Doctoral Thesis

December 2024

The impacts of spatio-temporal shifts in vertebrate herbivore communities on the functioning of the Icelandic tundra

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The impacts of spatio-temporal shifts in vertebrate herbivore communities on the functioning of the Icelandic tundra

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A 150 ECTS Academic Dissertation Presented in Candidacy for the
Degree of Doctor of Philosophy in Environmental Sciences

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Hvanneyri, December 2024

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This thesis should be cited as:

Mathilde Defourneaux, 2024, *The impact of spatio-temporal shifts in vertebrate herbivore communities on the functioning the Icelandic tundra*, PhD thesis, Environmental sciences, Agricultural University of Iceland, 75 pages. ISBN 978-9935-512-51-2

Vitna skal til þessarar ritgerðar sem:

Defourneaux, M. (2024). *The impact of spatio-temporal shifts in vertebrate herbivore communities on the functioning the Icelandic tundra* [Breytingar á samfélögum grasbíta í tíma og rúmi: áhrif á virkni íslenskra túndruvistkerfa]. Doktorsritgerð. Landbúnaðarháskóli Íslands, Hvanneyri. 75 bls. (á ensku, með íslenskum útdrætti). ISBN 978-9935-512-51-2

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Clarification of contribution

I hereby declare that this project is based on my own observations, is written by me, and that it has not been previously submitted to another university degree, neither in part nor in whole. The three accompanying papers are my own work, done under the supervision and with the assistance of my supervisors Isabel C. Barrio (Agricultural University of Iceland), James D. M. Speed (Norwegian University of Science and Technology) and Noémie Boulanger-Lapointe (University of Victoria).

My contributions to the three papers presented in this thesis were as follows:

Paper I: I conceptualised the research and developed the methodology with Isabel C. Barrio, James D.M. Speed, and Noémie Boulanger Lapointe. I performed data analysis, interpretation, and manuscript writing, which was reviewed and approved by all co-authors. I also handled correspondence with the journal for publication.

Paper II : I designed the research together with Isabel C Barrio, James D. M. Speed and Noémie Boulanger-Lapointe. The methodology was developed in collaboration with my supervisors, Laura Barbero-Palacios (PhD student, Greenland Institute of Natural Resources), and Jonas Schoelynck (University of Antwerp). I secured funding for the field survey and sample processing. I planned and collected, with the help of field assistants, all the data presented in the paper during a field survey in the Eastern Highlands of Iceland in 2022. Sample processing was carried out at the Agricultural University of Iceland with the help of students, and at the University of Antwerp under the supervision of Jonas Schoelynck. I conducted the data analysis and interpretation. I wrote the manuscript, which was reviewed by all co-authors. I corresponded with the scientific journal to which the paper was submitted.

Paper III: I conceptualised the research and developed the methodolgy with Isabel C Barrio, James D. M. Speed and Noémie Boulanger-Lapointe. I secured funding for the field survey and sample processing. I planned, and collected all the data presented in the paper during one field surveys in the Eastern Highlands of Iceland in 2022 with the support of field assistants. Sample processing was carried out at the Agricultural University of Iceland with the help of students, and at the University of Antwerp under the supervision of Jonas Schoelynck. I analysed and interpreted the data, and wrote the original manuscript that was revised and approved by all co-authors.

Mathilde Defourneax

Abstract

Rapid environmental changes in the Arctic tundra are driving shifts in herbivore populations, distribution, and phenology, affecting the structure of herbivore community. These changes will have consequences to ecosystem structure and function through the direct effects of herbivores on vegetation biomass and biogeochemical cycles. Yet, the effects of herbivores on ecosystem functions, particularly within a multispecies context, are still poorly understood. Addressing these knowledge gaps in tundra rangelands, which are grazed by both wild and domestic herbivores, is an urgent task to ensure the development of sustainable management practices.

Using Icelandic rangelands as a case study, I investigated how changes in herbivore communities affect tundra ecosystem functions across various spatial and temporal scales, with a focus on nutrient recycling. Specifically, I aimed to: **1)** track changes in herbivore community composition through time, **2)** assess the impact of herbivore on vegetation biomass, **3)** measure the faecal nutrient contributions of different herbivores species, and **4)** evaluate the role of herbivores on nutrient distribution. I analysed long-term data to assess shifts in herbivore populations and their impacts on vegetation at a regional scale. Additionally, through extensive fieldwork in 2022, I examined herbivore effects on vegetation, faecal nutrient deposition, and nutrient transport at landscape and local scales in high-elevation rangelands. Specifically, I measured rates of aboveground biomass consumption, faecal nutrient content and faecal deposition rates of pink-footed goose, sheep and reindeer, and forage quality at 21 sampling sites throughout the growing season. Near-infrared reflectance spectroscopy (NIRS) models were calibrated to estimate faecal nutrient content.

Results from the thesis indicate rapid changes in the Icelandic herbivore community: over the past 40 years, the dominant herbivores shifted from domestic (mainly sheep) to wild herbivores, led by the large increase in pink-footed goose. Overall, herbivores consumed a small percentage (4%) of total plant biomass, but this reached up to 30% in localised areas in the Eastern Highlands toward the end of the growing season. Although the goose population consumed less biomass than the sheep population, geese contributed significantly more to faecal nutrient deposition, especially early in the growing season when nutrient content in their faeces was highest. There was no clear connection between forage quality and herbivore consumption, but areas with low-quality forage showed more nutrient deposition through faeces. These findings highlight the potential of herbivores to redistribute nutrient across the landscape and provide insights into the role of herbivores in shaping tundra ecosystems through their effects on nutrient cycling, particularly in the context of strong and rapid ongoing herbivore community changes.

Keywords: herbivore, tundra, population changes, zoogeochemistry, nutrient, range management

Ágrip

Hraðar umhverfisbreytingar á norðurslóðum hafa í för með sér breytingar á stofnstærð, útbreiðslu og atferli grasbíta, sem hefur áhrif á samfélagsgerð þeirra. Þær breytingar munu síðan hafa afleiðingar fyrir byggingu og virkni vistkerfa, einkum vegna beinna áhrifa grasbíta á lífmassa gróðurs og hringrásir næringarefna. Þrátt fyrir það eru áhrif grasbíta á virkni vistkerfa enn illa þekkt, sérstaklega þegar um er að ræða samspil margra tegunda grasbíta. Mikilvægt er að bæta þekkingu á þessum áhrifum í túndruvistkerfum sem nýtt eru af mismunandi grasbítum, bæði villtum grasbítum og búfé, til að tryggja þróun sjálfbærrar landnýtingar.

Ég rannsakaði hvernig breytingar á samfélögum grasbíta hafa áhrif á virkni íslenskra túndruvistkerfa á mismunandi kvörðum í tíma og rúmi, með áherslu á hringrásir næringarefna. Markmið rannsóknarinnar voru einkum að: 1) fylgjast með breytingum í samsetningu samfélaga grasbíta yfir tíma, 2) meta áhrif grasbíta á lífmassa gróðurs, 3) mæla næringarefnainnihald í skít mismunandi grasbítategunda og 4) meta hlutverk grasbíta við dreifingu næringarefna. Ég greindi langtímagögn til að meta breytingar á stofnum grasbíta og áhrif þeirra á gróður á stærri svæðum. Að auki kannaði ég staðbundin áhrif og landlagsáhrif grasbíta á gróður, næringarefnainnihald í skít þeirra og flutning næringarefna í hálendisvistkerfum með umfangsmikilli vettvangsvinnu árið 2022. Í því fólst að mæla neyslu á ofanjarðarlífmassa gróðurs, magn og næringarefnainnihald í skít heiðagæsa, kinda og hreindýra, ásamt fóðurgæðum á 21 sýnatökustað yfir vaxtartímabilið. Nær-innrauð endurkastsgreining (NIRS) var notuð til að meta næringarefnainnihald í skít þessara tegunda.

Niðurstöður ritgerðarinnar sýna hraðar breytingar í íslenska grasbítasamfélaginu síðustu 40 árin. Hlutfall búfjár (aðallega kindur) sem var ríkjandi áður hefur dregist saman og hlutfall villtra grasbíta hefur aukist, einkum vegna mikillar fjölgunar heiðagæsa. Grasbítar neyttu að jafnaði lítils hlutfalls (4%) af heildarlífmassa gróðurs, en staðbundin neysla náði allt að 30% sums staðar á Austurhálendinu undir lok vaxtartímabilsins. Þrátt fyrir að gæsastofninn neyti minna lífmassa en kindur, lögðu gæsir verulega meira til af næringarefnum í skít, sérstaklega snemma á vaxtartímabilinu þegar næringarefnainnihald skítsins var hæst. Ekki fannst skýr tenging milli fóðurgæða og neyslu grasbíta, en á svæðum með lág fóðurgæði lagðist hlutfallslega meira til af næringarefnum með skít en á svæðum með hærri fóðurgæði. Þessar niðurstöður varpa ljósi á getu grasbíta til að dreifa næringarefnum um landslag og sýna fram á hlutverk þeirra í mótun túndruvistkerfa í gegnum áhrif þeirra á hringrásir næringarefna, einkum með hliðsjón af þeim hröðum breytingum sem eru að verða á grasbítasamfélaginu.

Lykilorð: grasbítar, túndra, breytingar á stofnum, áhrif dýra á hringrásir næringarefna, næringarefni, beitarstjórnun

Résumé

La toundra arctique subit des changements environnementaux et des politiques de gestion rapides. Ceux-ci affectent les populations, la distribution et la phénologie des herbivores, modifiant ainsi la composition des communautés. De telles transformations risquent d'impacter la structure et le fonctionnement de ces écosystèmes, en raison de l'effet des herbivores sur la biomasse végétative et sur les cycles biogéochimiques. Cependant, le rôle des herbivores dans la fonctionnalité des écosystèmes, particulièrement dans un contexte multi-espèces, reste peu étudié. Il est donc urgent d'étudier l'effet des changements des communautés d'herbivores sur le fonctionnement de la toundra, en particulier dans les zones de pâturages qui sont utilisées à la fois par des espèces sauvages et du bétail, afin de développer des pratiques de gestion adéquates.

À partir de l'étude du cas des pâturages islandais, j'ai étudié l'impact des changements dans les communautés d'herbivores sur le fonctionnement de la toundra, à différentes échelles spatiales et temporelles, tout en me focalisant sur le recyclage des nutriments. Mes objectifs étaient les suivants: 1) identifier les modifications de la composition des communautés d'herbivores au fil du temps, 2) évaluer l'impact direct des herbivores sur la biomasse végétative, 3) mesurer la déposition de nutriments par les excréments de plusieurs espèces d'herbivores et 4) analyser le rôle des herbivores dans la redistribution des nutriments. Pour ce faire, j'ai utilisé des données démographiques afin d'identifier les changements dans les communautés et d'évaluer leur effet sur la végétation à l'échelle régionale. Lors d'une campagne de terrain menée en été 2022, j'ai étudié l'impact des herbivores sur la biomasse végétative, la déposition et le transport de nutriments à l'échelle paysagère et locale. J'ai sélectionné 21 sites d'échantillonnage où j'ai mesuré les taux de consommation de biomasse végétative, la teneur en nutriments des fèces et la déposition des fèces des oies à bec court, des moutons et des rennes au cours de la saison. Enfin, j'ai étalonné des modèles multi-espèces basés sur la spectrophotométrie dans le proche infrarouge pour estimer la teneur en nutriments des fèces.

Mes résultats montrent une évolution rapide de la communauté d'herbivores en Islande : autrefois dominée par des espèces domestiques, principalement des moutons, elle est désormais principalement constituée d'espèces sauvages, en particulier les oies à bec court, dont la population a fortement augmenté au cours des 40 dernières années. Les herbivores consomment une faible part de la biomasse végétative totale (4 %), bien que ce taux puisse atteindre 30 % localement, notamment sur les plateaux de l'Est en fin de saison de croissance végétative. Bien que les oies consomment moins de biomasse que les moutons, elles contribuent fortement à la déposition de nutriments, surtout en début de saison de croissance, lorsque leurs fèces sont les plus riches en nutriments. Nous n'avons pas trouvé de lien clair entre la qualité du fourrage et sa consommation, mais les zones de fourrage moins nutritives présentent une déposition accrue de nutriments via les fèces. Nos résultats illustrent le potentiel des herbivores à redistribuer les nutriments dans le paysage, et nous éclairent sur leur rôle dans le façonnage des écosystèmes de toundra via leurs effets sur le cycle des nutriments, en particulier dans le contexte de changements rapides dans la composition des communautés d'herbivores.

Mots-clés: herbivore, toundra, changements de population, zoogéochimie, nutriment, gestion des pâturages.

Acknowledgements

I would like to express my deepest gratitude to my supervisors, Isabel, James, and Noémie, whose wisdom, guidance, and responsiveness have been invaluable. Their unwavering support and encouragement to pursue research questions that fascinated me have profoundly shaped my journey as a PhD student. They are not only exceptional supervisors but also remarkable people, whose kindness, warmth, and openness have created enriching interactions. I sincerely hope that this is just the beginning of many future collaborations and research projects together.

I am deeply thankful to Charlotte, Anya, Björk, Ludivine and Chris, whose essential help during fieldwork in the highlands made it possible to complete this research. Their joyful spirits and positive attitudes, even in the face of the worst possible weather (including a storm on our very first day), were an inspiration. My thanks also go to the Nattúrustofa Austurlands, particularly Katrín, Guðrún, Halldór, and the late Skarphéðinn, for their logistical support, insightful advice, and the working facilities and storage space they so generously provided. Special thanks to the local hunting communities who helped us to find reindeer, and to Lilja and Björn, who welcomed us warmly into their turf house at Sænautasel. Their hospitality, complete with hot chocolate, pancakes, and cosy bedding, provided warmth and comfort during our stay, especially when it snowed in the middle of summer! A huge thank you to Laura, my dedicated fieldwork companion, whose adventurous spirit and cheerful "hobbit" mood made every day in the field a real adventure. From the Icelandic Highlands to the high Arctic of Iqaluktuuttiaq, she brought invaluable skills and an incredible taste for food. (We still need to write that fieldwork recipe book!)

I am also grateful to my interns and lab assistants: Janine, Snæi, Manon, Nori, and Sebastian, who helped me to meticulously mill, weigh, and tablet hundreds of plant and faecal samples. Their hard work and dedication made it possible to complete this PhD on time. Thanks as well to Katarina at Antwerp University and the Tromsø team (UiT) : Hanna and Kari-Anne, for their precious help for NIRS calibration.

To my "office crew"—Stephen, Solveig, Anna, Phoebe, Sumji, and Mariana—thank you for creating a supportive, upbeat environment in which we grew as researchers and colleagues. I am also grateful to the Tundra ecological Lab for their precious feedback and friendly atmosphere during this thesis.

Finally, to my family—my parents, my siblings Éloïse and Pierre, and my partner Léo— for your support in this journey. Becoming an ecologist has been more than a career; it has shaped who I am, and I am grateful for your encouragements, especially when it meant being far away for extended periods. A special thanks to my grandmother, who first sparked my curiosity about the North as a kid, and to my dear friend Audrey, who called me every two weeks to cheer me on and keep me motivated during the final stages of the writing process.

Completing my PhD is more than earning a diploma; it marks the end of an incredible chapter of my life in Iceland. I have found here a warm, vibrant community, traditional music sessions, an interest in photography and mountaineering, and wonderful neighbors who helped me grow in countless ways. There are many dear friends and family members who have shared this journey with me. To each of you, thank you for being part of this transformative experience.

List of original papers

The present thesis is based on three publications, which will be referred throughout the thesis by their Roman numerals.

I. Defourneaux, M., Barrio, I.C., Boulanger-Lapointe, N., Speed, J.D.M., 2024. Long-term changes in herbivore community and vegetation impact of wild and domestic herbivores across Iceland. Ambio 53, 1124–1135. https://doi.org/10.1007/s13280-024-01998-6 [**published**]

II. Defourneaux, M., Barbero-Palacios, L., Schoelynck, J., Boulanger-Lapointe, N., Speed, J.D.M., Barrio, I.C., 2024. Capturing seasonal variations in faecal nutrient content from tundra herbivores using Near Infrared Reflectance Spectroscopy. in rev. Science of the Total Environment. [**submitted**]

III. Defourneaux, M., Speed, J.D.M., Boulanger-Lapointe, N., Schoelynck, J., Barrio, I.C., 2024. Nutrient redistribution by herbivores across a tundra landscape. in prep. [**manuscript**]

Two additional papers related to the topic of this thesis, in which I participated as a co-author, were also published during the course of the work:

Boulanger-Lapointe, N., Ágústsdóttir, K., Barrio, I.C., **Defourneaux, M.**, Finnsdóttir, R., Jónsdóttir, I.S., Marteinsdóttir, B., Mitchell, C., Möller, M., Nielsen, Ó.K., Sigfússon, A.Þ., Þórisson, S.G., Huettmann, F., 2022. Herbivore species coexistence in changing rangeland ecosystems: First high resolution national open-source and open-access ensemble models for Iceland. Science of The Total Environment 845, 157140. https://doi.org/10.1016/j.scitotenv.2022.157140

Barbero-Palacios, L., Barrio, I.C., García Criado, M., Kater, I., Petit Bon, M., Kolari, T.H.M., Bjørkås, R., Trepel, J., Lundgren, E., Björnsdóttir, K., Hwang, B.C., Bartra-Cabré, L., **Defourneaux, M.**, Ramsay, J., Lameris, T.K., Leffler, A.J., Lock, J.G., Kuoppamaa, M.S., Kristensen, J.A., Bjorkman, A.D., Myers-Smith, I., Lecomte, N., Axmacher, J.C., Gilg, O., Den Herder, M., Pagneux, E.P., Skarin, A., Sokolova, N., Windirsch, T., Wheeler, H.C., Serrano, E., Virtanen, T., Hik, D.S., Kaarlejärvi, E., Speed, J.D.M., Soininen, E.M., 2024. Herbivore diversity effects on Arctic tundra ecosystems: a systematic review. Environ Evid 13, 6. https://doi.org/10.1186/s13750-024-00330-9

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1. Introduction

Herbivore distribution, abundance, and migration patterns in the Arctic tundra are rapidly shifting. These shifts are affecting the composition of local herbivore communities, with potential widespread consequences for ecosystem structure and function. Yet, the effects of herbivores on ecosystem functions, particularly within a multispecies context, are poorly understood. There is an urgent need to clarify these effects in tundra rangelands, which are important socio-economical systems used for livestock grazing. Understanding herbivore impacts in such systems will help for effective land management.

In this introduction, I begin by describing the particular and severe constraints conditions of the Arctic tundra, and review the effect of climate change and human activities on its herbivore communities. I then discuss the role of herbivores in tundra ecosystems, particularly how they influence ecosystem functions through both consumption and waste deposition and highlight the apparent knowledge gaps related to their effects on biogeochemical cycles. Knowledge in this field is partly prevented by the lack of affordable methodologies to assess herbivore nutrient contributions through faecal inputs, so I describe the use of Near Infrared Reflectance Spectroscopy (NIRS) as a potential tool to bridge this gap. I then consider the implications of using tundra as a managed rangeland, highlighting the combined impacts of livestock grazing and wild herbivores, and the resulting management conflicts. Finally, I present the Icelandic tundra as a case study, focusing on its herbivore community, grazing system, and ongoing socio-ecological concerns about rangeland sustainability.

1.1 Changes in herbivore communities in the Arctic tundra

The Arctic tundra, characterized by vast, treeless landscapes, is a constraining environment for herbivores. The climatic conditions are severe, with extended winters and most of the precipitation falling as snow; the growing season is extremely brief, lasting only 1.5 to 4 months (Bliss et al. 1973). In addition, tundra ecosystems are limited by low nutrient availability, particularly nitrogen (N) and phosphorus (P), which are essential for plant growth. These conditions result in a low aboveground primary productivity (Barsdate and Alexander 1975), typically less than 200 $g.m^{-2}$ (Bliss et al. 1973). At the start of the growing season, as the vegetation begins to grow, nutrients stored in the soil by microorganisms are rapidly released, creating a sharp aboveground nutrient pulse, that gradually decreases as the season progresses (Westergaard-Nielsen et al. 2021). The resulting vegetation is usually patchy and low-lying (Virtanen and Ek 2014), and consists mainly of shrubs, graminoids (sedges, grasses and rushes), forbs, and numerous mosses and lichens.

Only few vertebrate herbivore species can cope with the harsh conditions of the Arctic tundra. The species richness of local herbivore communities rarely exceeds 14 species, with most of the herbivores being small- to medium-sized mammal and birds species (Barrio et al. 2016; Speed et al. 2019b). In terms of large herbivores, only reindeer (*Rangifer tarandus* L., Caribou in North America), and muskox (*Ovibos moschatus* Z.) are associated to the tundra ecosystem (Olofsson and Post 2018). Reindeer are by far the most widespread large herbivore in the tundra and have been domesticated in some parts of the region (Røed et al. 2018).

Ongoing environmental changes are affecting herbivore populations in the Arctic, causing significant changes in their distribution, abundance and phenology (e.g., timing of migration). The Arctic is warming nearly four times faster than the global average (Rantanen et al. 2022) leading to a northward expansion of boreal species and range shifts of Arctic species (i.e., borealization, Speed et al. 2021). Additionally, fluctuations in winter conditions (i.e., increased precipitation, higher temperatures), and more frequent extreme weather events lead to the formation of thick ice cover, limiting the access to food resources. Winter disturbances have a devastating impact on wild reindeer populations, many of which are declining (Uboni et al. 2016), and disrupt the population cycle of small rodents and ptarmigan (Kausrud et al. 2008; Fuglei et al. 2020). In turn, changes in agricultural practices in wintering grounds have led to substantial population increases of migratory waterfowl (Fox and Leafloor 2018). These changes in herbivore populations are expected to reshape communities, with potentially large consequences on biotic structures and ecosystem functions (Schmidt et al. 2017). Despite a growing body of literature addressing the impacts of herbivores in the tundra, the effects of herbivores on ecosystem functions in a multispecies context remain unclear (Barbero-Palacios et al. 2024). A greater understanding of the complex effects of changes in herbivore communities across the tundra biome is crucial to predict how future herbivore assemblages may restructure tundra environments.

1.2 The impact of herbivores on ecosystem functions

Despite low diversity and limited biomass (Fløjgaard et al. 2021; Greenspoon et al. 2023), herbivores are a very important component of tundra ecosystems (Oksanen et al. 1981; Oksanen and Oksanen 2000). Herbivores can exert a strong top-down control over primary production by consuming vegetation biomass. They also contribute to nutrient availability by converting plant biomass into urine and faeces (Barthelemy 2016), body fluids (Ferraro et al. 2023), or carcasses (Barton et al. 2013). Finally, they modify their physical environment by trampling, both directly through physical damage and habitat destruction, and indirectly by altering soil abiotic properties such as bulk density, pore structure, temperature, moisture, pH and organic matter (Tuomi et al. 2021). By influencing their environment through different pathways, herbivores affect numerous key ecosystem functions, which in turn, can influence plant-soil feedbacks, by either accelerating or decelerating rates of primary production, nutrient cycling and microbial activities (Hobbie and Villéger 2015; Wang et al. 2023, Meyer and Leroux 2024).

1.2.1 Consumptive effects of herbivores on vegetation biomass and biogeochemical cycles

Through their direct consumption of plant material, herbivores affect primary production and biogeochemical cycles. In tundra ecosystems, herbivores typically consume less than 10% of net aboveground primary production, although in high-density areas, they can consume up to 50-90% (Jefferies et al. 1994). Despite low overall consumption, herbivore feeding significantly affects plant productivity and ecosystem processes through soil-plant feedbacks (Wardle et al. 2004). By consuming plants, herbivores reduce photosynthetic tissue and limit CO_2 uptake by plants, affecting the carbon (C) balance of tundra ecosystems (Sjögersten et al. 2008; Falk et al. 2014).

Herbivores in tundra ecosystems are relatively selective feeders, showing preferences for specific species or plant groups based on their nutritional needs and digestive capacity (Schmidt et al. 2018). Both forage quantity and forage quality are important determinants of habitat and diet selection by herbivores in the Arctic tundra (Van Der Wal et al. 2000; Iversen et al. 2014). When available, herbivores target nutrient-rich, easily digestible plant species that are high in N and P, and low in C (Sheremetev 2023). Not only can this selective behaviour affect plant biomass and survival (Crawley et al. 2021), but it can also alter the composition of plant litter and recycling pathways. Selective foraging affects decomposition rates and microbial activity, with outcomes dependent on local conditions such as productivity, grazing history, and the occurrence of predators (Stark 2007; Forbes et al. 2019, Figure 1.1). Typically, in nutrient-rich areas, herbivores can stimulate compensatory plant regrowth from grazing-tolerant plant species, increasing productivity and litter quality, which accelerates nutrient cycling (Du Toit and Olff 2014). In contrast, in nutrient-poor areas, selective feeding of herbivores on N-rich plants alters plant competitive outcomes and promotes the dominance of N-poor plants, which are often rich in C and produce litter that is harder to decompose, resulting in slower decomposition and a fungal-dominated soil microbiome (Pastor and Naiman 1992). Long-term studies show that herbivores have lasting effects on biogeochemical cycles through their consumption of vegetation (Forbes et al. 2019). Specifically, their selective foraging behaviour can influence soil nutrient limitation and alter ecosystem stoichiometry (Daufresne and Loreau 2001), sometimes shifting communities from nitrogen- to phosphorus-limited systems (Sitters et al. 2019).

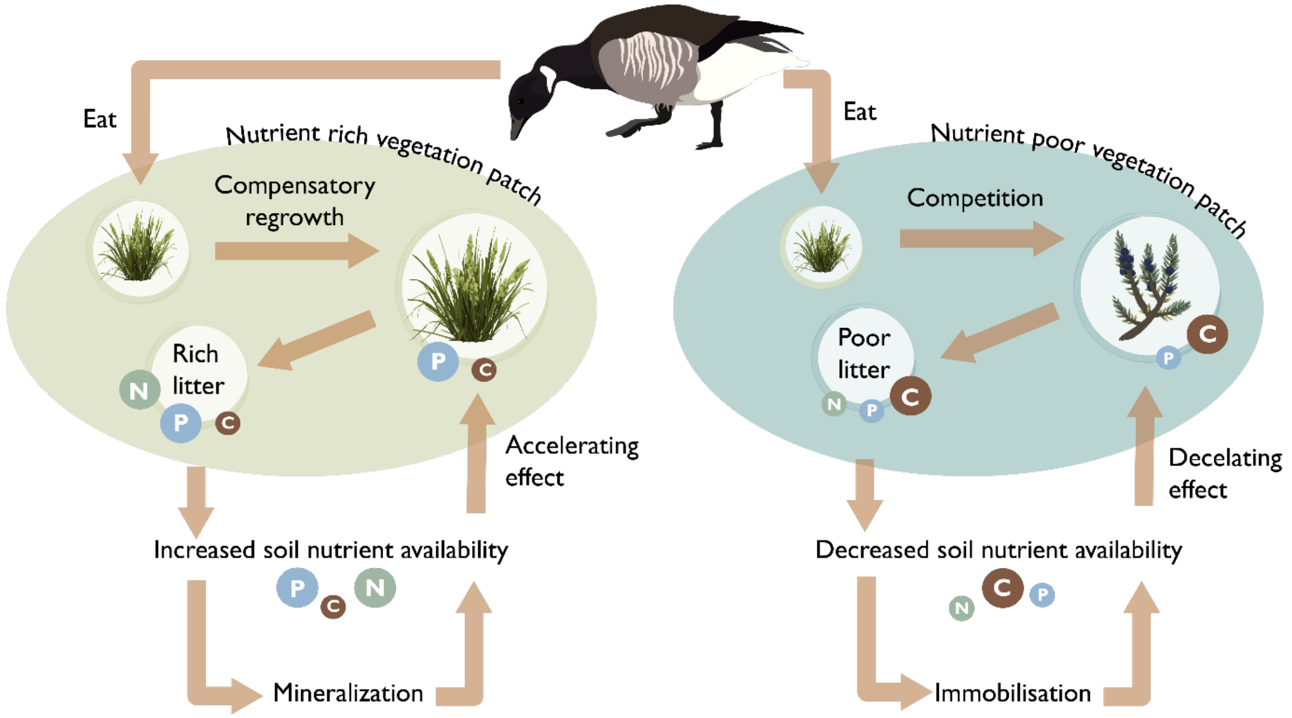

Figure 1.1: Conceptual model of herbivore-selective foraging and its effects on nutrient cycling. On the left, herbivores consume abundant, nutrient-rich plant species with low C:N and C:P ratios, which promotes compensatory plant regrowth and increases primary productivity. This process generates high quality litter that enhances soil nutrient availability and accelerates mineralisation rates. On the right, when nutrient-rich plant species are scarce, herbivores reduce their abundance, and promote more competitive nutrient-poor vegetation (i.e., high C:N and C:P). This process leads to increased production of low quality litter, which reduces soil nutrient availability, promotes microbial immobilisation, and slows decomposition rates.

1.2.2 The effect of herbivore waste on biogeochemical cycles

Herbivores convert plants into nutrient-rich wastes (e.g., faeces, urine, and carrion) that are more easily degradable than plant litter (Yang et al. 2019). Each waste type differs in its nutrient content, frequency of deposition, and persistence in the ecosystem (Subalusky and Post 2019). Faecal waste in particular, is a common input that is rich in readily available organic N and P (Sitters et al. 2017). By providing faecal waste, herbivores directly increase soil nutrient availability (Bazely and Jefferies 1985; Barthelemy et al. 2015) and strongly influence biogeochemical cycles in tundra ecosystems (Roy et al. 2022; Beard et al. 2023). Faecal deposition can locally enhance microbial growth, increase N and C mineralisation, promote plant productivity, and influence plant composition (Van Der Wal et al. 2004; Barthelemy 2016). However, the impact of faecal matter on tundra ecosystems depends on both its nutrient concentration, and its C:N:P stoichiometry. Indeed, faecal stoichiometry, specifically the nitrogen to carbon (C:N), phosphorus to carbon (C:P) and nitrogen to phosphorus (N:P) ratios, can affect the ability of soil microorganisms and plants to assimilate nutrients (Sitters et al. 2014; Sitters et al. 2017), thereby influencing whether an ecosystem becomes more N or P limited (Daufresne 2021). For example, differences in faecal quality among herbivores in temperate Europe, particularly their faecal N:P ratios, significantly affect plant communities and biomass, with plant biomass decreasing and plant community evenness increasing as faecal N:P increases (Valdés-Correcher et al. 2019). Although faecal inputs are lower in tundra regions compared to temperate regions (Wolf et al. 2013), recent research suggests that this contribution may be underestimated (Barthelemy et al. 2015). Nutrient inputs from herbivores can have a significant impact, particularly in areas where they congregate (Ruess et al. 1989; Roy et al. 2022), rest (Mosbacher et al. 2016), or visit repeatedly (Ferraro et al. 2024).

1.2.3 Species-specific traits mediate the impact of herbivores on ecosystem functions

The impact of herbivores on ecosystem functioning varies between herbivore species because different species have different sets of traits that mediate how herbivores use food resources and the amount of nutrients they return to ecosystems (Atkinson et al. 2024). Body size, through its influence on metabolic rate, is a key factor in determining the impact of herbivores on tundra ecosystems (Legagneux et al. 2014; Atkins et al. 2015). Larger herbivores tend to consume more low-quality forage due to their higher total energy requirements, resulting in higher C:N ratios in their faeces (le Roux et al. 2020). In contrast, smaller herbivores with higher metabolic rates, require large amounts of N. They therefore select N-rich forage which reduces faecal C:N ratios (Sitters and Olde Venterink 2021a). Similarly, due to their skeletal investment requirements, larger herbivores are expected to require more P, and to excrete proportionally less P (May and El-Sabaawi 2024). Additional traits, such as digestive physiology (e.g. hindgut fermenter, cloacal foregut fermenter, de Iongh et al. 2011) and feeding strategies (grazers, browsers or mixed-feeders, Hodgson et al. 2015) can significantly determine impacts of herbivores on ecosystems. Accordingly, faecal quality has been shown to vary significantly between species (Gálvez-Cerón et al. 2013; Barbero-Palacios et al. 2023), and several studies have explicitly assessed nutrient concentrations in the faeces of tundra herbivores, including geese and reindeer (Fivez 2014; Barthelemy et al. 2015; Beard et al. 2023). However, knowledge about interspecies differences remains limited, in part because the high cost of sample analysis is often prohibitive. Alternatives such as Near-Infrared Reflectance Spectroscopy (NIRS) could provide cost-effective assessments but require calibration with local samples of known chemical composition before the method can be widely implemented (Dixon and Coates 2009). Given the specificity of NIRS-based models most applications have traditionally focused on calibrating models for single species (i.e., monospecific models) at a particular location. There is increasing interest in developing multispecies models for broader ecological applications, although current models lack carbon estimation and are limited to mammalian herbivores in non-tundra environments (Villamuelas et al. 2017; Tolleson and Angerer 2020).

1.2.4 Seasonal variation in herbivore impact on ecosystem functioning

An additional source of variability in herbivore impacts on ecosystem functions is seasonality. Tundra herbivores have adapted to withstand highly seasonal and nutrient-poor conditions. Some vertebrates migrate to avoid the harsh winter conditions, others hibernate, while species such as voles and lemmings remain active under the snow cover (Reid et al. 2012; Soininen et al. 2015). Such differences in adaptation to winter conditions lead to strong seasonal population fluctuations throughout the year, and results in intense temporal variation in the impact of grazing on vegetation (Hik and Jefferies 1990; Ims and Fuglei 2005; Petit Bon et al. 2020).

Moreover, herbivores adjust their food preferences throughout the growing season, in response to phenological changes in food quality (Iversen et al. 2014). Early in the season, they tend to be more selective, favouring more palatable phenological stages (Iversen et al. 2014). However, to cope with the strong seasonal fluctuations, herbivores may shift their dietary preferences towards specific plant species, groups, or parts depending on their availability (Anderson et al. 2012). For example, upon arrival to their Arctic breeding grounds, geese consume large amounts of nutrient-rich belowground material (e.g., rhizomes) to replenish their reserves before nesting, especially when aboveground vegetation is still scarce (Fox et al. 2006). Seasonal changes in diet and plant nutrient content, as well as changes in life history, have been hypothesised to affect the amount of nutrients herbivores return from their faeces (Gálvez-Cerón et al. 2013; Čupić et al. 2021; Barbero-Palacios et al. 2023).

1.2.5 The impact of herbivore movements on nutrient redistribution

Herbivores exploit different habitats across spatio-temporal scales to maintain their body stoichiometric balance (Moore et al. 2010; Leroux et al. 2017), which is essential for survival, fitness, and reproduction (Van Beest et al. 2023). Given the limited availability of nutrients in Arctic ecosystems and the strong seasonality, plant-herbivore interactions at northern latitudes are driven by nutritional pulses, and herbivores tend to congregate in nutrient-rich areas, where resources are available in large quantities (i.e., grazing lawns, McNaughton 1984). In the long term, the combined effect of rapid compensatory regrowth and waste deposition (Ferraro et al. 2024) can result in a positive feedback that creates nutrient hotspots across the landscape, that are preferably revisited (Earl and Zollner 2017, Ferraro et al. 2023). Yet, some herbivores may complete their activities in different areas, for instance by feeding in one habitat, and resting in another. By doing so, they redistribute nutrients across the landscape (Polis et al. 1997; McInturf et al. 2019; Ellis-Soto et al. 2021). For instance migratory geese in their wintering ranges have been shown to move significant amounts of nutrients from agricultural fields, where they feed, to managed wetlands, where they roost, affecting food availability and habitat quality (Post et al. 1998).Thus, herbivore-induced nutrient fluxes can result in a transfer from nutrient-rich to nutrient-poor areas (Wolf et al. 2013; McInturf et al. 2019). Over large spatio-temporal scales, these processes create spatial heterogeneity that influence ecosystem functioning through bottom-up processes (Ferraro et al. 2021; Trepel et al. 2024). Such directional transfer of nutrients has been observed in muskoxen, which redistribute substantial amounts of nitrogen in tundra from nutrient-rich to nutrient-poor areas (Mosbacher et al. 2016).

Estimates suggest that herbivore-induced nutrient fluxes can be substantial in terrestrial ecosystems, especially in the case of large mammals (Wolf et al. 2013; Doughty 2017), or migratory birds (Post et al. 2008). These fluxes are thought to have been more evenly distributed during the Late Pleistocene

(Wolf et al. 2013). Currently, much of this capacity is concentrated in Africa, where extensive megafauna remains (Doughty et al. 2016). Nevertheless, this process remains important even in ecosystems with low herbivore biomass, such as the tundra (Mosbacher et al. 2016). This is partly because in less productive environments, herbivores are likely to forage in multiple areas to meet their nutritional needs (Polis et al. 1997). Yet, despite the recognition of herbivore-induced nutrient fluxes in tundra ecosystems, much of the existing research focuses on local scale nutrient transfer and overlooks the implications of herbivore movements (Stark et al. 2015), and the quality of nutrient fluxes (Sitters et al. 2015).

1.3 Tundra as managed rangelands: the interplay between livestock production and range sustainability

Many tundra regions serve as rangelands, with long traditions of extensive livestock grazing, such as sheep and reindeer husbandry (Ross et al. 2016; Stark et al. 2023), which have shaped the landscapes for centuries (Bråthen et al. 2017; Barrio et al. 2018). Addressing the role of herbivores on ecosystem functions in a multispecies context is particularly essential in these systems. When livestock graze alongside wild herbivores, conflicts can arise between stakeholders, as spatial overlap is often perceived as a sign of resource competition between wild and domestic species, and thus a threat to farming industries (Pozo et al. 2021). These conflicts are particularly acute in low-productive environments, where high herbivore densities can further constrain primary production (Mysterud and Austrheim 2008). In turn, livestock grazing in these marginal environments can have negative environmental consequences (Ross et al. 2016), especially when the grazing history of large herbivores is short. This is because such systems are expected to lack resilience from herbivory due to the limited tolerance to grazing of the native vegetation (Cingolani et al. 2005), which potentially leads to prolonged recovery times even after grazing is fully stopped (Price et al. 2022). Specifically, it has been shown that in environment with short grazing history that the intense livestock grazing y can cause vegetation shifts (Olofsson 2006), land degradation and erosion (Archer and Stokes 2000), and affect nutrient distribution patterns (Augustine 2003). Understanding the impacts of both domestic and wild species is essential for developing effective management strategies, particularly in the context of a changing world where the preservation of fragile biomes is critical. Although progress has been made, there are still important gaps in our knowledge of how these changes in herbivore communities can affect ecosystem structure and function, especially biogeochemical cycles, and are often overlooked in regions such as Iceland (Soininen et al. 2021; Barbero-Palacios et al. 2024).

1.4 The Icelandic tundra: a case study

Iceland lies within the sub-Arctic belt, with most of the country above the potential tree line (i.e. approx. 200-300 m a.s.l.), covered by tundra vegetation, and largely uninhabited. The Icelandic tundra is extensively used as grazing land for sheep and is subject to significant anthropogenic impacts, including climate change and changing management policies (Arnalds and Barkarson 2003). With comprehensive records of herbivore populations and relatively simple trophic linkages, Iceland provides a fantastic case study for investigating how changing herbivore communities may affect functions in tundra ecosystems, particularly biogeochemical processes, with the potential to provide valuable insights for management practices.

1.4.1 The herbivore community of Iceland: migratory birds, reindeer and livestock

The Icelandic vertebrate herbivore community has a species richness comparable to other Arctic ecosystems (Barrio et al. 2016) and includes 12 vertebrate species (eight wild, four domestic; **Figure 1.2**). Wild herbivores include birds, such as waterfowl and the rock ptarmigan (*Lagopus muta* L.), and feral reindeer (*Rangifer tarandus* L.), introduced in the early XVII^th^ century (Þórisson 1981). Unlike other tundra systems, small herbivorous mammals are largely absent. The domestic mouse (*Mus musculus* L.*)*, the wood mouse (*Apodemus sylvaticus* L.*)* and rabbits (*Oryctolagus cuniculus* L.) were introduced but are only found at low densities in proximity to human settlements (Bengtson et al. 1989).

Among waterfowl species, six species have been listed as strict herbivores (i.e., species that feed exclusively on plant material, Wilman et al. 2014; Speed et al. 2019b). These birds are all migratory and are present in Iceland from spring to autumn during reproduction (i.e., the pink-footed goose *Anser brachyrynchus* L., the greylag goose *Anser anser* L., the whooper swan *Cygnus cygnus* L.) or transit through Iceland in spring and autumn, before and after nesting further west, in Greenland. These include part of the pink-footed goose population, the white-fronted goose *Anser albifrons flavioris S*., the brent goose *Brenta bernicla* L. and the barnacle goose *Brenta leucopsis* B. Most species overwinter in Great Britain, Northern Ireland and Scotland (Alisauskas 2000). However, small groups may also stay in Iceland throughout the year (Alisauskas 2000).

As elsewhere in the Arctic tundra, waterfowl populations in Iceland have increased rapidly over the past 50 years (Fox and Leafloor 2018). Causes include the increased availability of food resources in agricultural landscapes, habitat protection and hunting bans (Fox et al. 2017). In particular, the Icelandic pink-footed goose population has increased from 8 450 individuals recorded in 1950 to 485 509 individuals in 2021 (Brides et al. 2021) with most of the population concentrated in the Eastern Highlands. In 2000, it was estimated that about a quarter of the breeding pairs in the Icelandic-Greenlandic population (i.e., about 7 300 pairs), were breeding in this area (Skarphéðinsson and Þórisson 2001).

Rock ptarmigans and reindeer are described as locally migratory species in Iceland, using different parts of the country throughout the year. Ptarmigans remain in lowland areas during the breeding season (mid-

April to August), move to the Highlands during the fall (September to October), and spend the winter at mid-elevation (November to mid-April; Gardarsson 1971). Icelandic rock ptarmigan populations are hunted and currently in decline (Fuglei et al. 2020). Reindeer are the only wild large herbivore in Iceland. Introduced on four occasions from Finnmark (Norway) between 1771 and 1787, reindeer were intended to be herded after the Sami tradition (Þórisson 1981). Today, reindeer are confined to Eastern Iceland, the only region where they have survived (Þórisson 1981), and managed as game. Their territory is geographically constrained by two large glacial rivers, with the largest herds historically located near the large Vatnajökull glacier. The total population has doubled in the last decade and was estimated to be around 10 000 individuals in 2022 (Þórisson 2018). Compared to other Arctic locations, reindeer migrations in Iceland are highly constrained and limited to short distances and elevation movements. Reindeer tend to occupy high-elevation rangelands in the summer before moving down to the lowlands in the winter (Þórisson 2018).

Domestic herbivores are exclusively mammals: the sheep *Ovis aries* L., the horse *Equus caballus* L., the cattle *Bos taurus* L., and the goat *Capra hircus* L., all Icelandic breeds. They were introduced by the first settlers in the ninth century (Adalsteinsson 1981). Most of the livestock are kept indoors during the winter (October-May) due to the harsh climatic conditions. During this time, they are fed on hay grown on pastures close to the farms, with the addition of concentrate pellets (Ross et al. 2016). During the summer, domestic herbivores are released into the fields as soon as the weather permits (Ross et al. 2016). Cattle and goats are kept in fenced fields adjacent to farms, in the lowlands. Management of horses is poorly documented, but most horses are kept in fenced pastures in the lowlands year-round (Gudmundsson and Dyrmundsson 1994), although there have been some observations of horses roaming freely in the Highlands (personal observation). Sheep (ewes and lambs) are the only livestock that roam completely free for part of the summer, usually from one month after lambing in early May, and until mid-September when they are gathered for the sheep round up (*réttir*) (Ross et al. 2016, Figure 1.3). The grazing season was traditionally set by local customs (Johannesen et al. 2013), but now sheep are released into the Highlands later in spring to reduce their impact on the ecosystem (Simpson et al. 2004). The exact timing varies each year based on current climate conditions (Archer and Arnalds 1983), with grazing usually limited to a maximum of three months (Johannesen et al. 2013).

From early spring to late autumn, sheep are kept for about a month adjacent to farms, just like other livestock. Sheep are abundant in Iceland, with 401 022 individuals in 2020 (Statistics Iceland 2022). Sheep grazing in the Highlands is an environmental concern and has been associated with increased rangeland degradation and soil erosion (Barrio et al. 2018), especially in the late 70s, when their population peaked at 900 000 individuals (Arnalds and Barkarson 2003). Since then, government restrictions and quotas have reduced sheep numbers, yet 45% of Icelandic land area remains in poor condition, with the majority located in the central Highlands (Arnalds et al. 2023).

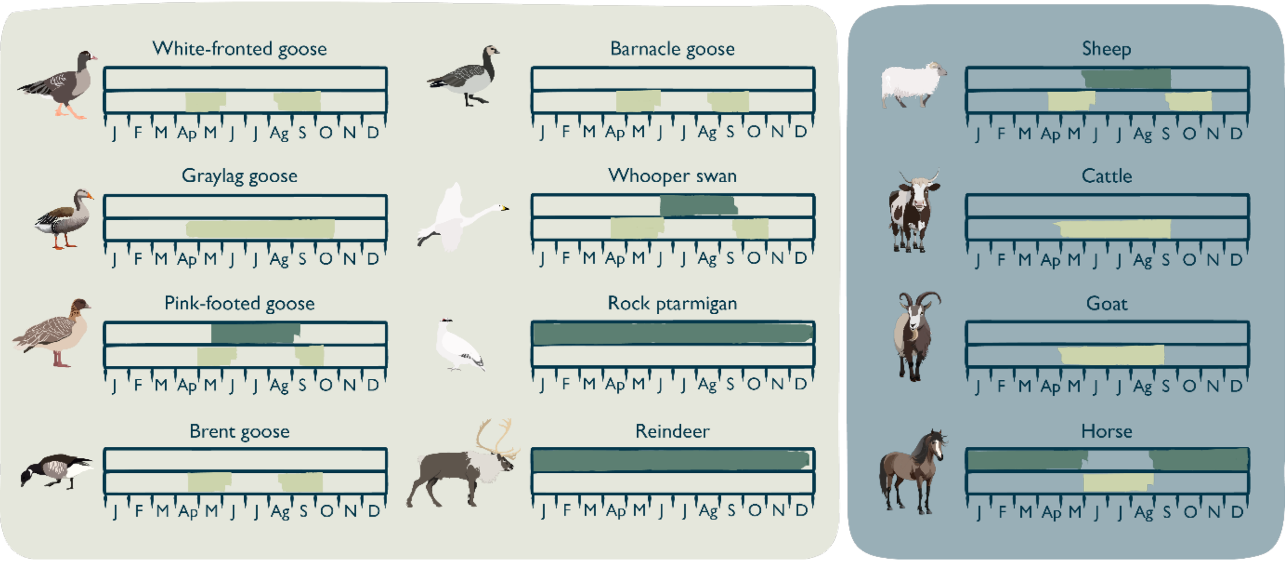

Figure 1.2: Wild (beige background) and domestic (blue background) herbivore species present in Iceland and their seasonal use of rangelands (top bars, dark green) and fertilized pastures (lower bars, light green) on a monthly scale. Species, listed from top to bottom, left to right, include: white-fronted goose (*Anser albifrons flavioris S.*), greylag goose (*Anser anser* L.), pink-footed goose (*Anser brachyrhynchus* L.), brent goose (*Branta bernicla* L.), barnacle goose (*Branta leucopsis* B.), whooper swan (*Cygnus cygnus* L.), rock ptarmigan (*Lagopus muta* L.), and reindeer (*Rangifer tarandus* L.) (beige panel); sheep (*Ovis aries* L.), cattle (*Bos taurus* L.), goat (*Capra hircus* L.) and horse (*Equus caballus* L.) (blue panel).

1.4.2 The interconnected grazing systems of Iceland: herbivore distribution patterns in Iceland

Livestock production is an important part of the Icelandic culture and economy (Arnalds 2019), with sheep production (i.e., for meat and wool) accounting for around 13% of the agricultural output. This strong farming legacy is reflected by the fact that 60% of the total surface of the country is considered as grazing land (Stefánsson et al. 2020). For the most part, sheep farms are scattered in the lowlands along the coast, with access to more distant areas in the Highlands for summer grazing.

Grazing lands are privately or publicly owned (Arnalds and Barkarson 2003). Private grazing lands are mostly found in the lowlands, adjacent to farms. They are used for grass production to supplement livestock, or for direct grazing by livestock (Fridriksson 1972), and are often fertilised and seeded, making them highly productive. They account for 40% of the total grazing area (Stefánsson et al. 2020). Most rangelands are publicly owned and divided into different administrative units (i.e., grazing commons). Each unit is used for sheep grazing by different farms. Grazing commons are largely located in the Highlands, uninhabited areas above the potential tree line (at approx. 200-300 m a.s.l.), where the vegetation is typical of tundra ecosystems (Óskarsdóttir et al. 2024). Rangelands are usually not amended, and lightly managed. Rangelands account for 60% of the grazing area available in Iceland (Stefánsson et al. 2020).

Despite major differences in management practices, improved pastures and rangelands remain closely interconnected as wild herbivores use both land types at different times of the annual cycle (**Figure 1.2**). Reindeer and ptarmigans only use rangelands, whereas some waterfowl such as the white-fronted goose are found in improved pastures during spring and autumn staging (**Figure 1.4**), and the pink-footed goose uses both pastures and rangelands during summer.

1.4.3 The predator-free tundra: the role of management policies as top-down control for large herbivore populations

The Icelandic tundra ecosystem is unique compared to other regions, with a simplified two-level system due to the lack of top-down control of herbivore populations by large predators. The only predators are the arctic fox (*Vulpes lagopus*; Pálsson et al., 2016), raptors (mainly the gyrfalcon, *Falco rusticolus*) and ravens (*Corvus corax*). These predators have minimal control over sheep and reindeer populations, but significant impact on rock ptarmigan and pink-footed geese (Nielsen 1999). Parasites such as warble flies and mosquitoes are absent, further reducing natural mechanisms of population control. As a result, reindeer populations are mainly limited by hunting pressure and to a lesser extent by food availability (Þórisson 2018). Hunting pressure has a strong influence on the spatial distribution of reindeer in Iceland, causing them to move long distances and seek refuge in less accessible, higher elevation areas near glaciers during the summer (Þórisson 2018). Sheep, on the other hand, are mostly restricted by current legislation and quotas (Arnalds and Barkarson 2003). In the absence of predators in grazing areas, sheep are typically scattered in small groups (usually one ewe and two lambs).

Figure 1.3: Seasonal sheep roundup (réttir) in Iceland. Sheep are herded from Highland rangelands (left page) down to the lowlands (right page) around mid-September, where they are sorted and allocated back to their respective farms (2023).

1.4.4 Shared tundra rangelands: consequences for ecosystems functions and land sustainability

During the growing season, pink-footed goose, reindeer and sheep use the same low-productivity rangelands in the Icelandic Highlands, opening the door to potential competition for resources (Boulanger-Lapointe et al. 2022; Möller 2024). To date, there is no evidence of dietary overlap between the three species in the Icelandic tundra, and no direct assessment of the pink-footed goose diet in Iceland. However, pink-footed goose, sheep and reindeer are all known to be relatively selective species, seeking high quality aboveground vegetation that is rich in N and P and relatively low in tannins (Sheremetev 2023). Thus, they generally feed on a mixture of dicotyledons (e.g., *Bistorta vivipara*), sedges (e.g., *Carex bigelowii*), grasses (e.g., *Poa* sp., *Festuca richardsonii*, and *Calamagrostis neglecta*), horsetails (*Equisetum arvense* and *E. variegatum*), and dwarf shrubs (e.g., *Salix* sp.) in various proportions, depending on their life history stage, and plant availability (Skogland 1980; Thórhallsdóttir and Thorsteinsson 1993; Fox et al. 2006; Fox et al. 2007; Anderson et al. 2012; Þórisson 2018). Specifically, when released in the Highland rangelands, sheep consume horsetail and dwarf shrubs in abundance (Thórhallsdóttir and Thorsteinsson 1993). Later in the season, graminoids, especially sedges, make up a large proportion of both sheep and geese diets, while reindeer increasingly rely on dwarf shrubs (Þórisson 2018). Studies from Svalbard show that geese supplement their diet by grubbing (i.e., the process of digging into the soil with their beaks to break up plant roots, rhizomes and other belowground vegetation), especially during the pre-breeding period, when aboveground primary production has yet to commence and belowground plant rhizomes represent a rich source of food (Fox et al. 2007; Speed et al. 2010).

The spatial overlap and shared food resources between wild and domestic herbivores in the Highlands, coupled with increasing wild herbivore populations and limited food availability for sheep production, is becoming a concern in Iceland (Barrio and Arnalds 2023; Möller 2024). The emerging conflicts between sheep farming and increasing wildlife populations could threaten the sustainability of tundra ecosystems as extensive rangelands. In addition, extensive sheep grazing in the Highlands, for example, has already been linked to land degradation and severe soil erosion (Barrio et al. 2018), as well as changes in plant community structure (Marteinsdóttir et al. 2017). Despite these pressing environmental issues, the effects of herbivores on ecosystem functions in Iceland, particularly within a multispecies grazing context, have been largely overlooked. How herbivore communities are changing in Iceland and how this translates into biogeochemical cycles, remains unclear. Yet, such aspects are essential to bring nuance into the role of herbivores in land sustainability, to unravel the increasing conflict between wild and domestic herbivores in natural rangelands, and to develop appropriate management practices.

Figure 1.4: A flock of white-fronted geese (*Anser albifrons flavirostris*) staging in a fertilized grassland in mid-April, Hvaneyri, Iceland (2024).

1.5 Research questions and objectives of the thesis

In this thesis, I investigated how changes in herbivore communities affect tundra ecosystem functions at different spatio-temporal scales (i.e. regional, landscape and local), with a particular focus on nutrient recycling. I investigated the dynamics of herbivore communities and the effects of multispecies herbivore assemblages on vegetation biomass and nutrient cycling. I examined how the impact of herbivores varies according to management regimes (i.e., improved fertilised grasslands and unimproved rangelands), herbivore species, and seasonality. A deeper understanding of how different herbivores influence ecosystem functioning will provide valuable insights to guide management and conservation efforts in tundra ecosystems, where both wild and domestic herbivores graze.

I used both existing long-term data, and field measurements to address the following research questions (Q) (**Figure 1.5**):

Q1. Has the Icelandic herbivore community changed over time?

To assess changes in species densities, community composition, and metabolic biomass (**Paper I**), I compiled national population records from different sources, and assembled herbivore traits (i.e., body weight, metabolic rates, grazing time) from the literature and existing databases.

- **Q1.1. How has the composition of herbivore communities changed over the past decades? (Paper I)**
  I predicted a shift from livestock-dominated systems to wild herbivore dominance due to a decline in livestock because of the introduction of quotas in the late 1980s (Arnalds and Barkarson 2003), and increasing migratory goose populations (Alisauskas 2000).

- **Q1.2. How have wild and domestic herbivore biomass changed over time? (Paper I)**
  I expected a rise in wild herbivore biomass, reflecting the numerical increase in waterfowl, but predicted that domestic species would still contribute more metabolic biomass due to their larger body size and metabolic rates compared to wild herbivores (Hudson et al. 2013).

Q2. What is the impact of herbivores on vegetation?

To estimate the direct impacts of herbivores on vegetation at regional (**Paper I**) and local scales (**Paper III**), I used aboveground plant biomass consumption rates as a proxy. For regional estimates, I combined herbivore traits (i.e., grazing time, dry matter intake, body weight) with satellite-derived estimates of aboveground primary production. This approach allowed for the calculation of consumption rates across two types of grazing lands under different management regimes (i.e., improved fertilised grasslands and unimproved rangelands, **Paper I**). At the site level, I conducted field measurements throughout the growing season in high-elevation rangelands where sheep, geese, and reindeer co-occur, enabling a detailed estimation of herbivore consumption (**Paper III**).

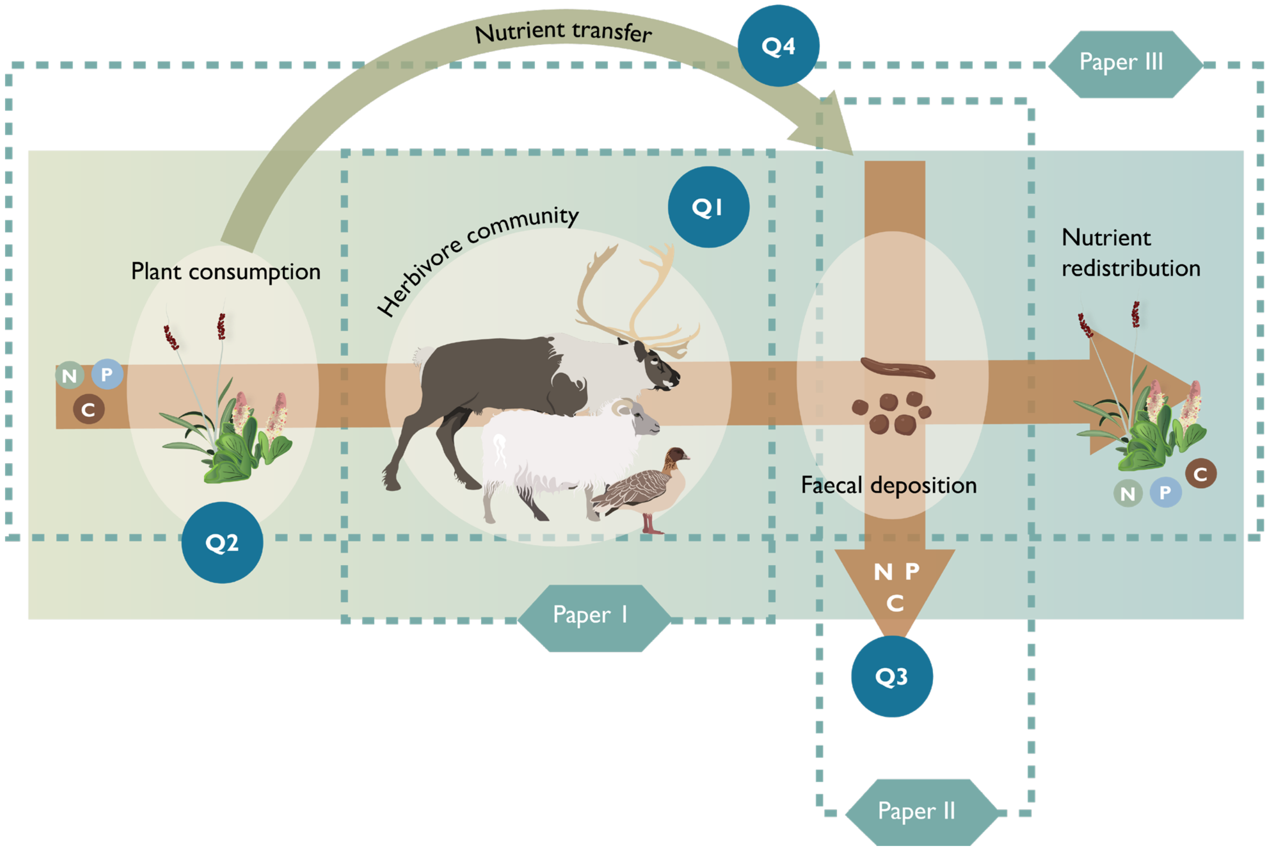

Figure 1.5: Research framework illustrating the impact of herbivores on the Icelandic tundra. The figure shows the main research questions (Q1-Q4) related to changes in herbivore communities (**Q1**), their effects on vegetation (**Q2**), nutrient deposition (**Q3**), and nutrient redistribution within tundra ecosystems (**Q4**). The research questions are addressed in three different research papers, indicated by the green hexagon shapes.

- **Q2.1. What are the impacts of wild and domestic herbivores on vegetation biomass? (Paper I)**
  I hypothesised that domestic herbivores would consume more plant biomass than wild species, with higher consumption rates in the lowlands due to their higher productivity and large populations of livestock (Fridriksson 1972).

- **Q2.2. Does herbivore consumption vary throughout the growing season? (Paper III)**
  I expected consumption rates to increase as the growing season progresses, driven by the growing nutritional needs of juvenile herbivores and the decline in forage quality as plants senesce (Mosbacher et al. 2016).

Q3. How much nutrients do herbivores deposit across the landscape?

To address both methodological and information gaps regarding the deposition of nutrient from herbivores, I developed a tool based on NIRS to measure nutrient content in tundra herbivore feces (**Paper II**), examined how nutrient content and stoichiometry vary across different herbivore species throughout the growing season (**Papers II**), and estimated the nutrient deposition from herbivores at landscape and site levels based on field measurements (**Paper II** and **III**).

- **Q3.1. Can NIRS be used to predict faecal nutrient concentrations using near-infrared spectroscopy for tundra herbivores? (Paper II)**
  I built both monospecific and multi-species models that were calibrated against samples of known chemical content. I predicted that monospecific models would perform better for each species and nutrient than multi-species models due to the increased complexity of the later. Still, I expected multi-species models to provide reliable estimates of faecal N, P, and C, as has been shown for European and American mammalian herbivores (Villamuelas et al. 2017; Tolleson and Angerer 2020).

- **Q3.2. Do faecal nutrient content and stoichiometry vary among herbivore species**? (**Paper II**)
  I hypothesised that faecal nutrient concentrations would differ among herbivore species. Specifically, I expected reindeer and sheep to show similar nutrient profiles due to their comparable digestive systems and similar diets (Mysterud 2000; Þórisson 2018), while geese faeces would contain higher levels of N and P, and lower C:N and C:P ratios compared to ruminants, due to their short retention time, low digestibility, and more selective diet (Karasov and Douglas 2013).

- **Q3.3. Do faecal nutrient content and stoichiometry vary throughout the growing season (Paper II)**
  I expected faecal stoichiometry to change throughout the growing season reflecting changes in herbivore life history (Čupić et al. 2021), diet quality and composition (Gálvez-Cerón et al. 2013), and plant phenology (Chapin et al. 1975). Specifically, I expect faecal stoichiometry decrease over the growing season, as herbivores start to build up reserves to survive winter conditions and prepare for reproduction (Barboza and Parker 2008), and as plants senesce relocating nutrients like N and P to belowground structures or litter (Chapin et al. 1975; Petit Bon et al. 2020).

- **Q3.4. How much nutrients do each herbivore deposit in the Icelandic tundra? (Paper II and III)**
  I anticipated that geese would contribute more nutrients due to their large populations and high defecation rates, compared to sheep or reindeer (Fivez 2014; Dessborn et al. 2016; Beard et al. 2023).

Q4. What is the contribution of herbivores to nutrient redistribution in tundra ecosystems?

To investigate the potential for herbivores to redistribute N, P, and C across the landscape, I combined field measurements of herbivore consumption, faecal deposition, and forage quality and quantity (**Paper III**).

- **Q4.1. Is herbivore consumption driven by forage quality? (Paper III)**
  I expected that higher N and P concentrations in forage would increase plant biomass consumption by herbivores, because of selective feeding on nutrient-rich patches (Van Langevelde et al. 2008). In turn, higher C concentrations would lead to reduced herbivore consumption rates. I predicted these patterns to be reflected in plot-level plant stoichiometry, with herbivores preferring to graze in areas with low C:N and C:P, maximizing their intake of N (essential for protein synthesis and metabolism) and P (used for tissue and bone formation, and metabolism) (Weterings et al. 2018; Balluffi-Fry et al. 2022).

- **Q4.2. Is there a link between forage quality and faecal deposition? (Paper III)**
  I predicted that geese would concentrate nutrient deposition in nutrient-rich areas due to their reduced mobility during nesting (Lazarus and Inglis 1978). In contrast, larger, more mobile herbivores like sheep and reindeer would redistribute nutrients more evenly, potentially transporting nutrients from nutrient-rich feeding patches to nutrient-poor resting areas (Stark et al. 2015).

2. Material and methods

In this thesis, I use different approaches to investigate the effect of spatio-temporal changes in herbivore community composition on vegetation, nutrient cycling and redistribution in the Icelandic tundra (**Figure 1.5**). These approaches varied in spatial (i.e., regional in **Paper I** to landscape in **Paper II** and local in **Paper III**) and temporal scales (i.e., decades in **Paper I**, to seasonal scales in **Papers II** and **III**), as well as in the type of data used (i.e., literature, open-source remote sensing data in **Paper I**, and field-collected data in **Paper II** and **III**).

Specifically, at the regional scale (**Paper I**), I assessed changes in herbivore community composition, density, biomass and consumption by synthesizing information available from literature and open-source remote sensing data for all of Iceland. This analysis spanned several decades, from 1986 when population records become available for domestic and wild herbivores in Iceland to the present. At a landscape and local scale (**Papers II** and **III**), I conducted seasonal analysis of plant biomass consumption by herbivores, faecal nutrient content and quality (**Paper II**) and herbivore nutrient redistribution (**Paper III**). These studies were based on an extensive fieldwork campaign conducted in the Eastern Highlands, where the herbivore community is the most diverse, and where both livestock and large populations of wild herbivores co-exist (Boulanger-Lapointe et al. 2022). Specific details on the methods and data analysis are provided in each of the chapters. In this section, I provide a general overview of the methods used in this thesis, starting with a description of the field-based data collection, and then explaining how each of the research questions presented in section 1.5 were assessed.

2.1 Field data collection

2.1.1 Study area

The study was conducted in the Eastern Highlands of Iceland, in Fjótsdalshreppur and Múlaþing (65.3234 °N, 15.3062 °E, **Figure 2.1**). The area comprises 6,415 km^2 and is characterised by a marked elevational gradient from 300 to 1833 m a.s.l. The highest peak is Mount Snæfell, a dormant volcano. The area includes broad wet valley bottoms, barren areas at higher elevations, as well as glaciers and permanent snow on mountain peaks. The area is typically snow covered until early–mid June. The study area is characterized by variable soil types, mainly brown and gleyic andosol with considerable carbon, allophane, and ferrihydrite content, resulting of the volcanic activity (Arnalds 2015). Permafrost is found at high elevations on the edges of Mount Snæfell and the large Vatnajökull glacier (Farbrot et al. 2007). Mean temperature ranges from -3.5°C in winter (October to Mai, based on average monthly temperatures), and 6.5 °C in summer (June to September, based on average monthly temperatures) (Icelandic Meteorological Office Database 2024), and precipitation varies between 710 mm and 830 mm (Óskarsdóttir et al. 2024).

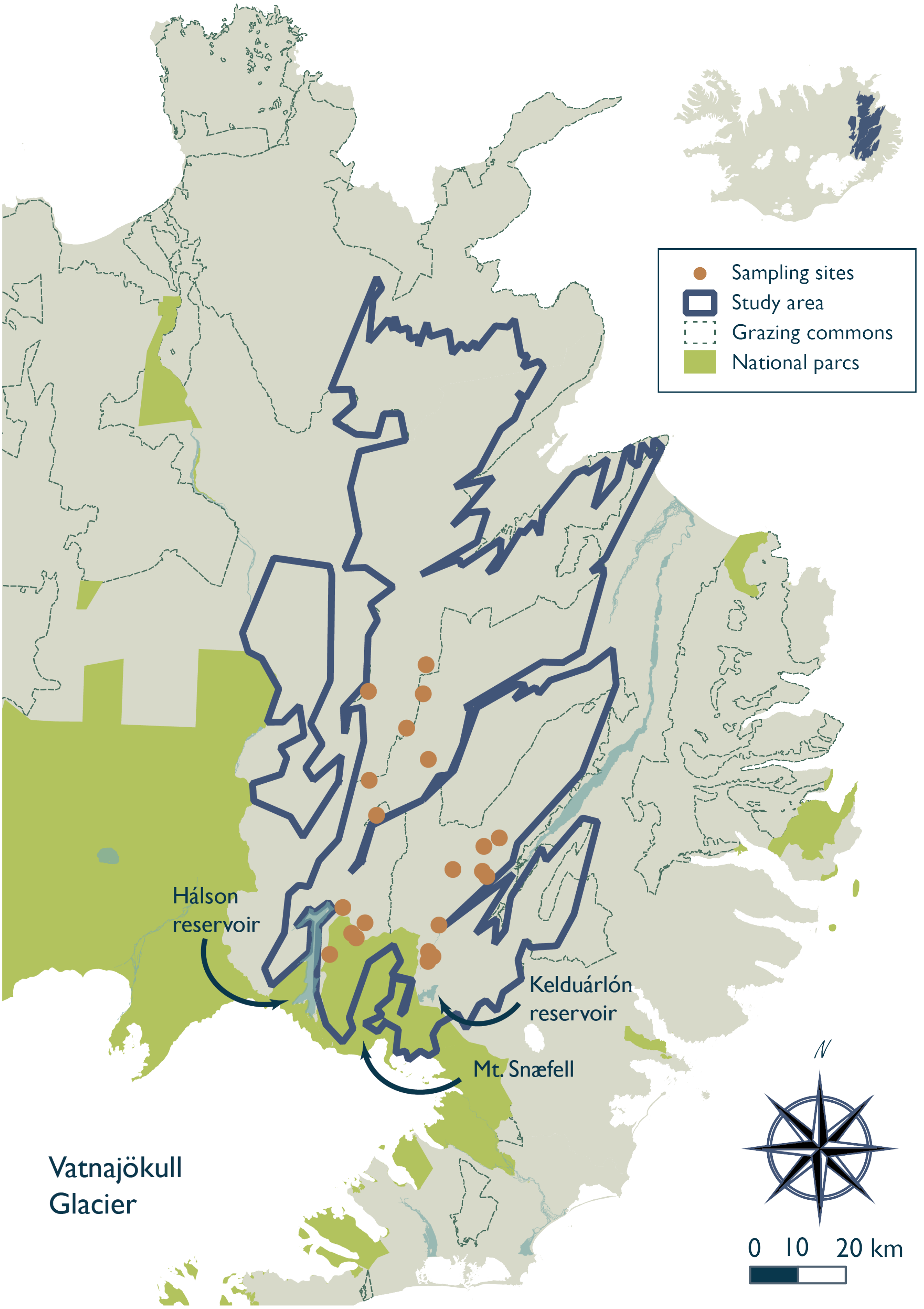

Figure 2.1: Map of the study area in the Eastern Highlands of Iceland. The study area, outlined in dark blue, encompasses land above 300 m a.s.l., where large breeding populations of the pink-footed goose (*Anser brachyrhynchus*), sheep (Icelandic breed, *Ovis aries*), and feral reindeer (*Rangifer tarandus*) coexist. Sampling sites are indicated with ochre dotes within the sampling area. Grazing commons are indicated by dashed green lines, and light green areas indicate the boundaries of national parks. The southern edge of the study area is defined by the Hálson reservoir, Mount Snæfell, and the Vatnajökull glacier.

The vegetation is characteristic of subarctic-alpine tundra (Óskarsdóttir et al. 2024) and is highly heterogeneous, alternating extensive barren areas, and patches of low-lying vegetated areas including heathlands, grasslands, marshes, and peat bogs (Ottósson et al. 2016). The most extensive areas of heathlands are located north of Mount Snæfell and East of Fjallgarðar and are used as winter and autumn grazing area by reindeer, and more recently as summer pastures and calving areas. They consist of a mixture of deciduous (e.g., *Salix herbacea, S. arctica*) and evergreen dwarf shrubs (e.g., *Empetrum nigrum*), sedges (e.g., *Carex bigelowii*), grasses (e.g., *Festuca rubra*) and forbs (e.g., *Bistorta vivipara,* and *Silene acaulis*) (Óskarsdóttir et al. 2024). Marshes and peat bogs are mostly dominated by hydrophilic *Carex* species (e.g. *Carex bigelowii*, *Carex nigra*, *Eriophorum sp.*) and horsetails (e.g., *Equisetum arvense* and *Equisetum variegatum*).

As part of a power plant development project, three large reservoirs were constructed along the glacial river Jökulsá á Dal, that traverses the study area: Hálslón (2006), Kelduárlón, and Ufsarlón (2008), leading to significant anthropogenic disturbances. One of the most notable impacts was the flooding of a major pink-footed goose breeding ground, along with the submersion of 1% of vegetation in the study area (i.e. 63 km^2), which was primarily used as an important grazing lawn by local herbivores (Óskarsdóttir et al. 2024). Aeolian deposits from wind erosion, which occur when water levels in the reservoirs are low, negatively affect forage quality and grazing patterns (Arnalds et al. 2010; Óskarsdóttir et al. 2024). Such effects of sand abrasion have been observed in other parts of Iceland (Thórhallsdóttir 2007). Additionally, infrastructure development around the power plant, including the construction of roads and bridges, increased the accessibility and human activity in the area. Increasing human presence, especially outdoor tourism, is believed to have caused significant disturbances to local wild herbivore populations (Óskarsdóttir et al. 2024). For instance, the recent depletion of local reindeer herds from the area which have increasingly moved to coastal regions, is suspected to be linked to increased human activity in the area (Þórisson 2018).

2.1.2 Herbivore community in the Eastern Highlands

The main herbivores present in the Eastern Highlands are pink-footed goose, sheep and reindeer (**Figure 2.2)**. The Eastern Highlands serve as the largest breeding and moulting ground for the Icelandic-Greenlandic pink-footed goose population and are the only region in Iceland where reindeer are found. Like much of the Icelandic Highlands, the area has a long history of extensive sheep farming. Sheep numbers in the area have declined since the introduction of a livestock quota in the 1980s (Arnalds and Barkarson 2003). Additionally, an outbreak of scrapie, a transmissible spongiform encephalopathy in 1990 led to culling all sheep in the region (Sæmundsen et al. 2014). Despite some recovery, sheep numbers have not returned to their previous levels (Sæmundsen et al. 2014). Swan and ptarmigan are also found in the area, but their presence is scattered and at much lower densities.

2.1.3 Sampling design

During summer 2022, 21 sites were established across the study area (**Figure 2.2**). These sites were randomly selected based on the probability of the occurrence of the three focal herbivore species: pink-footed goose, sheep and reindeer (Boulanger-Lapointe et al. 2022). My selection assumed a positive correlation between the probability of occurrence and the density of herbivores, assuming that a higher probability of occurrence would imply higher densities of the corresponding herbivore species. Specifically, I selected 7 sites with a probability of occurrence of at least 0.49 for each herbivore species, so that sites would be dominated respectively by each species. Sites were at least 1 km from each other, and to minimize potential human disturbances, all sites were located at least 1.5 km away from the main roads, and between approx. 535 m and 675 m elevation. Abundant plant species included a mix of evergreen (e.g., *Empetrum nigrum*, *Loiseleuria precumbens*, *Harrimanella hypnoides*) and deciduous (e.g., *Salix*

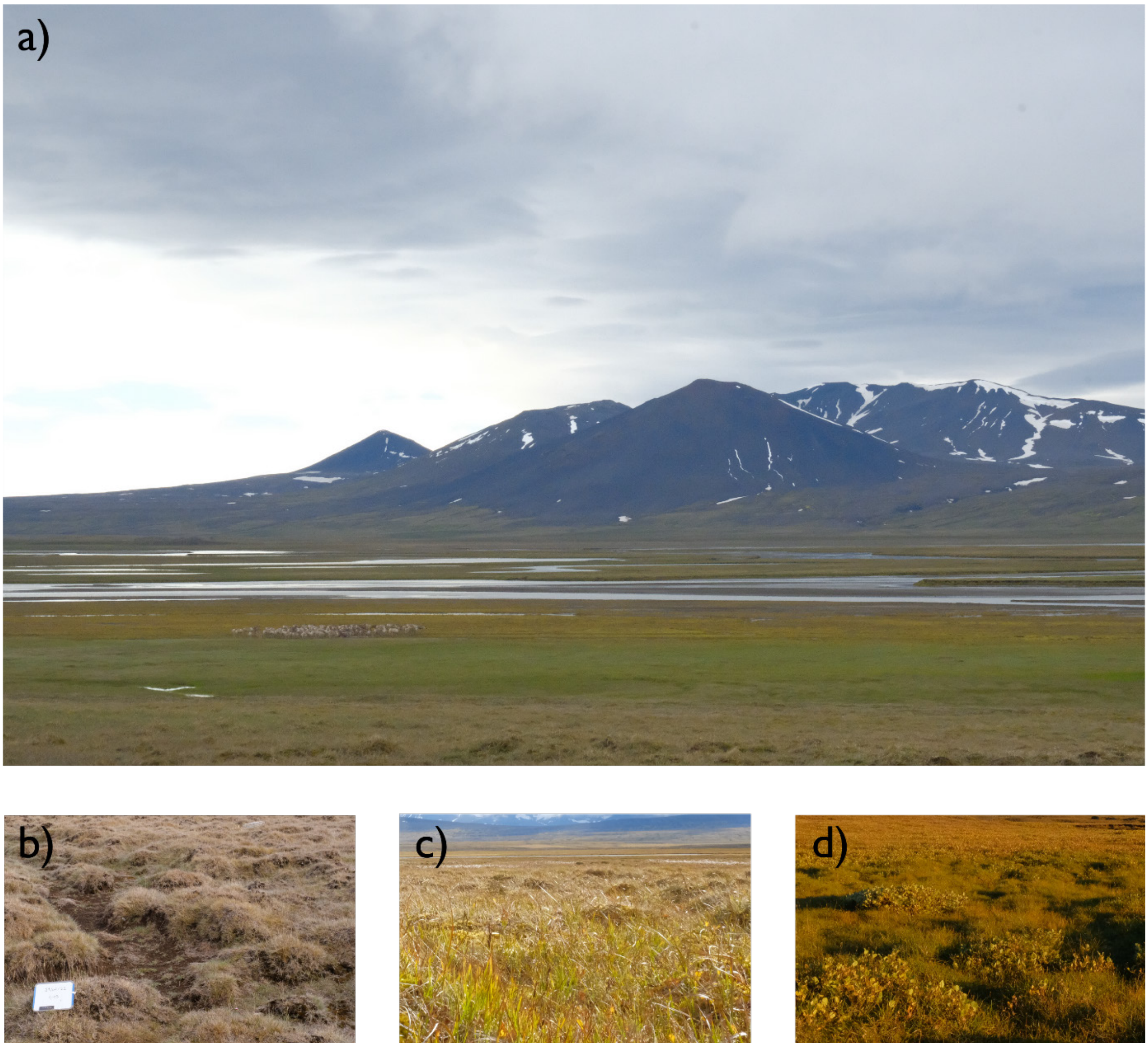

Figure 2.2: Photos of the study area in the Eastern Highlands of Iceland. (a) A large herd of reindeer (*Rangifer tarandus*) grazing with Mount Snæfell in the background. Sampling sites include covered by various type of grazed vegetation, including grasses (b), sedges (c) and deciduous shrubs (d)(2022).

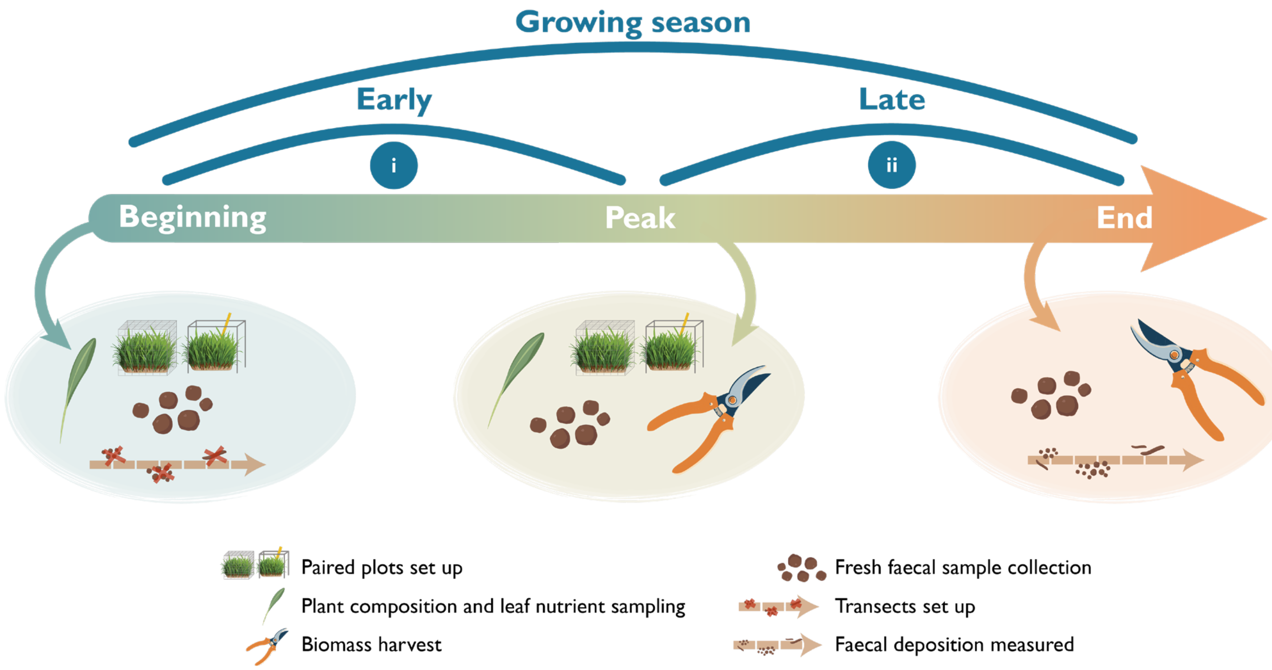

Figure 2.3: Diagram illustrating the sample collection timeline. Vegetation biomass was harvested at the peak and end of the growing season to estimate aboveground biomass consumption by herbivores during the early (i) and late (ii) growing season (see **section 2.3**). Fresh faecal samples were collected at the beginning, peak, and end of the growing season to assess faecal nutrient content (see **section 2.4.1**). In addition, three 100 m transects were cleared of faeces at the beginning of the season and faecal deposition measured at the end to estimate total seasonal faecal deposition (see **section 2.4.3**). At the beginning and peak of the growing season, exclosure cages were set up, plant community composition was assessed, and fully developed leaves were sampled to measure plant nutrient content (see **section 2.5**).

arctica, *Salix lanata*, *Salix herbacea*) shrubs, sedges (e.g., *Carex bigelowii*, *Carex nigra*, *Eriophorum angustifolium*), grasses (e.g., *Poa alpina*, *Festuca richardsonii*), forbs (e.g., *Silene acaulis*, *Bistorta vivipara*), and pteridophytes (e.g., *Equisetum arvense*, *Equisetum variegatum*) in various proportions (**Figure 2.2**). Sites were visited three times during the growing season 2022, at the beginning (late June-early July), peak (late July-early August) and end (late August-mid September) to estimate herbivore aboveground plant biomass consumption during early and late growing season (**section 2.3**), faecal deposition throughout the entire growing season (**section 2.4.3**), and measure forage quantity and quality (**section 2.5**) (**Figure 2.3**, **Paper III**). During each sampling to. fresh faecal matter was also collected in the sampling area (**Figure 2.3**, **section 2.4.1**, **Paper II and III**).

2.2 Assessing changes in herbivore community composition (Q1)

Changes in herbivore community composition were assessed for Iceland (**Q1.1**). Population data for Icelandic vertebrate herbivores was retrieved from diverse published and unpublished sources (see **Paper I** for details). Population time series had variable temporal coverage, but overall, complete national population records were available for all species since 1986. The composition of the herbivore community in each year, between 1986 and 2020 was assessed in a multivariate framework based on the relative abundance of herbivore species, to investigate whether there had been directional changes in herbivore community composition over time.

To combine population data across different herbivore species, I calculated the metabolic biomass (MB) for the entire herbivore community and for domestic and wild herbivores separately (**Q1.2**). MB is an allometric function that scales herbivore by their daily energy requirements (Hatton et al. 2015), allowing comparisons between species and the estimation of herbivore pressure in multispecies assemblages. MB was first calculated at the species level by combining body weight and metabolic rate information from the literature (see **Paper I** for details). Species-specific MB was extrapolated to the population level by multiplying by the abundance of the species in a given year, scaled by the amount of time spent grazing per year. Values were summed across domestic, wild and all herbivore species, and standardised by the sum of grazing areas in kilometre squares to obtain the metabolic biomass of the different herbivore groups per kilometre square in each year. Trends in the metabolic biomass of wild, domestic, and total herbivores from 1986 to 2020 were assessed using general additive model framework, which allows for the detection of non-linear trends in time series data, while minimising fine-scale bias. In addition, a sensitivity analysis was carried out to assess the uncertainties in the estimates.

2.3 Estimating herbivore impact on vegetation (Q2)

Herbivore aboveground plant biomass consumption was assessed at regional (**Paper I**) and local (**Paper III**) scales as a proxy for direct herbivore impacts on vegetation. At the regional scale, herbivore aboveground consumption was assessed separately for improved pastures and unimproved rangelands for all domestic and wild species between 1986 and 2020 (**Paper I; Q2.1**). Specifically, I compiled data on herbivore population records from 1986 to 2022 from different sources, information on grazing duration (days per year) in each type of grazing land, and daily dry matter intake (in kg $DW.day^{-1}$) for each herbivore species available in the literature. As for the trends in metabolic biomass (see **2.2**), trends in biomass consumption by wild, domestic, and total herbivores were assessed using non-linear regression analyses, coupled with a sensitivity analysis, to assess uncertainties in the estimates.

To assess seasonal changes in plant biomass consumption by herbivores at local scale (**Paper III; Q2.2**), I quantified herbivore consumption of aboveground plant biomass twice during the growing season (i.e. early and late, **Figure 2.3**) in the Eastern Highlands. During this time, the Eastern Highlands are mainly used by pink-footed geese, sheep and reindeer, so I assumed that my measurements of plant biomass consumption reflected consumption by these species only. To measure herbivore consumption, I used the moving cage method (McNaughton et al. 1996). This method accounts for potential compensatory regrowth of plants that can occur after grazing, and is used to reduce the resulting bias, that usually leads to underestimation of consumption rates (McNaughton et al. 1996). Specifically, I established 3 paired plots (i.e. open control and cage) at each sampling site at the beginning of the growing season. At the peak of the growing season, aboveground biomass was harvested at soil or moss level in the open control and associated cage plot, and the paired plots were moved to a new location that had been exposed to grazing earlier in the season. A second harvest was made at the end of the growing season and to reflect herbivore consumption during the late growing season. In total, I harvested aboveground biomass 6 times per site (3 paired plots) at the peak and end of the growing season, for a total of 252 biomass samples for the entire sampling season across sites. Each biomass sample was air-dried and weighed using a precision balance. Local aboveground herbivore consumption was calculated as the difference between the open control and caged aboveground biomass, standardised by the biomass from the open control plot. Consumption rates between the early and late growing seasons were compared using an inferential statistical framework to assess seasonal changes in herbivore consumption.

2.4 Estimating herbivore faecal nutrient contribution (Q3)

2.4.1 Developing of a tool to estimate herbivore faecal nutrient content

Fresh faeces were collected from the three focal herbivore species: pink-footed goose, sheep and reindeer in the Eastern Highlands of Iceland at the beginning, peak and end of the growing season 2022 (**Figure 2.3)**. To ensure accurate species identification, faeces were collected next to sighted individuals. Approximately 30 samples were collected per species per sampling session, resulting in a total of 298 samples (96 for pink-footed goose, 112 for sheep, 90 for reindeer). After collection, all samples were stored at -20°C until further processing.

Back in the laboratory, the faecal samples were thawed subsequently dried at 40°C for at least 48h, and ground into a thin powder. I sub-sampled 300 mg of material and pressed it into 15 mm diameter tablets using a hydraulic press with 4 tonnes pressure. Approximately 1 g of powder was taken from 191 samples to quantify N, P and C concentrations (% DW) using traditional laboratory methods at the University of Antwerp (more details are provided in **Paper II**). All tablets were scanned three times using a NIRS instrument (ASD LabSpec 4) with a contact probe attachment to measure the reflectance in the near infrared (from 350 to 2500 nm).

Since no model calibrations existed for faecal nutrient concentrations of Arctic herbivores, I first had to develop calibration models for using NIRS to predict faecal nutrient content (**Q3.1**). Based on the set of 191 faecal samples, both analysed by traditional laboratory methods and scanned with a NIRS instrument, I developed monospecific and multispecies (i.e., mammals only and all three herbivore species together) calibration models to assess faecal nutrient concentrations (N, P, and C) and ultimately faecal quality (C:N, C:P and N:P) (details of model calibration are provided in **Paper II**). Monospecific and multispecies models were calibrated using a partial least square regression (Geladi and Kowalski 1986) coupled with machine learning techniques to avoid overfitting (Burnett et al. 2021). The predictive abilities of each model were measured and compared to assess their performance in predicting faecal nutrient content.

2.4.2 Assessing herbivore faecal nutrient concentrations

Applying the NIRS multispecies models to the full set of faecal samples scanned with a NIRS instrument, I predicted faecal nutrient concentrations for the three herbivores across the growing season (beginning, peak and end), to assess differences between herbivore species (**Q3.2**) and along the growing season (**Q3.3**) using inferential statistics (**Paper II**).

2.4.3 Assessing nutrient deposition by different herbivores

Faecal nutrient deposition (total N, P and C) was estimated at a fine seasonal scale for the whole study area (**Paper II**), and at the site level for the whole summer (**Paper III**). Over the growing season, I encountered different type of faeces for sheep and reindeer, either clumps or individual pellets due to variations in diet for reindeer and/or differences in life history (e.g., lamb or adults for sheep). Therefore, I calculated the average faecal dry weight (g DW) of a typical faecal deposition from five faecal subsamples per herbivore species and type of faeces (i.e., approx. 10 g of fresh sheep and reindeer from a clump or one individual pellet, and a full dropping for geese). I determined the average water content of the faecal depositions after oven drying at 40°C for 2 days and used these values to calculate the initial dry biomass of a typical faecal deposition. Using the same approach.

To assess herbivore faecal nutrient deposition at the landscape scale (**Paper II; Q3.4**), I combined the data collected in the field (faecal nutrient content and dry weight of each faecal deposition) with data obtained from local sources (herbivore densities (individuals.km^{-2}) and grazing duration (days) over the sampling periods at the beginning, peak and end of the season, and average defecation rates (defecation events.day^{-1}), all compiled from the literature (see **Paper II** for details). Changes in faecal nutrient deposition among herbivores and throughout the growing season were assessed using inferential statistics.

At the site level (**Paper III**), faecal deposition was measured throughout the entire growing season using three 100 m long and 1 m wide transects, from the centre of the site outwards. At the beginning of the growing season, faeces were removed from the transect (Barrio et al. 2021). The same transects were visited again at the end of the growing season to assess faecal deposition for each herbivore species. Clumps were counted as a whole, while pellets were counted individually. Herbivore faecal nutrient deposition was assessed by combining faecal nutrient concentrations and weight of the estimated faecal deposition data, with local faecal deposition. Nutrient deposition from herbivore faeces were compared between species and sampling site in a regression framework.

2.5 Evaluating the role of herbivores in nutrient redistribution (Q4)

I assessed the potential for herbivores to redistribute nutrients by estimating forage quality (N, P and C concentration, with C:N, C:P and N:P ratios) and quantity at each of the 21 sampling sites. Specifically, to see if herbivores would preferentially forage in nutrient-rich patches and then redistribute these nutrients to nutrient-poor patches, I analysed the relationship between forage quality and quantity, with herbivore consumption (**Q4.1**), along with their faecal deposition patterns (**Q4.2**).

Forage quality and quantity were assessed on each control plots, when the paired plots were first established or moved to their new location, at the beginning and peak of the growing season (**Figure 2.3**). Plant community composition was assessed using the point intercept method using a 50 cm x 50 cm metal frame with 25 pins. In each plot, point intercept was performed by vertically lowering a 3 mm diameter pin through 25 holes evenly spaced 10 cm apart. The number of intercepts ('hits') of each vascular plant species from each of the 25 pins was recorded separately. Dead vascular plant material was all recorded as "*standing dead*" to separate living and dead biomass. Living material was only considered later in the analysis, and all intercepts by plant species were summed by pin to calculate the average number of hits per pin. For woody species, hits of woody and deciduous parts were not separated. Non-vascular vegetation (i.e. mosses or lichens) were only recorded if touched at the lowest level, as well as soil, litter or rocks. I targeted 9 plant species that are known to be important food resources for the pink-footed geese, sheep and reindeer throughout the growing season and that are abundant in the study area. These species included two deciduous shrubs (i.e. *Salix arctica* and *Salix herbacea*), four grasses (i.e. *Festuca richardsonii*, *Calamagrostis neglecta*, *Poa alpina*, *Deschampsia alpina*), one pteridophyte (i.e. *Equisetum arvense*), one forb (i.e. *Bistorta vivipara*), and one sedge (i.e. *Carex bigelowii*). I converted the average number of hits per pin for each key plant species obtained from the point intercept measurements to biomass (DW $g.m^{-2}$) using a weighted linear regression model (Bråthen and Hagberg 2004). Conversion factors were taken from Ravolainen et al. (2010). Futher details on the application of these models in Iceland can be found in Mörsdorf (2015).

Simultaneously to the community composition assessment, fully developed leaves (ca. 3 g) were randomly collected from the 9 target plant species at each site. Samples were stored pressed in tea bags during fieldwork. Back in the laboratory, samples were dried in an oven at 40°C and ground to a fine powder. Subsamples of 150 mg of milled material were pressed into 15 mm diameter tablets using a hydraulic press with 4 ton pressure, similar to the procedure used for faecal samples (see section **2.4.1**). The nutrient content (N, P and C) of each plant species was estimated using the Arctic Alpine NIRS calibration models (Murguzur et al. 2019). As this is the first time those models have been used in Iceland, I compared the values predicted by the models with a sub-sample of 44 (for C and N) and 34 (for P) samples analysed using traditional laboratory methods (i.e. see **Paper III** for details).

The total amount of nutrients available in each plot and forage quality (C:N, C:P and N:P) were calculated by multiplying the plant biomass by the corresponding nutrient concentration for a given species. Values were summed for all key forage species present in each paired plots, and were standardised by the total forage biomass retrieved from the point intercept. To investigate the relationship between forage quality and herbivore consumption (**Q4.1**) I used general linear mixed models where I accounted for the environmental variability in each paired-plot, and the quantity of available forage. To assess the relationship between forage quality and faecal nutrient deposition from the different herbivore species (**Q4.2**), I used a regression framework and modeled herbivore nutrient depositon as a function of forage quality and herbivore species at the sites-level.

2.6 Statistical analysis and data availability

Throughout the thesis, data summaries and analyses were performed in the R statistical software 4.3.2 (R Core Team 2024), using relevant packages for different analyses. Specifically, the *vegan* (Oksanen et al. 2013) and *mass* (Ripley et al. 2013) packages were used to assess changes in herbivore community composition using NMDS, and *mgcv* (Wood and Wood 2015) was used to build the general additive models and assess trends in herbivore abundance, metabolic biomass and forage intake (**Paper I**). The *pls* (Mevik and Wehrens 2015) and *prospectr* (Stevens et al. 2015) packages were used for the NIRS faecal calibration models, and the *emmeans* package (Lenth et al. 2024) was used to examine seasonal and interspecific differences in faecal nutrient content (**Paper II**). Finally, the *glmmTMB* package (Brooks et al. 2024) was used to examine the relationship between forage quality, herbivore consumption and faecal deposition (**Paper III**). Statistical code and data for each chapter are available in open (**Papers II,** https://github.com/Mathilde-Def/nirs_calibration_nutrient_iceland) and private (**Paper I and III**, unpublished) repositories (https://github.com/Mathilde-Def/herbivore_community_iceland, https://github.com/Mathilde-Def/herbivore_nutrient_redistribution)

3. Results

3.1 Changes in the Icelandic herbivore community over the past decades (Q1)

The compilation of herbivore population trends in Iceland over the last four decades revealed a transition from a livestock to a wildlife-dominated herbivore community (**Paper I; Q1.1**). However, this pattern of a wildlife-dominated herbivore community was not supported when looking at metabolic biomass, where wild species only accounted for approximately 14% of the total herbivore biomass.

Herbivore densities in Iceland increased to a large extent between 1986 and 2020. The densities of most wild herbivore species increased, except for white-fronted goose, greylag goose and ptarmigan, which decreased. Among livestock, sheep were by far the most important, but their numbers decreased steadily after the implementation of livestock quotas in the late 1980s. In turn, other livestock, including cattle, horses and goats increased in density. Of the wild species, birds (waterfowl and ptarmigans) were the most abundant, with reindeer making up only a small proportion of the total community and being found only in the East of the country. Historically, sheep and ptarmigan were the most abundant herbivores in Iceland, representing 26% and 55.4% of the herbivore community respectively in terms of density, in 1986. Today, the pink-footed goose is also among the most abundant herbivore species, accounting for 27.8% of the total herbivore population in 2020, and reflecting its large increase between 1950 (2.21 ± 0.03 individuals km^{-2}) and 2020 (7.54 ± 0.08 individuals km^{-2}). In contrast sheep represent 25.1%, and ptarmigans 26.8% in 2020.

The observed changes from a domestic- to a wild-dominated herbivore community were mainly driven by a rapid increase in pink-footed goose populations and a decrease in sheep abundance. However, livestock still dominated the herbivore community with their high metabolic biomass, reaching an average of 130 kg.km^{-2}.year^{-1} compared to 13.50 ± 1.06 kg.km^{-2}.year^{-1} for wild species. Concurrent to the decline of the sheep population, the total herbivore metabolic biomass decreased by 19.40% between 1986 and 2020 (**Paper I; Q1.2**).

3.2 Impact of herbivores on vegetation (Q2)

The impact of herbivores on Icelandic vegetation, as measured by the estimated consumption of aboveground biomass by herbivores, decreased in improved pastures and in rangelands between 1986 and 2020 (**Paper I; Q2.1**). Specifically, the total forage intake decreased by 6.16% in improved pastures and by 14.60% in rangelands. Total forage intake by herbivores was consistently higher on improved land than in rangeland (t test; $t = 87.4$, $df = 684.55$, p value < 0.001). Similar to the patterns in metabolic biomass, livestock contributed significantly more to total aboveground plant biomass consumption than wild species, consuming a substantial proportion of the net primary production (NPP) in both rangelands and improved pastures. Total consumption by wild herbivores was only 0.10 ± 0.01% and 0.21 ± 0.02%

in improved grasslands and rangelands, respectively. In comparison, livestock consumed an average of 2.35 ± 0.13% to 2.65 ± 0.20% of the total primary productivity in improved lands and rangelands, respectively.

Finer scale resolution at the site level and across the growing season (**Paper III; Q2.2**) revealed that herbivore consumption of aboveground biomass is not evenly distributed across high elevation rangelands, as I measured strong differences in herbivore consumption between sites. In addition, field measurements showed a significant increase in herbivore consumption between the early and late growing seasons (ANOVA, $F_{(1)} = 6.12$, p-value = 0.01), with herbivores consuming 8.6 ± 5.4 % and 34.3 ± 8,8 % of aboveground biomass, respectively.

3.3 Faecal nutrient contribution of herbivores (Q3)

3.3.1 Tools to estimate faecal nutrient content

Multispecies NIRS-based calibration models proved to be an efficient, low-cost tool for assessing nutrient faecal content across different herbivore species and throughout the growing season (**Paper II; Q3.1**). Specifically, I found that both the monospecific models, and multispecies (i.e., mammalian and all species) models, performed well (high R^2 and low RMSEP) in predicting N and C content in an independent validation dataset. The performances of the multispecies models including all three herbivores reached an R^2 of 0.88 and a RMSEP of 0.21 g DW for N; an R^2 of 0.76 and a RMSEP of 0.12 g DW for P; and an R^2 of 0.97 and a RMSEP of 0.64 g DW for C. In comparison, the monospecific models achieved predictive performances based on the external validation of $R^2 \geq 0.78$, RMSEP $\leq$0.31 g DW; $R^2 \geq 0.79$, RMSEP $\leq$ 1.09 g DW for N and C, respectively. Monospecific phosphorus calibration models were performed with less accuracy, probably due to the small sample size and low variance of P concentrations compared to the spectral data. A model for P could only be run for geese. The model achieved an R^2 of 0.77 for a RMSEP of 0.05 g DW.

3.3.2 Differences in faecal nutrient content and quality among herbivores

Based on the multispecies model, I was able to estimate faecal N, P and C concentrations, and C:N, C:P and N:P ratios for the main Icelandic tundra herbivores. Significant differences in faecal nutrient concentrations and quality were observed between species (**Q3.2**), with large fluctuations throughout the growing season (**Q3.3**). At the beginning and the peak of the growing season, faecal concentrations of N, P, and C were relatively stable for all species, except for reindeer, where C concentrations peaked at 44.38 % DW at the peak of the growing season. However, distinct patterns emerged toward the end of the growing season. Faecal N decreased in all three species. Faecal P also drastically declined in geese and reindeer, but remained unchanged in sheep (0.6% DW). Faecal C concentrations were more variable: in geese, faecal C increased significantly between the peak and late season, whereas it decreased in reindeer and remained stable in sheep. Overall, sheep faeces consistently contained 1.5 times more nitrogen than geese or reindeer faeces, which had similar nitrogen levels (i.e., about 2.70% DW) from the beginning to the peak of the growing season. However, towards the end of the season, the nitrogen concentrations in sheep faeces dropped to levels similar to those found in reindeer (2.31 and 2.39% DW, respectively), while N in geese faeces decreased by almost half to about 1.60% DW. Reindeer faeces consistently contained the highest levels of faecal P, and geese the lowest, reaching less than half the levels of reindeer.

C:N ratios were similar in the three species at the beginning of the growing season. These values remained unchanged in geese and sheep during the peak of the season, but increased significantly in reindeer. By the end of the growing season, the C:N ratio had doubled in geese and increased slightly in sheep, reaching levels similar to those observed in reindeer, where the C:N ratio had stabilised. In contrast, the C:P ratios were much more stable throughout the season and did not differ significantly between geese, sheep, and reindeer. The only notable change occurred towards the end of the season, when the C:P ratio in geese faeces increased sharply and tripled. Finally, the N:P ratios remained relatively constant all species throughout the growing season, with geese consistently having the highest ratios, and reindeer the lowest.

3.3.3 Nutrient contributions by different herbivores

At the scale of the study area, geese contributed the most to the nutrient budgets of the Icelandic tundra, while reindeer contributed the least (**Paper II; Q3.4**). This pattern was consistent with observations at the local scale (**Paper III**), where geese were responsible for most of the faecal N, P, and C inputs, whereas reindeer faeces were almost absent. Herbivore faecal nutrient contributions of N and P peaked at the beginning of the growing season and gradually decreased toward the end, in tune with the overall decrease in herbivore faecal quality during the season. Interestingly, estimates of faecal nutrient deposition at the site level (**Paper III**) were higher than those calculated for the broader study area (**Paper II**). Specifically, field estimates indicated that geese deposited an average of 3.85 g DW.m^2 of N, 0.59 g DW.m^2 of P, and 55.30 g DW.m^2 of C, whereas I estimated a total of 1.21 g DW.m^2 of N, 0.18 g DW.m^2 of P, and 17.70 g DW.m^2 of C when calculated at the broader scale.

3.4 Herbivore induced nutrient distribution (Q4)

Forage nutreint availability and forage quality decreased significantly between early and late growing season, while forage biomass did not differ significantly (**Paper III**). There was no clear relationship between nutrient availability or forage quality and herbivore consumption of aboveground plant biomass in either the early or late season (**Q4.1**). However, nutrient availability was negatively associated with nutrient deposition for N, P and C in both sheep and geese, with higher nutrient deposition where nutrients were less available (**Q4.2**). The patterns were consistent for both herbivore species, but the contribution of geese was consistently higher than that of sheep.

4. Discussion

This thesis presents a pioneering assessment of long-term changes in the Icelandic herbivore community, spanning over 70 years and multiple herbivore species, including both domestic and wild species. This dataset represents the most comprehensive record of terrestrial herbivores in Iceland to date (**Paper I**). Main findings revealed that domestic species have a larger impact on vegetation biomass than wild species in both rangelands and improved grasslands, although overall consumption rates have declined in the past decades (**Paper I**). In high-elevation tundra, however, herbivore impact on vegetation is strongly marked by seasonality, with consumption rates peaking toward the end of the growing season (**Paper III**). Additionally, this thesis introduces the first multispecies NIRS calibration model to assess faecal N, P, and C in tundra ecosystems, contributing to the affordability and standardisation of methodologies for investigating the role of herbivores in nutrient cycling (**Paper II**). The availability of these cost-effective methods paves the way for new research on herbivore diets, digestive physiology, and their effects on biogeochemical cycles, key components for understanding their role in ecosystem functioning in a multispecies context. Along with the model, I provide the first faecal nutrient estimates for pink-footed geese, reindeer and sheep in Iceland, revealing clear differences between these herbivores and changes throughout the growing season (**Paper II**). Notably, my findings highlight the substantial nutrient deposition by geese in high elevation tundra. Finally, I present evidence for herbivore-mediated nutrient transport in the Icelandic tundra, emphasising the critical role of herbivores in influencing biogeochemical cycles in these ecosystems (**Paper III**).

4.1 Long-term changes in herbivore communities and metabolic biomass

Despite uncertainties arising from data compiled from multiple sources, consistent trends in herbivore community composition and metabolic biomass were observed in Iceland over the last four decades (**Paper I**). Since 1990, there has been a noticeable shift from livestock to wild herbivore dominance, probably driven by the increasing waterfowl populations (Alisauskas 2000). Despite their large numerical increase, wild herbivores still represented a small fraction of the total metabolic biomass of herbivores, compared to livestock. This disparity is likely due to the limited number of reindeer, the only large wild herbivore in Iceland, which contribute minimally to the total wild herbivore biomass (Austrheim et al. 2011). Similar transitions from livestock to wild herbivore dominance have been documented in other Nordic countries, such as Norway, where a resurgence of large wild ungulates and a decline in domestic species have been observed (Austrheim et al. 2011). These shifts in herbivore communities were interpreted as passive trophic rewilding (Speed et al. 2019a). Trophic rewilding, in the sense of restoring native herbivore assemblages, has been proposed as a strategy for preserving Arctic ecosystems in the face of climate change (Olofsson and Post 2018). For example, the grazing by large herbivores in Arctic tundra has been shown to mitigate the effects of climate change by protecting carbon stored in permafrost (Windirsch et al. 2022), influencing albedo by reducing shrub cover (Malhi et al. 2022), and potentially reducing greenhouse gas emissions by promoting graminoid species, and limiting moss cover, which favour CO_2 uptake by vegetation (Falk et al. 2015; Lara et al. 2017). However, ecosystems with a short evolutionary history of grazing, such as Icelandic high-elevation rangelands, may have limited resilience to increased herbivore pressure. Characterized by low primary productivity, these areas are especially vulnerable to degradation, including soil erosion (Cingolani et al. 2005; Marteinsdóttir et al. 2017). For example, despite the exclusion of sheep grazing in some areas of the Highlands, no significant vegetation recovery has been observed, highlighting the long-lasting effects of grazing on ecosystem structure and function (Mörsdorf et al. 2021). Therefore, introducing or encouraging an increase in herbivore populations and thus of grazing pressure in Iceland may not be an appropriate management tool for the conservation of Highland rangelands.

4.2 Contrasted impact of herbivores on vegetation consumption and faecal deposition

4.2.1 Larger offtake from livestock compared to wild herbivores in both improved grasslands and rangelands

My results indicate that livestock exert a greater impact on vegetation than wild species, due to their greater metabolic biomass and energy requirements (**Paper I**). However, wild herbivores, in particular geese, consume an increasing proportion of net primary production in both improved grasslands and rangelands. Geese, the dominant wild herbivore, are highly selective feeders, preferring nutrient-rich plants in large quantities (Durant et al. 2004). Fertilised grasslands provide abundant high-quality forage necessary to build energy reserves prior migrating to nesting and moulting sites (Fox and Abraham 2017). This increased access to nutrient-rich forage during staging may play an important role in the recent increase of geese populations in northern Europe (Mason et al. 2018), as has been long recognised for North American migratory goose populations (Jefferies et al. 2003).

The increased plant biomass consumption by geese in improved grasslands can reduce forage availability to livestock (Baldi et al. 2001; Bjerke et al. 2021), and create tensions with farmers in the lowlands. To moderate this conflict, proposed solutions often include culling and financial compensation (Eythórsson et al. 2017). Interestingly, some studies suggest that geese may not always reduce grass yields and could even increase nutrient availability through their faecal inputs (Gorosábel et al. 2019). Therefore, investigating the nutrient feedback from geese in these ecosystems could provide a more nuanced understanding of the potential for wildlife conflict in improved grasslands.

While similar concerns to those in improved grasslands exist in rangelands, regional level estimates suggest a moderate consumption of plant biomass from wild and domestic herbivores. However, field measurements revealed strong spatial and temporal variation, with consumption rates reaching up to

30% in some high-elevation rangelands, where 25% of the Icelandic-Greenlandic pink-footed goose population nests and coexists with sheep and reindeer (Skarphéðinsson and Þórisson 2001; Boulanger-Lapointe et al. 2022) (**Paper III**). Comparable consumption rates have been observed at other locations throughout the Arctic, such as goose colonies in the High Arctic, where snow geese (*Chen caerulescens atlantica* K.) consume from 30% and up to 60% of the annual production of graminoids (Cargill and Jefferies 1984; Legagneux et al. 2012). These high consumption rates can locally impact vegetation structure and ecosystem function. Strong consumption rates have been shown, for example, to alter nutrient dynamics and potentially affect soil fertility and plant community composition (Sitters et al. 2019).

4.2.2 Differences in faecal quality and deposition between herbivores in tundra rangelands

I found strong variation in faecal nutrient content among tundra herbivores, suggesting that different herbivores contribute uniquely to biogeochemical cycling and nutrient turnover (**Paper II**). Specifically, I found that larger herbivores such as reindeer and sheep had more similar, and higher faecal nutrient concentrations than geese, likely due to differences in digestive systems, size and dietary preferences (Karasov and Douglas 2013; Sitters and Olde Venterink 2021a). The faecal nutrient concentrations and stoichiometry I observed in Icelandic herbivores were consistent with previous findings for reindeer (Barthelemy et al. 2015; Beumer et al. 2017) and geese (Bazely and Jefferies 1985; Dessborn et al. 2016; Beard et al. 2023) in tundra ecosystems, and for sheep in rangelands (Wang et al. 2018).

Faecal N:P ratios were higher in geese than in reindeer, suggesting that geese may promote N return to ecosystems over P (Beard et al. 2023), whereas reindeer may promote P cycling in the Icelandic tundra. Species differences in faecal stoichiometry can have strong local effects on N and P cycling by controlling the availability of nutrients to plants or soil microorganisms (Sitters and Olde Venterink 2021b). Despite the relatively short time that geese spend in high altitude rangelands, they were the main contributors to faecal nutrient inputs, surpassing sheep in nutrient deposition. This pattern was observed at both landscape (**Paper II**), and local (**Paper III**) scales. Nitrogen deposition from geese (769 $kg.km^{-2}$ and 2 090 $kg.km^{-2}$ for respectively landscape and local scales estimates) was higher to local average atmospheric deposition (<100 kg $N.km^{-2}.y^{-1}$, Arnalds 2015), and to levels observed in other areas with high goose densities (Post et al. 1998). However, estimates of N, P and C deposition by geese were higher at the site level (**Paper III**) than at the landscape level (**Paper II**) by 3 times. These findings emphasise the important role that geese play in nutrient cycling, particularly in promoting nitrogen return, and highlight the importance of considering species-specific contributions to nutrient dynamics in high-elevation rangelands.

The combined effect of increasing wild herbivore populations, coupled with earlier arrival of geese to their breeding grounds across the Arctic (Doiron et al. 2015; Ross et al. 2017) suggests that faecal nutrient deposition from geese will continue to be an important source of zoogenic nutrient inputs to these ecosystems. Geese concentrate their faecal inputs in specific areas, near water bodies and in densely vegetated regions, especially when they are less mobile during the breeding or the moulting season, creating localised nutrient hotspots (Van Geest et al. 2007; Sjögersten et al. 2010). At low goose densities, this concentrated faecal deposition can have positive effects on vegetation and microbial communities (Bazely and Jefferies 1985; Hik and Jefferies 1990; Beard et al. 2023), but at high densities, excessive goose grazing can shift plant species composition towards less palatable species (Sjögersten et al. 2010), and contribute to freshwater eutrophication in areas where they congregate in large numbers (Hessen et al. 2017). Further research is needed in Iceland to better assess the long-term role of faecal deposition from different herbivores on ecosystem functions. Such research could help clarify how variations in nutrient deposition patterns affect vegetation dynamics, microbial communities, and overall ecosystem health, especially in sensitive tundra environments.

4.3 The effect of seasonality on herbivore impact in tundra rangelands

Tundra ecosystems are highly seasonal environments, characterised by harsh winters, nutrient scarcity, and a brief, but marked growing season. Early in the growing season, there is a rapid release of nutrients that drives fast primary production followed by quick vegetation senescence (Chapin et al. 1975; McLaren et al. 2017; Westergaard-Nielsen et al. 2021). This dynamic is supported by the strong seasonal variation in forage quality observed in this thesis (**Paper III**). In addition, my research demonstrates that seasonality affects not only vegetation but also herbivore impacts, particularly in terms of consumption rates, faecal nutrient content, and nutrient deposition in tundra ecosystems.

Herbivore consumption rates in tundra ecosystems increased by more than threefold later in the growing season, likely because herbivores require more forage as plants begin to senesce. As offspring grow and their biomass increases, herbivores need more nutrient-rich forage, particularly high in N and P to support protein synthesis (Elser et al. 1996), and skeletal growth (May and El-Sabaawi 2024). Moreover, herbivores need to store resources for migration, winter survival, or reproduction (Wypkema and Ankney 1979; Barboza and Parker 2008). Increased herbivore consumption of plant biomass late in the growing season suggests that herbivores can have a strong top-down control on vegetation. This enhanced grazing pressure is likely to potentially slow down the recovery of heavily grazed tundra ecosystems by increasing the mortality of the more susceptible plant species and limiting their ability to regrow, reducing primary production (Brown and Allen 1989; Hik and Jefferies 1990), and promoting the expansion of less palatable plant species (Eskelinen and Oksanen 2006; Yu et al. 2011).

Interestingly, my results also highlight that faecal nutrient deposition is highest early in the growing season, when faeces contain higher concentrations of N, P, and C. The seasonal decline in faecal nutrient content is likely due to a decline in plant quality over time (**Paper III**), as palatable species translocate nutrients such as N and P into their belowground structures before senescence (Hahn et al. 2007; Happonen et al. 2022; Zhao et al. 2023). This pattern has also been observed in temperate and alpine ecosystems, where nutrient concentrations in faeces decrease as the season progresses (Kamler et al. 2004; Barbero-Palacios et al. 2023). More generally, the early-season nutrient pulse from herbivore faeces aligns with the typical nutrient burst seen at the beginning of the growing season in tundra ecosystems (Chapin et al. 1975; McLaren et al. 2017; Westergaard-Nielsen et al. 2021), emphasizing the critical role that herbivores play in nutrient turnover at this time. Therefore, in contrast to their top-down influence on vegetation later in the season, herbivores promote strong bottom-up control through nutrient deposition earlier in the growing season by increasing the amount of nutrients available for plants.

4.4 The role of herbivores in nutrient transport in tundra rangelands

In this thesis, I demonstrate that herbivores consumed forage plants irrespective of their quality at the community level, while consistently transporting and depositing nutrient-rich waste in vegetation patches with low nutrient availability across the landscape (**Paper III**). These results highlight the important role of herbivores in nutrient transport and redistribution, supporting ecological theories of nutrient transfer across ecosystems (Polis et al. 1997; McInturf et al. 2019; Ellis-Soto et al. 2021).

The lack of a clear relationship between herbivore consumption patterns and nutrient availability at the community level may be driven by factors not accounted for in my study. For example, I measured biomass consumption for the whole herbivore assemblage, but the presence and abundance of different herbivores with contrasting dietary preferences could mask species-specific patterns. Some studies have suggested that geese may select patches with intermediate nutrient levels as a trade-off between vegetation biomass and quality (Van De Koppel et al. 1996; Hassall et al. 2001), whereas larger herbivores such as sheep and reindeer tend to prioritise patches with higher biomass in their summer range (Van Der Wal et al. 2000; Mårell and Edenius 2006). Furthermore, within the same species, individual foraging preferences can vary considerably, influenced by factors such as herbivore density (Mobæk et al. 2012; Austrheim et al. 2014), interspecific competition (La Morgia and Bassano 2009), predation avoidance (Weterings et al. 2018), and human barriers. Understanding the drivers of consumption in a multispecies context is essential for a more accurate assessment of how herbivores influence nutrient distribution and cycling in ecosystems.

Notably, the fact that herbivores transferred more nutrients to low-quality forage areas challenges the assumption that herbivores primarily accelerate nutrient cycling in high-quality patches but have the opposite effect in nutrient-poor patches (Pastor and Naiman 1992; Stark 2007; Forbes et al. 2019). These results support evidence that herbivores can enhance nitrogen availability in less productive habitats by moving nutrients from nutrient-rich to nutrient-poor patches in the Arctic tundra (Post et al. 1998; Stark et al. 2015; Mosbacher et al. 2016; Ferraro et al. 2021). Such redistribution of nutrients could have significant long-term effects on plant productivity and ecosystem functioning, with the potential to increase nutrient availability in previously nutrient-poor patches. Experimental studies in tundra ecosystems have demonstrated the long-term beneficial effects of herbivore faecal deposition in low quality areas, promoting nutrient uptake by plants and enhancing growth (Barthelemy et al. 2015). Over time, this process could make these areas more attractive to herbivores, potentially leading to feedback loops that further increase nutrient concentrations and plant productivity (Bazely and Jefferies 1985; Bardgett and Wardle 2003).

4.5 Management implications for Icelandic rangelands

The impact of wild and domestic herbivores, particularly geese and sheep, on vegetation in Icelandic rangelands presents unique management challenges, especially in the Highlands. These areas are sensitive to disturbance and are often in poor ecological condition, making them especially vulnerable to grazing (Arnalds et al. 2023). While herbivore consumption rates have historically been high in Icelandic rangelands with limited primary production, recent increases in productivity (Raynolds et al. 2015), and reductions in sheep biomass (**Paper I**) have led to decreased grazing pressure. This shift offers new opportunities for land restoration, which could be enhanced through strategic management interventions (Mulloy et al. 2019).

Overall, my results emphasise the need to account for seasonality when looking at the role of herbivores in nutrient cycling and ecosystem function. The presence of herbivores early in the growing season in the tundra appears to be essential for nutrient turnover, but careful management is required to prevent excessive grazing pressure and ensure the health of rangelands, especially in the late season when plant recovery may be slower (Hik and Jefferies 1990). Implementing management strategies such as controlled grazing duration which account for the impact of wild herbivores (i.e., geese and reindeer) in the rangelands could help maintain rangeland conditions and mitigate the risk of overgrazing during this critical period. Although both wildlife and livestock coexist throughout Iceland, they are still often managed independently (Arnalds and Barkarson 2003) and detailed data on land use by herbivores, particularly for waterfowl species, remains scarce (Arzel et al. 2006). There is a need for systematic efforts to gather and synthesise data on both livestock and wildlife at regional and local scales. I hope that the integrated assessment presented in this thesis will serve as a foundation for collaborative wildlife and livestock management across the country. Insights from Icelandic tundra rangelands may have broader implications for other systems with similar conditions, such as alpine and northern rangelands. Developing a nuanced understanding herbivore interactions and ecosystem feedback in these regions could inform effective conservation and management strategies areas that share similar bioclimatic and ecological characteristics.

5. Conclusions

In this thesis, I assessed changes in the herbivore community in Iceland over the past decades and contributed to a deeper understanding of the role herbivores play in tundra ecosystem functions, particularly in relation to vegetation biomass, nutrient cycling, and nutrient transport. My results underscore the importance of considering both seasonality and species identity when evaluating herbivore impacts on tundra ecosystems. Additionally, they highlight the importance of addressing wildlife and livestock simultaneously, given that they often coexist in tundra ranges. Overall, this thesis addressed important regional knowledge gaps, resolved methodological limitations, and provided insights for managing tundra rangelands in high-latitude, multispecies contexts. Main take home messages include:

- Herbivore communities are shifting from being domestic to wild-dominated, but domestic species still account for most of the metabolic biomass.
- Domestic herbivores have a greater impact on vegetation biomass than wild species in both improved grasslands and rangelands, although their overall consumption has decreased over time.
- Differences in faecal nutrient composition between herbivores suggest that they contribute differently to nutrient cycling. In particular, geese add substantial amounts of nutrients to high-elevation tundra rangelands.
- Seasonality influences the impact of herbivores on ecosystem functioning: nutrient input from herbivore faeces was greater early in the growing season, while herbivore biomass consumption increased during the late season.
- Herbivores redistribute nutrients across the landscapes in high elevation rangelands, accumulating nutrients in nutrient-poor areas, which could be particularly important for tundra ecosystems.
- Cost-effective tools, such as NIRS provide promising results for predicting faecal nutrient contents in tundra herbivores, and could thus be used to increase our understanding of nutrient transfer within tundra ecosystems.
- There is a need for adapted management policies that account for seasonality and integrate the impacts of both wild and domestic herbivores. These policies could help balance the benefits of herbivores with rangeland sustainability, particularly during the late season.

6. Future work

To build upon the findings of this thesis, the following areas for future research can be proposed:

- Consistently reporting spatially and temporally explicit data on local herbivore population densities, and waterfowl migration timing is essential. I suggest strengthening collaboration with stakeholders to gather this valuable information.
- Investigating and clarifying diet preferences among different herbivore species in the Icelandic tundra will help uncover potential competition between wild and domestic herbivores.
- Expanding NIRS calibration model to other species and biogeographic regions could provide valuable insights into how body size, digestion, and diet influence faecal nutrient content and stoichiometry in tundra ecosystems, potentially enhancing our understanding of nutrient cycling across ecosystems.
- Further developing experimental approaches, such as size-selective exclosure experiments, will improve our understanding of herbivore effects on nutrient dynamics, separately and in combination, on tundra ecosystems. These experiments have shown promise and have already been implemented in international initiatives (e.g., Herbivory network, https://herbivory.lbhi.is/).
- Investigating the drivers of herbivore habitat use in relation to biogeochemistry could be advanced by integrating telemetry data with stoichiometric models. This approach, although relatively expensive, has great potential for Iceland, because telemetry studies on sheep and reindeer are already in place. Reinforcing coordination and collaboration across institutions could enhance data collection and analysis.
- Herbivores, particularly waterfowl like geese, play a key role in nutrient transport between terrestrial and aquatic systems. Investigating these cross-boundary nutrient dynamics in Iceland could provide insights into how herbivores influence both types of ecosystems and support more integrated management strategies.
- Applying modelling frameworks, like individual-based models (IBM) and Stoichiometric distribution models (StDM), adapted to multispecies interactions in tundra ecosystems, could provide valuable predictions regarding herbivore impacts under future environmental conditions. This would allow for more effective long-term management in the face of climate change.

7. Funding

This work was supported by the Icelandic Research Fund (grant number 217754 and 2410773-051); the Nordic Borealization Network (NordBorN, funded by NordForsk grant number 164079); and Landsvirkjun (grant number NÝR-22-2022 and NÝR-26-2023).

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Ambio
https://doi.org/10.1007/s13280-024-01998-6

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THE ROYAL SWEDISH ACADEMY OF SCIENCES

RESEARCH ARTICLE

Long-term changes in herbivore community and vegetation impact of wild and domestic herbivores across Iceland

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Received: 15 September 2023 / Revised: 18 January 2024 / Accepted: 8 February 2024

Abstract Changes in wild and domestic herbivore populations significantly impact extensive grazing systems, particularly in low productive environments, where increasing wild herbivore populations are perceived as a threat to farming. To assess the magnitude of these changes in Iceland, we compiled time series on herbivore populations from 1986 to 2020 and estimated changes in species densities, metabolic biomass, and consumption of plant biomass in improved lands and unimproved rangelands. We compared estimates of consumption rates to past and present net primary production. Overall, the herbivore community composition shifted from livestock to wildlife dominated. However, wild herbivores only contributed a small fraction (14%) of the total herbivore metabolic biomass and consumption (4–7%), and livestock dominated the overall herbivore biomass. These insights highlight the necessity of developing improved local integrated management for both wild and domestic herbivores where they coexist.

Keywords Herbivory · Land management · Livestock · Metabolic biomass · Vegetation impact · Wildlife conflicts

INTRODUCTION

By consuming plants, depositing waste and trampling, herbivores have a strong effect on ecosystem processes and functions (Olofsson 2009; Forbes et al. 2019). However, the magnitude and direction of herbivore impacts depend on multiple environmental factors, including ecosystem productivity (Burkepile and Parker 2017), and herbivore densities (Austrheim et al. 2014) and identities (Hempson et al. 2015; Wang et al. 2019). For instance, African savannas experience vegetation shifts with declines in grass or shrubs depending on the balance between grazing and browsing herbivores (Staver et al. 2021). Thus, changes in the composition of herbivore communities can determine the impact that herbivores have on ecosystems.

Worldwide, human management and environmental changes are driving changes in herbivore populations. The escalating demand for meat has led to increased livestock production in most countries, often replacing wild species and homogenizing herbivore communities (Hempson et al. 2017). Most of this intensification has occurred in managed agricultural lands, while rangelands have been abandoned in regions with high intensification of meat and dairy production (Alkemade et al. 2013; Godde et al. 2018). Conversely, wild species can benefit from changes in agricultural practices; for example, the abundance of migratory waterfowl has increased in the Arctic because of the enhanced food availability in their wintering ranges (Fox and Abraham 2017), and the densities of wild cervids have increased with recent changes in land use and population management in Norway, effectively replacing grazing livestock in some regions (Speed et al. 2019). The interplay between wild and domestic herbivores poses both management and societal challenges, particularly in low-productive ecosystems where increasing herbivore populations may constrain primary productivity and exacerbate conflicts between stakeholders (Mysterud and Austrheim 2008). Indeed, the spatial overlap between livestock and wild herbivores is often interpreted as a potential indicator of resource competition and is perceived as a threat to farming industries, while also potentially affecting populations of protected wildlife (Pozo et al. 2021). Understanding the relative impact of domestic and wild species is crucial for effective management policies in a changing world.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13280-024-01998-6.

In Iceland, the vertebrate herbivore community is composed of a mixture of wild and domestic animals, where birds are the only native herbivores. In the last decades, changes in agricultural policies have led to a reduction in the abundance of sheep by nearly half, following the introduction of a livestock quota in the early 1980s (Arnalds and Barkarson 2003). In turn, as in other parts of the Arctic, the numbers of migratory waterfowl (i.e., Anatidae) have greatly increased (Smith et al. 2020). Upon arrival in Iceland in early spring, geese and swans stage in improved agricultural lands (Fox et al. 1992), where livestock also graze for part of the season. The potential competition for resources between livestock and wild herbivores on improved grasslands (i.e., fertilized pastures including hay fields and grazing pastures) is becoming a concern for farmers (Jóhannesdóttir et al. 2017). Such concerns are extending to less productive rangelands in the highlands, where sheep graze during the summer months and spatially overlap with waterfowl suggesting that competition can also occur (Boulanger-Lapointe et al. 2022). However, limited evidence exists on the impact of waterfowl on sheep farming, and the broader consequences of herbivore community changes in both improved and unimproved land remain unclear.

This study aims to assess changes in the Icelandic herbivore community over the last decades and their impact on vegetation at a national scale. Specifically, our questions are as follows: (1) has herbivore community composition shifted over time? We anticipate a transition from a livestock-dominated to a wild-dominated system due to changes in Icelandic agricultural policies and an increasing migratory goose population. If such a shift has occurred, (2) do changes in herbivore community composition correlate with shifts in densities of particular herbivore species? And (3) are these changes reflected more broadly in the relative metabolic biomass (i.e., the animals' daily energy requirements) of wild and domestic herbivores? While the overall herbivore population may still grow, community shifts are likely related to fewer sheep and more waterfowl, with increasing metabolic biomass of wild herbivores relative to domestic species. Given their differing sizes and energy needs, we wondered: (4) do these changes translate to divergent impacts of wild and domestic herbivores on net primary production of improved and unimproved lands?.

MATERIALS AND METHODS

Study area

This study focuses on grazing areas used by domestic and wild herbivores in Iceland, which encompass 60% of the country (Stefánsson et al. 2020). About 40% of the grazing areas consist of fenced, improved grasslands located close to the farms in the lowlands (i.e., below 200 m a.s.l.). Improved grasslands are privately owned by farmers and are managed through fertilization and planting. These improved lands are used for hay production and/or as grazing pastures. In contrast, unimproved rangelands are mainly communally owned lands usually located at higher elevations characterized by low-productivity subarctic tundra vegetation, and used for extensive livestock grazing. Rangelands are managed as natural ecosystems and include a mosaic of tundra habitats, including heathlands, wetlands and natural grasslands (Thorhallsdottir 1997).

Vertebrate herbivore community

Iceland's vertebrate herbivore community encompasses domestic and wild species, including a total of 11 vertebrate herbivores (Table 1). Introduced by the first settlers in the ninth century, domestic livestock include sheep (*Ovis aries)*, cattle (*Bos taurus*), horses (*Equus ferus caballus*) and goats (*Capra hircus*) (Thomson and Simpson 2006). All livestock receive supplementary food during winter when, except for horses, animals are kept indoors. Cattle, goats and sheep are released to improved pastures in spring (Fridriksson 1972). Sheep are then grazed on unimproved rangelands from mid-June to mid-September (Ross et al. 2016). Horses mainly use unimproved rangelands year-round, but can be moved to improved pastures during the mating season (Magnússon and Magnusson 1990). On unimproved rangelands, horses use a more restricted area than sheep (unmapped), usually at lower elevations and closer to farms (i.e., horses do not graze in most highland rangelands).

Wild herbivores include feral reindeer (*Rangifer tarandus*), several species of geese, whooper swans (*Cygnus cygnus*) and rock ptarmigan (*Lagopus muta*). Reindeer were introduced in the seventeenth century and are confined to East Iceland's rangelands, where they are managed as game (Þórisson 2018). Waterfowl, including geese and swans, migrate from their wintering grounds (i.e., England, Scotland, and Ireland) to improved pastures in Iceland during spring and autumn. Among them, the Greenland white fronted goose (*Anser albifrons flavirostris*), the brent goose (*Branta leucopsis*) and the barnacle goose (*Branta bernicla*) continue their migration to Greenland where they breed (Fox et al. 1983); others, mainly pink footed geese (*Anser brachyrhynchus*), move to unimproved highland areas during summer to breed (Fox et al. 1992). Ptarmigans inhabit rangelands year-round and move seasonally to higher elevation (Gardarsson 1971).

Herbivore abundance data

A long-term herbivore abundance dataset for Iceland, spanning 11 vertebrate species (Table 1), was compiled

Table 1 The vertebrate herbivore community in Iceland includes domestic and wild species that are native or introduced. Their use of improved and unimproved grazing areas in Iceland is briefly described

Species	Status	Use of grazing areas in Iceland	
		Improved lands	Unimproved lands
Cattle (*Bos taurus* L.)	Domestic, introduced	Grazing pastures during growing season (May to Sept)	-
Icelandic Horse (*Equus ferus caballus* L.)	Domestic, introduced	–	Mostly grazed on rangelands year-round, but in the last 30 years, lowland fens have increased in importance as grazing area during summer
Icelandic sheep (*Ovis aries* L.)	Domestic, introduced	Grazing pastures during spring and autumn, i.e., after lambs are born and after *réttir**	Grazing area for ewes and lambs during the growing season (mid-June to mid-September)
Goat (*Capra hircus* L.)	Domestic, introduced	Grazing pastures during the growing season (May to Sept)	-
Greenland white fronted goose (*Anser albifrons flavirostris* S.)	Wild, native	Stopover during spring and autumn, before migrating to breeding sites in Greenland. Arrival peak passage between 20 and 25 April and early May	-
Greylag goose (*Anser anser* L.)	Wild, native	Staging and breeding area from spring to autumn. Arrival usually two weeks before pink footed geese and departure after the pink footed geese. A small part of the population recently became resident in Iceland (about 5%**)	-
Pink footed goose (*Anser brachyrynchus* B.)	Wild, native	Stopover during spring and autumn. Peak of arrival early May (8th of May). Part of the population continue the migration to Northeast Greenland breeding area in summer (perhaps 15–25%, Frederiksen et al. 2004)	Breeding area during summer (from mid-May to late August)
Brent goose (*Branta bernicla* L.)	Wild, native	Stopover during spring and autumn before migrating to breeding areas in northeast Greenland	-
Barnacle goose (*Branta leucopsis* B.)	Wild, native	Stopover during spring (i.e., end of April to late May) and autumn before migrating to breeding areas in East Greenland	-
Whooper swan (*Cygnus cygnus* L.)	Wild, native	Stopover during spring and autumn	Breeding area during summer
Rock ptarmigan (*Lagopus muta* M.)	Wild, native	–	Stay year-round
Reindeer (*Rangifer tarandus* L.)	Wild, introduced	–	Stay year-round

*The “réttir” corresponds to the collection of sheep from the rangelands after the summer

**Expert communication

from diverse published and unpublished sources with variable temporal and spatial coverage (Supplementary Material S1). Complete national population records for all species were available since 1986. Yearly livestock records since 1950, were retrieved from the national statistics database (Statistics Iceland 2022). Reindeer census data came from yearly aerial surveys in early July (Þórisson 2018). Waterfowl abundance data were derived from autumn colony censuses in UK wintering areas (Fox et al. 1998; Mitchell et al. 2010; Brides et al. 2021), as these estimates provide an accurate estimate of the abundance of waterfowl in Iceland during the summer months (Frederiksen et al. 2004). Most censuses were conducted yearly except for the barnacle geese and whooper swans, for which censuses were conducted every 5 years (Supplementary Material S1). One waterfowl species (the brent goose) was not included in the dataset due to lack of long-term consistent census data. Population estimates for the rock ptarmigan were based on biannual censuses (i.e., early May and early August, respectively, estimating summer and winter population) in East Iceland extrapolated to the entire country (Magnússon et al. 2004). Those estimates slightly overestimate the overall ptarmigan population (Sturludóttir 2015), but are nonetheless the longest and best available time series to date.

Herbivore densities were calculated by dividing abundance estimates by the total grazing area in Iceland (Stefánsson et al. 2020). The total grazing area is the sum of commonly and privately owned rangelands and improved lands. Full details on the database are provided in Supplementary Material S1.

Metabolic biomass of wild and domestic herbivores

Metabolic biomass (MB) is an allometric function that represents an animal's daily energy requirements. MB enables comparisons among species and allows estimating herbivore pressure in multi-species assemblages (Hatton et al. 2015). We calculated the species-specific metabolic biomass derived from Kleiber's (1932) equation based on the body mass (BW) and the metabolic rate (MR) of species i:

$$\mathrm{MB}_i = \mathrm{BW}_i^{\mathrm{MR}_i}$$

As no data on the age or sex of individuals were available for most of the species, we used the average mass of an adult obtained from the literature (Supplementary Material S2). For the metabolic rate, we used species-averaged estimates for birds and mammals (i.e., respectively 0.71 and 0.64; Hudson et al. 2013).

Population level estimates of metabolic biomass ($\mathrm{PMB_i}$, kg·year^{-1}) were calculated multiplying the species-specific metabolic biomass, by the abundance of the species in a given year and scaled by the amount of time spent grazing per year (G_i; G_i ranges from 0 to 1, 1 being for species grazing all year round and less for species that use the grazing areas seasonally; Supplementary Material S2).

PMB values were summed across species for the entire herbivore community ($\mathrm{PMB_{total}}$), and for wild and ($\mathrm{PMB_{wild}}$) and domestic ($\mathrm{PMB_{livestock}}$) species separately and standardized by the sum of grazing areas in kilometre squares.

Forage intake of wild and domestic herbivores in improved and unimproved land

Dry matter forage intake (DMI; DM kg year^{-1}) was used to estimate plant consumption by wild and domestic herbivores in improved lands and rangelands. Livestock DMI values were calculated following Holecheck (1998), using a value of 2% of the animals' body mass (kg) for ruminants and 3% for horses. DMI values of wild birds (waterfowl and ptarmigan) were extracted from literature. Data were either Iceland-specific, from comparable arctic or subarctic environments, or from closely related species (Supplementary Material S2). DMI values were multiplied by the abundance of each species and the number of days spent grazing in either improved lands or rangelands separately. Values were summed across the herbivore community ($\mathrm{DMI_{total}}$), livestock ($\mathrm{DMI_{livestock}}$) and wild species ($\mathrm{DMI_{wild}}$) and were standardized by the area of each type of land.

DMI was converted to carbon-based units (kg C year^{-1} km^{-2}), assuming that plants contain 45% of carbon (C) on average (Ma et al. 2018). We compared those values with yearly net primary production (NPP, in kg C year^{-1} km^{-2}) obtained from MODIS MOD 17 satellite derived products (Running and Zhao 2021) available from 2000 to 2021. We computed the average NPP for each year separately for improved lands and rangelands, using the map of grazing areas in Iceland (Stefánsson et al. 2020), and estimated the proportion of NPP consumed by wild and domestic herbivores in each type of land.

Accounting for parameter uncertainties

The calculations presented above are based on best available estimates of the parameters in the equations. Yet, most sources did not report a measure of variability, although these parameters are known to vary. To consider this variability, we simulated 100 replicates where each parameter varied stochastically by being perturbed by 10% from the baseline values, assuming a normal distribution (Supplementary Material S3).

Data analysis

Changes over time in herbivore community composition were analysed using Nonparametric Multidimensional Scaling (NMDS). We computed a Bray–Curtis dissimilarity matrix based on the density of each herbivore species in each year. Species composition was plotted using two axes to visualize temporal changes between consecutive years (Matthews et al. 2013).

Generalized Additive Models (GAM, Hastie and Tibshirani 1990) were employed to analyse temporal trends of species-specific densities, metabolic biomass, and forage intake. GAMs allow for the detection of nonlinear trends in time series data while ignoring fine-scale bias (Fewster et al. 2000). Year was modelled as a cubic spline to account for interannual variation. Herbivore densities were modelled assuming a gamma distribution which is appropriate for positive continuous variables; other response variables were modelled as Gaussian (Supplementary Material S4). Net changes in herbivore densities, metabolic biomass and forage intake were assessed after predicting each variable during the first (1986) and the last year (2020) of records. While this analysis blurs the nonlinear dynamics, it provides an overview of net changes in population sizes. Differences in forage intake within improved and unimproved lands were assessed with a *t* test.

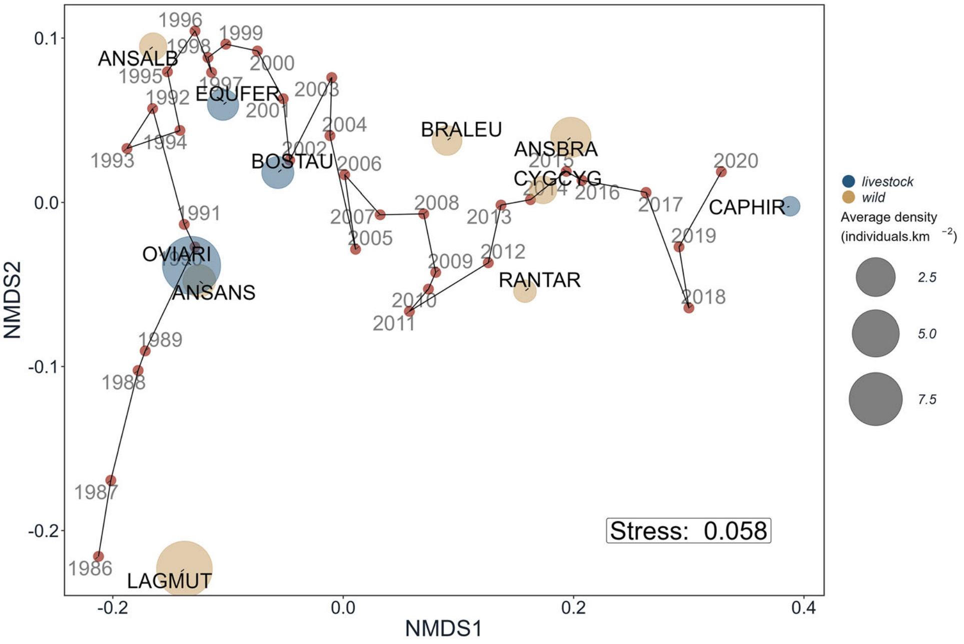


Fig. 1 NDMS visualizing changes in herbivore community composition in Iceland from 1986 to 2020. The solid line represents the trajectory of the overall herbivore community between years. Blue points are livestock species and yellow are wild species. Size of the points represents the average density (individuals km^{-2}) of each species. LAGMUT = rock ptarmigan, OVARI = sheep, ANSANS = Greylag goose, ANSALB = White fronted goose, EQUFER = horse, BOSTAU = cattle, BRALEU = Barnacle goose, CYGCYG = whooper swan, RANTAR = reindeer, ANSBRA = pink footed goose, CAPHIR = goats

All statistical analyses were carried out in R version 4.2.3 (R Core Team 2023). The packages *mass* (Ripley et al. 2013) and *vegan* (Oksanen et al. 2013) were used to run the NMDS, and *mgcv* (Wood and Wood 2015) for GAM. Unless stated otherwise, mean values and standard errors are presented.

RESULTS

Changes in herbivore community composition

From 1986 to early 2000, herbivore community composition was constrained to the left of the axis 1 of the NMDS plot (Fig. 1), with a clear directional trend from the bottom to the top of axis 2. After 1999, the trajectory moved downward on axis 2 and towards the right, parallel to axis 1. Species broadly clustered in two main groups across the biplot, with most livestock species (sheep, horses, and cattle) located at the left of the plot, and most wild species (barnacle goose, whooper swan, pink footed goose and reindeer) located towards the central part of the plot.

Changes in the densities of herbivores

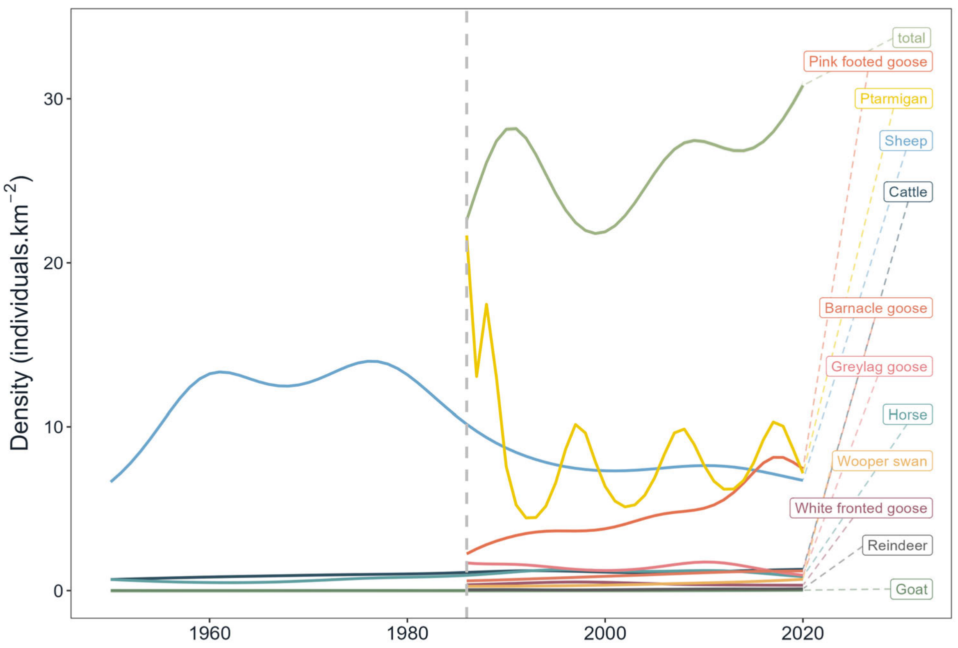
Between 1986 and 2020, when records were available for all species, total herbivore density significantly decreased by 29.30% (Supplementary Material S4, Fig. 2a). The estimated density of herbivores declined from 37.60 ± 0.06 individuals km^{-2} in 1986 to 26.60 ± 0.06 individuals km^{-2} in 2020, reaching a minimum in 1993 with 20.60 ± 0.04 individuals km^{-2}.

Population densities of the 11 species analysed displayed significant fluctuations between 1986 and 2020. Most herbivore populations increased, except for the sheep, white fronted goose, greylag goose and ptarmigan (Supplementary Material S5 and S6). Among livestock, sheep remained the most abundant herbivore in Iceland throughout the time series. By 2020, sheep constituted 25% of the total herbivore density contrasting with 4.89%, 3.17%, 0.09% for cattle, horses and goats, respectively. Sheep densities peaked at 13.90 ± 0.07 individuals km^{-2} in 1978, prior to the implementation of the livestock quota in the 1980s. Ptarmigan exhibited densities comparable to sheep, but fluctuated greatly over time, with a peak density of 21.90 ± 0.28 individuals km^{-2} in 1986. In turn, the density of pink footed goose increased from 2.21 ± 0.03 individuals km^{-2} in 1950 to 7.54 ± 0.08 individuals km^{-2} in 2020, consolidating its position as one of the most abundant herbivores, representing 29.10% of the total herbivore density in 2020.

Changes in metabolic biomass of wild and domestic herbivores

Total herbivore metabolic biomass (PMB$_{\text{total}}$) decreased by 19.40% (Fig. 2b, Supplementary Material S6), declining from a peak of 154.30 ± 0.31 kg km^{-2} in 1986 to

(a) Herbivore densities



(b) Herbivore metabolic biomass

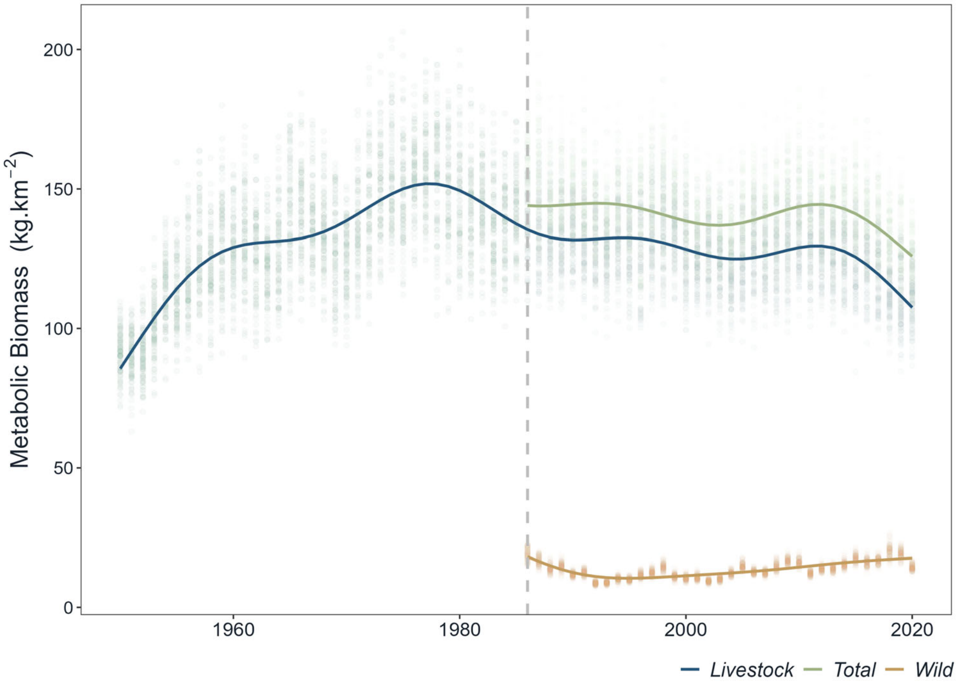


Fig. 2 Changes in the densities of the main vertebrate herbivore species (**a**) and in metabolic biomass of domestic and wild herbivores (**b**) in Iceland between 1950 and 2020. Green curves indicate the pooled density (**a**) and pooled metabolic biomass (**b**) of all herbivore species. Vertical grey dashed lines in 1986 indicate the starting point when data for all species becomes available. Coloured curves result from GAM. Light coloured surfaces represent the standard error of the GAM estimates and the points represent estimates of metabolic biomass, resulting from the uncertainty analysis

124.40 ± 0.31 kg km^{-2} in 2020. This decrease was primarily driven by changes in livestock metabolic biomass. Specifically, $PMB_{livestock}$ decreased by 20.40%, from 135.30 ± 0.18 kg km^{-2} in 1986 to 107.60 ± 0.34 kg km^{-2} in 2020 with an average of 130 kg km^{-2} over the entire period. In contrast, PMB_{wild} varied substantially during this time, but remained considerably lower than $PMB_{livestock}$ throughout the period, with an average of 13.50 ± 1.06 kg

km^{-2}. Current values (17.50 ± 0.83 kg km^{-2}) are commensurate to estimates from 1986 (18.10 ± 0.91 kg km^{-2}).

Before 1986, data were only available for $PMB_{livestock}$. In 1950, values of $PMB_{livestock}$ were comparable to those in 2020 (85.50 ± 0.76 kg km^{-2} and 107 ± 0.76 kg km^{-2}, respectively). However, $PMB_{livestock}$ underwent significant changes over this interval, peaking in 1978 at the historical maximum of 151.70 ± 0.41 kg km^{-2}.

Forage intake of wild and domestic species

Total forage intake by herbivores (DMI_{total}) between 1986 and 2020 was significantly higher in improved lands than in rangelands (*t* test; $t = 87.4$, df = 684.55, *p* value < 0.001). Overall, forage intake significantly changed in each land type and species group during the study period (Supplementary Material S4). Total forage intake decreased in both rangelands and improved land (Fig. 3a) but the magnitude of the decline was greater in rangelands (14.60% vs. 6.16%).

When considering each group of herbivores separately, forage intake by livestock decreased between 1986 and 2020 in both land types, and this decline was stronger in rangelands (20.60% vs. 9.22%: Fig. 3a). The estimated intake by wild species also decreased in rangelands by 18.60% (from 373 ± 24.4 kg C $year^{-1}$ km^{-2} in 1986 to 304 ± 22.4 kg C $year^{-1}$ km^{-2} in 2020), but increased in improved lands by 72.50% (from 118 ± 13.2 kg C $year^{-1}$ km^{-2} in 1986 to 202 ± 13.2 kg C $year^{-1}$ km^{-2} in 2020). Still, dry matter intake by wild species remained overall consistently low compared to $DMI_{livestock}$, as it represented on average 3.62% of the total herbivore consumption in improved lands and 7.13% in unimproved lands.

Total net primary production (NPP) was on average higher in improved land compared to rangeland (mean values recorded from 2000 to 2020 were, respectively, $179\,421 \pm 7771$ kg C km^{-2} $year^{-1}$and $118\,905 \pm 6136$ C km^{-2} $year^{-1}$). Between 2000 and 2020, the NPP increased in improved lands and rangelands by, respectively, 10.50% and 8.00%, but NPP was more variable in improved lands (sd = 20 560 vs. sd = 16 235) (Supplementary Material S7). When put in perspective with the estimates of average forage intake by herbivores, total wild herbivore consumption only accounted for $0.10 \pm 0.01\%$ and $0.21 \pm 0.02\%$ in improved grasslands and rangelands, respectively. In comparison, livestock consumed on average $2.35 \pm 0.13\%$ to $2.65 \pm 0.20\%$ of the total primary productivity (Fig. 3b), in improved and unimproved areas.

DISCUSSION

This study pioneers an assessment of long-term shifts in Iceland's herbivore community, juxtaposing managed improved grasslands and rangelands. We observed an initial transition from a livestock-dominated to a wild-dominated community since 1986, in tune with ongoing farmer's concerns. Yet, by 2020, wild species still contributed only 13.9% of total herbivore biomass, with livestock forage intake far surpassing that of wild herbivores. Interestingly, our analyses indicate a decline in herbivore forage intake since 1986, particularly in rangelands. This may be due to a higher dependency on cultivated and imported fodder, which has been the tendency in the past decades (Helgadóttir and Hopkins 2013). Conversely, wild herbivore consumption in improved lands increased, yet their overall intake remained modest.

Results from NMDS suggested a shift from livestock to wildlife dominance by the mid-1990s and a diversification of livestock. This shift aligns with global trends in waterfowl population growth, notably the pink footed goose, alongside with local livestock management shifts, like the implementation of a livestock quota in the 1980s and renewed efforts for the conservation of goat breeds (Dýrmundsson 2005). Similar transitions from livestock to wild dominance have been documented in other Nordic countries, like Norway, where a recovery of large wild ungulates and a decline in domestic species has been reported (Austrheim et al. 2011). These transitions have been interpreted as trophic rewilding (Speed et al. 2019). While the observed changes in herbivore densities indicate that trophic rewilding might have also happened in Iceland, those results do not hold in terms of metabolic biomass, where the metabolic biomass of wild herbivores remained much lower than that of livestock. A potential explanation could be the limited number of large ungulates in Iceland which could increase the biomass of wild herbivore species in response to the decrease in livestock biomass (Austrheim et al. 2011).

The total average metabolic biomass of herbivores in Iceland (141 ± 2.03 kg km^{-2} in 2020) ranks among the lowest values recorded in Europe, including both livestock and wild species (190–16 000 kg km^{-2}) (Fløjgaard et al. 2021) but is commensurate to what is observed in other high latitude ecosystems (108 kg km^{-2} in 2015, Speed et al. 2019). Herbivore metabolic biomass in Iceland has declined since 1986; largely driven by domestic herbivores. Assuming that this pattern was maintained before 1986, it is likely that Iceland had reached a maximum value of metabolic biomass in the late 70 s, when the densities of livestock species peaked. Given the short evolutionary history of grazing in Iceland, where mammalian herbivores were introduced in historical times, this might have significant ecological implications as land recovery is usually limited in areas characterized by a short grazing history (Price et al. 2022).

Livestock consumed more plant biomass than wild species, but their forage intake remained far below than in

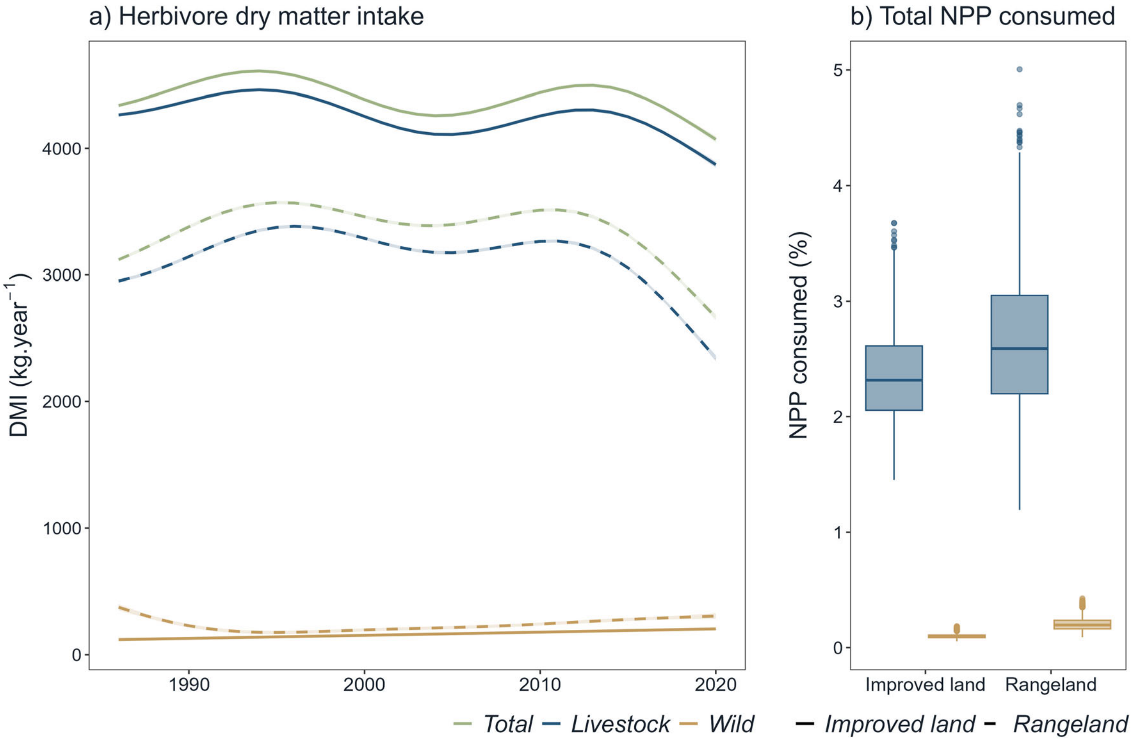


Fig. 3 Wild and domestic herbivore dry matter intake between 1986 and 2020 (**a**), and proportion of plant biomass consumed by wild and domestic herbivores between 2000 and 2020 on Icelandic grazing areas (**b**). Coloured smooth curves in (**a**) result from GAM

other Northern European rangelands (1.43–5.36% vs. 18.6–24.3%, Wolf et al. 2021). Wild species consumed on average less than 0.3% of the net primary production, while livestock consumed approximately 2% in both land types, which is in stark contrast to global averages (11% NPP for wild mammals; Pedersen et al. 2020). Total herbivore biomass consumption decreased, likely driven by livestock reduction, which was modest in improved lands, therefore relaxing the historical pressure exerted in those lands.

Consequences for management

This study sheds light on shifting herbivore pressure across two distinct land types: improved grasslands, extensively modified by human activities, and rangelands, managed as more natural ecosystems. As such, the management implications of changing herbivore dynamics in these areas differ significantly.

Improved grasslands, where most livestock are grazed, have expanded over the last century due to agricultural advancements and expansion of government subsidies (Wald 2010; Helgadóttir and Hopkins 2013). Enhancements like nitrogen-based fertilizers have boosted grass nutritional quality and crop yields, benefiting both livestock production and waterfowl populations (Jefferies et al. 2003; Fox and Abraham 2017). However, increasing waterfowl densities on improved lands can lead to conflicts between wild and livestock species. Such tensions can arise due to perceived competition and the greater investments that farmers make on improved pastures compared to rangelands, and have been reported from grazing areas worldwide (Baldi et al. 2001; Mason et al. 2018). While culling and financial compensation are proposed solutions (Eythórsson et al. 2017), interactions between wild and domestic species, particularly via vegetation, can complicate management strategies. As waterfowl often arrive before livestock are released in the pastures and they form large flocks during migration, they might have concentrated impacts and affect the amount of vegetation and plant species available later (Bjerke et al. 2021). However, some studies have shown that geese do not interfere with livestock feeding and may not reduce the yield of fertilized pastures, but can instead increase nutrient availability for grasses (Gorosábel et al. 2019). Investigating potential positive interactions between these species, especially considering the lower impact of geese compared to livestock, warrants further research.

In contrast, rangelands, managed with less intensity, endure harsh climates, and exhibit lower productivity. These areas are more sensitive to disturbances compared to improved grasslands and are often deemed to be in poor condition (Arnalds et al. 2023). Grazing practices (e.g., length of grazing period and stocking density) vary among grazing commons (Arnalds and Barkarson 2003). While concerns of conflict akin to those in improved lands exist, our findings suggest that despite the spatial overlap between wild and domestic species (Boulanger-Lapointe et al. 2022) wild species have a moderate consumption of plant biomass in rangelands. Similar observations in Norwegian rangelands point to limited competition in low density, unfenced settings (Speed et al. 2019). Facilitation, rather that competition, is more plausible in low-productive ecosystems (Barrio et al. 2013). In turn, reduced herbivore pressure in rangelands presents an opportunity for their restoration coupled with strategic management changes (Mulloy et al. 2019).

Knowledge gaps identified

While this study encompasses an extensive temporal scale, spanning over 70 years for several herbivore species, and represents the most comprehensive long-term dataset available for terrestrial herbivores in Iceland, certain limitations should be acknowledged. Our analyses addressed the inherent uncertainties associated with the compilation of data from diverse sources. Despite these uncertainties, it is noteworthy that our results demonstrated consistent patterns in herbivore community changes, metabolic biomass, and herbivore dry matter forage intake. Our assumptions reveal important data gaps for the study of herbivore community dynamics in high-latitude managed grazing systems.

Information related to herbivore land use, including finer scale data on spatial and temporal use remain very scarce and poorly monitored for many waterfowl (Arzel et al. 2006). Similarly, systematic efforts are needed to collect and synthesize data from local and regional sources for livestock species. Further research and monitoring will allow exploring approaches based on finer spatial and temporal resolution that could reveal areas or periods more prone to wildlife conflicts, where wild and domestic species coexist. Such analyses will provide information on the potential interactions between species and help disentangling management conflicts by locally adapting management practices.

CONCLUSIONS

Wildlife and livestock conflicts occur in many places around the world, including Iceland. Yet, studies exploring the relative impact of wild species compared to livestock remain scarce. The long population records available in Iceland allowed us to evaluate the potential vegetation impact of domestic and wild herbivores at a national scale. Consistent long-term spatially and temporally explicit data might be the key to further solve these issues. Stakeholders play a valuable role in providing such information, and this paper stands as a call to develop collaborations.

Acknowledgements We would like to thank Ólafur K. Nielsen and Erla Sturludóttir for ptarmigan population data, Skarphéðinn Þórisson for reindeer census data; Carl Mitchell, Antony D. Fox, and Kane Bride for waterfowl census data; and Landgræðslan for sharing grazing area data and Emmanuel P. Pagneux for his help with MODIS data. Funding for this project was provided by the Icelandic Research Fund (Grant No. 217754; TUNDRAsalad). This paper is dedicated to the memory of Skarphéðinn Þórisson who tragically passed away in July 2023.

Author contributions MD, ICB, JDMS, and NB-L contributed to conceptualization; MD, ICB, JDMS, and NB-L provided methodology; MD involved in formal analysis and investigation; MD involved in writing—original draft preparation; ICB, JDMS, and NB-L involved in writing—review and editing; ICB involved in funding acquisition; ICB, JDMS, and NBL involved in supervision.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interest to disclose.

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Ambio

Supplementary Information

This supplementary information has not been peer reviewed.

Long-term changes in herbivore community and vegetation impact of wild and domestic herbivores across Iceland

Supplementary material S1. Population data for herbivore species in Iceland

Supplementary material S2. Estimates of body mass, forage intake and grazing time for each herbivore species obtained from the literature

Supplementary material S3. Evaluation of the uncertainty of the metabolic biomass and herbivore forage intake estimates

Supplementary material S4. Results from the Generalized Additive Models

Supplementary material S5. Species-specific herbivore density trends

Supplementary material S6. Estimated net changes between 1986 and 2020

Supplementary material S7. Averaged yearly net primary productivity within improved lands and rangelands in Iceland from 2000 to 2020

Supplementary material S1. Population data for herbivore species in Iceland

Domestic species

Livestock numbers during winter (i.e., sheep, horses, cattle, and goats) were retrieved from national statistic records[1]. Demographic groups encompassed the total number of individuals for each herbivore species, including scarce details regarding young (<1 year old), adult males (>1 year old for sheep, 4 years old for horses), female and yearling (grouped), and non-reproductive individuals.

Reindeer

Reindeer census data were derived from aerial surveys conducted yearly in early July every by the East Iceland Nature Research Centre (Náttúrustofa Austurlands)[2]. Census categories include young (1-2 years old) and adult males (>3 years), females and yearlings (indistinguishable), and calves (2 months).

Waterfowl

Waterfowl abundance data were obtained from the World Waterfowl Trust (**Table S1**). Annual colony censuses were conducted in October-November in the wintering areas in the UK (i.e., Scotland, Ireland) for Greenland white fronted geese, greylag and pink footed geese[3–5]. Censuses for barnacle geese and whooper swan occurred every 5 years and were done by aerial surveys. These counts encompassed returning adults and some non-migratory individuals residing year-round in the UK. Still, these colony censuses represent an unbiased estimate of the abundance of waterfowl present in Iceland during the summer months[6]. One waterfowl species (i.e., the brent goose, *Branta bernicla*) was not included in this study due to the lack of long-term consistent census data. However, the population was estimated to be relatively stable from the late 60s to 2000 (from 8000-13 000 individuals 18 000- 24 000)[7], and to slightly increase until 2014 (32 000 individuals, or a density of 0.5 individuals.km^{-2})[8], representing 5.2% of the overall waterfowl population in Iceland.

Rock ptarmigan

Population estimates for the rock ptarmigan were provided by the Icelandic Institute of Natural History. They were extrapolated from annual census conducted in East Iceland to represent the entire country population (Magnússon et al., 2004). Biannual censuses in early May and early August from 1981 to 2021 approximated summer and winter populations. For our study, we used a yearly average based on both estimates standardized by the number of months in summer (3) and in winter (9). Those estimates slightly overestimate the overall ptarmigan population [10], but are nonetheless the longest and best available time series to date.

Table S1. List of herbivores in Iceland and dataset descriptors of their abundance. Time period and frequency respectively correspond to the first and last year of population census records and the frequency of population census.

Species	Time period	Frequency	References
Greenland white fronted goose (*Anser albifrons flavirostris)*	1983-2020	Yearly	[3]
Greylag goose (*Anser anser)*	1953-2020	Yearly	[4]
Pink footed goose (*Anser brachyrynchus)*	1950-2020	Yearly	[4]
Brent goose (*Branta bernicla*)	NA	NA	NA
Barnacle goose (*Branta leucopsis)*	1959-2020	5 years	[4]
Whooper swan (*Cygnus cygnus)*	1986-2020	5 years	[5]
Rock ptarmigan (*Lagopus muta)*	198-2020	Yearly	[9]
Reindeer (*Rangifer tarandus)*	1964-2020	Yearly	[2]
Cattle (*Bos taurus)*	1950-2020	Yearly	[1]
Icelandic Horse (*Equus ferus caballus)*	1950-2020	Yearly	[1]
Icelandic sheep (*Ovis aries)*	1950-2020	Yearly	[1]
Goat (*Capra hircus)*	1950-2020	Yearly	[1]

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Supplementary material S2. Estimates of body mass, forage intake and grazing time for each herbivore species obtained from the literature

Literature searches for relevant data on body mass, forage intake and grazing time were carried out on scientific search engines (Web of Science, Google Scholar, Scopus) on December 2022. We searched for common name (full e.g., pink footed goose and short e.g., goose, swan) or Latin names of the species, in addition to the expressions "*Iceland*" or "**arctic*" or "*North**, and "*forage intake*" or "*DMI*" or "*dry matter intake*" or "*offtake*" or "*body weight*". For Icelandic breed-specific information we added "*Iceland*" or "*Icelandic breed*".

For grazing time on improved pasture and rangelands, qualitative information was prevalent, especially for livestock species. Information on timing of year-to-year livestock release to pastures and waterfowl arrival were truly lacking in the literature, as well as regional variations.

Due to the absence of local forage intake data of free-ranging animals and the specificities of Icelandic mammal breeds, values of daily dry matter intake (DMI) for mammals (livestock and feral reindeer) were estimated following Holecheck (1998). This involved assigning a value of 2% of body mass for ruminants and 3% for horses. DMI values of wild birds (waterfowl and ptarmigan) were extracted from the literature, either directly from the species in Iceland, from the same species in a comparable arctic or subarctic environment, or from a closely related species when no species-specific data were available. For example, DMI values for graylag and Greenland white-fronted geese were based on data from pink footed goose, a species that has a similar diet and body weight.

Table S2. Adult averaged species-specific values for body weight (BW), dry matter intake (DMI), and grazing time (total Gtot, improved lands Gimp and rangelands Grang). These variables correspond to the average adult body mass, the amount of dry vegetation ingested within a day (in kg.day^{-1}), the proportion of days spent grazing within a year and the number of days spent grazing in improved grasslands and rangelands.

Species name	**BW (kg)**	**DMI (kg.day^{-1})**	**Gtot (day and proportion)**	**Gimp/Grang (days)**	**References**
Greenland white fronted goose (*Anser albifrons flavirostris*)	2.64	0.20	71 (0.19)	71 / 0	[2–4]
Greylag goose (*Anser anser)*	3.30	0.20	178 (0.49)	178 / 0	[4–8]
Pink footed goose (*Anser brachyrynchus)*	2.51	0.20	160 (0.44)	68 / 92	[4–7,9,10]
Barnacle goose (*Branta leucopsis)*	1.68	0.15	75 (0.21)	75 / 0	[4,11–15]
Whooper swan (*Cygnus cygnus)*	9.35	0.24	183 (0.50)	91 / 92	[4,16,17]
Rock ptarmigan (*Lagopus muta)*	0.50	0.06	365 (1.00)	0 / 365	[18,19]
Reindeer (*Rangifer tarandus)*	80	1.60	365 (1.00)	0 / 365	[20]
Cattle (*Bos taurus)*	470	9.40	123 (0.34)	123 / 0	[21–23]
Icelandic Horse (*Equus ferus caballus)*	379	11.4	365 (1.00)	109 / 256	[24–26]
Icelandic sheep (*Ovis aries)*	65	1.30	184 (0.5)	92 / 92	[27]
Goat (*Capra hircus)*	56.25	1.12	123 (0.34)	123 / 0	[28]

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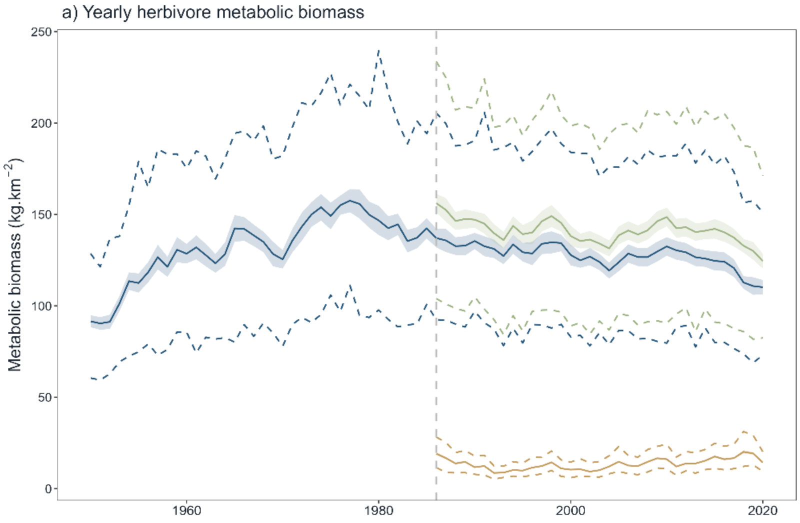
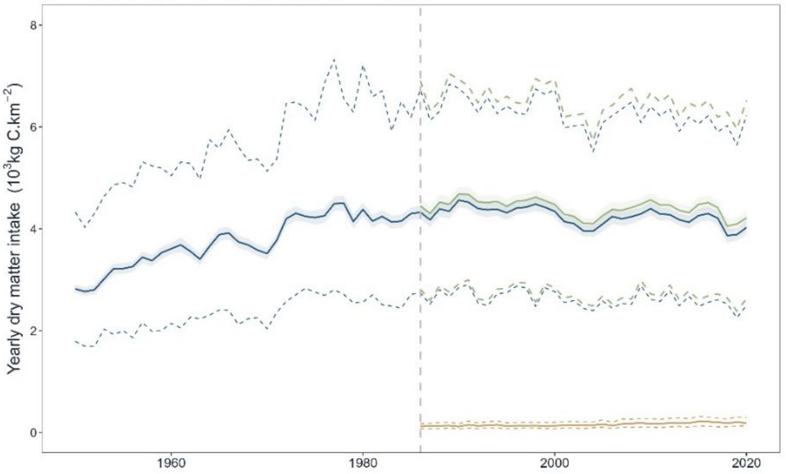
Supplementary material S3. Evaluation of the uncertainty of the metabolic biomass and herbivore forage intake estimates

The analyses presented in this study are based on best available estimates for the parameters in the equations. Although these parameters (e.g., the average body mass of a species of herbivore or the time that animals graze on each type of land) are known to vary, most sources did not report a measure of variability. Most records for population size, body mass and grazing time reported a single value with no associated estimate of variability. To account for parameter uncertainty in our analyses, we simultaneously estimate 100 replicates of each parameter (i.e., in the case of metabolic biomass estimates, parameters were: body weight (BW_i), number of individuals (N_i) and total grazing time (G_i); for forage intake estimates, parameters were: dry matter intake (DMI_i), and grazing time in improved lands ($Gimp_i$) and rangelands ($Grang_i$)) by perturbing the baseline levels reported in **Supplementary material S1** by 10%, assuming that variables were normally distributed. After computing the PMB and DMI at the species level, we estimated the metabolic biomass and the forage intake for the total, domestic and wild herbivore species separately by conducting 100 iterations, with resampling, to generate estimates for each year in the period from 1950 to 2020. We calculated the standard error for these estimates within each herbivore group and year. Additionally, we estimated the yearly lower and upper limits of the estimates by summing maximum and minimum values of the PMB and DMI across each herbivore group (**Figure S3**). Uncertainty estimates were run on R version 4.2.3 (R Core Team 2023).



b) Yearly herbivore forage intake in improved lands



c) Yearly herbivore forage intake in rangelands

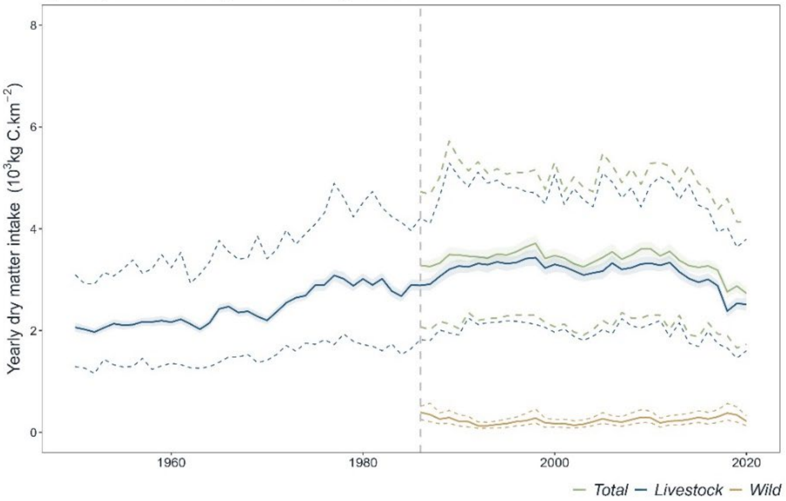


Figure S3: Uncertainty generated for the yearly herbivore metabolic consumption (a), biomass consumption in improved lands (b) and rangelands (c). Solid lines, dashed lines and shaded area represent respectively the mean, the minimum and maximum and the standard error of the yearly estimates.

Supplementary material S4. Results from the Generalized Additive Models

We used penalized regression splines to estimate the smooth term of the general additive model. Degrees of freedom were estimated to be optimal during the computation of the model using cross validation and a control parameter of maximum 4 threads. "Year" was modelled as a cubic spline.

Table S4: Selected results from GAM models. *Tot*, *Wild, Dom, Imp* and *Rang* stand for total, wild herbivore species, domestic herbivore species, improved lands, and rangelands. OVARI = sheep, BOSTAU = cattle, EQUFER = horse, CAPHIR = goats, RANTAR = reindeer, ANSALB = White fronted goose, ANSANS = Greylag goose, ANSBRA = pink footed goose, BRALEU = Barnacle goose, CYGCYG = whooper swan, LAGMUT = rock ptarmigan.

Variable	**Edf**	**ref.df**	**Statistics (F)**	**p_value**
Total herbivore density				
D_{tot}	8.986608	8.999936	3709.0846	< 0.001
Species specific herbivore density				
D_{OVIARI}	8.94	9.00	1602.70	< 0.001
D_{BOSTAR}	8.56	8.94	613.13	< 0.001
D_{EQUFER}	8.94	9.00	2225.27	< 0.001
D_{CAPHIR}	8.99	9.00	9560.57	< 0.001
D_{RANTAR}	7.80	7.98	1237.81	< 0.001
D_{ANSALB}	5.08	5.33	561.04	< 0.001
D_{ANSANS}	5.82	5.98	397.07	< 0.001
D_{ANSBRA}	7.95	8.01	1488.39	< 0.001
D_{BRALEU}	4.28	4.73	1031.97	< 0.001
D_{CYGCYG}	4.45	4.84	2100.00	< 0.001
D_{LAGMUT}	9.00	9.00	1788.97	< 0.001
Total herbivore metabolic biomass				
MB_{tot}				
Group-specific herbivore metabolic biomass				
MBW_{ild}	8.94	9.00	827.60	< 0.001
MB_{Dom}	4.52	4.92	25.01	< 0.001
Total herbivore forage intake				
DMI_{Tot_Imp}	8.93	9	1167	<0.001
DMI_{Tot_Rang}	8.93	9	1740	<0.001
Group specific herbivore forage intake				
DMI_{Wild_Imp}	6.54	6.81	428313	<0.001
DMI_{Wild_Rang}	6.23	6.48	24464	<0.001
DMI_{Dom_Imp}	8.93	9.00	988	<0.001
DMI_{Dom_Rang}	6.23	6.48	24464	<0.001

Supplementary material S5. Species-specific herbivore density trends

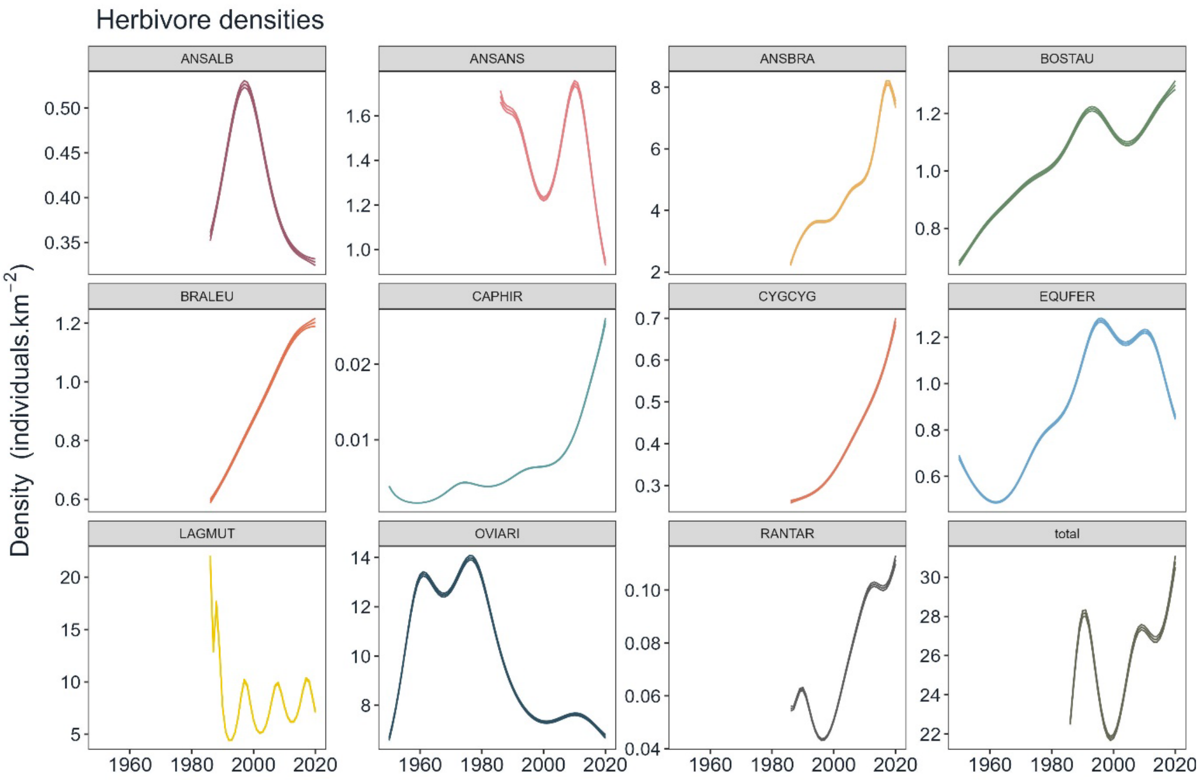


Figure S5: Species specific density trends in Iceland from fitted Generalized Additive Models with optimal degrees of freedom selected based on cross validation. Please note the different scales on the y-axes. OVARI = sheep, BOSTAU = cattle, EQUFER = horse, CAPHIR = goats, RANTAR = reindeer, ANSALB = White fronted goose, ANSANS = Greylag goose, ANSBRA = pink footed goose, BRALEU = Barnacle goose, CYGCYG = whooper swan, LAGMUT = rock ptarmigan. Blue gradients correspond to livestock species and red gradient wild species. Shaded areas around the lines represent the standard error of the estimates.

Supplementary material S6. Estimated net changes between 1986 and 2020

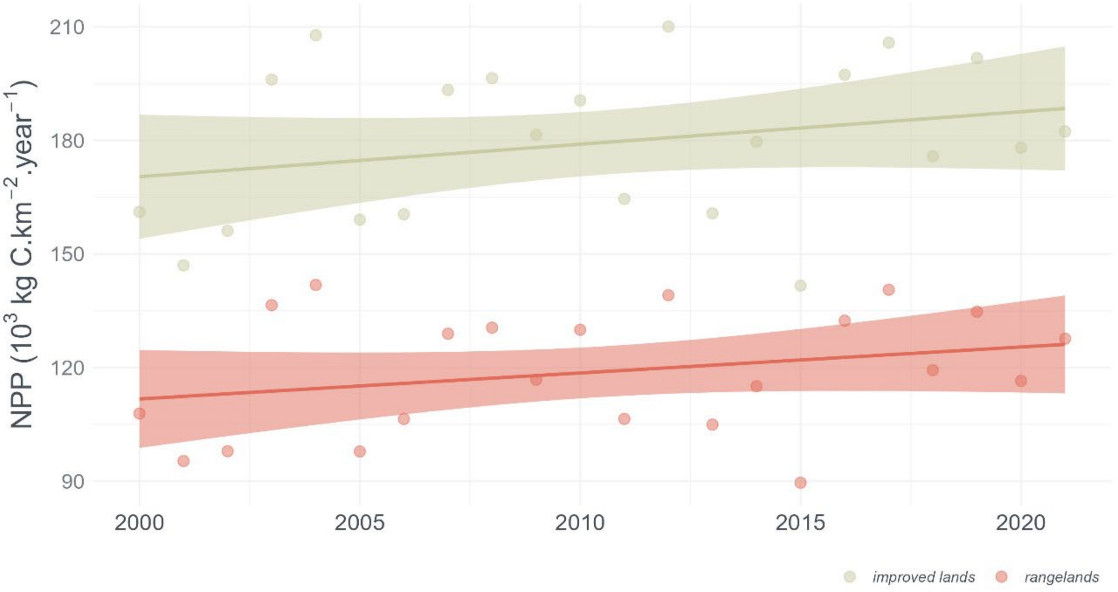
Table S6: Estimated net changes between 1986 and 2020 for herbivore densities, metabolic biomass, and forage intake.

Variable	Value in 1986	Value in 2020	Net changes*
Total herbivore density			
D_{tot}	22.6	30.8	36.4
Species specific herbivore density			
D_{OVIARI}	10.12	6.73	-33.70
D_{BOSTAU}	1.11	1.30	17.00
D_{EQUFER}	0.93	0.85	-8.43
D_{CAPHIR}	0.004	0.03	522.19
D_{RANTAR}	0.05	0.11	102.66
D_{ANSALB}	0.36	0.32	-8.02
D_{ANSANS}	1.67	0.94	-44.46
D_{ANSBRA}	0.94	7.44	231.47
D_{BRALEU}	0.59	1.20	101.94
D_{CYGCYG}	0.26	0.69	165.06
D_{LAGMUT}	21.70	7.17	-66.90
Total herbivore metabolic biomass			
MB_{tot}	144	126	-12.60
Group-specific herbivore metabolic biomass			
MBW_{ild}	18.1	17.5	-2.86
MB_{Dom}	135	108	-20.60
Total herbivore forage intake			
DMI_{Tot_Imp}	9537	8925	-6.42
DMI_{Tot_Rang}	6780	5745	-19.80
Group specific herbivore forage intake			
DMI_{Wild_Imp}	321	449	40.10
DMI_{Wild_Rang}	929	675	-27.4
DMI_{Dom_Imp}	9579	8724	-8.93
DMI_{Dom_Rang}	6711	5386	-19.8

*net changes of herbivore densities, metabolic biomass and forage intake were computed as 100 x $(V_2 - V_1)/V_1$, where V_1 is the estimated value for the earlier year and V2 is that for the last year.

Supplementary material S7. Averaged yearly net primary productivity within improved lands and rangelands in Iceland from 2000 to 2020

a) Annual net primary productivity in Icelandic grazing areas



b) Proportion of NPP consumed by herbivore from 2000 to 2020

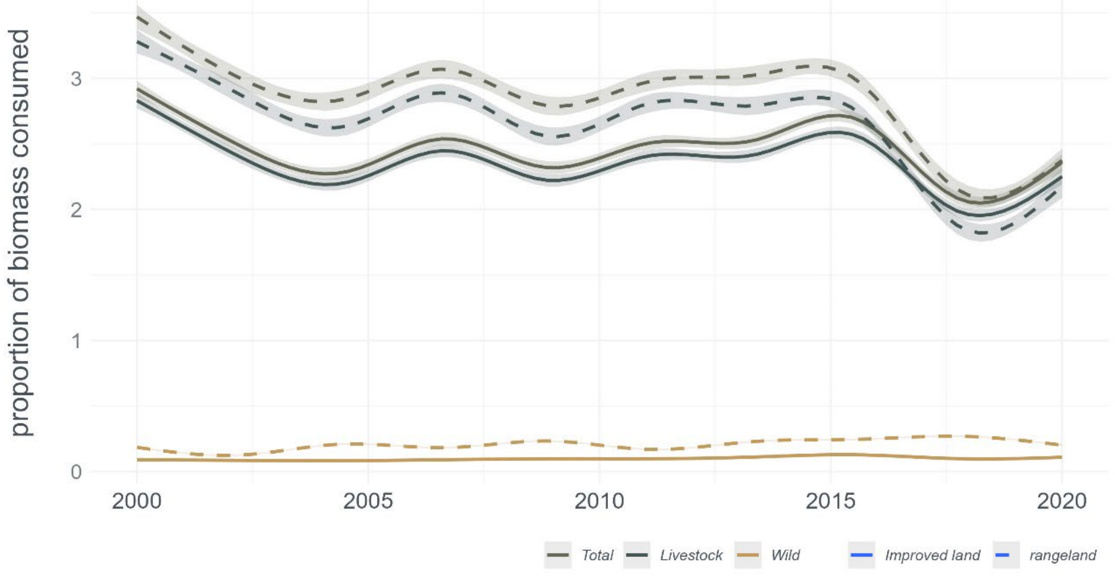


Figure S5: Averaged yearly net primary productivity (a) and proportion of plant biomass consumed by herbivores in grazing areas of Iceland (b) between 2000 and 2020. Solid lines correspond to improved lands and dashed lines to rangelands.

II

Capturing seasonal variations in faecal nutrient content from tundra herbivores using Near Infrared Reflectance Spectroscopy

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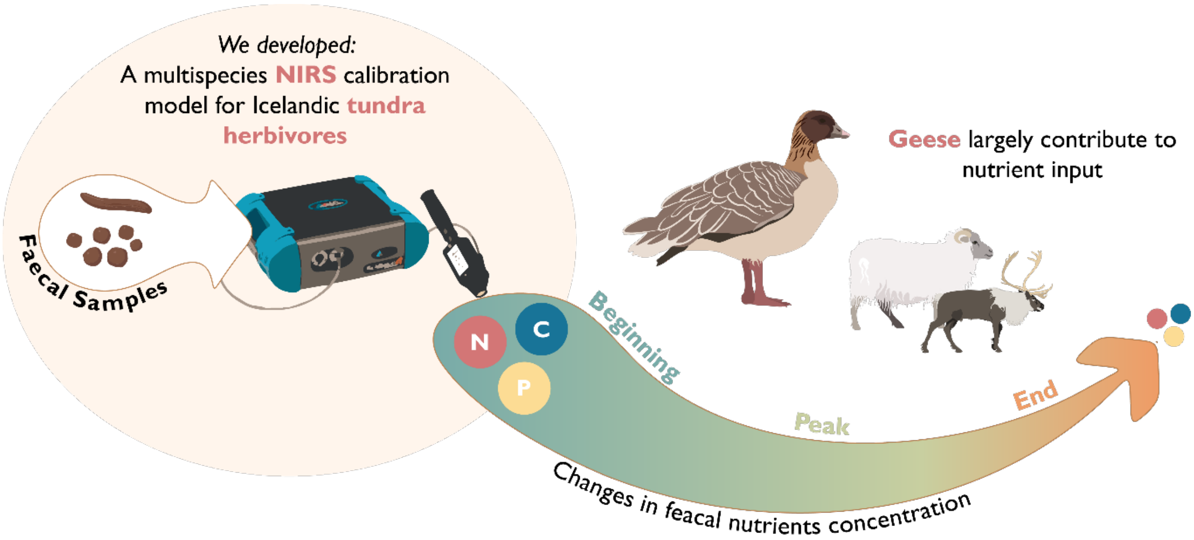
Highlights:

- First multispecies NIRS models to estimate faecal N, P and C in common tundra herbivores.
- Herbivores significantly influence biogeochemical cycles in the tundra.
- Faecal stoichiometry varies between species and throughout the growing season.
- Most of herbivore nutrient input occur early in the growing season
- Geese contribute the most to total faecal nutrient deposition in Icelandic tundra

Graphical abstract:



Abstract:

Herbivores contribute to nutrient cycling in tundra ecosystems through their wastes (e.g., faeces, urine). However, their contribution might vary among species and over time during the growing season likely due to differences in body size, digestive physiology, and variations in diet composition and quality. Capturing such fine-scale variability requires intensive sampling, but traditional wet-lab methods for measuring nutrient concentration and stoichiometry in animal faeces are relatively expensive. To address this challenge, we developed a low-cost alternative using Near-Infrared Spectroscopy. Using a set of 191 fresh faecal samples, both scanned with NIRS and analysed by traditional wet-lab methods, we calibrated a general model for the main Icelandic tundra herbivores (i.e., pink-footed goose, *Anser brachyrynchus*, reindeer, *Rangifer tarandus* and sheep, *Ovis aries*) to assess faecal nutrient concentrations (nitrogen, phosphorus, and carbon) and stoichiometry (C:N, C:P, N:P). The multispecies models explained between 76 and 91% of variation between samples. We then applied the models to over 300 samples and assessed changes in faecal nutrient concentration, and stoichiometry of the three herbivores throughout the growing season. We found a general decline in faecal quality throughout the growing season, with higher N and P concentrations at the beginning and peak of the season, and higher C:N and C:P. Our results show that faeces of the three herbivores have a similar faecal stoichiometric ratio, except at the end of the growing season. Geese contribute disproportionately to the nutrient pools of Icelandic rangelands due to their high defecation rate and large population. These results provide important insights into how different herbivore species can influence the biogeochemistry of nutrient-limited tundra rangelands throughout the growing season, and a general model for faecal nutrient content of tundra herbivores.

Keywords: zoogeochemistry, nitrogen, phosphorus, carbon, faecal stoichiometry, dung, herbivore, NIRS

1. Introduction:

Herbivores consume plant biomass, digest, and release nutrients such as nitrogen (N), phosphorus (P) and carbon (C) through the deposition of faeces and urine. By doing so, they contribute to soil biogeochemistry (Schmitz and Leroux, 2020) and affect multiple ecosystem processes and properties, including primary productivity (Bazely and Jefferies, 1985; Leroux and Loreau, 2010), plant community composition (Barthelemy et al., 2015), and decomposition dynamics (Sitters et al., 2014; Wang et al., 2018).

In nutrient-limited ecosystems, such as the tundra, herbivores play a crucial role in nutrient recycling (Beard et al., 2023; Roy et al., 2022). They locally release large amounts of readily available organic P and N in their faeces (Bryant et al., 1983; Fivez, 2014), which are essential nutrients for plant and microbial growth (Bowman et al., 1993; McLaren and Buckeridge, 2019). However, nutrient return in faeces depends not only on where herbivores deposit their faeces, and how much nutrients the faeces contain, but also on their C:N:P stoichiometry. Indeed, the stoichiometry of faeces, specifically the ratios of nitrogen to carbon (C:N), phosphorus to carbon (C:P), and nitrogen to phosphorus (N:P), can influence the capacity of soil microorganisms and plants to assimilate these nutrients (Sitters et al., 2017, 2014), and can ultimately determine the direction of nutrient limitation, particularly whether an ecosystem becomes more N- or P-limited (Daufresne 2021). For instance, differences in faecal quality among herbivores in temperate Europe, specifically their faecal N: P ratios, significantly impact plant communities and biomass, with a decrease in plant biomass and an increase in plant community evenness as faecal N:P increase (Valdés-Correcher et al., 2019).

The amount of nutrients contained in faeces can vary widely among species due to differences in diet (Hahn et al., 2007; Sitters and Olde Venterink, 2021; Wrench et al., 1997), body size (Vanni and McIntyre 2016; le Roux et al. 2020) and digestive physiology (de Iongh et al., 2011). In addition, the concentration of nutrients contained in faeces changes over time for a given individual due to large variations in the quality and availability of forage plants in seasonal environments (Barbero-Palacios et al., 2023; Gálvez-Cerón et al., 2013). Several studies have explicitly assessed nutrient concentrations in the faeces of tundra herbivores, including geese and reindeer (Barthelemy et al., 2015; Beard et al., 2023; Fivez, 2014). However, little is known about how nutrient concentrations differ between tundra herbivores, and throughout the growing season, as variations are often overlooked due to the prohibitive cost of faecal nutrient content analyses (**Supplementary material 1**), Near-Infrared Reflectance Spectroscopy (NIRS) offers a quick, non-destructive, low-cost alternative that allows for multiple analyses with limited sample material. Specifically, NIRS is a method that measures the absorption of light from organic bonds in molecules (such as C-H, N-H, O-H) in the visible and near-infrared light spectrum (Xiaobo et al., 2010). NIRS can be used to reliably estimate the concentration of a wide range of chemical components in various types of samples, including C, N and P in plants (Murguzur et al., 2019; Petit Bon et al., 2020a) and N and P in mammalian faeces (Tolleson and Angerer, 2020; Villamuelas et al., 2017). NIRS-based models can also provide meaningful qualitative and quantitative information on the species identity (Tuomi et al., 2023), individual physiology (Dixon and Coates, 2009), variation in diet quality (e.g., crude protein and forage digestibility, Showers et al. 2006) and composition (e.g., Walker et al. 2002; Molle et al. 2023). Thus, the estimation of chemical components and traits from NIRS-based models can be especially useful when animals cannot regularly be sampled or observed, like in wildlife research and management (Petit Bon et al. 2020a, Dixon and Coates 2009). However, NIRS models are often limited to the sample populations on which they are based, as they require an empirical calibration based on spectral data matching with reference samples. This limitation restrains the use of NIRS for ecological studies, as the range of ecological contexts is often not accounted for when developing population-specific calibration models. In the case of a small and homogeneous population, it is recommended that a minimum of 50-75 independent samples be used to calibrate the model as the complexity of the models increases. In more heterogeneous populations, a minimum of 150 samples is recommended (Marten et al., 1984). As a result, NIRS-based models have historically been developed in an agricultural context and/or focused on a single crop (e.g., Cougnon et al. 2016), or herbivore species (e.g., Dixon and Coates 2009). There is a growing interest in developing multispecies NIRS calibration models to enable the application of NIRS to broader ecological contexts. For instance, Villamuelas et al. (2017) successfully calibrated a model to predict faecal N from free-ranging European herbivores, and Tolleson and Angerer (2020) developed a NIRS-based model to assess faecal N and P in American ruminants (both domestic and wild). However, these models have limited application in a biogeochemical context because they do not estimate C, preventing the description of faeces stoichiometry (C:N, C:P, N:P). Furthermore, these models were restricted to mammalian herbivores, excluding other common herbivore groups, such as birds (Speed et al., 2019), and were developed in environments other than tundra.

This paper presents the first attempt to estimate fecal nutrient concentrations (i.e., N, P and C) and stochiometry of tundra herbivores (i.e., including mammals and birds) based on spectral data. We used Iceland as a case study, focusing on the tundra ecosystem which is found in the central Highlands of the country. The Icelandic tundra is home to two large mammal species: the free-ranging Icelandic sheep (*Ovis aries*), and the feral reindeer (*Rangifer tarandus*), both introduced after human settlement (Adalsteinsson, 1981; Þórisson, 2018). The only native herbivores are birds (the pink-footed goose *Anser brachyrhynchus*, the rock ptarmigan *Lagopus muta* and the whooper swan *Cygnus cygnus*, Boulanger-Lapointe et al. 2022). Icelandic herbivore communities are undergoing profound changes, with decreasing livestock and an increasing wild herbivore (Defourneaux et al., 2024). How such changes in herbivore communities will affect nutrient dynamics in the Highland ecosystems remains unknown, as the contribution of herbivores to nutrient deposition has never been estimated for this system.

Our objectives were fourfold: 1) to train monospecific NIRS models to assess faecal nutrient content (N, P and C) for three common tundra herbivores; 2) to calibrate a standardised multispecies (i.e, mammals, and mammals and birds together) NIRS model to estimate faecal nutrient content and stoichiometry of Icelandic tundra herbivores; 3) to assess differences in faecal nutrient concentrations and stoichiometry between herbivore species, throughout the growing season; and 4) to estimate the nutrient inputs from different herbivore faeces to the tundra. We predicted that monospecific models would perform well for each herbivore species and nutrient; and that the performance of multispecies models would be lower than the monospecific models, as they are more complex. We then applied these models to predict nutrient concentrations in a larger set of samples, expecting that faecal nutrients would vary between species and across the growing season. Specifically, we hypothesised that reindeer and sheep would have similar faecal nutrient concentrations and stoichiometry, due to their similar digestive systems and overlapping diets (Mysterud, 2000; Þórisson, 2018). In turn, we expected geese faeces to contain more N and P in their faeces and to have lower C:N and C:P ratios compared to ruminants, due to their short retention time, low forage digestibility, and high diet selectivity (Karasov and Douglas 2013). In addition, we expected faecal faeces stoichiometry to decrease over the growing season as aboveground vegetation senesces, and N and P content is translocated to belowground material or lost in the litter (Chapin et al., 1975; Petit Bon et al., 2020b). Finally, we hypothesised that geese would contribute more nutrients as they are more numerous and defecate more frequently.

1. Material and methods

1.1. Study area and study species

Sampling was carried out in the Eastern Highlands of Iceland above 300 m a.s.l. (**Figure 1**, 65.3234 °N, 15.3062 °E), where the mean annual temperature is 0.2°C (Icelandic Meteorological Office Database, 2024), and annual precipitation ranges between 710 mm and 830 mm (Óskarsdóttir et al., 2024).

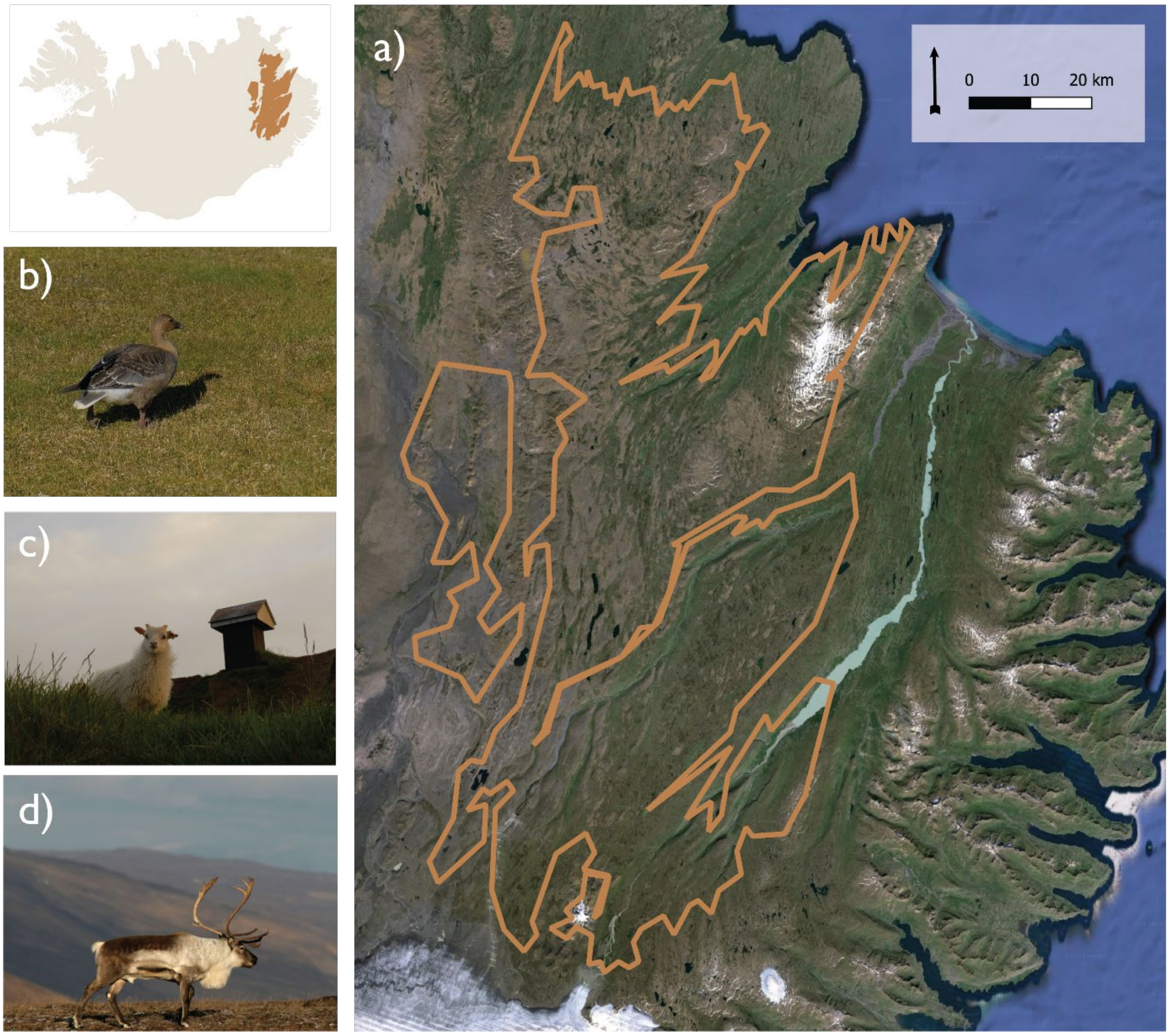


Figure 1: Study area in Eastern Highlands of Iceland (a), with the orange line delimiting areas above 300 m a.s.l. where the distribution of three vertebrate herbivores overlap: the pink footed geese *Anser brachyrynchus* (b), the domestic sheep *Ovis aries* (Icelandic breed, c), and the feral reindeer *Rangifer tarandus* (photo: Skarphéðin Þorisson, d)

The area is 6415.07 km^2, and has a vegetation characteristic of tundra ecosystems, with a mosaic of barren and low-lying vegetated areas including areas of heathland dominated by evergreen and deciduous dwarf shrubs (e.g., *Salix* sp. and *Empetrum sp.*), natural grassland, and *Carex* bogs (Arnalds et al. 2010; Óskarsdóttir et al. 2024). Only a few vertebrate herbivore species use the area during the growing season: the breeding pink-footed goose, the feral reindeer and the Icelandic sheep. The reindeer is the only species present year-round in the area but tends to move to lower elevations during the winter (Þórisson, 2018). Pink-footed geese and sheep are only present during the summer (from mid-June to mid-September, Defourneaux et al. 2024). Occasionally, the whooper swan and the rock ptarmigan are found in the area, but they are present at lower densities (Sturludottir et al. 2018; Brides et al. 2021) and tend to prefer lower elevation sites during the growing season (Gardarsson, 1971). They were therefore excluded from this study.

1.2. Faecal sample: collection and preparation

Faecal samples were collected in summer 2022. Sampling targeted the three main herbivore species present in the Icelandic tundra (i.e., sheep, reindeer, pink-footed goose), with contrasting digestive physiology (i.e., ruminant and cloacal fermenter), and included both adult and juvenile individuals to capture potential variation in faecal in nutrient concentrations. We collected samples at three times during the growing season, at the beginning (June 20th - July 9th), peak (July 24th - August 8th), and end (August 25th - September 10th), across the study area. Samples were collected as fresh as possible next to observed individuals to ensure accurate species identification (e.g., to distinguish clearly between reindeer and sheep faeces). The freshness of the samples was assessed by their odour and their generally shinier and darker aspect (Hibert et al., 2011). As an exception, we collected reindeer faeces that were ca. one day old at the end of the growing season, as it was difficult to approach the animal during the hunting season (from late July-August). The herds were located using GPS collar data provided by *Náttúrustofa Austurlands* and local knowledge from hunters.

We treated each faecal pile as a single sample, regardless of whether the pile consisted of individual pellets, loose droppings, or formed a compact clump. A total of 309 faecal samples were collected, with a minimum of 30 samples per species and sampling season. Samples were kept cold for few days during fieldwork, before being stored at -20°C until processing.

After thawing, each faecal sample was randomly subsampled from 3-4 different parts of the pile (i.e., because nutrient content can vary within the pile) to produce a homogeneous composite of approximately 3 g of dry matter. Each composite was then oven dried at 40°C to constant weight and milled in a ball mill (Retsch mixer mill model mm 200) at a frequency of 300 Hz for 1.5 min (**Figure 2,** 2).

1.3. Laboratory analysis

1.3.1. Laboratory measurements

To calibrate NIRS models, we required samples with known nutrient concentrations. Therefore, from the 309 available ground samples, we selected 195 samples using a stratified sampling to ensure that each species and sampling session was adequately represented. For this subset, wet laboratory analysis was used to assess faecal N, P and C concentrations (**Figure 2,** 3a). Specifically, we used a Flash 2000 CN analyser (Thermo Fisher Scientific, Waltham, MA, U.S.A.) to assess faecal C and N concentrations (on subsamples of 10 mg; detection limit = 0.005%). Total P content was determined by acid digestion with H_2SO_4, salicylic acid and H_2O_2 (on subsamples of 300 mg; detection limit = 0.03 mg/L) and followed by calorimetric analysis (Skalar SAN++; Breda, The Netherlands; Walinga et al. 1989).

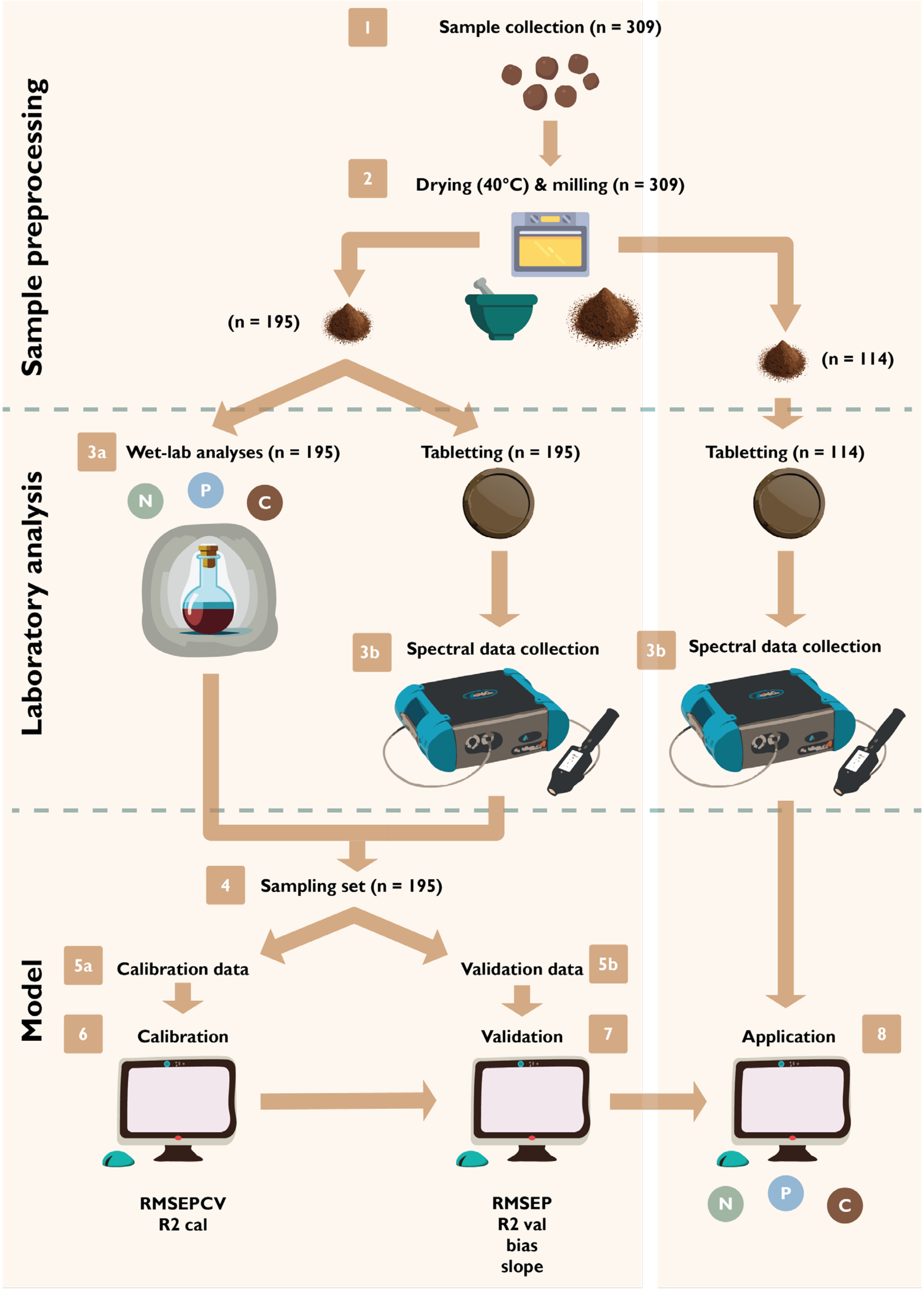


Figure 2: The use of Near-Infrared spectral data to predict nutrient concentrations (N, P and C) from tundra herbivore faecal material. Faecal samples were collected from the field (1), and are pre-processed in the lab after being stored at -20°C (i.e., oven dried and milled, 2). For a subset of 195 samples (left side of the diagram) nutrient concentration was measured using wet-lab analyses (3a) and spectral scans of pressed samples (tablets; 3b). The resulting dataset (4) was split into a calibration dataset (80% of the full dataset, 5a) and validation dataset (20%, 5b), which were used to calibrate (6) and validate (7) a Partial Least Squares (PLS) regression model. On the right side: new samples are processed (n = 114), and spectral data are collected. The nutrient concentrations are estimated using the

coefficients from the validated model (8). Samples from calibration, validation and application were used for further analyses to assess differences in herbivore faecal quality throughout the growing season.

1.3.2. Spectral data collection

Approximately 300 mg of the ground faecal material was pressed into tablets (Ø 15 mm, 1.3 mm thick) using a 4-tonne hydraulic press. The tablets were then dried at 40°C for 2.5 hours to remove any water films that may have formed, near infrared absorption patterns (Givens et al., 1997). Tablets were then stored in desiccators, at room temperature (approx. 20°C), to keep them dry until scanning. Each tablet was scanned three times on the same surface using a spectroradiometer (ASD LabSpec 4) and a contact probe attachment (**Figure 2,** 3b). The spectroradiometer covered a wavelength range of 350 to 2500 nm, with a 1.4 interval resolution in the 350-1000 nm range, and a 2 nm interval resolution in the 1000-2500 nm range, generating 1214 data points per sample and scan.

1.3.3. Spectral data formatting

Following the guidelines of Burnett et al. (2021), the spectral measurements were transformed to log(1/ reflectance) and averaged per sample. We then corrected the spectral data using a splice correction to remove the gap between the 100 nm and 1800 nm wavelengths resulting from the sensor overlap (Grillini et al., 2023). We also removed the visible part of the spectrum (350 nm-1100 nm) and wavelengths outside 2451-2500 nm to discard potential instrumental noise.

The calibration dataset included the 195 samples for which wet lab and spectral data were available (**Figure 2,** 4). The remaining scans (i.e., 114 samples) were retained for further model applications and nutrient concentration estimation.

1.4. Model calibration and validation

We used Partial Least Squares (PLS) regression to predict the faecal nutrient concentration (i.e., response variable) from the spectral measurements (i.e. predictors) (Martens and Naes, 1992). PLS regression is a suitable modelling approach for our dataset, because it can handle collinear predictors, such as the different wavelengths of a reflectance spectrum, as well as the larger number of predictor variables compared to the number of samples (Geladi and Kowalski, 1986). As PLS can be very sensitive to outliers (Xiaobo et al., 2010), we identified and removed them from the dataset (n = 14). To identify these values, we estimated the mean of the Mahalanobis distance and conducted a Principal Component Analysis (PCA) based on the spectral data, and discarding samples that were out of the cluster (Jackson and Chen, 2004). Outliers from the response variables were identified and removed from the dataset based on monospecific boxplots (Zuur et al., 2010). The dataset was separated by herbivore species to build monospecific models (**Table 1**). We separated each species dataset into a calibration (i.e., approx. 80%) and a validation set (i.e., approx. 20%, **Figure 2,** 5a and 5b, **Table 1**) and we ensured an equal representation of the sampling seasons.

To prevent model overfitting, we used permutations to estimate the optimal Number of Components (NoC) to include in the model, where each component is a linear combination of the original variables, that captures different patterns in the data (Serbin et al., 2014). The optimal NoC corresponds to the model with the first minimum RMSEP (prediction error; compared to the absolute minimum of the RMSEP) based on a 10-fold cross-validation (Xiaobo et al., 2010). We then developed mammal-specific (sheep + reindeer) and multispecies (sheep + reindeer + geese) models using the same method based on the same calibration and validation dataset from the monospecific models.

We used R statistical software 4.3.2 (R Core Team, 2023) to build our models, using *prospectr* (Stevens et al., 2015) and *pls* (Mevik and Wehrens, 2007) packages for the pretreatment of the spectral data and the partial least squares regression respectively.

Table 1: Overview of nutrient concentrations (N, P, and C, % dry matter) in faecal samples for each herbivore species, with the sample size (n) used for model calibration. The range indicates minimum and maximum nutrient concentrations measured via traditional wet-lab methods. Mean nutrient concentrations are presented with their respective coefficient of variation.

		Calibration data			**Validation data**		
Nutrient	**Herbivore**	**n**	**Range**	**Mean (cv)**	**n**	**Range**	**Mean (cv)**
	geese	41	1.27 - 6.72	2.37 (0.46)	10	1.7 - 3.86	2.27 (0.31)
N	sheep	57	1.66 - 4.6	3.1 (0.24)	15	1.86 - 4.03	2.99 (0.18)
	reindeer	43	1.99 - 3.39	2.53 (0.13)	11	2.02 - 2.89	2.53 (0.13)
	geese	41	0.13 - 0.53	0.29 (0.39)	10	0.15 - 0.5	0.28 (0.39)
P	sheep	53	0.32 - 0.77	0.52 (0.22)	14	0.41 - 0.67	0.54 (0.15)
	reindeer	45	0.45 - 1.19	0.76 (0.25)	12	0.46 - 1.23	0.78 (0.28)
	geese	41	28.12 - 44.74	36 (0.11)	10	32.42 - 39.27	35.56 (0.06)
C	sheep	57	33.94 - 44.72	41.66 (0.05)	15	38.14 - 44.23	41.96 (0.04)
	reindeer	43	35.05 - 46.2	42.28 (0.06)	11	37.26 - 45.69	42.35 (0.06)

1.5. Model performances and uncertainty of the estimates

The performance of the PLS models was evaluated using an internal 10-fold cross-validation based on the calibration data (**Figure 2**,5a), an independent validation based on the validation data (**Figure 2**,5b), and an uncertainty analysis (i.e., bootstrapping) based on both the calibration and validation data. Specifically, for each model, we calculated the variance explained (R^2) and the Root Mean Square Error of Prediction (RMSEP) as indicators of model accuracy. In addition, we estimated the bias, slope and intercept of the predicted and observed data based on the external validation. To understand the inherent uncertainties in the models when predicting new values based on faecal spectra, we used a permutation test (i.e., bootstrapping, Burnett et al. 2021), where we resampled the calibration data 500 times, ran the model, extracted the bootstrap coefficients and intercept, and applied these coefficients to the validation data to calculate the prediction intervals with the 95% confidence interval.

These steps were performed for each model (i.e., species specific, mammalian and all herbivores), and the estimates were compared to evaluate the performance of the monospecific and multispecies models for each nutrient (i.e., N, P and C).

1.6. Estimating differences in herbivore faecal nutrient content

We applied the multispecies NIRS calibration model to the remaining faecal samples to estimate N, P and C content (**Figure 2**, 8), and then evaluated the stoichiometric ratios (i.e., C:N, C:P and N:P). For one sample, the model predicted a negative value for phosphorus content. This value was adjusted to the minimum P value detected in chemical analyses (0.13% Dry weight DW; **Table 1**).

To assess differences in nutrient content (i.e., N, P and C) and in stoichiometry (C:N, C:P and N:P) between herbivore species, and across the growing season, we used a two-way ANOVA, with interaction between herbivore species and time within the season (nutrient ~ species × season). A post-hoc Tukey test (Hothorn et al., 2008) was used when the ANOVA results showed a significant interaction between season and species ($p>0.05$).

The ANOVAs were performed using using "*lme4*" (Bates et al., 2015) and "*lmerTest*" (Kuznetsova et al., 2017), and post-hoc Tukey packages were performed using the "*emmeans*" package (Lenth et al., 2024) in R statistical software 4.3.2 (R Core Team, 2023).

1.7. Estimating herbivore faecal nutrient contribution

To estimate nutrient contribution of faeces by the different herbivores during the growing season, we first estimated the average dry weight (in g) of a typical faecal deposition from five faecal subsamples per herbivore species (i.e., approx. 10 g of fresh sheep and reindeer, and 4 g of fresh geese). We determined their water content after oven drying at 40°C for 2 days and used these values to calculate the initial dry biomass of a typical faecal deposition.

Table 2: General information on the herbivore species in the study area. Dry faeces weight (g DW) was measured from 5 randomly selected faeces samples per species, collected during the study. Data on defecation rates (number of defecation events per day) and time spent in the area (days) were averaged from various literature sources. Local population sizes, provided by *Náttúrustofa Austurlands*, were used to estimate local densities (individuals.km^{2}). Means ± SD are shown for dry faeces weight and deposition rates. The absence of standard deviation for the daily defecation rates of reindeer is due to having only one reference.

	Pink-footed goose	**Reindeer**	**Sheep**
Faeces weight (g DW)	1.60 ± 0.79	18.68 ± 8.01	11.92 ± 5.06
Deposition rate (.days^{-1})	120.50 ± 32.00[a,b,c]	38.5 ± 0.00[d]	16.13 ± 7.00[e,f]
Grazing time (days)	92[g]	365[g]	92[g]
Population (ind)	121377[h,i]	1940[j]	45939[k]
Density (ind.km^{-1})	18.92	0.30	7.16
Body weight (kg)	2.64[l]	80.00[j]	65.00[m]
Yearly metabolic biomass (kg.km^{-1}.year^{-1})	9.50[g]	5.00[g]	26.11[g]

[a] Madsen, 1985

[c] Therkildsen and Madsen, 2000

[b] Chudzińska et al., 2016

[d] Kazmin and Abaturov, 2011

[e] Rollins et al., 1984

[f] Welch, 1982

[g] Defourneaux et al., 2024

[h] Skarphéðinsson and Þórisson, 2001

[i] Mitchell et al., 2010

[j] Þórisson, 2018

[k] Agricultural Ministry of Iceland, 2024

[l] Speed et al., 2019

[m] Ross et al., 2016

2. Results

2.1. Calibration and validation of the nutrient models

All species studied had distinct spectral signatures (**Figure 3**, **Supplementary material 2**). On average, geese had the lowest reflectance, and sheep the highest, with reindeer in between.

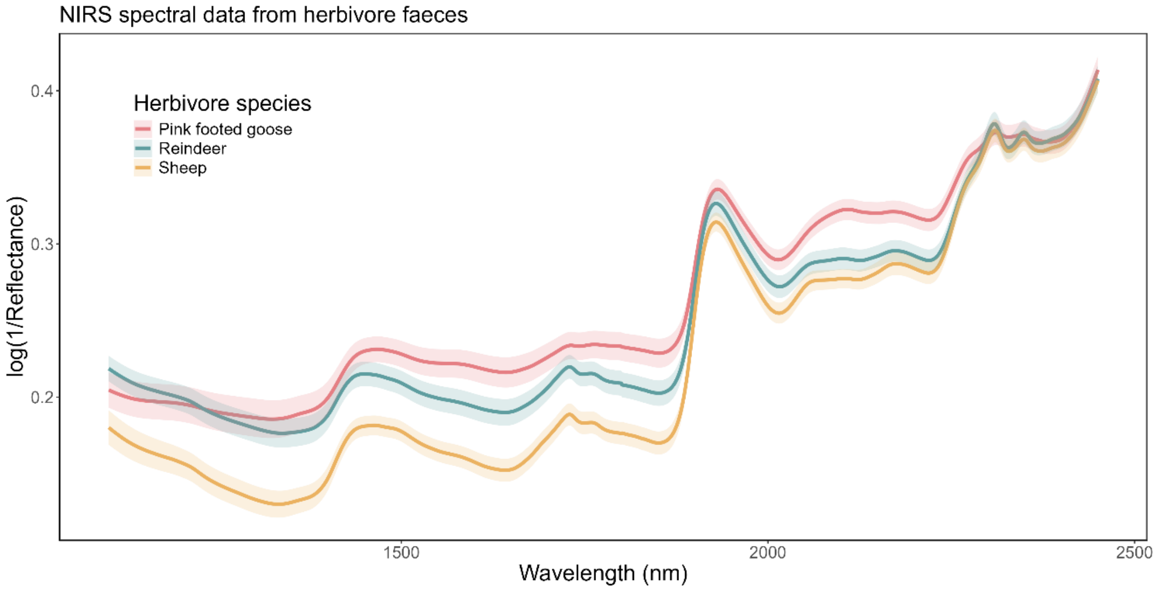


Figure 3: Typical reflectance spectra from faeces in the near infrared (1100-25000 nm) after log transformation. This figure is made by averaging all spectra per herbivore species, shaded surfaces correspond to the 95-confidence interval.

The variation of nitrogen content observed in the samples used for the calibration and validation was particularly small for reindeer (coefficient of variation cv = 0.13) compared to geese (cv = 0.46) and sheep (cv = 0.24) (**Table 1**). Phosphorus concentrations were lower compared to nitrogen and carbon, and showed less variability between the samples, with coefficients of variation ranging between 0.25 and 0.39 (**Table 1**). The variation of carbon content in geese faeces (cv = 0.11), was large compared to reindeer (cv = 0.06) and sheep (cv = 0.05).

Table 3: Performance of calibration models for herbivore faecal nutrient concentrations (N, P and C). *n* refers to the number of samples used for the calibration and the validation, while *NoC* is the Number of Components used in the model calibration. *R^2* and *RMSEP* (Root Mean Square Error P) are calculated from the internal cross validation (calibration data), and the external validation (validation data). *Bias* (prediction -observation), and *intercept* and *slope* are derived from the projection of observed vs predicted values from the validation set. Models for reindeer and sheep faecal P could not be calibrated because of low sample size and limited variance in P concentrations; these are reported as NA.

	Calibration set				**Validation set**					
Model	**n**	**NoC**	**R^2**	**RMSECV**	**n**	**R^2**	**RMSEP**	**Bias**	**Intercept**	**Slope**
N										
geese	41	10	0.79	0.26	10	0.78	0.31	-0.01	-0.65	1.29
sheep	57	5	0.81	0.28	15	0.91	0.16	-0.04	0.19	0.95
reindeer	43	7	0.89	0.08	11	0.93	0.08	-0.01	-0.36	1.15
reindeer + sheep	100	6	0.86	0.22	26	0.87	0.18	-0.06	0.07	1
reindeer + sheep + geese	141	12	0.83	0.25	36	0.88	0.21	-0.03	-0.36	1.15
P										
geese	41	5	0.49	0.07	10	0.77	0.05	0	0.09	0.69
sheep	57	NA	NA	NA	15	NA	NA	NA	NA	NA
reindeer	43	NA	NA	NA	11	NA	NA	NA	NA	NA
reindeer + sheep	98	5	0.45	0.13	26	0.31	0.16	0.03	0.37	0.38
reindeer + sheep + geese	139	6	0.63	0.13	36	0.76	0.12	0.02	0.14	0.71
C										
geese	41	10	0.91	0.59	10	0.79	0.92	-0.64	3.69	0.91
sheep	57	10	0.83	0.51	15	0.9	0.55	-0.15	6.53	0.85
reindeer	43	6	0.82	0.85	11	0.77	1.09	0.09	13.34	0.68
reindeer + sheep	100	11	0.84	0.68	26	0.84	0.77	-0.07	7.53	0.82
reindeer + sheep + geese	141	12	0.92	0.91	36	0.97	0.64	0.03	-0.52	1.01

We found that both monospecific, and multispecies models (i.e., mammalian and all all-species) models, performed well (high R^2 and low RMSEP) in predicting nitrogen and carbon content from an independent validation dataset (**Table 3, Supplementary material 3**). In particular, the monospecific models achieved predictive performances based on the external validation of $R^2 \geq 0.78$, RMSEP ≤ 0.31 g DW; $R^2 \geq 0.79$, RMSEP ≤ 1.09 g DW for N and C, respectively. The multispecies model performance reached an R^2 of 0.88 and a RMSEP of 0.21 g DW for N; and an R^2 of 0.97 and a RMSEP of 0.64 g DW for C. However, models for P were less accurate and the geese-based model reached an R^2 of 0.77 for a RMSEP of 0.05 g DW. Sheep and reindeer models for P could not be run, likely due to the small sample size and low variance of P concentrations compared to the spectral data (see **Table 1** for details). The multispecies model for predicting P had higher predictive ability ($R^2 = 0.76$, RMSEP = 0.12 g DW), but it still had lower predictive ability compared to the N and C models.

2.2. Differences in herbivore faecal nutrient content between species and throughout the growing season

After applying the multispecies calibration models to predict faecal N, P and C across a larger number of samples, we found large variations in faecal nutrient concentrations and stoichiometry throughout the growing season and between herbivore species (**Figure 4**, **Supplementary material 4**). In general, faecal N and P concentrations remained similar during the early (i.e., beginning to peak) growing season. In contrast, towards the end of the season faecal N drastically decreased (up to half of the early season levels), while faecal P decreased more progressively. An exception was observed in sheep faeces, where the P concentration remained constant throughout the entire season, at 0.33-0.53% DW.

Specifically, at the beginning and peak of the season, total N concentrations in sheep faeces were 1.5 times higher (3.60 % DW) than those in geese and reindeer faeces, which had similar levels (i.e., approx. 2.70% DW). However, by the end of the growing season, sheep and reindeer had similar levels of faecal N levels (respectively 2.31 and 2.39% DW), while geese showed a drastic decrease, with almost half of the nitrogen content compared to the peak of the growing season (approx. 1.60% DW). Conversely, reindeer consistently had the highest faecal P concentrations throughout the season, and geese the lowest, with less than half of the reindeer values (0.21 - 0.33 % DW vs 0.66 - 0.78 % DW for geese and reindeer respectively).

Overall, faecal C concentrations were highly variable. Geese followed expectations and showed similar levels of faecal C during the beginning and peak seasons, before increasing towards the end of the growing season (32.14 to 37.45 % DW). In contrast, reindeer faeces showed a strong increase in C content from beginning to peak (38.84 % DW to 44.38 % DW), before decreasing to reach similar levels as sheep towards the end of the growing season (41.79 % DW). Sheep, on the other hand, did not show any significant changes in C content throughout the growing season, and remained constant at approx. 41.00 % DW. Overall, faecal C, was higher in sheep and reindeer than in geese (**Figure 4**).

Faecal stoichiometry, mean C:N and C:P ratios, increased during the season for all herbivore species. Despite significant differences in faecal N, P and C, all three species had relatively similar C:N and C:P levels at the beginning of the season. The C:N ratio increased during the growing season, while C:P remained relatively constant. However, the faecal quality of geese decreased

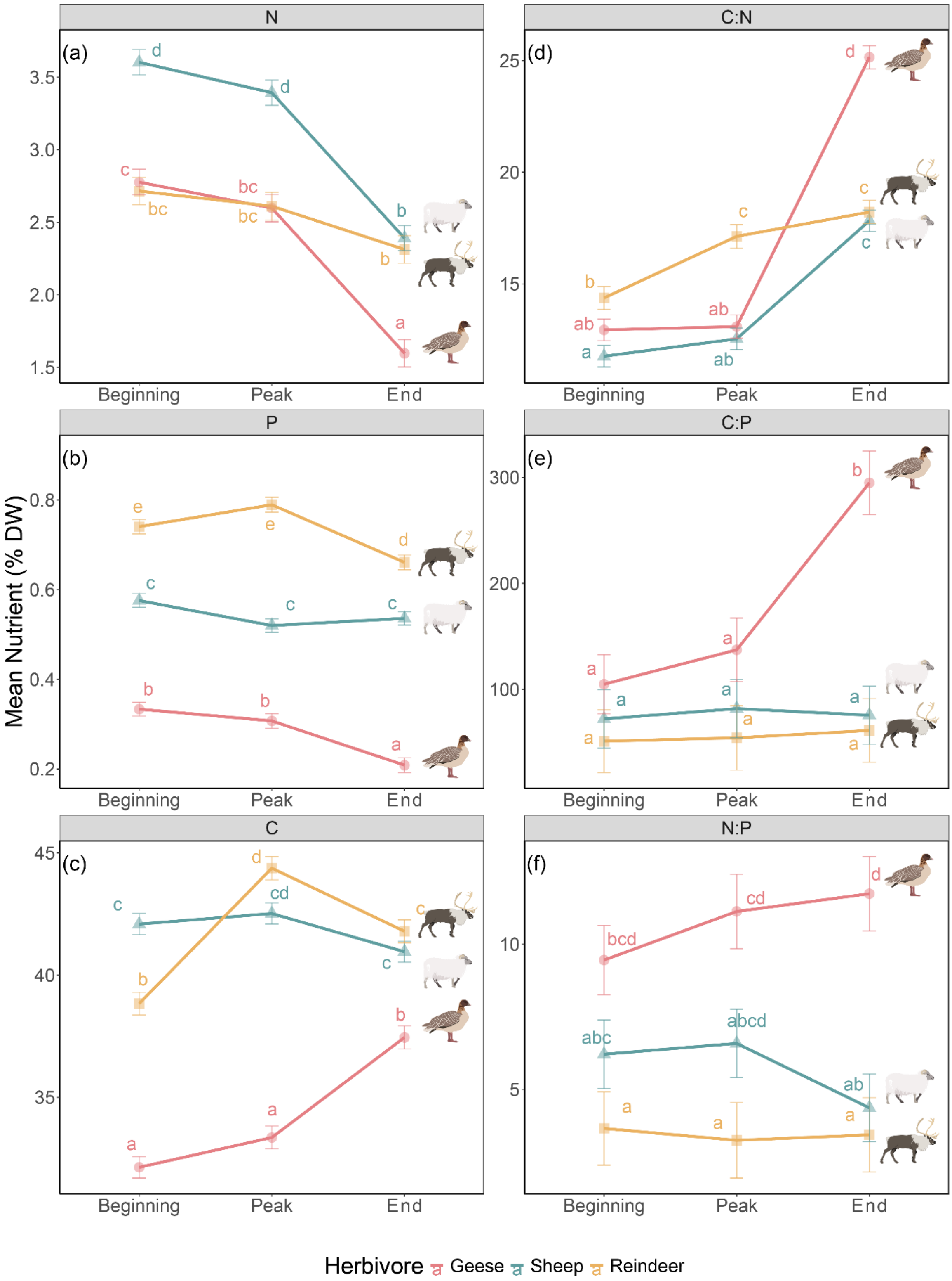


Figure 4. Seasonal faecal nutrient content variation (% DM, mean and se) for nitrogen N (a), phosphorus P (b), carbon C (c), carbon to nitrogen ratio C:N (d), carbon to phosphorus ratio C:P (e), nitrogen to phosphorus ratio N:P (f) for the main Icelandic herbivore species in the beginning, peak and late growing season. Significant differences between herbivore species are indicated at each time during the growing season with letters.

significantly towards the end of the growing season, with C:N and C:P levels 1.5 and 3 times higher than those observed in reindeer and sheep by 1.5 and 3 times respectively.

In contrast, faecal N:P ratios were rather stable in geese, sheep and reindeer. However, the values were consistently twice as high in geese than in reindeer or sheep, respectively 9.45 - 11.74 and 3.43 - 6.58.

2.3. Faecal nutrient input by different herbivore species

Throughout the growing season, geese consistently contributed more N, P and C than sheep and reindeer, due to their higher population density and defecation rates (**Figure 5, Table 2**). In contrast, reindeer, deposited the least amount of nutrients. Specifically, from the beginning to the peak of the growing season, geese deposited twice as much N and C as sheep, and more than three times as much as reindeer. Similarly, geese deposited 7 times as much P as reindeer, and 1.5 times as much as sheep. At the end of the growing season, however, N and P deposition substantially decreased significantly by one third and 1.5 times at the end, respectively, to reach similar deposition levels to those of sheep (99.52 kg.km^{-2} for N and 22.72 kg.km^{-2} for P).

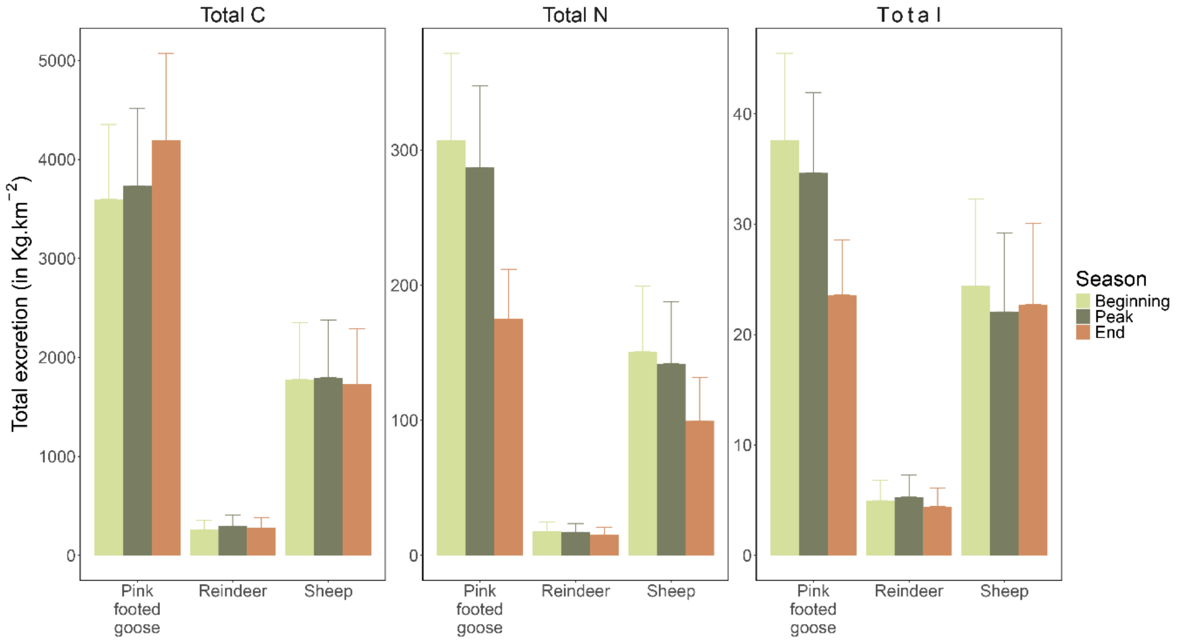


Figure 5: Estimates of the seasonal nutrient contributions (N, P, and C) per km² for pink-footed geese, sheep, and reindeer in the Icelandic tundra. These values were calculated using local species densities, daily defecation rates, time spent grazing, mean faecal dry weight, and the average nutrient concentrations (N, P, and C) across the growing season. The 95% confidence intervals are shown, reflecting the variation in faecal DW and daily defecation rates.

3. Discussion

We have developed the first NIRS-based model for predicting faecal N, P and C of tundra herbivores, based on the three main Icelandic species found in high-elevation rangelands. Our study demonstrates the potential of NIRS scanning as an efficient, low-cost tool for assessing faecal nutrient content across different herbivore species and throughout the growing season. We found strong seasonal variation in herbivore faecal nutrient content among tundra herbivore species, suggesting that different herbivore species contribute uniquely to biogeochemical cycling and nutrient turnover. However, we found that faecal quality (C:N and C:P) of herbivores did not strongly differ along the growing season, except for geese, where C:N and C:P in geese faeces increased strongly towards the end of the growing season. Finally, we found that geese were consistently the largest contributors to nutrient budgets in the Icelandic tundra, probably due to their large population and defecation rate, highlighting their role in biogeochemical cycles.

3.1. Methodological aspects: A more affordable, standardised approach to assess variation in faecal nutrient content over the growing season

The spectral signatures found in the present study had a similar profile to that observed for mammalian (Tolleson and Angerer, 2020; Villamuelas et al., 2017). Although our calibration dataset was small compared to the variability within our calibration set, both monospecific and multispecies calibrations had high and similar predictive abilities. Model performance was comparable to existing NIRS multispecies models for other herbivore communities (Villamuelas et al., 2017), and plants in similar environments (Murguzur et al., 2019). Although the low RMSEP of the reindeer faecal nitrogen model could reflect some homogeneity in the calibration data, as reindeer faecal samples were mostly collected from the same herd during each sampling session. This could also mean that the model does not generalise as well across reindeer populations. This result demonstrates that a single multispecies NIRS calibration model can effectively estimate N, P and C content, and stoichiometric ratios, in the faeces of Icelandic tundra herbivores, where herbivore digestive systems and size are highly contrasted. Similar models for estimating nutrient content in leaves, litter (Murguzur et al., 2019; Petit Bon et al., 2020a; Smis et al., 2014), and soils (Petit Bon et al., 2020b) have already been developed for tundra ecosystems. Thus, by providing a first attempt at multispecies NIRS-based models for estimating faecal nutrient concentrations of Icelandic tundra herbivores, our study contributes to the standardisation and affordability of nutrient analysis in tundra ecosystems. This advancement will facilitate comparisons for nutrient analysis between plants, herbivores and soils, providing valuable insight into nutrient transfer within tundra ecosystems.

3.2. Differences in faecal nutrient content among tundra herbivores

The faecal nutrient concentrations and stoichiometry we observed in Icelandic herbivores are similar to those previously reported for reindeer (Barthelemy et al., 2015; T. Beumer et al., 2017) and geese (Bazely and Jefferies, 1985; Beard et al., 2023; Dessborn et al., 2016) in tundra, and sheep in rangelands (Wang et al., 2018). Our analyses revealed considerable interspecific and seasonal variation, much of which can be attributed to differences in digestive physiology, dietary preferences, and body weight. As expected, reindeer and sheep generally had closer C:N and C:P ratios than geese, probably due to their similarities in body size and digestive systems. However, the rapid increase in faecal C, and C:N during the peak of the growing season in reindeer faeces compared to sheep may be due to differences in diet. Although reindeer and sheep often have overlapping diets during summer (Mysterud, 2000), studies in Iceland have shown that reindeer consume a greater proportion of small deciduous shrubs (i.e., *Salix sp.*) which are higher in C content, while sheep prefer grasses and sedges, which are richer in N (Murguzur et al., 2019; Þórisson, 2018).

Unexpectedly, geese faeces generally had lower nutrient concentrations than those of sheep or reindeer, despite their digestive system (e.g., cloacal fermentation), which is usually associated with high quality faeces due to the shorter retention time, lower digestibility and higher diet selectivity, compared to ruminants (Karasov and Douglas 2013). They are also much smaller than reindeer or sheep, which means that they typically require less P for skeletal investment (May and El-Sabaawi, 2024). However, previous research in nutritional ecology suggests that geese may digest protein (the main source of assimilated N) as efficiently as other herbivores of similar size (Buchsbaum et al., 1986) and rely on symbiotic gut microflora to enhance nutrient assimilation (Durant, 2013), which may underestimate their ability to efficiently digest their food resources. Furthermore, waterfowl faeces are combined with urine in the form of highly soluble uric acid and ammonium ions, which are likely to be rapidly assimilated by the ecosystem (Beard et al., 2023). In particular, the microorganisms and uric acid present in geese faeces, together with the higher nutritional quality of the faeces compared to vegetation, are thought to make geese faeces a valuable food source for reindeer and sheep (van der Wal and Loonen 1998).

Overall, the observed decline in faecal quality in herbivore faeces over the growing season is likely to reflect a decline in plant quality (Hahn et al., 2007). Similar declines in nutrient concentrations over the growing season have been reported for palatable plant species, as they translocate their

N and P to belowground structures prior to senescence (Happonen et al., 2022; Zhao et al., 2023). Moreover, as the growing season progresses, and preferred forage plant species become less available, herbivores may resign themselves to consuming less nutritious, readily available plants to meet their metabolic needs (Gálvez-Cerón et al., 2013). Such shifts in dietary preferences have been documented for geese and reindeer in other Arctic tundra sites (Audet et al., 2007; Cadieux et al., 2005; Mårell, 2006; Zhao et al., 2019).

Lastly, the decrease in nutrient concentrations towards the end of the growing season may be due to geese preparing for overseas migration, and reindeer for winter and calving, which require substantial amounts of N, P and C for respectively protein synthesis, tissues (i.e., new feathers and antlers), and fat, which are essential elements for the herbivore survival (Barboza and Parker, 2008; Wypkema and Ankney, 1979). In contrast, sheep are kept indoors, and do not show changes in P or C. Furthermore, the N:P ratio showed little variation over the growing season for all three species, which may indicate that herbivores maintain a stoichiometric balance in their bodies to meet their metabolic needs (Sitters and Olde Venterink, 2018; Sterner et al., 1992).

However, caution should be taken when relating differences in dietary preferences to variations in faecal nutrient content between the different herbivore species, because the signal can be blurred by physiological differences between species, which can affect nitrogen absorption and fermentation rates (Leslie et al., 2008). Larger datasets with a more diverse range of herbivores are needed to draw more precise conclusions about the influence of functional group on faecal nutrient content or stoichiometry. Greater integration of nutritional ecology within the field of zoogeochemistry may to unravel the complexities in interpreting these differences.

3.3. Implications for ecosystem functioning and biogeochemical cycles

One of the most exciting findings is that seasonality has a significant effect on the quality of herbivore faeces. In Icelandic tundra rangelands, most nutrient turnover from herbivores in occurs in a very short period, when geese and sheep are present during the growing season. Our results show that nutrient turnover from faecal deposition is particularly pronounced from the beginning to the peak of the growing season, as indicated by the generally consistent decline in faecal N and P concentrations. These results are consistent with other studies that have investigated seasonal changes in faecal nutrient content in temperate and alpine ecosystems (Barbero-Palacios et al., 2023; Kamler et al., 2004). In addition, increases in C:N and C:P ratios towards the end of the growing season, particularly in geese, suggest that N and P release to the soil may be slower than earlier in the season. This is because nutrient release rates from herbivore faeces tend to decrease as C:N and C:P ratios increase (Sitters et al., 2014).

From a broader perspective, the higher nutrient concentrations and lower stoichiometric ratios recorded in faeces early in the season are consistent with strong nutrient pulses are typically recorded in tundra early in the growing season (Chapin et al., 1975; McLaren et al., 2017; Westergaard-Nielsen et al., 2021), highlighting the role of faecal nutrient deposition on these pulses. We did not observe significant changes in N:P ratio throughout the growing season for neither of the three herbivores. However, higher faecal N:P ratio in geese than those in reindeer, suggesting that geese could promote N return to ecosystems over P (Beard et al., 2023), whereas reindeer promote P in the Icelandic tundra. Ultimately, species differences in faecal stoichiometry are likely to have strong local effects on N and P cycling, controlling the availability of these nutrients to plants or soil microorganisms.

3.4. Management implications

Our extrapolations of faecal nutrient deposition in the area over the growing season are broad approximations, but they fall in the range of those observed in other grazing systems. In particular, total faecal P and N appear to be generally higher than in other tundra ecosystems, at higher latitudes (about 370 kg.km^{-2}.year^{-1} for muskox only, Mosbacher et al. 2016), and much lower than in alpine tundra, where large herbivores are present year-round (Barbero-Palacios et al., 2023), in line with estimates of places where geese breed in large colonies (about 175 kg.km^{-2}.year^{-1}; Post et al. 1998).

The faecal N deposited by herbivores is comparable in magnitude to the observed annual atmospheric nitrogen inputs (<100 kg N.km^{-2}.y^{-1}, Arnalds 2015). Therefore, the annual return of herbivores in our study area may also represent an important nutrient pathway and may play a role in the biogeochemical cycles of Icelandic rangelands, especially for nitrogen. To our knowledge, there are no available estimates of atmospheric P inputs in Iceland.

Most of the nutrient addition was driven by geese, despite their relatively short presence in the area. These results support the extensive literature on the important role of geese in nutrient recycling in tundra ecosystems through defecation (Koltz et al., 2022). While livestock (mainly sheep) generally have a greater impact on vegetation than wild herbivores (mainly pink-footed geese) in Icelandic rangelands (Defourneaux et al., 2024), geese contribute far more to faecal nutrient deposition despite their small size. In Eastern Iceland, breeding densities can reach up to 70 nests.km^{-2} (Stefánsson et al., 2022), suggesting that they are less common in the rest of the landscape, and that their impact on nutrient pools may be more concentrated than expected Since the late 1980s, the Icelandic herbivore community has been shifting from a domesticated to a wild-dominated, due to a decline in the domestic sheep population and an increase in the abundance of pink-footed geese (Defourneaux et al., 2024). In addition, geese are arriving at their breeding grounds across the Arctic earlier and extending their presence on the tundra (Doiron et al., 2015; Ross et al., 2017). Thus, faecal N and P deposition from geese is likely to increase in the future. Some studies have already highlighted the strong positive responses of vegetation and microbial communities to increased geese faecal deposition in the Arctic (Bazely and Jefferies, 1985; Beard et al., 2023; Hik and Jefferies, 1990), but changes in vegetation cover, especially towards less palatable species (Sjögersten et al., 2010), and the potential for freshwater eutrophication due to large aggregations of geese (Hessen et al., 2017), are growing concerns in the tundra, and should be further addressed in Iceland. Unlike reindeer or sheep, which are expected to redistribute nutrients across the landscape due to their mobility during the growing season (Wolf et al., 2013), geese tend to concentrate their faecal inputs in specific areas during at beginning of the growing season, especially near water bodies and in areas of dense vegetation. This spatially concentrated nutrient loading creates localised hotspots of enrichment. Understanding when and where herbivores deposit faeces is crucial to predicting how ecosystems might respond to allochthonous nutrient inputs from herbivores. This is particularly important in the context of changing herbivore communities and should be further investigated to better assess the role of faecal deposition in ecosystem functioning.

4. Conclusions

By developing the first multispecies NIRS-based open-source model to quantify faecal nutrient concentrations (i.e., N, P and C) in different herbivore species (i.e., pink-footed geese, reindeer and sheep) in the Icelandic tundra, we take an important step towards making faecal nutrient analysis more affordable and standardised. In this comparative study, we highlight the strong variation in faecal nutrient content and stoichiometry between herbivore species and draw attention to the large amount of high-quality faecal input supplied early in the season, particularly by geese. We emphasise the importance of considering seasonality and species identity when assessing the role of herbivores in tundra biogeochemical cycles. Extending the NIRS model to other species and regions could provide valuable insights into how body size, digestion, and diet influence faecal nutrient content and stoichiometry in tundra ecosystems. Finally, we draw attention to the strong ongoing changes in herbivore community composition in northern rangelands, which are expected to have a substantial impact on nutrient dynamics in the Icelandic tundra.

Data accessibility statement

R script-based NIRS calibration development, prediction models and all data used in this study will be stored online upon acceptance of the manuscript.

Author contributions

MD, ICB, JDMS, and NB-L contributed to conceptualization; MD, ICB, JDMS, NBL, LBP and JS provided methodology; MD was involved in formal analysis, investigation and visualization; MD was involved in writing—original draft preparation; ICB, JDMS, NBL, NBL, LBP and JS were involved in writing—review and editing; ICB and MD were involved in funding acquisition; ICB, JDMS, and NBL were involved in supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Anya Boardman, Björk Kristjánsdóttir, Charlotte Wagner and Ludivine Panot for fieldwork and sample collection, and Janine G. Lock, Eleanor Greer, and Katharina Wilfert for lab processing. We are very grateful to the lab of Kari Anne Bråthen at The Arctic University of Norway (UiT), especially Hanna Böhner and Francisco J. A. Murgurzur, which kindly shared their expertise in NIRS. Finally, we would like to thank Náttúrustofa Austurlands and WWT for sharing precious data on herbivore population.

Fundings

This work was supported by the Icelandic Research Fund (grant number 217754 and 2410773-051); the Nordic Borealization Network (NordBorN, funded by NordForsk grant number 164079); and Landsvirkjun (grant number NÝR-22-2022 and NÝR-26-2023). JS is grateful to the Research Foundation–Flanders (FWO) for funding the Scientific Research Network: Zoogeochemistry, Alchemists of the Wild (project No. W001522N) and the Bijzonder Onderzoeksfonds of the University of Antwerp for research funding (project No. 44158).

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Supplementary Information

This supplementary information has not been peer reviewed.

Capturing seasonal variations in faecal nutrient content from tundra herbivores using Near Infrared Reflectance Spectroscopy

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Supplementary material 1: Comparison of cost and time for wet-lab methods vs. near infrared spectroscopy (NIRS) for sample processing (excluding machine costs)

Supplementary material 2: Distribution of the spectral data included in the NIRS calibration

Supplementary material 3: Results from species-specific and multispecies NIRS calibration model

Supplementary material 4: Differences in faecal nutrient concentration and quality from Icelandic tundra herbivore species

Supplementary material 1: Comparison of cost and time for wet-lab methods vs. near infrared spectroscopy (NIRS) for sample processing (excluding machine costs)

These estimates assume that samples have already been preprocessed (i.e., dried, milled, weighed and pressed), and that the necessary equipment is available. Labor costs are not included. The costs for wet-lab methods reflect the prices offered in Antwerp, where the analyses were conducted.

Table S1.1: Cost and time for wet-lab methods vs. near infrared spectroscopy (NIRS) for sample processing. Costs are reported per samples in Euros. Preparation time and processing time refer respectivelly to the time required for machine warm up and sample analysis. The number of samples that can be processed in one batch is indicated in parentheses. In braquet is reported the amount of samples that can be processed in one batch. To make the methods comparable, the total processing time refers to the time required to analyze a single sample.

	Wet-lab methods	**NIRS**
C : N analysis, unitary cost (€)	3.46	0
N : P analysis, unitary cost (€)	10.13	0
Total unitary cost for C : N : P (€)	13.59	0
Preparation time (h)	0	20
Processing time C:N (h)	0.25 (1)	NA
Processing time N:P (h)	23 (40)	NA
Total processing time (min)	30 (1)	0.5 (1)

Supplementary material 2: Distribution of the spectral data included in the NIRS calibration

Two-dimensional non-metric multidimensional scaling (NMDS) is used to assess dissimilarities in spectral signatures of samples from the different herbivore species.

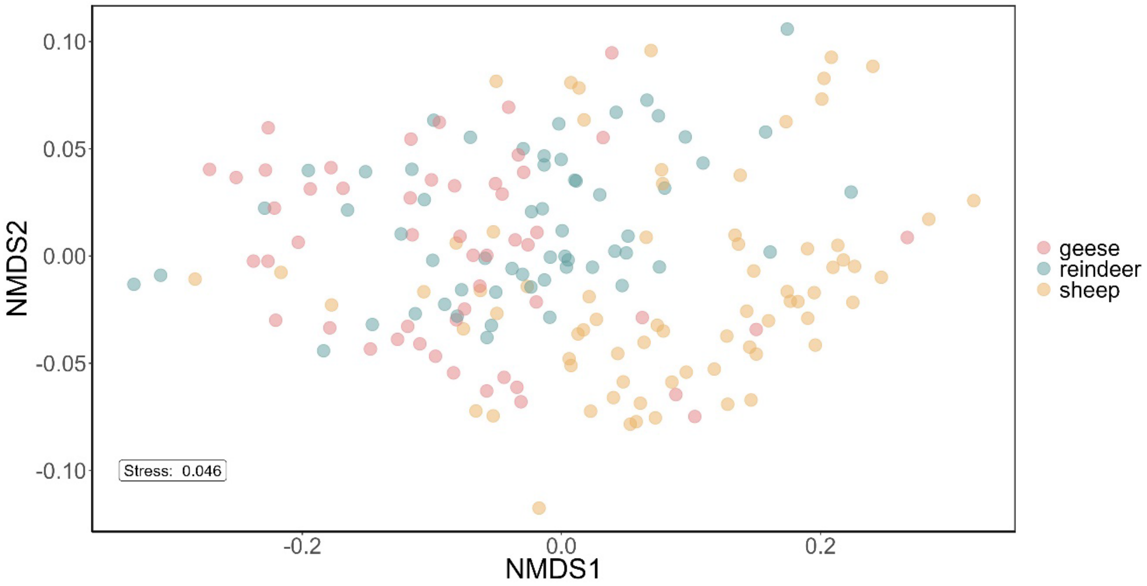

Figure S2.1: NMDS of the spectral data used in the NIRS calibration model for herbivore faecal nutrient content. Each point indicates sample position in the NMDS analysis. Color indicates herbivore species identity.

Supplementary material 3: Results from species-specific and multispecies NIRS calibration model

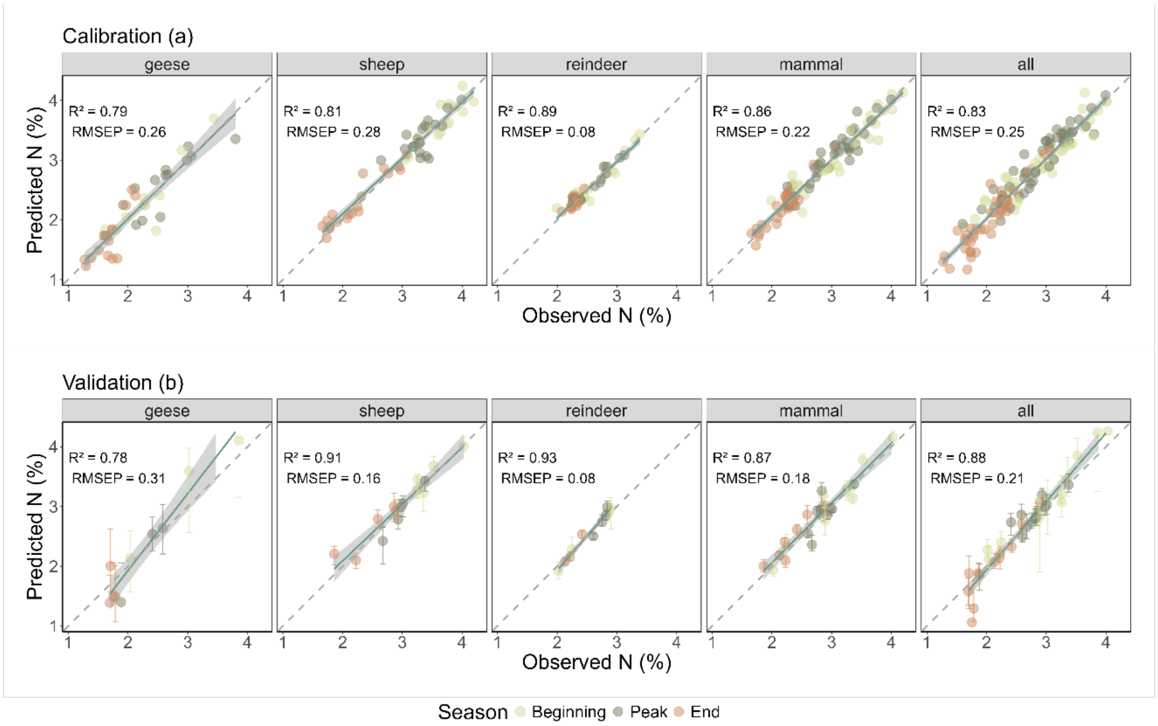

Figure S3.1: Cross-validation (a) and external validation (b) of monospecific and multispecies Icelandic tundra herbivore models for predicting faecal nitrogen (N) content (% dry weight). Each plot displays the variance explained (R^2) and root mean square error of prediction (RMSEP) for either cross-validation or external validation. Predicted values (% DW) are derived from calibration models based on spectral data, while observed values (% DW) are obtained from traditional wet-lab methods. The 95% confidence intervals shown in the validation plots were calculated using bootstrapping analysis. Colors indicate the timing within the growing season when each faecal sample was collected.

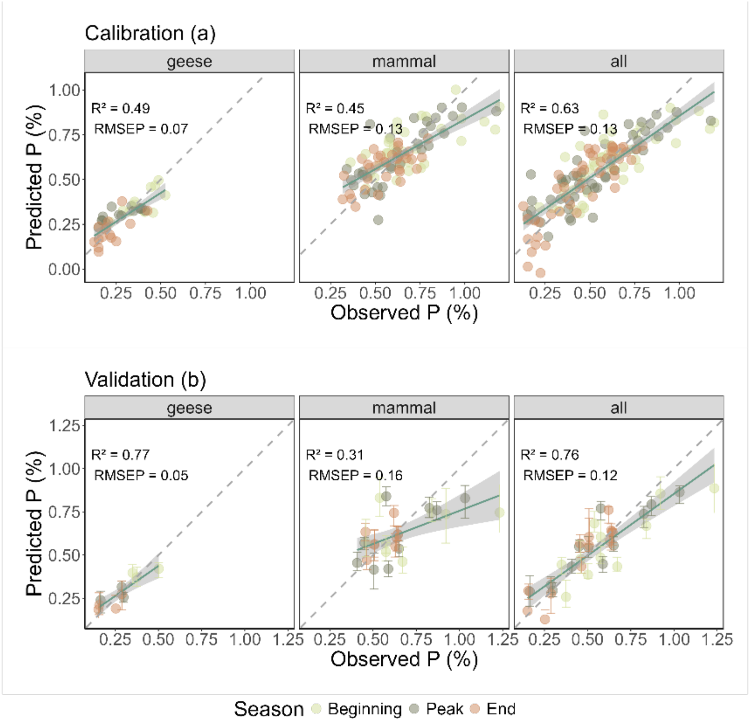

Figure S3.2: Cross-validation (a) and external validation (b) of monospecific and multispecies Icelandic tundra herbivore models for predicting faecal phosphorus (P) content (% dry weight). Each plot displays the variance explained (R^2) and root mean square error of prediction (RMSEP) for either cross-validation or external validation. Predicted values (% DW) are derived from calibration models based on spectral data, while observed values (% DW) are obtained from traditional wet-lab methods. The 95% confidence intervals shown in the validation plots were calculated using bootstrapping analysis. Colors indicate the timing within the growing season when each faecal sample was collected.

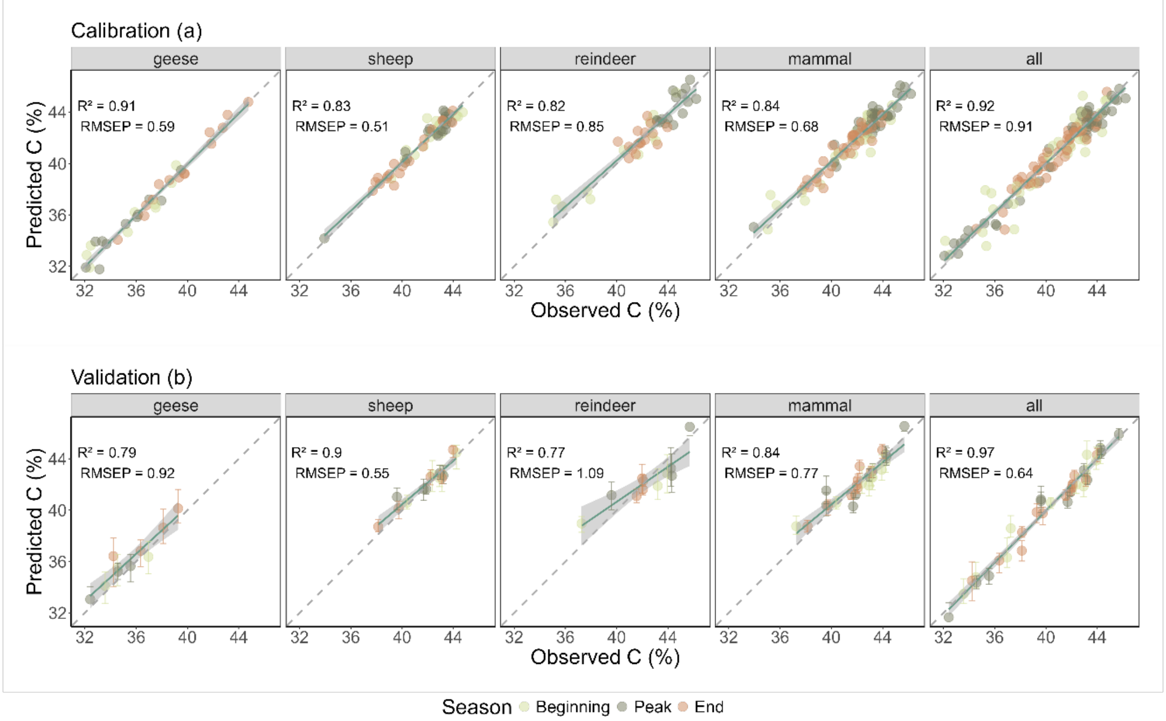

Figure S3.3: Cross-validation (a) and external validation (b) of monospecific and multispecies Icelandic tundra herbivore models for predicting faecal carbon (C) content (% dry weight). Each plot displays the variance explained (R^2) and root mean square error of prediction (RMSEP) for either cross-validation or external validation. Predicted values (% DW) are derived from calibration models based on spectral data, while observed values (% DW) are obtained from traditional wet-lab methods. The 95% confidence intervals shown in the validation plots were calculated using bootstrapping analysis. Colors indicate the timing within the growing season when each faecal sample was collected.

Supplementary material 4: Differences in faecal nutrient concentration and quality from Icelandic tundra herbivore species

Table S4.1: Number of samples by herbivore species, age (i.e. adult or juvenile) and timing in the growing season. This includes all the data collected in the field and used for the analysis, after removing the outliers.

Herbivore	Age	Beginning	Peak	End
geese	adult	32	30	30
geese	juvenile	4	NA	NA
sheep	adult	30	29	29
sheep	juvenile	7	8	9
reindeer	adult	28	29	30
reindeer	juvenile	3	NA	NA

Table S4.1: Summary of the two-way ANOVA analysing the differences in faecal nutrient content (% DW) and stoichiometry among herbivore species (geese, reindeer and sheep), and throughout the growing season. N = nitrogen, P = phosphorus, C = carbon, C:N = carbon to nitrogen ratio, C:P = carbon to phosphorus ratio, and N:P = nitrogen to phosphorus ratio

Nutrient	Term	df	Sumsq	Meansq	Statistic	P value
C	season	2	424.93	212.46	31.48	< 0.001 ***
	herbivore	2	3635.36	1817.68	269.31	< 0.001 ***
	season:herbivore	4	665.91	166.48	24.67	< 0.001 ***
N	season	2	49.61	24.8	90.52	< 0.001 ***
	herbivore	2	35.79	17.9	65.32	< 0.001 ***
	season:herbivore	4	7.93	1.98	7.24	< 0.001 ***
P	season	2	0.27	0.14	16.56	< 0.001 ***
	herbivore	2	9.34	4.67	568.84	< 0.001 ***
	season:herbivore	4	0.24	0.06	7.22	< 0.001 ***
C : N	season	2	3008.65	1504.32	179.96	< 0.001 ***
	herbivore	2	532.21	266.11	31.83	< 0.001 ***
	season:herbivore	4	1036.87	259.22	31.01	< 0.001 ***
C : P	season	2	205240	102620	3.74	0.025 *
	herbivore	2	793835.1	396917.6	14.46	< 0.001 ***
	season:herbivore	4	425498	106374.5	3.87	0.004 **
N : P	season	2	21.58	10.79	0.22	0.806 *ns*
	herbivore	2	2590.66	1295.33	25.84	< 0.001 ***
	season:herbivore	4	178.24	44.56	0.89	0.471 *ns*

III

Nutrient redistribution by herbivores across a tundra landscape

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Abstract

Through their daily movement and behaviour, herbivores can actively redistribute nutrients across the landscape from where they eat to where they rest and defecate. In this way, herbivores can create heterogeneity in nutrient distribution across the landscape, often reinforcing nutrient-rich areas by using them more. The magnitude of herbivore impacts could be affected by the composition of the herbivore community, as different species have varying behaviours and effects on the ecosystem.. How different herbivores contribute to nutrient recycling and redistribution is a particularly relevant question in nutrient-limited ecosystems such as tundra rangelands that are undergoing strong changes in herbivore community composition. We collected data on nutrient availability in forage plants, aboveground plant biomass consumption by herbivores, and fecal deposition of migratory pink-footed geese, domestic sheep, and feral reindeer at 21 sampling sites in Icelandic tundra rangelands throughout the growing season, to understand the role of a multi-species assemblage of herbivores in nutrient redistribution. We used near-infrared spectroscopy to estimate nutrient (nitrogen, phosphorus and carbon) content and quality (C:N, C:P and N:P) of forage plant species and herbivore faeces. We showed that overall herbivore consumption significantly increased over the growing season, while forage quality decreased and the biomass of forage plants remained unchanged. Herbivore consumption was not significantly related to forage quality, but herbivores, particularly geese, deposited more nutrients in patches where forage quality was lower, indicating a transport of nutrients from rich-to-poor patches. Our findings challenge the assertion that herbivores generally induce positive feedbacks in nutrient dynamics in tundra systems, and highlight the potential for different herbivore species to induce nutrient transport in tundra rangelands to varying extents. By studying how different herbivores contribute to nutrient recycling and distribution in the Icelandic tundra, we emphasize the importance of relative changes in consumer densities to understand herbivore induced landscape heterogeneity and dynamics.

Keywords: Nutrient fluxes, herbivores, tundra, ecosystem subsidies, zoogeochemistry, feedbacks

1. Introduction

Herbivores play a crucial role in nutrient cycling and strongly influence biogeochemical cycles by consuming plant material, digesting, and providing nutrient-rich subsidies such as urine, faeces, and carrion to the soil (Schmitz 2008). Through their daily movements and behaviour, herbivores can actively redistribute nutrients across the landscape from areas where they eat to where they rest, nest and ultimately defecate (Polis et al. 1997). Herbivore nutrient transport has been reported in many studies, ranging from savanna ecosystems (Veldhuis et al. 2018) to tundra (Dessborn et al. 2016; Mosbacher et al. 2016). By actively transporting nutrients across the landscape, herbivores influence the spatial structure of ecosystems, affecting plant nutrient availability and recycling, with the potential to drive nutrient ratios and limitation (i.e., Leroux and Loreau 2010; Daufresne 2021). This, in turn, can influence plant-soil feedbacks, by either accelerating or decelerating rates of primary production, litter decomposition, and microbial activities (i.e., mineralisation, respiration) at large spatio-temporal scales (Abbas et al. 2012; Ferraro et al. 2021), creating spatial heterogeneity and dynamics.

The magnitude and direction of herbivore impact on nutrient cycling is largely determined by the identity and the density of herbivores present in the community (Pastor and Naiman 1992; Bakker et al. 2004). Herbivores with different digestive physiology (i.e., ruminant, cloaca digestive system body mass (le Roux et al. 2020) and migratory behaviours (i.e., migratory vs sedentary, McInturf et al. 2019) have different diet preferences, exploit resources differently (i.e., grazers, browsers, mixed feeders, Wrench et al. 1997) and produce subsidies of varying quality at different times of the year (Defourneaux et al., in prep). Moreover, different herbivores spread nutrients within and across ecosystems to varying extents depending on their range of movement and daily behaviour (Earl and Zollner 2014).

In tundra ecosystems, resources are limited because of the short growing season and strong nitrogen and phosphorus co-limitation (Nadelhoffer et al., 1991). To exploit these patchy resources, herbivores move across the landscape and typically congregate where nutrient availability in forage plants is high, as their fitness and survival depends on nutrient intake (Van Beest et al. 2023). This aggregation intensifies their impact on nutrient cycling and creates a positive feedback loop, by providing nutrients via waste deposition in areas where nutrient content is already high (Hik and Jefferies 1990; Elschot et al. 2015). In contrast, other studies suggest that herbivores can decelerate nutrient cycling, especially when feeding in nutrient poor systems. This is because herbivores are expected to slow down decomposition by promoting plants with low nutrient quality, resulting in a slow-decomposing litter which favours soil fungi (Pastor et al. 1988).

Despite these general predictions, grazing effects on biogeochemical processes can vary widely, even within ecosystems of similar levels of nutrients. For instance, recent studies have found that herbivores may unexpectedly increase in soil nutrients in nutrient poor habitats as a result of nutrient translocation by herbivores moving between habitats, and thus, redistributing nutrients (Stark et al. 2015); and few attempts have tried to empirically quantify these fluxes (Mosbacher et al. 2016). Such results emphasised the need of incorporating herbivore-mediated nutrient transport into our understanding of biogeochemical processes across ecosystems with varying levels of nutrient. Yet, most studies focus on the effects of a single herbivore species and do not account for the diversity of herbivores present within an area (Barbero-Palacios et al. 2024). Understanding the role of herbivores in nutrient transport in a multispecies context can provide valuable insights into nutrient dynamics in tundra ecosystems at large spatial scales, which are essential for the management and conservation of these habitats.

Animal foraging and movement, often driven by nutrition, serve as crucial links to understanding nutrient cycling dynamics (Ellis-Soto et al. 2021). To gain a deeper understanding of herbivore-driven nutrient redistribution, we explored the relationship between nutrient availability, herbivore foraging behaviour at the community level, and nutrient deposition through herbivore faeces. We used Iceland as a case study, focusing on the tundra ecosystem found in the central Highlands of the country. The Icelandic tundra encompasses about 60% of the total grazing area of Iceland and is used by free roaming livestock and wild herbivores during the plant growing season (i.e., late June to early September, Defourneaux et al. 2024). In the eastern part of the country the herbivore community is dominated by three widespread tundra species: the pink-footed goose (*Anser brachyrhynchus* B.*)*, the domestic sheep (*Ovis aries* L.*)*, and the reindeer (*Rangifer tarandus* L.*)*. Concurrent to environmental changes over the last decades, herbivore communities in Iceland have increased in overall density and slowly shifted from a sheep-dominated community towards a wilder herbivore community (Defourneaux et al. 2024b). Understanding how different herbivore species mediate the spatial flow of nutrients and ultimately influence nutrient dynamics in tundra ecosystems is crucial for better management of the rangelands. Specifically, we aimed to answer the following research questions:

1) How do forage biomass, forage quality, nutrient availability, and herbivore consumption rates change throughout the growing season? Does the quantity of nutrients available (N, P, and C) and quality (C:N, C:P and N:P) in forage plant species drive herbivore consumption?

We expect forage biomass to be higher, but nutrient availability and forage quality to be lower later in the growing season as plants senesce. In turn, we predict greater herbivore consumption later in the season, to compensate for the decline in plant quality. Thus, we expect a strong relationship between the quantity of nutrients available in forage plant species and herbivore consumption, and we expect this relation to change over the growing season. Specifically, we expect higher levels of N and P to be associated with greater biomass consumption, and higher levels of C to be associated with reduced consumption. In landscapes where nutrients are available in limited quantity, herbivores tend to target nutrient-rich areas of the landscape, favouring plant species with higher in N and P content (Van Langevelde et al. 2008), while avoiding those with high C content . Thus, herbivores may seek for patches of low C:N and C:P ratios. The relationship with N:P is less clear, but larger herbivores may prefer plants with lower N:P ratio, as they require more P for skeletal investment (May and El-Sabaawi 2024). In contrast, small herbivores may prefer plants with higher N:P, because of their fast metabolism, and high N requirements (Sterner et al. 1992; Sitters et al. 2017). Thus, at the community level, it may be more difficult to detect a clear relationship between N:P levels and consumption, unless one functional group of species (small vs large) clearly dominates the herbivore community.

2) Is faecal nutrient deposition by herbivores greater in nutrient rich vegetation? Does the magnitude of nutrients deposited differ between herbivore species?

Specifically, we predict that nutrient return will be primarily driven by geese, as these are the more abundant species. We anticipate that faecal nutrient deposition from geese will be concentrated in nutrient-rich areas, due to their reduced mobility especially early in the season when they are nesting. In contrast, we expect larger, more mobile herbivores such as sheep and reindeer to distribute nutrients more evenly, potentially inducing nutrient transport from nutrient-rich patches, where they feed, to nutrient-poor patches, where they defecate and rest.

2. Methods

2.2. Study area

Sampling was conducted in the East highlands of Iceland, above 300 m a.s.l (**Figure 1**, 65.3234 °N, 15.3062 °E). Mean temperature ranges from -3.5°C in winter (October to Mai, based on average monthly temperatures), and 6.5 °C in summer (June to September, based on average monthly temperatures) (Icelandic Meteorological Office Database 2024), and annual precipitation varies between 710 mm and 830 mm (Óskarsdóttir et al. 2024). Permafrost is found at high elevation on the edge of the large Vatnajökull glacier (Farbrot et al. 2007). The vegetation is highly heterogeneous, and alternates between extensive barren areas, and small mosaics of low-lying vegetated areas including heathlands, natural grasslands, marshes, and peat bogs (Ottósson et al. 2016). Common plant species include a mixture of small woody species (e.g. *Salix sp., Empetrum* spp., *Vaccinium* spp.), rushes (e.g. *Kobresia myosuroides*), sedges (e.g. *Carex bigelowii*), and grasses (e.g. *Festuca richardsonii, Calamagrostis neglecta*) (Arnalds et al. 2010; Óskarsdóttir et al. 2024).

2.3. Herbivore species

Pink footed goose, sheep and reindeer overlap in the study area during the growing season (Boulanger-Lapointe et al. 2022). Pink footed goose are the most abundant species reaching densities of up to 28.7 nests.km^{-2} in breeding sites (Stefánsson et al. 2022), but overall represent a small fraction of the herbivore biomass (Defourneaux et al. 2024b). Other avian herbivores, like ptarmigan (*Lagopus muta*) and whooper swan (*Cygnus cygnus*) are also present in the area, but at a very low density, thus were not included in this study.

Throughout the growing season, pink-footed geese, sheep, and reindeer feed on a mixture of forbs (e.g., *Bistorta vivipara*), sedges (e.g., *Carex bigelowii*), grasses (e.g., *Poa* sp., *Festuca richardsonii*, and *Calamagrostis neglecta*), horsetails (*Equisetum arvense* and *E. variegatum*), and dwarf shrubs (e.g., *Salix herbacea* and *Salix arctica*). Early in the season, horsetails and shrubs make up a larger part of the sheep's diet, shifting towards sedges later in the season (Thórhallsdóttir and Thorsteinsson 1993). Graminoids make up the largest portion of the diet for both sheep and geese, particularly as the season progresses, while dwarf shrubs are more important in the reindeer's diet (Thórhallsdóttir and Thorsteinsson 1993; Þórisson 2018).

2.4. Sampling design

During summer 2022, we sampled 21 sites (**Figure 1**) randomly selected across the study area based on their accessibility and the probability of occurrence of each herbivore species (based on Boulanger-Lapointe et al., 2022). Our selection assumed a positive correlation between the

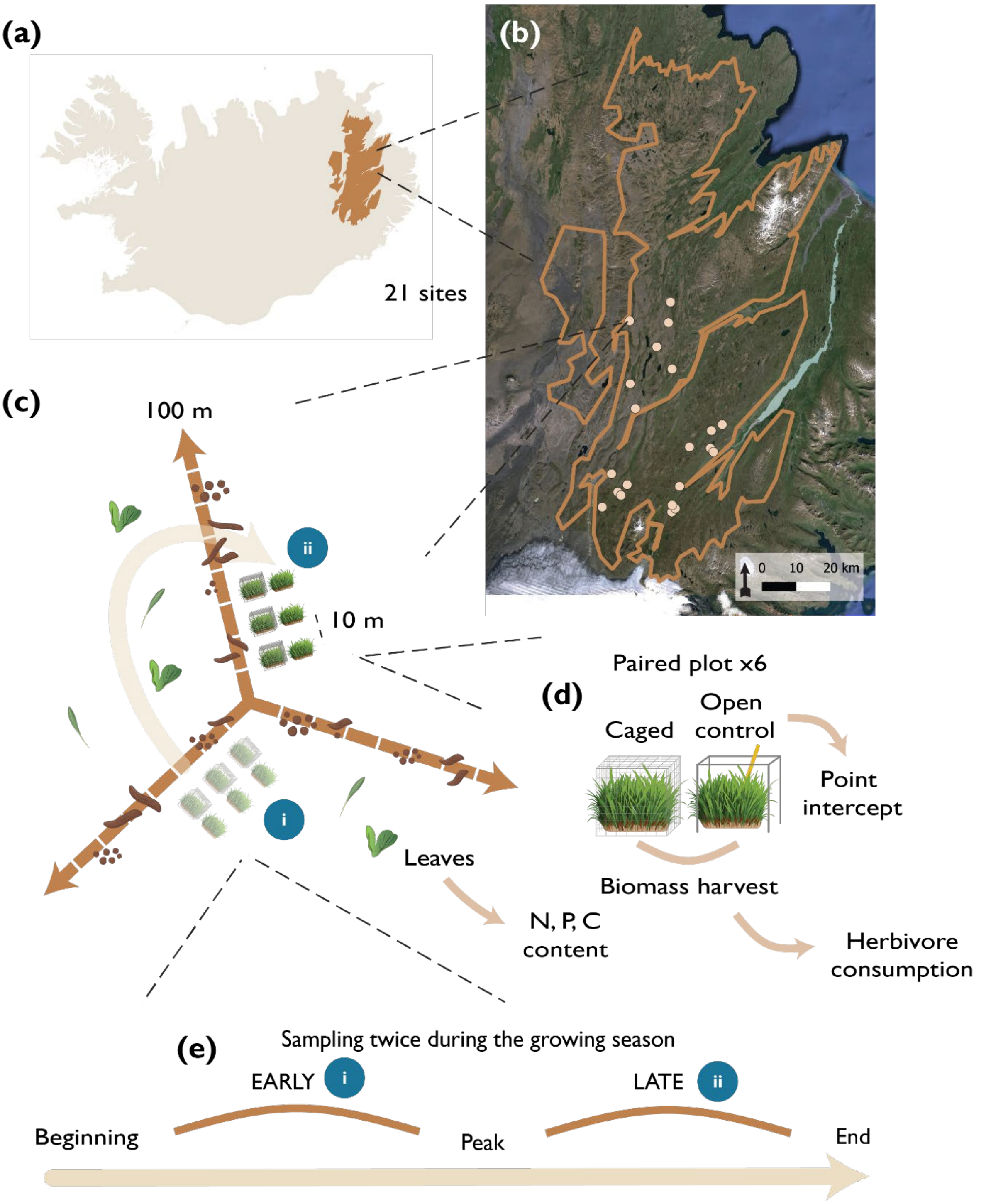

Figure 1: The study area is in the eastern Icelandic highlands (a). We sampled 21 sites (b), twice across the growing season 2022 (e). In each site, we set three 100 m long, 1m wide transects for pellet counts at the end of the growing season (c). We set 3 paired plots (cage and uncaged) to measure herbivore consumption through biomass harvests (d); these plots were moved across the sampling season (circular arrow) to represent respectively what has been consumed during early (i) and late (ii) season. Plant community composition was assessed on the open control plots when cages were set, using the point intercept method. We collected plant leaves form target species at each at the beginning and peak of the growing season.

probability of occurrence and density of herbivores. We selected 7 sites with a high probability of occurrence of each species (pink footed goose, sheep, and reindeer). All sites were selected at least 1.5 km away from main roads and 1 km to each other, to avoid excessive human disturbance and potential spatial autocorrelation. Sites were visited during three sampling sessions, at the beginning (20th of June - 9th of July), the peak (24th of July - 8th of August), and the end (25th of August - 10th of September) of the growing season.

2.5. Plant biomass consumption by herbivores

We used movable cages (McNaughton et al. 1996) to quantify herbivore consumption. In each sampling site, three paired plots (caged and open control plots, Ikea drawers Jonaxel 50x51x15 cm) were set up, with aboveground biomass collected twice during the growing season (at the peak to evaluate total herbivore consumption early in the season, and at the end, to assess herbivore consumption later in the growing season, **Figure 1**). The three paired plots were established at the beginning of the growing season along three 100 m transects irradiating from the centre of the site (**Figure 1**), 10 m apart at 10, 20 and 30 m from the centre of the sampling site. The paired plots were moved clockwise to the next transect after each biomass harvest, to account for potential compensatory regrowth of vegetation due to herbivory (McNaughton et al. 1996). Within each paired plot, aboveground plant biomass was harvested at moss or soil levels, in both the caged and open control plots in a central 33 x 33 cm square (i.e., to avoid edge effect). Biomass samples were air dried and weighted to the nearest 0.1 g upon return to the lab. We defined herbivore consumption (i.e., amount of aboveground plant biomass consumed by herbivores, in g DW.m^{-2}), as the difference in dry weight of biomass between caged and open control plots within each pair, adjusted by the biomass in open control plot. Negative values for biomass consumption were recorded in some sites due to high environmental variation between open control and caged plots.

2.6. Estimate of nutrient availability and forage quality

2.6.1. Forage biomass

Plant community composition was assessed twice during the growing season (beginning and peak) on the open control plots, and was used to estimate the biomass of forage species available for grazing. Specifically, we used a 50 x 50 cm point intercept frame with 25 points and recorded the average number of hits per pin of each species of vascular plants. We defined as forage plant species, a set of 9 key species known to be part of herbivore diet and be abundant in the area (Thórhallsdóttir and Thorsteinsson 1993; Anderson et al. 2012; Þórisson 2018). Key forage plant species included two deciduous shrubs (*Salix arctica* and *Salix herbacea*), four grasses (*Festuca richardsonii*, *Calamagrostis neglecta*, *Poa alpina*, *Deschampsia alpina*), one pteridophyte (*Equisetum arvense*), one forb (*Bistorta vivipara*), and one sedge (*Carex spp* including *C. bigelowii* and *Carex nigra*). From the point intercept data (IF), the biomass (BM) of each forage species was calculated using a conversion factor (Bråthen and Hagberg 2004; Ravolainen et al. 2010; see Mörsdorf 2015 for an application of this approach in Iceland). We defined total forage biomass as the sum of the biomass of the forage plant species, and total plant biomass as the sum of biomass of all vascular plant species. Standing senescent material was not included.

2.6.2. Forage nutrient content

To measure %N, %P and %C contained in forage plant species, we randomly harvested (approx. 1-3 DM g) of fully developed leaves from the 10 plant species from various individuals at each sampling site, avoiding the paired plots to not interfere with biomass harvest. Sample collection was made at the beginning and peak of the growing season. We targeted leaves which did not show any signs of insect herbivory nor diseases. We chose to focus only on aboveground vegetative parts of plants assuming that nutrient contents in the leaves will be a good proxy for what is contained in the plants (Zhang et al. 2021). Plant samples (n = 221) were pressed for storage in the field. After the field season, plant samples were oven dried at 40°C for 48h and stored in air-tight bags with silica gel in the fridge until further analysis. Plant samples from each species were pooled together at the site level and milled with a ball mill (Retsch mm 200 model mixer mill) at a frequency of 300 Hz for 1.5 min. About 150 mg of fine powder was pressed into tablets (Ø 15 mm, 1 mm thick) with a hydraulic press and 4 tons of pressure. If available, remaining material was put aside for further wet-laboratory analysis (n = 44, **Supplementary material 1**). The tablets were dried at 40°C for 2.5 hours to remove any potential water films which might affect the absorption patterns in the near infrared region (Givens et al. 1997), and were stored in desiccators at room temperature (approx. 20°C) until scanning. We scanned each tablet 3 times, on the same surface using a spectroradiometer (ASD LabSpec 4) with a contact probe attachment. We estimated total foliar N, P and C concentrations (% Dry Weight, DW) based on the Arctic-Alpine model (Murguzur et al. 2019). The model was developed including the same plant species, but from different biogeographical regions (i.e., Fennoscandia, Svalbard and French Alps). To ensure that the models could be used on Icelandic samples, we compared the modelled values of a subset of samples (n = 44 for N and C, and n = 34 for P) with foliar N, P and C concentration obtained from wet-laboratory analysis (**Supplementary material 1, Table S1.1**).

2.6.3. Nutrient availability and forage quality

We combined the estimated standing biomass (BM_{ij}) with the associated nutrient content (Nut_{ij}) for each forage plant species *i* to compute the total amount of N, P and C (in %DW) available per plot at the peak and late season (*j*). To make the estimates comparable across plots, the total amount of nutrients contained in the forage biomass in each plot was standardized by the total amount of forage available in each plot.

$$Total\ nut_j = \frac{\sum_{i,j} Nut_{ij}\ x\ BM_{ij}}{\sum_{i,j} BM_{ij}}$$

We defined forage quality as the C:N, C:P and N:P ratio.

2.7. Herbivore nutrient deposition

Within each sampling site, we set at the beginning of the growing season, three 100 m transects (**Figure 1**) from a central point outward, where we removed all herbivore pellets present in a 1 m width band (Barrio et al. 2021). At the end of the growing season, we identified and counted each pellet to evaluate faecal deposition rates over the whole summer (i.e., to estimate nutrient input by herbivores across the growing season).

In addition, we measured herbivore faecal nutrient content and faecal dry weight based on fresh faecal samples at the beginning, peak and end of the growing season (at least 30 samples per species and sampling session, Defourneaux et al., *in rev*). To measure faecal nutrient content, we randomly subsampled each faecal sample from at least 3-4 different parts of the pile (i.e., because nutrient content can vary among the pile) to obtain approx. 350 mg of dried matter. Faecal matter was oven-dried at 40°C for at least 24h, milled and pressed into tablets. We estimated N, P and C concentrations (%DW) using the faecal tundra herbivore NIRS calibration model from Defourneaux et al. (*in rev*).

We encountered different types of faeces throughout the season for sheep and reindeer (e.g., individual pellets or clumps). Thus, we estimated the average faecal dry weight (in grams) for each species on 5 samples per species and type of faeces, randomly selected within the total pool of samples. Specifically, for reindeer and sheep, we subsampled approximately 10 g of fresh faeces from a clump, or one individual pellet. For goose we used a full dropping. The samples were oven dried at 40°C for 2 days. By comparing the wet and dry weights, we estimated the dry weight of a full faecal deposition. Total herbivore nutrient deposition was estimated in each site for each herbivore species combining the faecal deposition, averaged faecal weight and average N, P and C concentration.

2.8. Statistical analysis

We first assessed seasonal differences (early vs. late) in aboveground biomass (for forage species and total biomass), nutrient availability and forage quality, and herbivore consumption, using a one-way ANOVA.

Herbivore consumption was modelled at the paired plot level, as a function of nutrient availability (N, P and C) or forage quality (C:N, C:P, N:P) (positive continuous variables), and timing during the growing season (early or late; qualitative variable, binomial) using a Generalized Linear Mixed Model with a Gaussian family. A statistical interaction between the two variables was included in the model to assess if the relationship between herbivore consumption and nutrient availability differed between seasons. Because of multicollinearity among the different chemical elements (i.e. N and P, Spearman rank correlation >0.90, **Figure S2.1**), separate models were fitted for each nutrient and the corresponding ratios, resulting in 6 different models, and we presented the results for N, C, C:N and N:P only. In all models, we fitted site identity as a random intercept to account for environmental variation and the hierarchical structure of the dataset (3 measurements per site). Plots where forage species were absent were excluded from the analysis (n = 3) as our question related to the connection between forage quality and herbivore consumption.

Herbivore nutrient deposition was modelled at the site level, as a function of nutrient availability (N, P and C), and herbivore species (pink-footed goose or sheep, as reindeer faeces were too few to include in analyses, factorial variable). A statistical interaction between the two variables was included in the model to assess if nutrient deposition in sites with different nutrient availability differed between herbivore species. To improve normality of the data, N, P and C deposition values were log-transformed prior to analysis, and were fitted as response variable using a Gaussian error distribution. Non-significant interactions were removed from the model.

For every model, data exploration was carried out following the protocol described in Zuur et al. (2010). We used diagnostic plots to test the assumptions of linearity, normality and homoscedasticity of residuals (Zuur and Ieno 2016). Unless stated otherwise, mean values and standard errors are presented. All analysis were run using R statistical software 4.3.2 (R Core Team 2024). The ANOVAs were conducted using using "*lme4*" (Bates et al. 2015) and "*lmerTest*" (Kuznetsova et al. 2017), and Posthoc Tukey analysis were performed using "*multcomp*" and "*emmeans"* packages (Hothorn et al. 2006; Lenth et al. 2024). We used glmmTMB (Brooks et al. 2017) to run the GLMM.

3. Results

3.1. Seasonal differences in aboveground biomass, herbivore consumption, nutrient availability and forage quality

Biomass of forage species was on average 78.8 ± 7.65 $g.m^{-2}$ per plot. The proportion of forage plant biomass in each plot represented on average 54 ± 2 % of the living vascular plant biomass, ranging between 3-100%. The total forage biomass did not significantly differ between early and late season (**Table S3.1**, ANOVA, F(1) = 0.69 , p value = 0.41). In turn, total aboveground biomass was significantly higher in the late growing season (**Table S3.1**, ANOVA, $F_{(1)}$ = 17 , p value < 0.001).

Nutrient availability (N, P and C), and forage quality (C:N, C:P and N:P) significantly differed between early and late season (**Table S2.1**). Forage N, P and C concentrations were all higher earlier in the season than late, whereas the C:N, C:P and N:P ratios were all lower early in the season than late. From the beginning to the peak of the growing season (approx. 31 days), herbivores consumed on average 8.6 ± 5.4 % of the total aboveground biomass available, while they consumed average 34.3 ± 8,8 % from the peak to the end of the growing season consumed (**Figure 2**). There was significantly less consumption (ANOVA, $F_{(1)}$ = 6.12, p-value = 0.01) during early season compared to late.

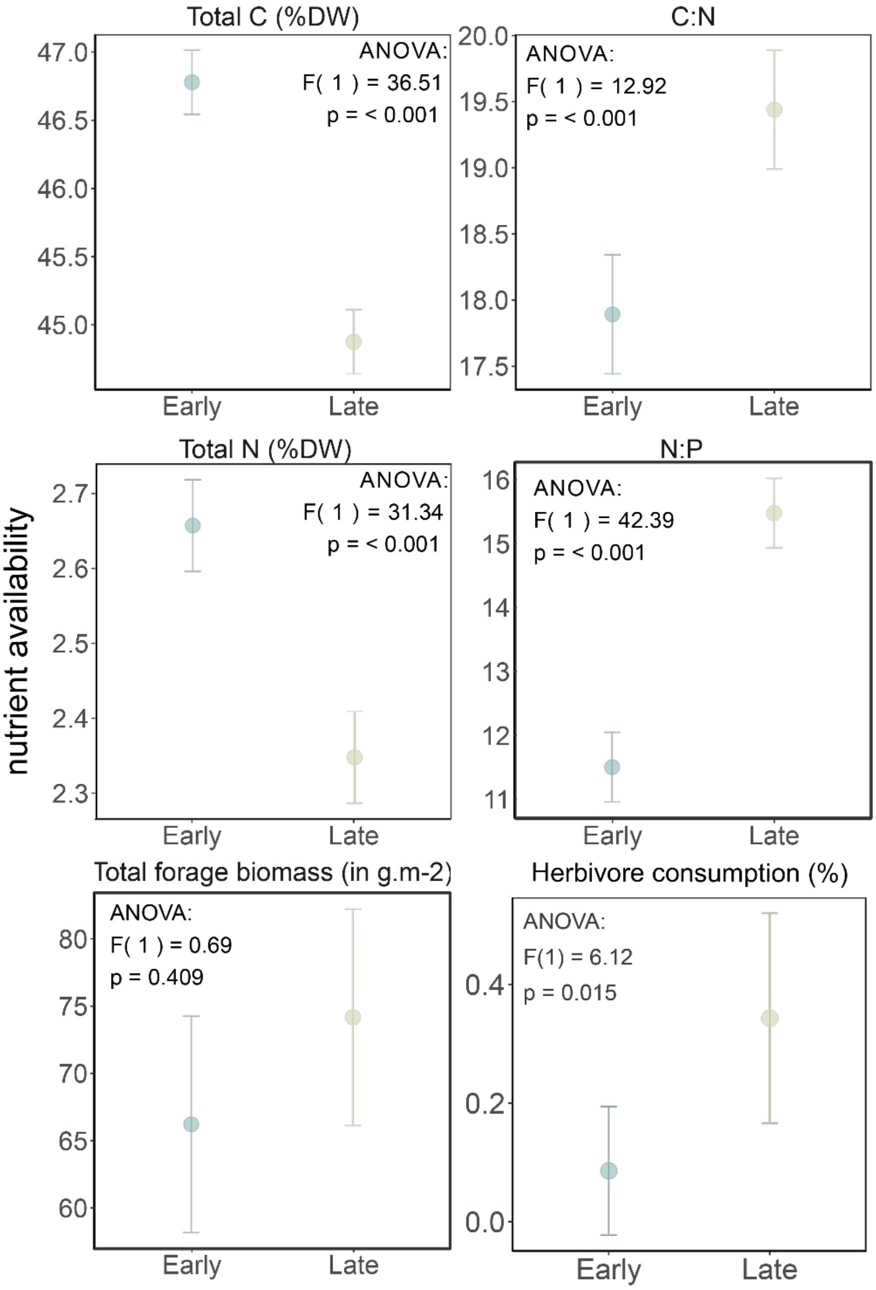

Figure 2: Differences in biomass of forage plants (in g. m^{-2}) and total living biomass (a), nutrient availability and forage quality (b), and consumption rates (c) between early and late season. Nitrogen, phosphorus and carbon concentrations (in %DW) were computed for the forage species available in each sampling plot. Ratios (C:N, C:P and N:P) were subsequentially assessed from the N, P and C concentrations. Means and 95 confidence intervals are displayed.

3.2. Effect of nutrient availability and forage quality on herbivore consumption

Nutrient availability and forage quality did not influence the consumption of aboveground plant biomass by herbivores in early or late season (**Figure 3, Supplementary material 4, Table 4.1**).

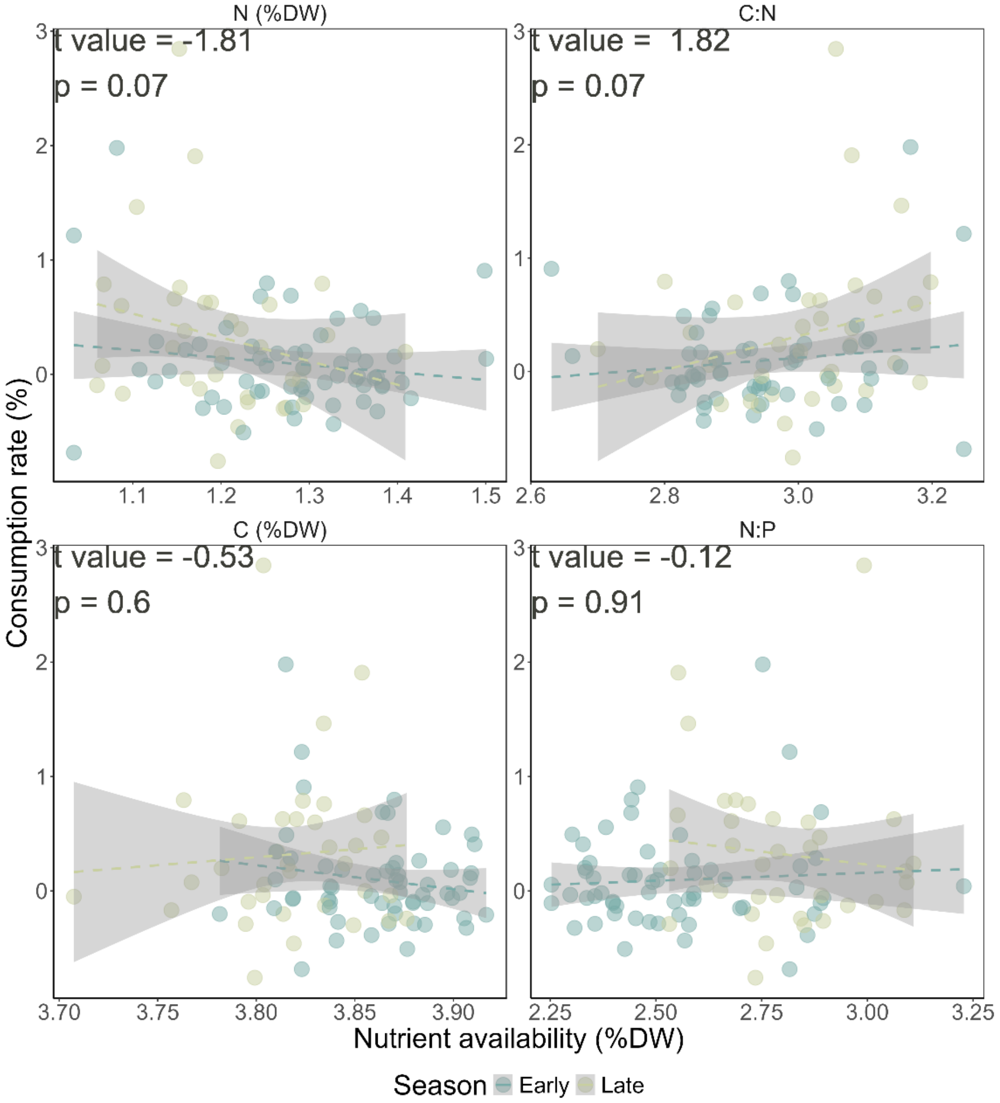

Figure 3: Effect of the nutrient availability and forage quality on aboveground plant biomass consumption by herbivores level during early and late growing season. Dashed lines (predicted mean) indicate non-statistically significant relationships (p >0.05). Shaded areas indicate 95% confidence intervals.

3.3. Effects of nutrient availability on herbivore nutrient deposition

Herbivores deposited on average 11.6 (0.66 - 47.0) g DW.m-^{2}, 1.78 (0.96 -7.94) g DW.m-^{2}, and 166 (104 - 646) g DW.m-^{2} of N, P and C, respectively. Overall, geese contributed the most to the total faecal deposition and reindeer the least (**Supplementary material 4, Table 4.2**). Indeed, reindeer faeces were only found at 5 of the sites, preventing the inclusion of this species in formal analyses by species. Nutrient availability was negatively associated with nutrient deposition for N, P and C in both sheep and geese, with higher deposition of nutrients where nutrients were less available (**Figure 4**). Herbivore species had a significant effect on nutrient deposition, with geese having a greater contribution than sheep.

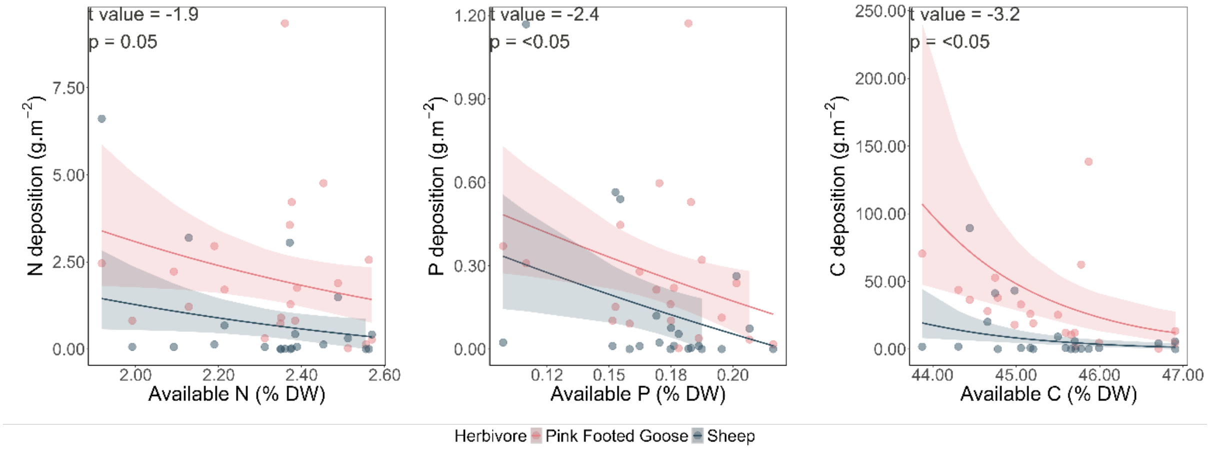

Figure 4: Relation between herbivore nutrient deposition (N, C and P, ing.m-^{2}) and nutrient availability in forage (N, P and C, %DW).

4. Discussion

In this study, we investigated the potential for herbivore nutrient redistribution at the community level in tundra ecosystems. Herbivores consumed significantly more plant biomass late in the season, when nutrient levels in forage plants were lower. In contrast, the amount of forage biomass remained constant throughout the growing season. Surprisingly, we found no significant relationship between nutrient availability or forage quality, or biomass and herbivore consumption at the community level, but herbivores consistently defecated more, and thus contributed more nutrients, in areas where nutrients were less available. The contribution of geese to faecal nutrient deposition was higher than that of sheep. Our results suggest that herbivores drive a net transport of nutrients from nutrient-rich to nutrient-poor tundra patches. This finding highlights the crucial role herbivores play in connecting biogeochemical cycles across different habitats.

4.1. Seasonal changes in herbivore consumption and forage quality

Herbivore consumption rates increased significantly, from 8% early in the growing season to 34% later. These values are much higher than regional estimates of herbivore biomass consumption, previously estimated at 2.65 ± 0.20% for Icelandic rangelands (Defourneaux et al. 2024). Such a large difference could be due to our sampling design, which focused on vegetation patches with good vegetation cover and likely to be used by herbivores, whereas previous estimates covered broader areas, including more bare ground and sparse vegetation patches, and thus diluting consumption rates. However, our results are consistent with global averages for tundra ecosystems, where $\leq$10% of annual vascular plant production is typically consumed by herbivores (Jefferies et al. 1994; Legagneux et al. 2012), and with areas of high herbivore aggregation, such as goose colonies, where consumption rates have been estimated to range from 30% to 80% (Cargill and Jefferies 1984).

Overall, our study shows that herbivore consumption in tundra ecosystems is highly variable, both spatially and temporally, with important shifts in biomass consumption occurring over a short period (30 days) during the growing season, and increasing grazing pressure late in the growing season. The seasonal increase in herbivore consumption observed in our study coincided with a decrease in forage quality, suggesting a possible connection between these two factors (Van Langevelde et al. 2008). Thus, as plants senesce, herbivores may require more forage to meet their energy needs, especially as offspring grow and increase biomass. Growing animals also require more N- and P-rich forage for protein production (Elser et al. 1996).

4.2. Absence of a relationship between herbivore consumption and forage quality

Contrary to our expectations, we found no significant relationship between nutrient availability or forage quality and herbivore consumption at the community level. Those results contradict existing models that predict a positive correlation between forage quality and herbivore consumption (Van Langevelde et al. 2008; Iversen et al. 2014). The presence and abundance of different herbivores with more contrasting diet preferences could blur consumption patterns at the community level. Several studies have shown that small and intermediate-sized herbivores are typically more sensitive to forage quality, as they require highly digestible food (Sheremetyev et al. 2017; Rozenfeld and Sheremetyev 2021; Sheremetev 2023). In contrast, larger herbivores are usually less selective, and may prioritise patches with higher forage quantity to maximise intake (Shipley 2007). For instance, reindeer in Svalbard have been observed to prioritise patches of high biomass over high quality forage at both landscape and patch scales (Van Der Wal et al. 2000). While some species of geese have been shown to feed more on patches with intermediate nutrient levels, as a trade-off between forage quality and quantity (Van De Koppel et al. 1996; Hassall et al. 2001).

Furthermore, individual foraging preferences can vary considerably within the same species influenced by factors such as herbivore density (Kausrud et al. 2006; Mobæk 2012; Mobæk et al. 2012), interspecific competition (La Morgia and Bassano 2009), chemical constraints (Forchhammer and Boomsma 1995), or predation avoidance (Hopcraft et al. 2010; Weterings et al. 2018). For instance, geese may feed near water bodies, that serve as refuges; while reindeer, may shift their diet to alternative food sources in response to hunting pressure and human disturbances (e.g. tourism). Sheep movements, on the other hand, may be constrained by natural and artificial barriers specific to Icelandic grazing system. Life history traits can further constrain foraging behaviour. For example, geese are restricted to nesting areas early in the season, limiting their access to optimal forage (Anderson et al. 2012). Moreover, our study focused on aboveground resources, potentially missing part of the herbivore diet, such as underground foraging by geese (e.g., grubbing, Pedersen et al. 2013).

Overall, herbivores respond to their heterogeneous environment in complex ways across spatial and temporal scales, making it difficult to identify the drivers of herbivore consumption in tundra ecosystems. Experimental approaches, such as size-selective exclosures, could help to capture species-specific consumption patterns at the patch level (Barrio et al. 2021). A deeper understanding of the dietary preferences of the three herbivore species coexisting in Iceland, would also help disentangle how they partition their food resources.

4.3. Nutrient accumulation from herbivore faeces in poor forage quality patches

The fact that herbivores transferred more nutrients to low-quality forage is consistent with growing evidence on the role of herbivores in nutrient transport and redistribution across ecosystems (Polis et al. 1997; McInturf et al. 2019; Ellis-Soto et al. 2021). As expected, nutrient transfer was mainly driven by geese, as also observed in (Defourneaux et al. in rev). Notably, no reindeer faeces were recorded during the study, indicating their limited impact on nutrient flow compared to the more abundant sheep and geese (Defourneaux et al. 2024; Defourneaux et al. in rev). However, we did not observe substantial differences between herbivore species of the direction of the nutrient transport; both sheep and geese deposited more nutrients in areas of low forage quality.

In tundra ecosystems, herbivores are generally thought to accelerate nutrient cycling, exerting a strong positive feedback on productive patches (Du Toit and Olff 2014). This is typically facilitated by compensatory plant regrowth, rapid decomposition of high-quality litter, and substantial nutrient inputs via herbivore waste. Conversely, herbivores are believed to exert a negative feedback on low-quality patches by favouring plants with lower nutrient content, thereby reducing litter quality (Pastor and Naiman 1992; Stark 2007). In such cases, faecal deposition may have a limited impact on plant productivity at the ecosystem scale due to its localised effects (Pastor et al. 1988). In contrast, our results suggest that herbivores consume plant biomass regardless of forage quality, but redistribute nutrients along a gradient of plant nutrient availability, effectively transporting nutrients across the landscape and depositing nutrient-rich waste in nutrient-poor areas. This is consistent with other studies in tundra environments that have shown that herbivores can increase nitrogen availability in less productive habitats by moving nutrients from nutrient-rich to nutrient-poor patches (Post et al. 1998; Stark et al. 2015; Mosbacher et al. 2016; Ferraro et al. 2021).

From a long-term perspective, nutrient inputs from herbivores in patches with lower forage quality could influence vegetation dynamics by providing ressources in labile nutrients (Sitters and Olde Venterink 2021) which are more easily decomposable that plant litter (Yang et al. 2019) . Long-term experiments suggest that herbivore faecal deposition can have lasting effects on patches with lower nutrient availability, ultimately improving plant nutrient acquisition and growth while creating nutrient hotspots through localised faecal deposition (Barthelemy et al. 2015). In areas where forage quality is low, this process may enhance the plant palatability, potentially making them more attractive to some herbivores. Previous studies in northern rangelands have shown that grazing can extend the availability of high-quality grasses throughout the growing season, highlighting the potential for grazing to facilitate improved forage quality later in the season (Mysterud et al. 2011).

Overall, to improve our understanding of the relative impacts of herbivores in a multispecies context at the landscape scale, we suggest incorporating large-scale approaches, that combine telemetry to track herbivore movement patterns with stoichiometric distribution models for assessing nutrient availability (Leroux et al. 2017; Balluffi-Fry et al. 2022). While these approaches would require substantial amounts of data, they could offer valuable insights by revealing "hotspots" of productivity resulting from herbivore activity.

4.4. Implications for management

Herbivore communities in the Arctic are changing rapidly with large increases in goose populations (Alisauskas 2000) and shifts between domestic and wild species (Defourneaux et al. 2024b). The spatial overlap of geese, sheep and reindeer has spilled a lot of ink in Iceland, where the increasing abundance of wild species is usually perceived as a threat to farming (Pozo et al. 2021). Investigating the contribution of different herbivores to nutrient budgets can provide valuable information on their relative impact on ecosystem functions, and in particular nutrient cycling. In high latitude tundra, the large amounts of faecal nitrogen and phosphorus deposited by smaller herbivores, like geese, appear to have important positive feedback to ecosystems, ultimately affecting forage quality, and creating vegetation pulses (Hik and Jefferies 1990; Beard et al. 2023). However, the direction and magnitude of such changes seems to vary considerably depending on the type of vegetation in which herbivores deposit their faeces (Sjögersten et al. 2010). More effort should be allocated to documenting the behaviour of herbivores in Icelandic tundra ecosystems to establish when and where their presence needs to be considered in the biogeochemical functioning of these ecosystems.

5. Conclusion

Our study provides strong evidence that herbivore consumption in Icelandic ecosystems is not determined by forage quality or quantity. Instead, a variety of factors, including individual preferences, environmental constraints, and life history traits, could shape their foraging behavior. Moreover, we provide the first evidence of herbivore-mediated transport of nutrients at the community level in Icelandic tundra rangelands. This finding emphasises the crucial role herbivores play in biogeochemical cycles across different habitats.

To effectively manage these ecosystems, it is essential to understand the complexity of herbivore foraging behavior and its impact on nutrient transport within a multispecies context. Emphasis should be placed on conducting studies that specifically measure the effects of different herbivores, both separately and in combination. This approach will help gaining in better understanding of the direction and magnitude of herbivore roles in nutrient transport and biogeochemical processes.

Acknowledgements

We would like to thank Anya Boardman, Björk Kristjánsdóttir, Charlotte Wagner and Ludivine Panot for fieldwork and sample collection, and Janine G. Lock, Eleanor Greer, Sebastian A. Damböck, Snæbjörn Jack and Katharina Wilfert for lab processing. Finally, we would like to thank Náttúrustofa Austurlands for their support in fieldwork.

Funding

This work was supported by the Icelandic Research Fund (grant number 217754 and 2410773-051); the Nordic Borealization Network (NordBorN, funded by NordForsk grant number 164079); and Landsvirkjun (grant number NÝR-22-2022 and NÝR-26-2023). JS is grateful to the Research Foundation–Flanders (FWO) for funding the Scientific Research Network: Zoogeochemistry, Alchemists of the Wild (project No. W001522N) and the Bijzonder Onderzoeksfonds of the University of Antwerp for research funding (grant number 44158)

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Supplementary Information

This supplementary information has not been peer reviewed.

Nutrient redistribution by herbivores across a tundra landscape

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Supplementary material S1: Assessment of nutrient availability within forage plant species

Supplementary material S2: Data exploration

Supplementary material S3: Differences in forage and total biomass, nutrient availability and forage quality, and herbivore consumption, during early and late growing season

Supplementary material 4: Results from regression analysis

Supplementary material S1: Assessment of nutrient availability within forage plant species

NIRS measurements:

Approximately 150 mg of the ground plant material was pressed into tablets (Ø 15 mm, 1.3 mm thick) using a 4-tonne hydraulic press. The tablets were then dried at 40°C for 2.5 hours to remove any water films that may have formed, near infrared absorption patterns (Givens et al. 1997). Tablets were then stored in desiccators, at room temperature (approx. 20°C), to keep them dry until scanning. Each tablet was scanned three times on the same surface using a spectroradiometer (ASD LabSpec 4) and a contact probe attachment. The spectroradiometer covered a wavelength range of 350 to 2500 nm, with a 1.4 interval resolution in the 350-1000 nm range, and a 2 nm interval resolution in the 1000-2500 nm range, generating 1214 data points per sample and scan.To evaluate the amount of N, P and C contained in the samples, we used the predictions from the arctic–alpine model (Murguzur et al. 2019). However, because this model was never used in Iceland before, we check the predictive abilities of the model on a subset of samples of know nutrient concentrations.

Thus, we analysed n = 44 samples for C and N and n = 34 samples for P of ground samples using wet laboratory. Specifically, we used a Flash 2000 CN analyser (Thermo Fisher Scientific, Waltham, MA, U.S.A.) to assess plant C and N concentrations (on subsamples of 10 mg; detection limit = 0.005%). Total P content was determined by acid digestion with H_2SO_4, salicylic acid and H_2O_2 (on subsamples of 300 mg; detection limit = 0.03 mg/L) and followed by calorimetric analysis (Skalar SAN++; Breda, The Netherlands; Walinga et al. 1989). We then used linear regression models to assess both the fit of the predictions (by analyzing the intercept and slope) and their accuracy (using the root mean square error of prediction RMSEP and the coefficient of determination R^2).

Table S1: Model parameters for the regression analysis between chemical content predicted from single leaves and tablets

Nutrient	Intercept	Slope	R2	RMSEP
C	-7.62	1.13	0.75	1.57
N	-0.043	1.06	0.93	0.20
P	0.076	0.95	0.82	0.045

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Givens, D. I., J. L. De Boever, and E. R. Deaville. 1997. The principles, practices and some future applications of near infrared spectroscopy for predicting the nutritive value of foods for animals and humans. *Nutrition Research Reviews* 10: 83–114. doi:10.1079/NRR19970006.

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Supplementary material S2: Data exploration

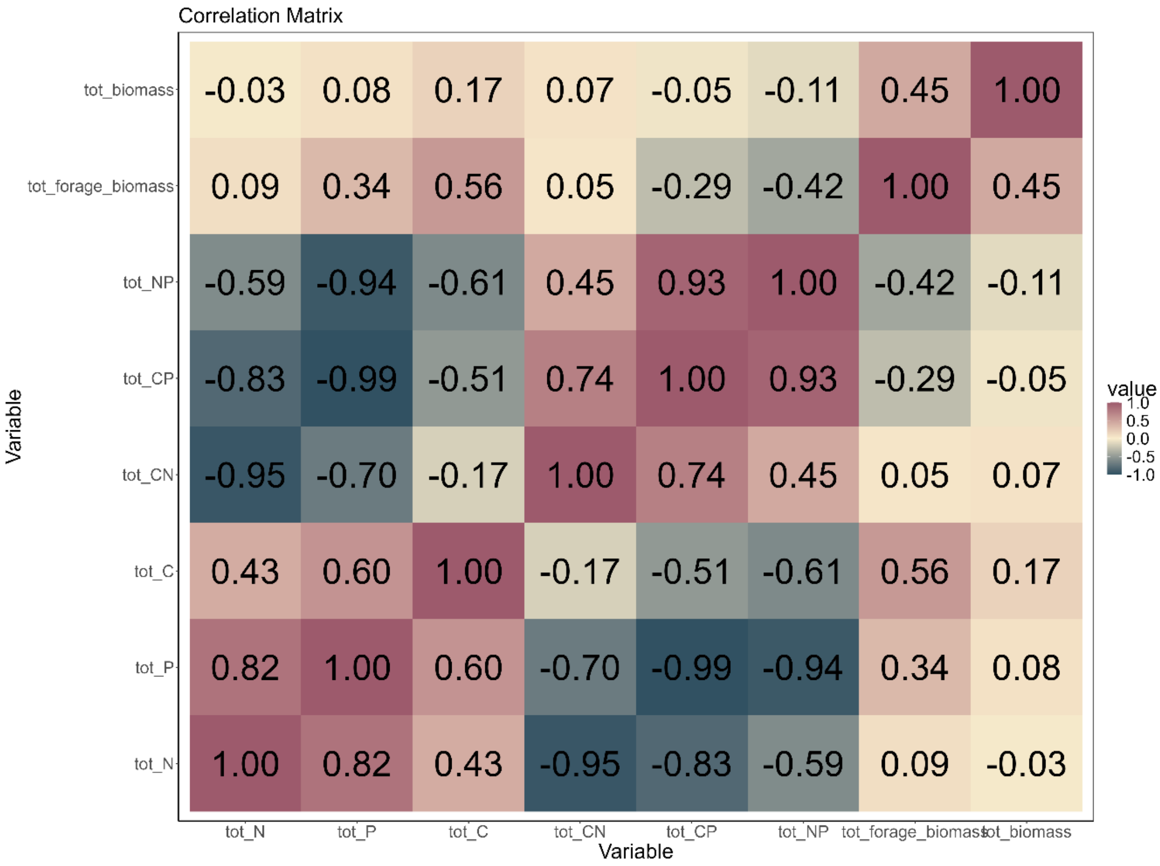

Figure S2.1: Correlation matrix showing correlations between variables assessing the total nutrient availability (N, P and C) and forage quality (C:N, C:P and N:P).

Table S2.1: Summary statistics (max, mean, median, min, standard deviation and standard error) of the plot level nutrient availability (total N, total P and total C) and forage quality

Nutrient	Max	Mean	Median	Min	sd	se
N	6.19	1.81	1.57	0.16	1.26	0.08
P	0.5	0.14	0.11	0	0.11	0.01
C	123.49	37.28	29.87	2.62	27.13	1.81
C.N	35.23	20.81	20.26	12.88	3.95	0.26
C.P	1677.32	331.15	302	137.5	184.65	12.34
N.P	56.32	15.41	14.38	8.71	5.78	0.39

Supplementary material S3: Differences in forage and total biomass, nutrient availability and forage quality, and herbivore consumption, during early and late growing season

Table S2.1: Summary of the one way ANOVA analysing the difference in forage and total biomass (g.m-2), nutrient availability (N, P and C, in %) and forage quality (C:N, C:P, N:P), and herbivore consumption rates (in %) at early and late growing season

Variable	df	sumsq	meansq	statistic	p value
N	1	2.09	2.09	31.34	< 0.001
P	1	0.14	0.14	55.71	< 0.001
C	1	79.24	79.24	36.51	< 0.001
C:N	1	52.5	52.5	12.92	< 0.001
C:P	1	211652.5	211652.5	31.39	< 0.001
N:P	1	346.07	346.07	42.39	< 0.001
Forage biomass	1	1388.92	1388.92	0.69	0.409
Total biomass	1	119502.5	119502.5	17	< 0.001

Supplementary material 4: Results from regression analysis

We modeled herbivore consumption as a function of nutrient availability or forage quality, as well as the timing within the growing season (categorized as B for peak or C for late, a qualitative binomial variable). We used generalized linear models with a Gaussian family for this analysis. Separate models were developed for each nutrient (N, P, and C) and their ratios (C:N, C:P and N:P), leading to a total of six models. To account for environmental variability, site identity was included as a random effect.

Table S4.1: Results from the regression analysis, herbivore consumption as a function of forage quality (in term of N%, P%, C%, C:N, C:P and N:P), seasonnality (B = early and C = late) and forage quantity.

Nutrient	term	estimate	std.error	t.value	p.value
N	Intercept	1.43	0.74	1.91	0.06
	late season	0.14	0.12	1.17	0.24
	tot_N	-1.05	0.58	-1.81	0.07
	tot_forage_biomass	0.00	0.00	0.14	0.89
P	Intercept	0.26	0.25	1.04	0.30
	late season	0.16	0.14	1.16	0.24
	tot_P	-0.93	1.26	-0.74	0.46
	tot_forage_biomass	0.00	0.00	0.29	0.77
C	Intercept	4.42	8.18	0.54	0.59
	late season	0.17	0.15	1.15	0.25
	tot_C	-1.13	2.13	-0.53	0.60
	tot_forage_biomass	0.00	0.00	0.36	0.72
C:N	Intercept	-2.30	1.32	-1.75	0.08
	late season	0.18	0.12	1.52	0.13
	tot_CN	0.82	0.45	1.82	0.07
	tot_forage_biomass	0.00	0.00	-0.15	0.88
C:P	Intercept	-0.77	1.13	-0.68	0.50
	late season	0.17	0.13	1.26	0.21
	tot_CP	0.16	0.2	0.76	0.44
	tot_forage_biomass	0.00	0.00	0.28	0.78
N:P	Intercept	0.20	0.89	0.22	0.82
	late season	0.24	0.14	1.63	0.10
	tot_NP	-0.04	0.33	-0.12	0.91
	tot_forage_biomass	0.00	0.00	-0.04	0.97

Table S4.2: Results from the regression analysis, herbivore faecal deposition as a function of forage quality (in term of N%, P%, C%) and herbivore species (sheep or gesse)

Nutrient	Term	Estimate	std.error	T value	P value
	Intercept	3.09	1.11	2.78	<0.05
N	herbivoresheep	-0.58	0.17	-3.47	<0.05
	tot_N	-0.91	0.47	-1.93	0.05
	Intercept	0.65	0.19	3.5	<0.05
P	herbivoresheep	-0.11	0.05	-1.94	0.05
	tot_P	-2.53	1.06	-2.39	<0.05
	Intercept	34.79	9.76	3.56	<0.05
C	herbivoresheep	-1.67	0.34	-4.87	<0.05
	tot_C	-0.70	0.21	-3.25	<0.05