East-Finnmark samples alone performed poorly in predicting samples from the other region. However, a calibration model with samples from both regions predicted samples from both regions well. In my analysis a small numbers of samples (few dozens) from East-Finnmark supplementing the much larger West-Finnmark calibration data was enough to improve model accuracy. This indicates that the FDA model is able to identify species-specific signals shared by samples from different regions, even when the spectra from those regions appears to differ markedly. This corroborates recent findings by Murguzur et al. (2019), presenting successful global calibrations to predict plant N (P and Si) content in samples across temperate and arctic regions (used also in Chapter II). The result indicates towards feasibility of expanding the current fNIRS calibrations to inter-regional or circumpolar ones.

Relevance of the fNIRS calibrations for tundra community and ecosystem research can be substantial, and the method could have benefited work in Chapters I and II of the thesis. In Chapter I, extensive vegetation damage surveys were linked with small rodent abundance index, providing a spatially explicit link between herbivores and plants. However, the two damage indices represented cumulative effects of rodents over two consecutive peak years, while the rodent snap trapping provided, in essence, a snapshot in time. Repeated pellet counts in fixed plots could have provided a more accurate result of the cumulative abundance of rodents over time, without compromising taxonomic accuracy. Moreover, the exclosure experiment plots and biomass harvest plots in Chapter I were not directly linked with small rodent abundance or presence, as index trapping in single quadrants is not an established practice. This is one clear example, of how plot-scale fecal pellet sampling and fNIRS could benefit studies aiming to link herbivore abundance and species composition with local changes in vegetation community composition. Such sampling, and the non-disruptive nature of NIRS on samples, would furthermore allow for analyzing collected feces for diet composition using DNA metabarcoding (Chapter III and Tuomi et al. unpublished), and hence directly link herbivore foraging and food consumption to vegetation damages and resulting changes in plant community composition. A different, and possibly even more compelling alternative for studying ecosystem nutrient cycling, process rates, and stoichiometric changes in plants and herbivore feces, would be to use NIRS to analyze plant, soil and fecal N, P, Si and e.g. batatasin III content (Murguzur et al., 2019; Rinnan and Rinnan, 2007; Steyaert et al., 2012) all in the same site. Such calibrations would have provided highly valuable strands of evidence also for Chapter II, where changes in plant N content and community-level secondary metabolites could be linked to herbivore forage quality and stoichiometry of herbivore feces.

3.5 Large ungulate trampling effects on tundra soil structure, biota and microclimate

In Chapter IV, I set out to conceptualize current knowledge on ungulate trampling effects on tundra soils and to review the existing empirical literature on the topic from polar tundra areas. I identified four distinct pathways describing how trampling can affect soil structure, biota and microclimate, which may interact and ultimately lead to trampling-induced changes in soil biogeochemistry (see Fig. 3 in Chapter IV). The four causal pathways depict both dynamics observed consistently across biomes (e.g. compaction, declines in biota) as well as effects that may be especially prevalent in tundra, most notably linked with changes in soil microclimate. The review revealed a dearth of research on trampling effects on tundra soils, with only 28 original papers retrieved. However, some clear patterns emerged and the review of empirical evidence indicated that many soil responses may involve non-linear dynamics and thresholds especially with trampling intensity. Most trampling effects appear to be also strongly constrained by local environmental conditions, including resident vegetation, soil moisture and soil organic matter (OM) content and ambient climate.

Grazing ungulates and livestock compact soils across temperate ecosystems (Beylich et al., 2010) as well as in cold systems, including alpine tundra and boreal forests (e.g. Donkor et al., 2002). In tundra, I found strong evidence for trampling-induced soil compaction in tundra soils, including permafrost soils and soils with high organic matter content. Trampling intensity emerged as a key determinant of soil compaction responses, with potential thresholds both at onset of compaction as well as at initiation of erosion (Gellatly et al., 1986; Monz, 2002). While reviewed studies with reindeer did not report increasing bulk density, compaction and erosion are often observed next to reindeer fences and areas of heavy footpath traffic (Moen and Danell, 2003). Moreover, increased bulk density does often associate with reindeer presence, but it may not be explicitly linked with trampling in literature (Stark et al., 2002) and hence not be included in the current review. Lacking theoretical context, bulk density measures may also go un-reported.

Resident vegetation biomass and community as well as soil moisture and organic matter content emerged as key context factors modulating the compaction response to increasing trampling intensity (e.g. Bryan, 1977; Gisladottir, 2006). For instance, seasonal variation in soil moisture conditions, e.g. during spring thaw, may increase susceptibility of soils with high OM content to trampling-induced compaction (Kevan et al., 1995). In tundra, soil permafrost may effectively protect soils from compacting, and cryogenic processes could in some cases counteract compaction and increase bulk density (cf. Krzyszowska, 1989). However, frost heaving is unlikely to recover the soil macro-aggregate structure important for soil biota, water regime and biogeochemical processes (Six et al., 2004) – hence, soil compaction may result in complex changes in soil structure, which may not be detected via bulk density alone.

Corroborating findings across biomes (Howison et al., 2017), the reviewed papers reported consistently declines in the abundance of soil mesofauna, including enchytraeid worms, nematodes, and springtails (Collembola) in response to trampling. Soil fauna may be susceptible to trampling-induced compaction but also direct mechanical damage (Beylich et al., 2010), and responses of functional groups are expected to differ (Sitters and Andriuzzi, 2019). While the reviewed papers indicated differences between and within taxonomic groups of soil fauna (e.g. Sørensen et al., 2009), little is known of which functional or feeding groups are most susceptible to trampling, or benefit from trampling-induced changes. For instance, soil nematodes of different sizes may vary in their response to trampling-induced compaction, changes in vegetation composition or abundance of soil bacteria (Sitters and Andriuzzi, 2019; Sørensen et al., 2009; Xue et al., 2013), while springtails may respond to changes in soil moisture regime (Hayward et al., 2004). Changes in soil fauna and decomposer trait composition could be driven by bottom-up processes, and their responses to trampling are likely to initiate trophic cascades below-ground (Sitters and Andriuzzi, 2019). Just as soil microbial responses to large ungulate grazers are poorly understood across biomes (Sitters and Andriuzzi, 2019), I found only two original studies addressing trampling effects of soil bacteria and fungi, indicating a fundamental research gap for understanding how large ungulates affect ecosystem functioning. Based on studies in agricultural systems, fungi may be in general more susceptible and affected by both compaction and direct damage, while bacteria may be more sheltered dwelling in the soil micro-pore space (Beylich et al., 2010; Six et al., 2004).

Trampling effects on soil may also be mediated by changes in vegetation biomass and community composition. In tundra, especially cryptogams are susceptible to mechanical damage and trampling, and ungulate presence is commonly associated with strongly reduced biomass of lichens and mosses, attributable specifically to trampling rather than foraging (Heggenes et al., 2017; van der Wal et al., 2001). Moss responses are of particular importance, as mosses are an abundant growth form in many tundra ecosystems, and form thick carpets with strong insulating effect (Soudzilovskaia et al., 2013). Thick moss carpets slow down spring thaw, suppress soil temperatures during summer and even out diurnal thermal variation (Blok et al., 2011). The reviewed papers reporting moss and temperature responses consistently reported declining moss biomass and mat thickness with trampling, and linked this with higher growing season soil temperatures (Olofsson, 2009; van der Wal and Brooker, 2004). In addition, reduced moss biomass – as well as in litter and lichen biomass – may change soil moisture regime and lead to increased evaporation of freely draining soils (Blok et al., 2011). However, these effects were not considered in the reviewed literature.

Changes in plant biomass and community composition link with changes in plant roots. In tundra, 70% of plant biomass locates below-ground, and roots have a crucial role in soil C dynamics e.g. via root exudation and macro-aggregate formation (Chapin and Ruess, 2001; Six et al., 2004). Based on the review, root responses to trampling are largely unknown. The reviewed studies indicated that roots are likely to respond to trampling, and that multiple mechanisms can lead to trampling-induced changes in roots. For instance, increasing thaw depth in permafrost areas may allow roots to grow in deeper soil layers, while shift in vegetation composition will translate to an altered root biomass and function (Chapin and Shaver, 1981; Ylänne et al., 2018). Changes in roots are likely interact with soil biota in tundra, as ungulate presence has been linked with declining abundance in root-feeding nematodes (Sitters and Andriuzzi, 2019).

Finally, trampling is likely responsible for driving changes in plant community composition over longer time-scale. Trampling-induced vegetation shifts may arise through non-selective damages that are especially harmful for slow plant growth forms (Briske, 1996; Lezama and Paruelo, 2016). Trampling-induced changes on soil structure, biota and microclimate are likely to modulate soil resource availability, especially those of nutrients (see below), and moisture (e.g. Howison et al., 2017; Zimov et al., 1995) with subsequent changes in plant community composition.

3.6 Large ungulate trampling effects on soil biogeochemistry and ecosystem process rates

Ungulates are generally thought to drive changes in soil nutrient cycling and ecosystem process rates by modifying the quantity and quality of litter entering the soil subsystem (Bardgett and Wardle, 2003; Sitters and Andriuzzi, 2019). However, the above-described trampling-induced changes in soil structure, biota, microclimate as well as plant roots are also likely to cascade down to soil nutrient pools and biogeochemical processes in a highly complex manner. Indeed, trampling effects may significantly promote, but also decelerate, nutrient cycling and ecosystem process rates (Sitters and Andriuzzi, 2019). Evidence from other biomes indicates that changes in abundance of soil biota or microbes may not accurately predict soil process rate responses, which may be explained by the primacy of decomposer traits over their abundance, or alternatively by complex interplay of soil physical and biological conditions (Sitters and Andriuzzi, 2019). Indeed, trampling-induced soil compaction and associated changes in soil porosity (Beylich et al., 2010; Six et al., 2004), may ultimately alter soil biotic processes, nutrient turnover and long-term carbon dynamics , with a potential to decelerate N mineralization and hence process rates (Schrama et al., 2013b).

In tundra reindeer pastures, accelerated ecosystem process rates and state-shifts from shrub to graminoid-dominated systems feature coupled changes in vegetation composition, litter decomposability and soil microbial community composition (Olofsson et al., 2004a; Stark et al., 2012). While such changes can be driven by additions of feces and urine, recent research from tundra indicates that inputs of labile nutrients alone is not sufficient to initiate a shift in ecosystem processes (Barthelemy et al., 2018). Soil nutrient levels and microbial activity were only seldom measured among the reviewed literature. However, trampling-induced changes in insulating vegetation cover seem to play a substantial role promoting process rates, as warming soils accelerate biotic soil processes, which are heavily limited by temperature in tundra (Davidson and Janssens, 2006). Indeed, reviewed papers linked increased soil temperature to higher rates of N cycling. Compared to the compaction-mediated effect on N cycling observed in temperate grasslands (Schrama et al., 2013b), the moss-temperature pathway could be more easily triggered in tundra if moss decline ensued with lighter trampling intensity than soil compaction. Based on the review, very little is known of trampling effects on ecosystem process rates: determining thresholds, mechanisms and net effects and their dependence on environmental context is a pressing knowledge gap for future research.

3.7 Multiple ecological roles of arctic mammalian herbivores

Research on ecological networks has increasingly recognized the need to co-consider both trophic and non-trophic interactions to realistically explain structuring and functioning of ecosystems and species communities (García-Callejas et al., 2018; Sanders et al., 2014; Fig. 3). While much of the recent work on multiple interactions networks focuses on describing how non-trophic effects may modify trophic dynamics (Kéfi et al., 2012; Sanders et al., 2014), some contributions have bridged nutritional processes (Cherif and Loreau, 2013) and non-trophic physical alteration of the environment to explain how animals alter ecosystem processes (Barot et al., 2007; Pascual et al., 2017; Sitters and Olde Venterink, 2015). Clearly, also herbivores' roles in food-webs and for ecosystem function are multifaceted, and involve both trophic and non-trophic effects (Sanders et al., 2014; Sitters and Andriuzzi, 2019). However, this complexity in herbivore roles and functional traits in e.g. grazed tundra ecosystems is poorly acknowledged, and hence a realistic view on herbivore effects on ecosystem processes is still emerging. For instance, I found only 9 studies that explicitly incorporated large herbivore trampling effects on tundra soil (3 simulations and 6 observational studies; Chapter IV). In my PhD thesis, I have highlighted two prominent activities of tundra keystone herbivores, i.e. dwarf shrub clipping by small rodents and trampling by large ungulates (Fig. 3, horizontal axis), and established that these activities can accelerate ecosystem process rates (Fig. 3, vertical axis). Specifically, both of these activities appear to link with herbivore mobility, and be highly density-dependent.

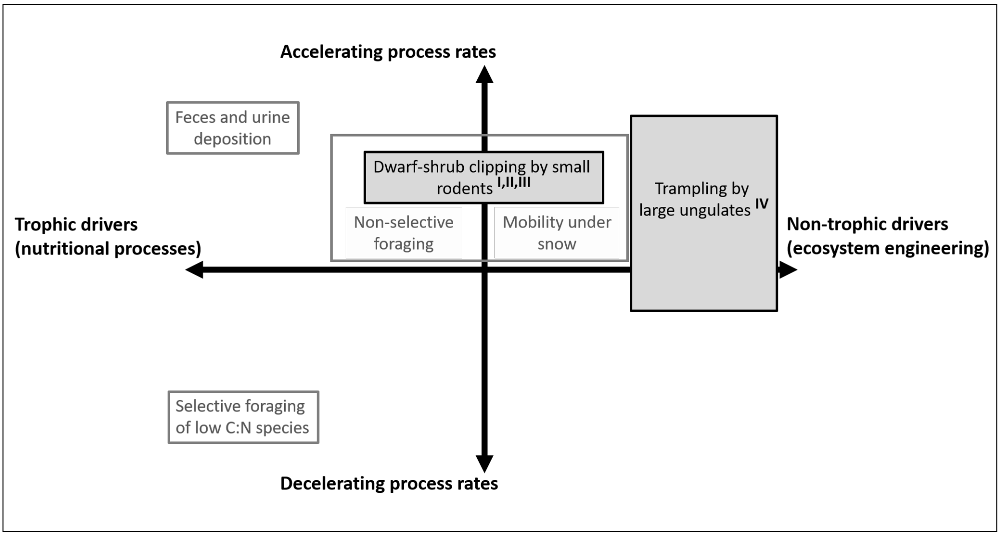

Figure 3. Hypothesized positioning of key herbivore drivers along two central conceptual axis of the thesis. Grey boxes indicate herbivore drivers covered in literature; black boxes with grey background indicate findings of this thesis. Roman numbers in superscript denote Chapter numbers.

Removal of “late successional” slow woody species and subsequent promotion of process rates has been previously reported in connection to beavers cutting large aspen in temperate forests (Pastor and Naiman, 1996). Despite a drastically different ecological context, rodents appear to cause similar effects in subarctic tundra (Chapter II). Unlike with beavers, causes for why small rodents clip poorly-palatable dwarf-shrubs remain unknown, as the interaction can be attributed to feeding under extreme resource limitation (Jefferies et al., 1994) or to removing obstacles to allow mobility under snow (Korslund and Steen, 2006). Herbivores experiencing nutrient deficiency due to low-quality forage may also be forced to increase their mobility to meet their stoichiometric demands (Simpson et al., 2010), and hence foraging and mobility may be tightly interlinked. In this way, the phenomenon of dwarf-shrub clipping may not be clearly assignable to a trophic or non-trophic interaction (Fig. 3). However, based on field observations both mechanisms may operate, as some cut shoots ("match sticks") are debarked while some are not. This, in turn, may depend on the species responsible for the cutting, with grey-sided voles typically debarking twigs (feeding) in contrast to lemmings (mobility; L.O. personal communication). Notably, *Empetrum* is found in diets of especially grey-sided voles in relatively high frequencies (Soininen et al., 2013b; Tuomi M. unpublished data); however it is unclear whether this results from feeding on berries or also on shoots. Cutting *Empetrum* shoots in the local feeding patch and feeding off the less-defended bark (Lavola et al., 2017) may outweigh all other choices, when the perceived habitat quality is low. Local vegetation composition and snow conditions, especially ground freezing (Ehrich et al., 2019), are plausibly key environmental controls of dwarf-shrub clipping in case of both foraging (with poor mobility and forage availability), and mobility.

Across ecosystems, effects of small herbivore mobility on ecosystem process rates is linked with tunneling and burrowing mammals, which are most studied among terrestrial ecosystem engineers (Coggan et al., 2018), and their impacts on soil and ecosystem processes have been addressed in also tundra (e.g. McKendrick et al., 1980). However, the role of trampling as a form of "process rate -altering" ecosystem engineering, non-trophic force is less clear (Fig. 3; Coggan et al., 2018). Even so, trampling effects are likely omnipresent (Sitters and Andriuzzi, 2019), as even small mammals have been found to cause soil compaction through repeated trampling in their runways (Pascual et al., 2017). In tundra, large ungulates moving in herds have the potential to induce physical and microclimatic changes both over large areas, and in spatially restricted game tracks (Fig. 3). While ecosystem engineering and non-trophic interactions have been widely observed to increase spatial heterogeneity (Coggan et al., 2018), whether this is the case also for ungulate trampling or dwarf-shrub clipping, is an interesting question for future.

Under which conditions trampling and dwarf-shrub clipping would promote net process rate acceleration or deceleration is currently unknown (Fig. 3). Direction of change is contingent on the interplay of different trophic and non-trophic herbivore effects and on capacity of the system to change in either direction. First, as fluctuating densities of small and large herbivores co-exist in tundra systems, their multiple activities modulating different drivers of ecosystem process rates are bound to interact (Fig. 3). For instance, if trampling decreased nitrogen mineralization rates though compaction, a simultaneous loss of insulating moss and increasing soil temperature might counteract this effect and promote higher decomposition rates in tundra. Primacy of selective feeding, trampling and excretion/urination effects are likely to be density-dependent and they may display density-dependent thresholds in their effects on soil characteristics and plant-soil interactions (Chapter IV). Second, ecosystem responses to multiple herbivore effects are constrained by the local biotic and abiotic context. Acceleration or deceleration of process rates with herbivore activities can be expected to occur in habitats where site characteristics (Grinath et al., 2019) allow for shifts in feedbacks between plants and soil, and between herbivores and patch forage quality. In general, the capacity of nutrient cycling to respond to physical ecosystem engineering depends on site abiotic constraints and "position along environmental gradients" (Grinath et al., 2019). For instance, ungulate trampling effects on nitrogen cycling via changes in soil temperature may be contingent on ambient air temperature; when growing season temperature is low, loss of insulation does not lead to warmer soils. Tundra soil susceptibility to compaction may depend on both site sensitivity and recovery capacity, which may be affected by e.g. site moisture conditions and presence of bio-turbating fauna, respectively. Rodent-induced shifts in plant community and process rates are likely contingent by the resilience of *Empetrum* as the prominent niche constructor. Generally, stoichiometric theory and mismatches between herbivores, plants and soil microbes (Cherif and Loreau, 2013) may represent a powerful framework for predicting the system's capacity to accelerate or decelerate (Sitters and Olde Venterink, 2015). Specifically, the N vs. C limitation of soil microbes may determine whether increased decomposition rates lead to net N mineralization or immobilization (Cherif and Loreau, 2013). For example, even if trampling increased microbial activity though warmer soils, faster decomposition rates could lead to net N immobilization by N-limited microbes (Cherif and Loreau, 2013); yet, inputs of herbivore excreta and urine may simultaneously alleviate microbial N limitation in tundra systems, and hence promote net N mineralization instead of immobilization (Cherif and Loreau, 2013; Fig. 3). As a critical starting point, addressing C vs. N limitation of microbes in grazed systems where trampling (Chapter IV) or dwarf-shrub clipping (Chapter II) has been found to increase nitrogen availability, would shed light on a key control of ecosystem process rate change. Similarly, stoichiometric mismatches could help to explain small rodent foraging and mobility behaviour in seasonal tundra ecosystems (Simpson et al., 2010).

4 Conclusions

To conclude, arctic herbivores display strong spatial-temporal density fluctuations, with a strong potential to affect dominant damage-intolerant, slow vegetation and soil characteristics. Depending on herbivore density and ecosystem context, both reindeer and small rodents can promote both decelerated and accelerated ecosystem process rates. In my thesis, I have argued that at least in some cases, this apparent idiosyncrasy of arctic herbivore effects on plant and ecosystem processes arises from insufficient recognition of multiple ecological roles of these animals (Fig. 3). Abundant past research has established that in low-productive systems selective grazing pushes the system towards decelerated process rates, while deposition or excreta and urine may increase process rates. However, these considerations ignore possibly the most prominent activities of high-density herbivore populations, namely trampling and devastation/clipping of poorly palatable dominant vegetation. The effects of trampling on soil process rates are mediated via multiple pathways (structure, biota and microclimate), and therefore the net effect of trampling alone on tundra process rates cannot be easily predicted. Moreover, the capacity of the system for increased process rates may vary between habitats, with niche constructing and legacy effects of *Empetrum* likely playing a central role for the resilience of a slow process rate state.

I found that in low-productive tundra, acceleration of ecosystem process rates by small and large herbivores appears to be strongly linked with mechanical damage leading to declined abundance of process-retarding slow evergreen dwarf-shrubs (Chapters I and II) or of cryptogams, which control soil thermal regime and biological process rates (Chapter IV). Based on my findings it is clear that only a joint consideration of trophic, nutritional and non-trophic interactions will allow for developing a realistic understanding on how arctic herbivores govern and modulate ecosystem processes.

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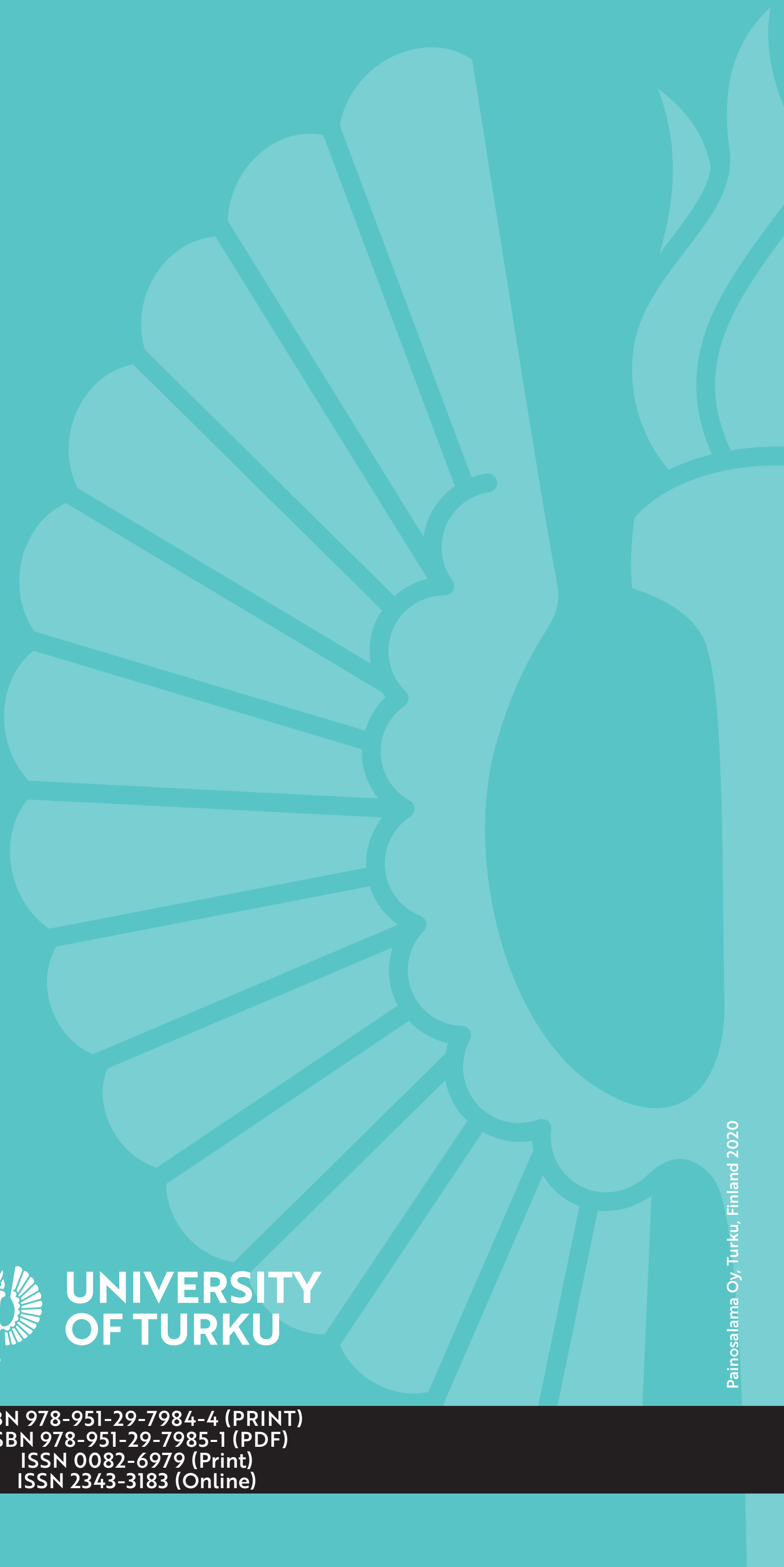

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