Influence of reindeer herbivory on Arctic ecosystem structure and functioning across spatial and temporal scales

Marcus P. Spiegel

Christ Church

University of Oxford



A thesis submitted for the degree of

Doctor of Philosophy

Supervised by:

Professor Marc Macias-Fauria

Michaelmas 2022

Abstract

Top-down and bottom-up forces interact to regulate ecosystem structure and functioning across Earth's biomes. In the Arctic, warming is outpacing the global average and driving extensive changes including increases in permafrost thaw and vegetation productivity. These ecosystem responses are mediated by herbivores, particularly reindeer, which are the only large herbivores presently widespread in tundra environments. Herbivory in the Arctic affects vegetation productivity, plant community composition, and soil thermal regimes, and thus has implications for the carbon cycle and energy balance potentially relevant to global-scale climate feedbacks. However, our understanding of these Earth system consequences is hindered by uncertainty as to whether herbivory remains a major control on ecosystem processes over larger, regional scales in the Arctic and how the effects of herbivory vary in space and time.

This thesis aims to detect and characterise the influence of reindeer herbivory from the regional to the plot scale and depending on the time since and duration of herbivory events. The research focussed on the Yamal Peninsula, where Indigenous Nenets mobile pastoralists manage the world's largest domesticated reindeer herds, and included analysis of remote sensing products and field-based data collection. The objectives of the thesis are addressed through three studies presented as separate research articles.

The first article, '**Top-down regulation by a reindeer herding system limits climate-driven Arctic vegetation change at a regional scale**,' used spatial comparisons to determine whether differences in vegetation across a large swath of the Yamal Peninsula were linked to variations in reindeer herbivory pressure. By creating new maps of herd sizes and decades-old migration routes and integrating these data with remote sensing products, this work found that higher reindeer density was linked to lower coverage of tall woody vegetation and less sensitivity of productivity to climate within this vegetation type. These findings were consistent across six separate lines of evidence, leading to the conclusion that reindeer have had a significant, albeit modest, effect at the regional scale that has limited the cover of tall woody vegetation and its growth and expansion with warming.

The second article, '**Heterogeneity in immediate and lagged effects of reindeer herbivory over spatially comprehensive fine scales**,' included landscape-scale analysis that involved conducting repeat unmanned aerial vehicle (UAV) surveys next to a campsite of Indigenous Nenets managing a large herd. The surveys occurred immediately before the herd arrived at the campsite, immediately after they had left the site to migrate onwards, and one month after the herd's activity to map vegetation changes, continuously over space at very fine, centimetre-scale resolution. The processing of the UAV imagery employed structure-from-motion (SfM) photogrammetry in a novel workflow that enabled detection of significant canopy height changes between surveys exceeding a spatially variable limit of detection based on photogrammetric and rasterisation uncertainty. The significant changes showed primarily decreases in vegetation height immediately after the herbivory event and increases one month later, but with high spatial heterogeneity, which nevertheless showed spatial structure. Evaluation of this spatial heterogeneity by mapping habitat types, deriving vegetation height, and incorporating reindeer GPS collar data revealed that areas with high reindeer activity showed evidence of reindeer browsing around the edges of erect shrubs and trampling of low-lying vegetation as well as lagged growth in low-lying vegetation one month later. Areas with lower herbivory pressure showed strikingly little change, despite belonging to similar habitat types, demonstrating the effects of a reindeer herbivory event on vegetation change within a growing season.

Lastly, the third article, '**Offsetting impacts of different size classes of herbivores on CO_2 uptake in a tundra ecosystem**,' employed a more traditional plot-based ecological approach to compare CO_2 fluxes within a seven-year-old exclosure experiment excluding three different size classes of herbivores within three different habitat types. Variations in fluxes were driven primarily by differences in photosynthesis, rather than respiration. Consistently, controls accessible to all herbivores were the weakest CO_2 sinks, but plots open to small herbivores and small- and medium-sized herbivores were progressively stronger CO_2 sinks than plots where all herbivores were excluded. After ruling out differences in litter cover and plant community composition, the most likely explanation for these dynamics included a combination of defoliation from reindeer and nutrient fertilisation by smaller herbivores. The effects of reindeer were most pronounced in willow meadows, whereas smaller herbivores had the largest influence within forb tundra. These findings highlight the importance of considering the different functions of herbivores and how they interact with different

environmental contexts in the Arctic to understand the aggregate, non-additive consequences for ecosystem processes.

Overall, this thesis demonstrates new methodologies for assessing the impacts of herbivores with spatially comprehensive measurements and offers novel insights into the effects of reindeer in tundra ecosystems. The impacts of reindeer were apparent and consistent across spatial scales, including at the regional scale, suggesting that they have significance for the Earth system. The lines of evidence showed that reindeer herbivory can limit the growth of shrubs in the Arctic, mediated by topography and landcover, with implications for ecosystem processes, namely carbon cycling. This work can inform future studies of Arctic herbivory and facilitate the inclusion of top-down regulation in ecosystem models, which is necessary to accurately predict the responses of tundra ecosystems to climate change and the resulting feedbacks.

Acknowledgements

This work would not have been possible without the support and contributions of many people. Thank you, first, to my supervisor, Marc Macias-Fauria for all the mentorship and inspiration you have provided to me since I arrived in Oxford over five years ago. You convinced me that Oxford was the right choice not once, but twice. You promised me you would do your best so that I would not regret my decision and told me we would have fun, and you did not let me down on either count. We have really "grabbed it by the antlers"! Thank you also to all the members of the Biogeosciences lab group, especially Maria Dance and Alejandra Mora-Soto, with whom I enjoyed exchanging ideas while sharing an office in St. Peter's College, and Nicola Kühn for a very successful and enjoyable collaboration.

I would like to thank my collaborators in Labytnangi, Russia for welcoming me into your lab group, as well. Sasha Sokolov made my fieldwork in Yamal possible and deserves credit for the incredible summer I spent in Erkuta in summer 2021. I cherish the substantial contributions of anthropologists Sasha Terekhina and Sasha Volkovitskiy to my research, as well as their hospitality and constant encouragement. Thank you also to Dina Yusupova, Kirill Shklyar, and Violetta Filippova for their friendship and support in the field, and to Nikita and Ilya Sokolov for their excellent work as field assistants. I am also grateful to the Indigenous Nenets people I met in Erkuta for welcoming me as one of their own, especially Efim Serotetto and his family for their partnership in my work. I would also like to give a special mention to Richie Kenton-Page, who was instrumental in the construction of the flux chamber I took with me to Russia.

I am grateful that I have many wonderful collaborators around the world, particularly Dorothée Ehrich, Isla Duporge, Taejin Park, and Jeff Kerby. I have learned many things from each of them, and I am proud of the work we have done together. I have been fortunate enough to be a part of multiple international projects – a Navigating the New Arctic grant led by Valeriy Ivanov, Peter Ungar, and John Ziker; CHARTER led by Bruce Forbes; and the Plant Functional Trait Courses led by Vigdis Vandvik and Brian Enquist. These groups each provided new opportunities to me during my DPhil and contributed to my intellectual development. Thank you also to Merritt Turetsky for her guidance in the early stages of this work and for her fieldwork advice.

I am also thankful for the community I have had in Oxford supporting me throughout my time here. Eleanor Thomson has been my greatest source of encouragement and a wonderful colleague. Josh Ettinger has been a great flatmate, collaborator, and friend with whom I have enjoyed sharing this DPhil experience. The friendship of my neighbours Sophie Cheng and Colin Hill made the covid lockdowns bearable. Nils Cwiekala and Alessa Röder have been my family away from home. Ryan Blank and Sam Heywood helped me through the last months of the work. Tina Christmann made the return to the department during covid far more enjoyable with her enforcement of the baking rota.

My DPhil would not have been possible without financial support from the Clarendon Fund Scholarship and Christ Church Clarendon Award, as well as CHARTER (European Union's Horizon 2020 research and innovation programme under Grant Agreement No. 869471) and the American Friends of Christ Church Scholarship. I am also grateful for fieldwork funding granted by EU INTERACT Transnational Access.

Lastly, thank you to my family who have supported me from afar and given me the best chance to succeed in my endeavours.

Table of Contents

Abstract **2**
Acknowledgements **5**
List of Abbreviations **9**

Chapter 1: Introduction **10**
1.1 Thesis rationale 11
1.2 Aims and objectives 15
1.3 Thesis structure 17
1.4 References 18

Chapter 2: Literature Review **24**
2.1 Scope 25
2.2 Large-scale vegetation trends in the Arctic 25
2.3 Effects of herbivores on tundra ecosystems 29
2.4 Remote sensing of herbivore impacts in the Arctic 35
2.5 References 37

Chapter 3: Methods and study area **48**
3.1 Overview 49
3.2 Study area 49
3.3 Data collection, processing, and analysis 54
3.4 References 63

Chapter 4: Top-down regulation by a reindeer herding system limits climate-driven Arctic vegetation change at a regional scale **67**
4.1 Chapter statement 68
4.2 Author contributions 68
4.3 Abstract 69
4.4 Plain language summary 69
4.5 Introduction 70
4.6 Materials and methods 74
4.7 Results 79
4.8 Discussion 85
4.9 Acknowledgments 87

4.10 Open research 88
4.11 References 88
4.12 Supplementary material 94

Chapter 5: Heterogeneity in immediate and lagged effect of reindeer herbivory over spatially comprehensive fine scales 100
5.1 Chapter statement 101
5.2 Author contributions 101
5.3 Abstract 102
5.4 Introduction 103
5.5 Materials and methods 106
5.6 Results 114
5.7 Discussion 121
5.8 References 125
5.9 Supplementary material 132

Chapter 6: Offsetting impacts of different size classes of herbivores on CO_2 uptake in a tundra ecosystem 138
6.1 Chapter statement 139
6.2 Author contributions 139
6.3 Abstract 140
6.4 Introduction 141
6.5 Materials and methods 143
6.6 Results 149
6.7 Discussion 152
6.8 References 156
6.9 Supplementary material 161

Chapter 7: Synthesis and conclusion 172
7.1 Summary 173
7.2 Main findings 173
7.3 Synthesis 175
7.4 Implications and future directions 178
7.5 References 180

Appendix 1: Additional co-authored articles 183

List of Abbreviations

AET: Actual evapotranspiration

AIC: Akaike information criterion

CAVM: Circumpolar Arctic Vegetation Map

CHM: Canopy height model

CSF: Cloth simulation filtering

DEM: Digital elevation model

DOP: Dilution of precision

DSM: Digital surface model

DTM: Digital terrain model

ER: Ecosystem respiration

EVI: Enhanced vegetation index

GEP: Gross ecosystem photosynthesis

GNSS: Global navigation satellite system

GPS: Global positioning system

ITEX: International Tundra Experiment

LiDAR: Light Detection and Ranging

LoD: Limit of Detection

MODIS: Moderate resolution imaging spectroradiometer

NDVI: Normalised difference vegetation index

NEE: Net ecosystem exchange

OTC: Open-top chamber

PAR: Photosynthetically active radiation

PCR: Principal component regression

PET: Potential evapotranspiration

RGB: Red, green, blue

RMSE: Root mean square error

SAR: Synthetic aperture radar

SEUW: Standard error of unit weight

SfM: Structure-from-motion

UAV: Unmanned aerial vehicle

VSI: Vegetation sensitivity index

YNAO: Yamal-Nenets Autonomous Okrug

Chapter 1:
Introduction



Photo: Marcus Spiegel

1.1 Thesis rationale

1.1.1 Top-down and bottom-up regulation in ecology

The relative importance of top-down and bottom-up forces in governing ecosystem productivity and biodiversity constitutes a classic question in ecology (Hairston et al., 1960; Hunter & Price, 1992; Power, 1992). Top-down regulation implies that herbivory controls plant populations, whereas bottom-up regulation suggests that climate and soil properties determine the growth and composition of the vegetation community with cascading influences up the trophic chain. Top-down and bottom-up forces are both present in nearly all biological systems, and the results of their interactions determine patterns in nature (Hunter & Price, 1992). Yet, contemporary ecosystem models, particularly carbon cycle models, rarely account for the influence of animals in ecosystem structure and functioning (Schmitz et al., 2018; Väisänen et al., 2014).

This omission likely stems not from a perceived lack of importance of top-down control, as regulation by herbivores has been found to be ubiquitous and significant in ecosystems across the globe (Jia et al., 2018), but rather due to the challenge of characterising animals' impacts. The strength and function of top-down regulation is highly site specific and depends on the local environmental conditions as well as the types and densities of herbivores present (Bernes et al., 2015; Jia et al., 2018; Ravolainen et al., 2011). When multiple herbivores are present in a system, their combined impacts are not necessarily cumulative, as their functions may not be overlapping, but instead complementary or even offsetting (Olofsson et al., 2013). For example, the combined ability of bovids to digest cellulose, suppressing woody vegetation, and equids to graze on less fibrous vegetation and promote short grass growth leads to more effective maintenance of open grasslands than results from the presence of either group individually (Macias-Fauria et al., 2020). Moreover, the impact of herbivores is more complex than simply reduced plant abundance, biomass, and productivity due to their consumption. Herbivory can promote higher diversity by disproportionately removing the most common species, for example, by targeting taller species that would otherwise dominate by limiting the availability of light for shorter plants under their canopy cover (Borer et al., 2014; Eskelinen et al., 2022). In addition to consumption, mechanisms by which animals affect the ecosystem include fertilisation via their faeces and urine and, particularly for large herbivores, trampling and perturbation of vegetation and soils (Enquist et al., 2020; Forbes et al., 2009; Tanentzap & Coomes, 2012). Trampling can alter surface temperature and chemical reactions in the soil directly, while herbivore-driven changes in the vegetation cover

can have additional below-ground implications (Schmitz et al., 2018; Tanentzap & Coomes, 2012). In the high latitudes, trampling by large herbivores can also affect soil thermal regimes by compacting snow and reducing its insulation strength, potentially protecting permafrost soils from thawing (Beer et al., 2020). Thus, top-down impacts occur via direct and indirect pathways and can regulate ecosystem structure and functioning by influencing both biotic and abiotic systems.

Despite this complexity, developing our understanding of top-down forces is an urgent research priority needed to predict ecosystem responses in the face of climate change and the current biodiversity crisis. There is growing interest in addressing the biodiversity and climate crises with "rewilding," which involves introducing ecosystem engineers, often large herbivores, into areas to restore self-sustaining provision of ecosystem services such as carbon sequestration (Pettorelli et al., 2018; Svenning, 2020). Yet, although theory and early evidence supports the alignment of these conservation efforts with environmental goals, more work is needed to link actions with impacts and tease apart context dependencies (Pettorelli et al., 2018). Consideration of how top-down regulation varies in space, over time, and depending on the animals present is essential for evaluating the role of existing herbivore assemblages and the potential for rewilding interventions. This nuance is important for accurate upscaling with ecosystem models, which is crucial for improving our assessment of future trajectories at multiple scales (Kristensen et al., 2022).

1.1.2 Large herbivores in the Arctic

In the Arctic, where warming is estimated to be occurring at four times the rate of the planet as a whole (Chylek et al., 2022), top-down regulation by herbivory interacts with rapid ecosystem responses to climate change. Warming is driving permafrost thaw (Crowther et al., 2016; Schuur et al., 2015), a positive carbon cycle feedback, as well as an increase in vegetation productivity, largely attributed to the growth and expansion of shrubs, especially tall shrubs (>0.4 m height) (Elmendorf et al., 2012; Myers-Smith et al., 2011, 2015; Myneni et al., 1997; Sturm et al., 2001). This latter response has complex climate feedbacks because although carbon is sequestered as aboveground biomass increases, shrub-dominated tundra has a lower albedo compared to other Arctic landcover types, causing more warming as less solar radiation is reflected (Macias-Fauria et al., 2020). Additionally, taller vegetation traps more snow in a thicker blanket, increasing winter soil temperatures and promoting permafrost thaw, which may accelerate even further as increased vegetation productivity causes a higher

presence of plant roots and consequent increases in microbial decomposition rates, referred to as “rhizosphere priming” (Kennedy, 2012; Keuper et al., 2020; Parker et al., 2021).

The influence of herbivores is superimposed on these climate-driven impacts. The Arctic herbivore assemblage is species-poor, especially when considering only large herbivores, which often have a disproportionately large effect on ecosystem functioning (Enquist et al., 2020). Whereas a diverse assemblage of large herbivores, including mammoth, woolly rhino, and wild horse, was present during the Pleistocene, only reindeer (same species as caribou, *Rangifer tarandus*) remain widespread in most Arctic regions (Olofsson & Post, 2018). Yet, reindeer have a substantial effect on tundra vegetation and counteract the impacts of warming in the Arctic directly by limiting shrub growth and expansion (Christie et al., 2015; Olofsson et al., 2009; Olofsson & Post, 2018). The combination of their activities has been shown to locally promote a shift from shrub- to graminoid- and forb-dominated vegetation, creating grasslands that often remain stable for years after the herbivory pressure ceases (Egelkraut et al., 2018; Forbes et al., 2009; Klein, 1968; Olofsson et al., 2001; Ricca et al., 2016). Tundra ecosystems can exist in these alternative stable states (Pausas & Bond, 2022; van der Wal, 2006), and theory suggests that reindeer may contribute to resilience in the Arctic by maintaining open landscapes (Kaarlejärvi et al., 2015).

However, these impacts of reindeer herbivory have been observed primarily where reindeer are concentrated over small areas due to management fences or experiments, and it remains uncertain whether top-down regulation is a major control on Arctic ecosystem structure and functioning over larger spatial scales. Furthermore, a recent meta-analysis of the impacts of reindeer on Arctic and alpine vegetation found that effects on vascular plants were inconsistent and highly context dependent (Bernes et al., 2015). More work is needed to explain the heterogeneity in reindeer impacts across the Arctic, quantify the effects on processes relevant to the Earth system, and include reindeer herbivory in ecosystem models. These developments can contribute to predictions of how tundra ecosystems will respond as warming continues and as reindeer numbers fluctuate, but they also may inform perspectives on the potential for megafaunal rewilding in the Arctic.

The grassland biome that dominated the high latitudes during the Pleistocene, termed the “mammoth steppe,” stored roughly 1000 Gt more soil carbon than today’s moss- and shrub-dominated tundra (Zimov et al., 1995, 2012). Although there is ongoing debate over the

extent to which this ecosystem was the result of top-down controls or bottom-up abiotic factors as well as the potential for its recreation under today's conditions (e.g., Monteath et al., 2021), proposals already exist to rewild the Arctic with megafauna as a natural climate solution (Macias-Fauria et al., 2020). Early results from the "Pleistocene Park" experiment, which has reintroduced large herbivores such as Yakutian horses, bison, and yak (amongst other taxa) into a fenced area in northeast Siberia, have shown evidence of lower soil temperatures and increased carbon storage in heavily grazed areas (Windirsch et al., 2022). These findings are exciting, but such ambitious initiatives are expensive and challenging to scale up (Macias-Fauria et al., 2020). Yet, opportunities exist to improve our understanding of large herbivores in the Arctic by studying the natural "experiments" already in progress, where reindeer are herded or move freely across landscapes, even if their function is more limited than that of a diverse assemblage of megafauna. This knowledge will help us evaluate the future of the Arctic with the current herbivore assemblage and under various top-down regulation scenarios.

1.1.3 The Yamal Peninsula

The Yamal Peninsula in West Siberia, Russia is a hotspot for rapid environmental change and industrial development. Climate change has caused tall shrub expansion (Forbes et al., 2010; Forbes & Stammler, 2009; Frost & Epstein, 2014) and thaw of the continuous permafrost layer underlying the peninsula, leading to frequent landslides and, in some instances, spectacular gas-emission craters over 50 m deep that appear overnight (Dvornikov et al., 2019; Verdonen et al., 2020; Walker et al., 2009). Exploration and extraction of hydrocarbons has led to the expansion of infrastructure, including roads, railroads, and pipelines (**Figure 1.1**), and a large influx of workers (Kumpula et al., 2011). Yet amidst this change, Indigenous Nenets on the Yamal tundra have continued their centuries-old practice of reindeer herding as a nomadic way of life (Forbes et al., 2009; Stammler, 2005). The Yamal Peninsula is home to the world's largest domesticated reindeer herds, and it was the only Russian region where breeding did not decline following the collapse of the Soviet Union (Stammler, 2002). Reindeer herbivory has had a constant influence on the land since at least the 1600's CE due to the resilience of the Yamal-Nenets social-ecological system (Forbes et al., 2009). If a regional signal of top-down control by reindeer were to be visible anywhere in the Arctic, it would be here.

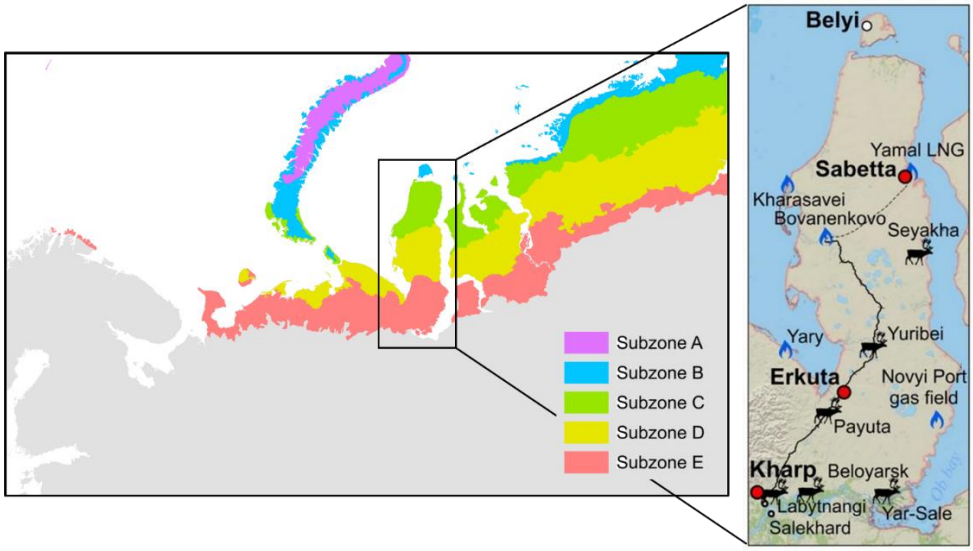


Figure 1.1: The location of the Yamal Peninsula. The coloured subzones are the bioclimatic subzones from the Circumpolar Arctic vegetation map (Walker et al., 2005). "Kharp," "Erkuta," "Sabetta," and "Belyi" are sites of long-term studies conducted by the Russian Academy of Sciences. Reindeer symbols represent slaughterhouses and flame symbols show centres of the hydrocarbon industry. The solid line through the peninsula is the existing railway line and the dashed line is a railway line under construction. Map of Yamal provided by Alexandra Terekhina and Alexander Volkovitskiy.

The studies I present in this thesis investigate the impacts of reindeer and their interactions with the vegetation, climate, and topography on Yamal. In **Chapter 3**, I describe the region and introduce my field sites in more detail. Interdisciplinary collaboration with social anthropologists who have built relationships with Nenets herders over many years has been critical to this work, which has relied on knowledge of herd movements to evaluate responses due to variations in herbivory pressure over space and time. These variations create the opportunity on Yamal to explain heterogeneity in the influence of reindeer within and between Arctic landscapes. Furthermore, despite the substantial proportion of Arctic landmass that is within Siberia, comparatively few studies of reindeer herbivory and ecosystem responses have taken place in this vast region (Bernes et al., 2015; Soininen et al., 2021; Virkkala et al., 2018). Thus, the Yamal-Nenets social ecological system provides an ideal natural laboratory for developing new insights into top-down regulation in the Arctic.

1.2 Aims and objectives

The overarching aim of this thesis was to detect the influence of reindeer herbivory and evaluate the heterogeneity in its effects on Arctic ecosystem structure and functioning over different spatial and temporal scales. Specifically, this aim was developed into four concrete research objectives.

Objective 1: Does reindeer herbivory have a regional-scale effect on tundra vegetation that can be detected using space-borne satellite imagery?

This objective seeks to determine whether local-scale impacts that have been documented under high levels of reindeer activity in the Arctic persist in comparisons at broader spatial scales. In my regional-scale work, I tested whether variation in reindeer herbivory pressure over space was linked to the distribution of landcover types, particularly the proportion of area covered by tall woody vegetation, and the sensitivity of vegetation productivity to variability in climate, quantified by the vegetation sensitivity index (VSI, after Seddon & Macias-Fauria et al., 2016). I hypothesised that these analyses would show differences at the regional scale consistent with the effects of reindeer. Specifically, I anticipated that areas with higher reindeer pressure would have lower coverage of tall woody vegetation and exhibit lower climate sensitivity, indicating that herbivory has caused decoupling between climate and productivity.

Objective 2: How does vegetation change across a landscape after the area is used for pastures along the migration route of a large reindeer herd?

At the landscape scale, I aimed to detect vegetation changes continuously over space, both immediately after a herd had camped in the area for a week and a month later to track the vegetation recovery. The vegetation changes were measured as changes in canopy height derived from photogrammetric reconstructions using successive unmanned aerial vehicle (UAV) surveys. I hypothesised that the impacts immediately after the herbivory event would be spatially heterogeneous and show decreases in vegetation height stemming from browsing or trampling depending on the vegetation present initially. I expected growth in the vegetation one month later to be widespread and more substantial where there was less disturbance from reindeer.

Objective 3: What is the resultant effect on ecosystem functioning when reindeer herbivory interacts with the effects of other herbivores within the local assemblage?

Using an herbivore exclosure experiment that cumulatively excludes three different size classes of herbivores, I aimed to compare responses not just in the vegetation present, but in ecosystem processes. Carbon fluxes were measured in the different exclosure plots and controls to determine photosynthesis, respiration, and the carbon balance at multiple points in the growing season. By comparing the impacts of different herbivore assemblages, I endeavoured to derive insights into the mechanisms by which different herbivores control

vegetation communities and ecosystem functioning. Since the exclosure experiment had only been established for seven years, a relatively short time span for community composition to shift in the tundra, I hypothesised that differences in the carbon balance driven by the herbivore assemblage would result mainly from consumption of and damage to the vegetation. Therefore, I predicted that plots accessible to more herbivores would have lower carbon uptake via photosynthesis and that differences in respiration would be insignificant.

Objective 4: How do landcover and topography mediate ecosystem responses to reindeer herbivory?

Within each of the first three objectives, I aimed to assess how the environmental context mediates the influence of herbivory I detected. The context was characterised by the landcover, or similarly habitat type, and the topography, considering the position within the surrounding landscape. These variables were used to search for consistent patterns in where reindeer herbivory is having significant impacts within the tundra and what these impacts entail. I hypothesised that a combination of the landscape positions where reindeer tend to spend most of their time and the vegetation most vulnerable to their herbivory would explain the spatial heterogeneity in the effects of reindeer. Reindeer often remain on upland areas to find relief from insect harassment, and their activities have been commonly observed to limit the growth of erect shrubs. Thus, I expected to detect effects of reindeer herbivory consistent with the inhibition of shrub expansion primarily in the upslope areas of landcover and habitat types where erect shrubs were growing.

1.3 Thesis structure

The above objectives are addressed in this thesis in three research articles, which form three separate chapters, with additional chapters providing background and synthesis. This chapter (**Chapter 1**) introduces the motivation behind the research and states the thesis' aims and objectives. **Chapter 2** provides context for the work by reviewing existing literature and identifying where knowledge gaps exist. **Chapter 3** gives additional details on the study area and describes the methods used in the data collection and analysis. **Chapters 4, 5,** and **6** present the different studies I conducted in the format of research articles. Although each article individually represents a complete study, the three chapters are complementary, showing a progression over different spatial scales, temporal scales, and responses assessed (**Table 1.1**). The results and conclusions are synthesised in **Chapter 7**, which also discusses the implications of the research and potential future directions.

Table 1.1: The research chapters in this thesis and how they vary in their spatial and temporal scales and measured responses.

Ch.	Title	Spatial scale	Temporal scale	Response
4	Top-down regulation by a reindeer herding system limits climate-driven Arctic vegetation change at a regional scale	Regional	Decades/long-term (cumulative impacts)	Vegetation proxies: landcover class and VSI
5	Heterogeneity in immediate and lagged effects of reindeer herbivory over spatially comprehensive fine scales	Landscape	Within a growing season	Plant trait: canopy height
6	Offsetting impacts of different size classes of herbivores on CO_2 uptake in a tundra ecosystem	Plot	7-year experiment	Ecosystem process: carbon fluxes

In addition, in **Appendix 1**, I include the first page of four additional research articles to which I have made substantial contributions during my DPhil. These articles have been published or are currently in review and relate to the work I present in my thesis in varying ways. The first article, "Multiscale mapping of plant functional groups and plant traits in the High Arctic using field spectroscopy, UAV imagery and Sentinel-2A data" (second author), presents an application of UAV mapping in the Arctic that links to my methodology in **Chapter 5**. I also include a second article related to research with UAVs, "Determination of optimal flight altitude to minimise acoustic drone disturbance to wildlife using species audiograms" (co-first author), which quantified the disturbance UAV noise causes to different animals, including reindeer. In "Seeing roots from space: aboveground fingerprints of root depth in vegetation sensitivity to climate in dry biomes" (second author), we applied the VSI metric employed in **Chapter 4** in southern Africa to assess links between root depth and vegetation sensitivity to climate. Lastly, "Fighting the climate spiral of silence: Lessons from a COP26 climate conversations campaign" (last author) addresses how we engage with the climate crisis. The pressing need to understand and respond to contemporary environmental challenges underpins much of the motivation behind the research I present in this thesis.

1.4 References

Beer, C., Zimov, N., Olofsson, J., Porada, P., & Zimov, S. (2020). Protection of Permafrost Soils from Thawing by Increasing Herbivore Density. *Scientific Reports*, *10*(1), 4170. https://doi.org/10.1038/s41598-020-60938-y

Bernes, C., Bråthen, K. A., Forbes, B. C., Speed, J. D. M., & Moen, J. (2015). What are the impacts of reindeer/caribou (Rangifer tarandus L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, *4*(4). https://doi.org/10.1186/s13750-014-0030-3

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler, P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown, C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M. J., … Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*(7497), 517–520. https://doi.org/10.1038/nature13144

Christie, K. S., Bryant, J. P., Gough, L., Ravolainen, V. T., Ruess, R. W., & Tape, K. D. (2015). The Role of Vertebrate Herbivores in Regulating Shrub Expansion in the Arctic: A Synthesis. *BioScience*, *65*(12), biv137. https://doi.org/10.1093/biosci/biv137

Chylek, P., Folland, C., Klett, J. D., Wang, M., Hengartner, N., Lesins, G., & Dubey, M. K. (2022). Annual Mean Arctic Amplification 1970-2020: Observed and Simulated by CMIP6 Climate Models. *Geophysical Research Letters*, *49*(13), 1–8. https://doi.org/10.1029/2022GL099371

Crowther, T. W., Todd-Brown, K. E. O., Rowe, C. W., Wieder, W. R., Carey, J. C., MacHmuller, M. B., Snoek, B. L., Fang, S., Zhou, G., Allison, S. D., Blair, J. M., Bridgham, S. D., Burton, A. J., Carrillo, Y., Reich, P. B., Clark, J. S., Classen, A. T., Dijkstra, F. A., Elberling, B., … Bradford, M. A. (2016). Quantifying global soil carbon losses in response to warming. *Nature*, *540*(7631), 104–108. https://doi.org/10.1038/nature20150

Dvornikov, Y. A., Leibman, M. O., Khomutov, A. V., Kizyakov, A. I., Semenov, P., Bussmann, I., Babkin, E. M., Heim, B., Portnov, A., Babkina, E. A., Streletskaya, I. D., Chetverova, A. A., Kozachek, A., & Mayer, H. (2019). Gas-emission craters of the Yamal and Gydan peninsulas: A proposed mechanism for lake genesis and development of permafrost landscapes. *Permafrost and Periglacial Processes*, ppp.2014. https://doi.org/10.1002/ppp.2014

Egelkraut, D., Aronsson, K.-Å., Allard, A., Åkerholm, M., Stark, S., & Olofsson, J. (2018). Multiple Feedbacks Contribute to a Centennial Legacy of Reindeer on Tundra Vegetation. *Ecosystems*, *21*(8), 1545–1563. https://doi.org/10.1007/s10021-018-0239-z

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Dorrepaal, E., Elumeeva, T. G., Gill, M., Gould, W. A., Harte, J., Hik, D. S., Hofgaard, A., Johnson, D. R., Johnstone, J. F., Jónsdóttir, I. S., Jorgenson, J. C., … Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, *2*(6), 453–457. https://doi.org/10.1038/nclimate1465

Enquist, B. J., Abraham, A. J., Harfoot, M. B. J., Malhi, Y., & Doughty, C. E. (2020). The megabiota are disproportionately important for biosphere functioning. *Nature Communications*, *11*(1), 1–11. https://doi.org/10.1038/s41467-020-14369-y

Eskelinen, A., Harpole, W. S., Jessen, M., Virtanen, R., & Hautier, Y. (2022). Light competition drives herbivore and nutrient effects on plant diversity. *Nature*, *March*. https://doi.org/10.1038/s41586-022-05383-9

Forbes, B. C., Macias-Fauria, M., & Zetterberg, P. (2010). Russian Arctic warming and "greening" are closely tracked by tundra shrub willows. *Global Change Biology*, *16*(5), 1542–1554. https://doi.org/10.1111/j.1365-2486.2009.02047.x

Forbes, B. C., & Stammler, F. (2009). Arctic climate change discourse: The contrasting politics of research agendas in the West and Russia. *Polar Research*, *28*(1), 28–42. https://doi.org/10.1111/j.1751-8369.2009.00100.x

Forbes, B. C., Stammler, F., Kumpula, T., Meschtyb, N., Pajunen, A., & Kaarlejärvi, E. (2009). High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences*, *106*(52), 22041–22048. https://doi.org/10.1073/pnas.0908286106

Frost, G. V., & Epstein, H. E. (2014). Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology*, *20*(4), 1264–1277. https://doi.org/10.1111/gcb.12406

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community Structure, Population Control, and Competition. *The American Naturalist*, *94*(879), 421–425. https://doi.org/10.1086/282146

Hunter, M. D., & Price, P. W. (1992). Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities. *Ecology*, *73*(3), 724–732. https://doi.org/10.2307/1940152

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., & Luskin, M. S. (2018). Global signal of top-down control of terrestrial plant communities by herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(24), 6237–6242. https://doi.org/10.1073/pnas.1707984115

Kaarlejärvi, E., Hoset, K. S., & Olofsson, J. (2015). Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. *Global Change Biology*, *21*(9), 3379–3388. https://doi.org/10.1111/gcb.12970

Kennedy, R. E. (2012). New views on changing Arctic vegetation. *Environmental Research Letters*, *7*(1). https://doi.org/10.1088/1748-9326/7/1/011001

Keuper, F., Wild, B., Kummu, M., Beer, C., Blume-Werry, G., Fontaine, S., Gavazov, K., Gentsch, N., Guggenberger, G., Hugelius, G., Jalava, M., Koven, C., Krab, E. J., Kuhry, P., Monteux, S., Richter, A., Shahzad, T., Weedon, J. T., & Dorrepaal, E. (2020). Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere priming. *Nature Geoscience*, *13*(8), 560–565. https://doi.org/10.1038/s41561-020-0607-0

Klein, D. R. (1968). The Introduction, Increase, and Crash of Reindeer on St. Matthew Island. *The Journal of Wildlife Management*, *32*(2), 350. https://doi.org/10.2307/3798981

Kristensen, J. A., Svenning, J.-C., Georgiou, K., & Malhi, Y. (2022). Can large herbivores enhance ecosystem carbon persistence? *Trends in Ecology & Evolution*, *37*(2), 117–128. https://doi.org/10.1016/j.tree.2021.09.006

Kumpula, T., Pajunen, A., Kaarlejärvi, E., Forbes, B. C., & Stammler, F. (2011). Land use and land cover change in Arctic Russia: Ecological and social implications of industrial development. *Global Environmental Change*, *21*(2), 550–562. https://doi.org/10.1016/j.gloenvcha.2010.12.010

Macias-Fauria, M., Jepson, P., Zimov, N., & Malhi, Y. (2020). Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190122. https://doi.org/10.1098/rstb.2019.0122

Monteath, A. J., Gaglioti, B. V., Edwards, M. E., & Froese, D. (2021). Late Pleistocene shrub expansion preceded megafauna turnover and extinctions in eastern Beringia. *Proceedings of the National Academy of Sciences*, *118*(52), e2107977118. https://doi.org/10.1073/pnas.2107977118

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., Speed, J. D. M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N. M., Baittinger, C., Trant, A. J., Hermanutz, L., Collier, L. S., … Vellend, M. (2015). Climate sensitivity of shrub

growth across the tundra biome. *Nature Climate Change*, *5*(9), 887–891. https://doi.org/10.1038/nclimate2697

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., MacIas-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4). https://doi.org/10.1088/1748-9326/6/4/045509

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., & Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, *386*(6626), 698–702. https://doi.org/10.1038/386698a0

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., & Oksanen, L. (2001). Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, *24*(1), 13–24. https://doi.org/10.1034/j.1600-0587.2001.240103.x

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*(11), 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x

Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761). https://doi.org/10.1098/rstb.2017.0437

Olofsson, J., te Beest, M., & Ericson, L. (2013). Complex biotic interactions drive long-term vegetation dynamics in a subarctic ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624), 20120486. https://doi.org/10.1098/rstb.2012.0486

Parker, T. C., Thurston, A. M., Raundrup, K., Subke, J., Wookey, P. A., & Hartley, I. P. (2021). Shrub expansion in the Arctic may induce large-scale carbon losses due to changes in plant-soil interactions. *Plant and Soil*, *463*(1–2), 643–651. https://doi.org/10.1007/s11104-021-04919-8

Pausas, J. G., & Bond, W. J. (2022). Feedbacks in ecology and evolution. *Trends in Ecology & Evolution*, *37*(8), 637–644. https://doi.org/10.1016/j.tree.2022.03.008

Pettorelli, N., Barlow, J., Stephens, P. A., Durant, S. M., Connor, B., Schulte to Bühne, H., Sandom, C. J., Wentworth, J., & du Toit, J. T. (2018). Making rewilding fit for policy. *Journal of Applied Ecology*, *55*(3), 1114–1125. https://doi.org/10.1111/1365-2664.13082

Power, M. E. (1992). Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy. *Ecology*, *73*(3), 733–746. https://doi.org/10.2307/1940153

Ravolainen, V. T., Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Henden, J.-A., & Killengreen, S. T. (2011). Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. *Basic and Applied Ecology*, *12*(8), 643–653. https://doi.org/10.1016/j.baae.2011.09.009

Ricca, M. A., Miles, A. K., Van Vuren, D. H., & Eviner, V. T. (2016). Impacts of introduced Rangifer on ecosystem processes of maritime tundra on subarctic islands. *Ecosphere*, *7*(3). https://doi.org/10.1002/ecs2.1219

Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M., Davies, A. B., & Goetz, S. J. (2018). Animals and the zoogeochemistry of the carbon cycle. *Science*, *362*(6419), eaar3213. https://doi.org/10.1126/science.aar3213

Schuur, E. A. G., McGuire, A. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., Hugelius, G., Koven, C. D., Kuhry, P., Lawrence, D. M., Natali, S. M., Olefeldt, D., Romanovsky, V. E., Schaefer, K., Turetsky, M. R., Treat, C. C., & Vonk, J. E. (2015). Climate change and the permafrost carbon feedback. *Nature*, *520*(7546), 171–179.

https://doi.org/10.1038/nature14338
Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, *531*(7593), 229–232. https://doi.org/10.1038/nature16986
Soininen, E. M., Barrio, I. C., Bjørkås, R., Björnsdóttir, K., Ehrich, D., Hopping, K. A., Kaarlejärvi, E., Kolstad, A. L., Abdulmanova, S., Björk, R. G., Bueno, C. G., Eischeid, I., Finger-Higgens, R., Forbey, J. S., Gignac, C., Gilg, O., den Herder, M., Holm, H. S., Hwang, B. C., … Speed, J. D. M. (2021). Location of studies and evidence of effects of herbivory on Arctic vegetation: a systematic map. *Environmental Evidence*, *10*(1), 1–21. https://doi.org/10.1186/s13750-021-00240-0
Stammler, F. (2002). Success at the Edge of the Land: Past and Present Challenges for Reindeer Herders in the West Siberian Yamalo-Nenetskii Autonomous Okrug. *Nomadic Peoples*, *6*(2), 51–71. https://doi.org/10.3167/082279402782311211
Stammler, F. (2005). *Reindeer Nomads Meet the Market: Culture, Property and Globalisation at the `End of the Land'*. Lit.
Sturm, M., Racine, C., & Tape, K. (2001). Increasing shrub abundance in the Arctic. *Nature*, *411*(6837), 546–547. https://doi.org/10.1038/35079180
Svenning, J. C. (2020). Rewilding should be central to global restoration efforts. *One Earth*, *3*(6), 657–660. https://doi.org/10.1016/j.oneear.2020.11.014
Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: Do browsing and grazing herbivores matter? *Biological Reviews*, *87*(1), 72–94. https://doi.org/10.1111/j.1469-185X.2011.00185.x
Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., & Stark, S. (2014). Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, *4*(5), 384–388. https://doi.org/10.1038/nclimate2147
van der Wal, R. (2006). Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, *114*(1), 177–186. https://doi.org/10.1111/j.2006.0030-1299.14264.x
Verdonen, M., Berner, L. T., Forbes, B. C., & Kumpula, T. (2020). Periglacial vegetation dynamics in Arctic Russia: decadal analysis of tundra regeneration on landslides with time series satellite imagery. *Environmental Research Letters*, *15*(10), 105020. https://doi.org/10.1088/1748-9326/abb500
Virkkala, A. M., Virtanen, T., Lehtonen, A., Rinne, J., & Luoto, M. (2018). The current state of CO2 flux chamber studies in the Arctic tundra: A review. *Progress in Physical Geography*, *42*(2), 162–184. https://doi.org/10.1177/0309133317745784
Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Raynolds, M. K., Comiso, J. C., Gubarkov, A. A., Khomutov, A. V., Jia, G. J., Kaarlejärvi, E., Kaplan, J. O., Kumpula, T., Kuss, P., Matyshak, G., Moskalenko, N. G., Orekhov, P., Romanovsky, V. E., Ukraientseva, N. G., & Yu, Q. (2009). Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index. *Environmental Research Letters*, *4*(4), 045004. https://doi.org/10.1088/1748-9326/4/4/045004
Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & The other members of the CAVM Team. (2005). The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, *16*(3), 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x
Windirsch, T., Grosse, G., Ulrich, M., Forbes, B. C., Göckede, M., Wolter, J., Macias-Fauria,

M., Olofsson, J., Zimov, N., & Strauss, J. (2022). Large herbivores on permafrost— a pilot study of grazing impacts on permafrost soil carbon storage in northeastern Siberia. *Frontiers in Environmental Science*, *10*(August), 1–17. https://doi.org/10.3389/fenvs.2022.893478

Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., Reynolds, J. F., & Chapin, M. C. (1995). Steppe-Tundra Transition: A Herbivore-Driven Biome Shift at the End of the Pleistocene. *The American Naturalist*, *146*(5), 765–794. https://doi.org/10.1086/285824

Zimov, S. A., Zimov, N. S., Tikhonov, A. N., & Chapin, I. S. (2012). Mammoth steppe: A high-productivity phenomenon. *Quaternary Science Reviews*, *57*, 26–45. https://doi.org/10.1016/j.quascirev.2012.10.005

Chapter 2:
Literature Review



Photo: Marcus Spiegel

2.1 Scope

The research conducted as part of this thesis investigated the role of herbivory within a changing Arctic. In this chapter, I begin by reviewing some of the biome-wide vegetation trends in tundra ecosystems before shifting to the impacts of herbivores, particularly reindeer, which are the most widespread large herbivores in the Arctic and the focus of most of my work. Since my objectives emphasised the detection of herbivory impacts over large spatial scales and explanation of the spatial heterogeneity in these impacts, my research employed remote sensing methods to generate observations that were continuous in space and covered large areas. Therefore, much of the literature reviewed here involves applications of remote sensing in the Arctic, which informed the study design and methods chosen for the research chapters in this thesis. I conclude by examining prior work specifically on using remote sensing to study herbivory in the Arctic, and throughout, I highlight knowledge gaps and suggest opportunities for further investigation.

2.2 Large-scale vegetation trends in the Arctic

2.2.1 Greening of the Arctic

Recognition of a greening trend in the northern high latitudes likely began with the work of Myneni et al. (1997), who showed a marked increase in plant growth over the circumpolar region between 1981-1999. They observed this trend using satellite-derived normalised difference vegetation index (NDVI), a metric based on spectral reflectance measurements that is strongly correlated with plant photosynthetic activity (Raynolds et al., 2008). Since this initial work, multiple studies have detected widespread increases in NDVI over high latitudes (e.g., Bhatt et al., 2017; Jia et al., 2003; Pouliot et al., 2008; Zhou et al., 2001), most often attributed to higher summer temperatures (Berner et al., 2020; Fraser et al., 2011; Zhu et al., 2016). These patterns have also been linked to a lengthening of the growing season, particularly advanced spring phenology (Park et al., 2016; Post et al., 2018), and declines in Arctic sea ice extent (Bhatt et al., 2010; Macias-Fauria et al., 2017). The increased plant growth has resulted in higher CO_2 uptake and carries implications for many local aspects of tundra ecosystems, such as hydrology, permafrost dynamics, food webs, and human use of Arctic landscapes (Epstein et al., 2012; Kennedy, 2012; Lucht et al., 2002).

However, the Arctic greening trend is not uniform in time or space. The relationship between temperature and NDVI has gradually weakened over time as the temperature limitation of vegetation growth has declined (Keenan & Riley, 2018; Piao et al., 2014). Despite the long-

term greening trend, there have also been periods when Arctic vegetation productivity appeared to be declining, or browning, such as from 2011-2014 (Phoenix & Bjerke, 2016). Roughly 20 times as much area has shown a greening trend rather than a browning trend during the satellite era (Park et al., 2016), but interpretations of these trends are complicated by pulse events within the time series such as extreme climatic events or disturbances that alter land cover (Treharne et al., 2019; Wang & Friedl, 2019).

Additionally, Arctic greening and browning trends are highly spatially heterogeneous and inherently scale-dependent (Myers-Smith et al., 2020). Comparisons between imagery at varying resolutions from different satellites or unmanned aerial vehicles (UAVs) have shown that the geographic patterns do not always align and that sub-meter resolution pixels are needed to capture the fine-scale variation observed in ground-based measurements (Assmann et al., 2020; Ju & Masek, 2016; Siewert & Olofsson, 2020). The proximal drivers of spatial variability in greening trends are not well understood, and in fact, the lack of a trend in tundra greenness in many locations despite pervasive increases in summer air temperatures merits further investigation (Berner et al., 2020; Myers-Smith et al., 2020). Possible explanations include other environmental constraints on plant growth such as nutrients and moisture, competing drivers of vegetation change, such as permafrost thaw, which also results from warming, and herbivory. The effects of both vertebrate and invertebrate herbivores on Arctic greening remain uncertain, but reindeer herbivory has been hypothesised to be strongly related to NDVI in Yamal (Miles & Esau, 2016). Yet, as in most of north-west Siberia, extensive greening was found in the southern part of the Yamal Peninsula, where there is intensive reindeer herding (Berner et al., 2020; Miles & Esau, 2016). Examining the correspondence between spatial variability in greening and herbivory pressure can help determine the strength of top-down regulation in modern tundra ecosystems.

2.2.2 Shrub expansion

The increase in vegetation biomass implied by Arctic greening has often been linked to the growth and expansion of shrubs (Martin et al., 2017; Tape et al., 2006). Early evidence of widespread increases in shrub abundance in Alaska based on comparisons of historic and modern aerial photographs was presented by Sturm et al. (2001), and more recent evidence from satellite imagery (Frost & Epstein, 2014), dendrochronology (Forbes et al., 2010), long-term ecological monitoring (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Myers-Smith et al., 2019), and Indigenous knowledge (Forbes & Stammler, 2009)

indicates that shrub expansion is a pan-Arctic phenomenon. Shrub increases occur in three general forms: (*i*) infilling of existing patches, either via lateral growth of shrubs or recruitment between patches; (*ii*) increase in growth, particularly in canopy height, which can include a change of growth form from prostrate (<0.1 m) and erect dwarf shrubs (0.1-0.4 m) to tall multi-stemmed shrubs (>0.4 m); and (*iii*) an advancing shrubline into areas previously beyond the range limit (Myers-Smith et al., 2011). The development of tall, tree-sized (>2 m) shrubs has been particularly notable in Yamal, where alder (*Alnus*) is the most abundant shrub genera at the treeline and willow (*Salix*) is most abundant farther north (Macias-Fauria et al., 2012).

Warmer air temperature has been the major driver of shrub growth and expansion, and passive warming experiments with open-top-chambers (OTCs), such as from the International Tundra Experiment (ITEX), support this link (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Post & Pedersen, 2008). Yet, the response of shrub growth to temperature is mediated by the environmental context. Temperature sensitivity is higher at sites with greater soil moisture, for taller shrubs growing at their range limits, and at the boundary between the Low and High Arctic (Myers-Smith et al., 2015). Snow dynamics have also been identified as a key control on shrub growth, as a positive feedback exists in which increased shrub abundance causes more snow trapping, leading to warmer soils, higher microbial activity, and more plant-available nitrogen, which promotes further shrub growth (Sturm et al., 2005). Recent work has found that nitrogen limitation consistently affects shrub individuals (Martin et al., 2022). Permafrost thaw can also increase nutrient availability, but the main impact of permafrost may be the creation of bare microsites with warm soils and few competitors where tall shrubs can establish within patterned-ground features (Frost et al., 2013). Similarly, cryogenic landslides on Yamal create concave, bare terrain where tall shrubs can emerge, as well (Verdonen et al., 2020). In addition to these abiotic factors, biotic drivers such as disease and herbivory may have important influences on shrub dynamics, but their role and interactions with climatic factors are complex and require further investigation (Myers-Smith et al., 2015).

Shrub expansion affects local food webs and ecosystem services, but it also may play a role in climate feedbacks within the Earth system. Although more carbon is stored as shrubs increase their above and below ground biomass, shrubs also promote warmer soils and permafrost thaw, which will likely release substantially more carbon than is sequestered in

biomass as climate warming continues (Sturm et al., 2005). Furthermore, shrub expansion leads to decreases in surface albedo and evapotranspiration-induced increases in atmospheric moisture content, both of which are additional positive climate feedbacks (Bonfils et al., 2012; Loranty & Goetz, 2012). Thus, improving our understanding of the controls on shrub expansion and the resulting climate feedbacks is necessary to better constrain climate change modelling.

2.2.3 High-resolution mapping

To enable the monitoring of changes in vegetation composition and plant traits that are occurring in the Arctic, remote sensing techniques beyond simply analysing NDVI have been employed to map vegetation. The Circumpolar Arctic Vegetation Map (CAVM), which classified the Arctic into 15 vegetation mapping units, was produced by Walker et al. (2005) based on regional experts' interpretations of existing maps, literature, and satellite imagery. The CAVM has been widely used as a base map in Arctic ecology studies and was updated in 2019 with a raster version at finer, 1 km resolution developed using an unsupervised classification routine (Raynolds et al., 2019). Although this biome-wide map provides an adequate overview of variation in land cover across the Arctic, its accuracy, estimated as only 39% in the original map and 70% in the raster version, is insufficient for incorporation into most analyses. Furthermore, vegetation in the Arctic is very spatially heterogeneous, such that there is often as much or more variation in cover within kilometre-scale pixels than between neighbouring pixels (Räsänen & Virtanen, 2019; Suvanto et al., 2014).

At the regional scale, more accurate land cover maps can be produced by combining higher spatial resolution satellite imagery with training data derived from *in-situ* observations using machine learning classification techniques (Duncan et al., 2019). For example, Wang et al. (2020) used Landsat satellite imagery (30 m resolution) covering a region in Alaska and north-western Canada to map annual land cover with over 80% accuracy and detected both disturbance-driven changes in forest area in the Boreal biome and climate-driven shrub expansion in the Arctic. In Yamal, Landsat imagery has also been used to map vegetation cover (Hofhuis et al., 2021; Verma et al., 2020), but the most detailed, recent land cover map over this region was produced by Bartsch et al. (2019) at 20 m resolution using Sentinel imagery with an approach incorporating unsupervised and supervised classification with assessment by local experts.

UAVs provide the opportunity to move from characterising broad land cover and vegetation cover to mapping plant functional types in tundra ecosystems due to their ability to capture imagery with much finer, centimetre-scale spatial resolution (e.g., Fraser et al., 2016; Orndahl, Ehlers, et al., 2022; Orndahl, Macander, et al., 2022; Thomson et al., 2021; Yang et al., 2021). These mapping efforts, which apply locally-calibrated classification models to reflectance data from multispectral sensors, have classified plant functional types with accuracies upwards of 80% in some cases (Fraser et al., 2016; Yang et al., 2021). Although UAV surveys are limited in the extent of the spatial area they cover, initial attempts to use UAV data to bridge between field data and satellite imagery have shown promise for producing more accurate regional maps that retain more detailed vegetation characterisations (Orndahl, Macander, et al., 2022; Thomson et al., 2021). As the availability of satellite imagery with metre and sub-metre resolution pixels continues to increase, our ability to accurately map Arctic vegetation communities and detect fine grain changes will improve even further.

In addition to mapping vegetation composition, remote sensing techniques can also be used to derive spatially continuous maps of plant traits. Plant chemistry can be inferred from spectral information, although employing regression models rather than the classification models used to determine plant functional types (Thomson et al., 2021). Physical traits, such as biomass, can also be estimated using empirical relationships with spectral bands (e.g., Berner et al., 2018; Räsänen et al., 2018), but they are more accurately predicted using approaches incorporating photogrammetry or active remote sensing (Cunliffe et al., 2020). Light detection and ranging (LiDAR) and UAV structure-from-motion (SfM) photogrammetry have been used to map vegetation structure with very high precision at the landscape scale (Alonzo et al., 2020), whereas synthetic aperture radar (SAR), captured by Sentinel-1, has been used for retrieval of tundra vegetation height over large extents (Bartsch et al., 2020). Applications of these techniques can provide insights into how vegetation structure, particularly shrub height, is changing over large scales and what is driving the spatial heterogeneity of these changes within and between tundra ecosystems.

2.3 Effects of herbivores on tundra ecosystems

2.3.1 Reindeer influence in the tundra

Top-down regulation from herbivores has been identified as a potentially important factor mediating the response of tundra ecosystems to climate change (Berner et al., 2020; Myers-

Smith et al., 2020). Since reindeer (same species as caribou, *Rangifer tarandus* L.) are the most widespread large herbivores in the Arctic, much of the existing research has focused on their impacts. Reindeer influence vegetation through a combination of their grazing, browsing, trampling (on both soil and snow), and addition of faeces and urine (Egelkraut et al., 2020). The combination of these activities leads to more complex impacts than those that would result simply from the defoliation from reindeer foraging, and a recent systematic review by Bernes et al. (2015) found that these impacts are highly context dependent, aside from a consistent reduction in lichen cover. Still, a large body of evidence from across the Arctic, reviewed by Olofsson & Post (2018), suggests that reindeer reduce the abundance of deciduous shrubs while promoting graminoids (e.g., Forbes et al., 2009; Kitti et al., 2009; Olofsson et al., 2001; Ricca et al., 2016). Further investigation of the mechanisms by which reindeer drive this shift and how they interact with other factors is necessary to understand the extent of this effect within the Arctic and explain how it varies in different environmental contexts.

The proposed mechanisms that contribute to a transition from moss- and shrub-dominated tundra to graminoid-dominated vegetation arise from multiple reindeer activities. Graminoids generally have higher tolerance to defoliation and damage than shrubs, allowing their rapid regrowth and recovery (Chapin III, 1980; Chapin III et al., 1980). Reindeer also deposit nutrients via their faeces and urine and promote warmer summer soils by disturbing the insulating moss layer, both of which favour enhanced nutrient cycling, often benefitting graminoids (van der Wal & Brooker, 2004). An increase in graminoid abundance leads to drying out of the soil due to their higher evapotranspiration rates, further limiting the growth of shrubs, which rely on high soil moisture (Zimov et al., 1995). Although each of these effects individually contributes to changes in the abundance of functional groups, simulation experiments have found that dramatic shifts in community composition require defoliation, trampling, and fertilisation working in combination (Barthelemy et al., 2015; Egelkraut et al., 2020).

In areas where heavy reindeer activity has supported graminoid-dominated vegetation, studies have found higher rates of nitrogen cycling as well as increased primary production (Olofsson et al., 2001, 2004; Sitters et al., 2019). These findings support the hypothesis that herbivores, rather than limiting ecosystem productivity by consuming vegetation, can actually facilitate enhanced productivity through shifts in plant community composition (Zimov et al.,

1995). Reindeer maintain these productive grazing lawns within a positive feedback loop, in which they fertilise and consume the nutrient-rich, easily-digestible forage (Forbes et al., 2009). In some cases, the vegetation has remained remarkably stable even a century after grazing ceased, driven by feedbacks stemming from increased nutrient turnover (Egelkraut et al., 2018).

The effect of reindeer on plant community composition is especially relevant given the widespread warming-driven shrub expansion in the Arctic. Following years of warmer temperatures linked to climate change (Olofsson et al., 2009) or experimental warming with OTCs (Post & Pedersen, 2008), shrub abundance increased markedly in the absence of herbivory but showed much smaller responses where reindeer were present. In a study where responses were monitored after the cessation of experimental warming, shrub increases continued where reindeer were excluded, but where reindeer herbivory occurred, shrub biomass returned to levels from before the experimental warming began (Kaarlejärvi et al., 2015). Warming has also been linked to increases in shrub height, but where reindeer are in high enough density, shrubs remain in a "browse trap" with small shrubs unable to grow into tall life stages regardless of summer temperature (Bråthen et al., 2017). This effect on shrub height has been observed in Fennoscandia and Yamal, where higher reindeer activity was linked with decreased height of willow shrubs (Kolari et al., 2019; Pajunen, 2009). Lastly, the impacts of herbivory interact with warming to affect the diversity of plant communities. Whereas warming in the absence of herbivores decreased species richness and led to the exclusion of species, reindeer herbivory promoted higher species gains and lower losses while facilitating cooccurrence (Kaarlejärvi et al., 2017; Post et al., 2021). This impact depends on the environmental conditions, as a separate study found that higher reindeer activity was linked to higher species richness in productive sites, but lower species richness in low-productive sites (Sundqvist et al., 2019). Thus, top-down control by reindeer remains important amidst rapid climate change and has the potential to counteract warming-driven impacts, but more work is needed to understand the extent of and heterogeneity in reindeer influence.

2.3.2 The Arctic vertebrate herbivore assemblage

While reindeer limit shrub expansion in modern tundra ecosystems, it has been postulated that a more diverse herbivore assemblage would likely exert an even stronger influence on the vegetation (Olofsson & Post, 2018). At the end of the Pleistocene, many large

mammalian herbivores, including mammoths, bison, woolly rhinoceroses, and horses were common in the Arctic. Some work suggests these animals maintained a highly productive graminoid- and forb-rich heterogeneous vegetation matrix that was widespread throughout the high northern latitudes, termed the "mammoth-steppe" (e.g., Zimov et al., 1995, 2012), although the relative role of herbivores and climate is still hotly debated (e.g., Monteath et al., 2021). As I described in **Chapter 1**, the ambitious Pleistocene Park experiment has been established in north-east Siberia using animal introductions to test the degree to which large herbivores can recreate the mammoth steppe within today's environmental conditions in the Arctic and secure higher and more resilient ecosystem carbon storage, sometimes referred to as the "Zimov hypothesis" (Macias-Fauria et al., 2020; Zimov, 2005). An important component of this hypothesis, in addition to vegetation changes, is the trampling and compaction of snow, which decreases insulation of the soil in winter, enabling it to freeze more deeply and preventing permafrost thaw (Beer et al., 2020). Early results from Pleistocene Park have demonstrated that the animals introduced into the area have had a strong effect on the abundance of woody vegetation, the soil carbon storage, and the vulnerability of the permafrost to thaw (Fischer et al., 2022; Macias-Fauria et al., 2020; Windirsch et al., 2022), but further investigation is ongoing to develop a mechanistic understanding of the effects and characterise the role of herbivore density and diversity.

The modern Arctic herbivore assemblage, although lacking the diversity of large herbivores, consists of many smaller herbivore species. Invertebrate herbivory is outside the scope of this thesis, but it does cause leaf damage across the tundra biome, albeit typically at low rates (Barrio et al., 2017; Rheubottom et al., 2019). There is also the herbivory of birds, including ptarmigans and geese, which can lead to the loss of vegetation cover as a result of their grazing and grubbing for roots and rhizomes (e,.g., Sjögersten et al., 2012; Speed et al., 2010; van Der Wal et al., 2007). Along the Hudson Bay coast, Jefferies et al. (2006) found that foraging by lesser snow geese led to widespread vegetation loss and soil degradation in coastal marshes. Such dramatic effects from goose herbivory have not been observed in tundra ecosystems in continental Europe, but goose populations are increasing in Europe and North America and are known to have an important role within ecosystem functioning in High Arctic Spitsbergen (Sjögersten et al., 2011).

Among Arctic mammalian herbivores, muskoxen are currently the only large herbivores other than reindeer with a wide distributional range, although they are much less widespread.

Similarly to reindeer, muskoxen affect vegetation dynamics especially via their trampling (Mosbacher et al., 2019). Small rodent herbivores, particularly lemmings and voles, are important to food webs and common in most Arctic ecosystems (Fufachev et al., 2019). Regular rodent cycles of 3-5 years cause oscillations in plant biomass, with the most substantial vegetation impacts occurring the year after a peak because of the strong impact of rodents on plants during the winter (Olofsson et al., 2012, 2013). Studies using exclosure designs that exclude only reindeer or both reindeer and small rodents have found that small rodents also limit the abundance of shrubs and their expansion with warming, but their impact was smaller than that of reindeer in the tundra and limited to dwarf shrubs (< 0.3 m height) (Lindén et al., 2021; Olofsson et al., 2009). Furthermore, the influence of small rodents extended to less palatable, evergreen shrubs, which they cut to create runways and nests under the snow (Lindén et al., 2021). These activities increased vegetation diversity by controlling the most dominant plant species. Lastly, small rodents also affect the nutrient dynamics in tundra ecosystems. Petit Bon et al. (2020) found that nutrient levels in vegetation were significantly higher in areas that had been disturbed by small rodents during the previous winter. Not only did rodents increase nutrient content more than reindeer did, but also their positive effect was weakened where reindeer were present. Even though the modern Arctic herbivore assemblage lacks many of the large herbivores of the past, the extant species still have unique functions that interact to create complex outcomes for ecosystem structure and functioning.

2.3.3 Carbon cycle responses

As I have already discussed, determining how Arctic carbon cycle dynamics will respond to climate change is an important research priority. Warming has strong effects on both methane and CO_2 emissions in the terrestrial Arctic, but here I focus mainly on CO_2, which has been measured more frequently in prior studies in the tundra and is the focus of my work in **Chapter 6**. Herbivory has been identified as one important factor mediating carbon cycle responses, and its impacts are typically assessed by measuring CO_2 fluxes using chamber measurement techniques within exclosures or across gradients of herbivory pressure. Yet, in a 2018 review of CO_2 flux chamber studies, only 13 studies were found that assessed the impact of herbivory, compared to 80 on air temperature and 36 on soil nutrients, and the authors characterised the knowledge level regarding disturbances like herbivory as “poor” and the importance of the topic as “urgent” in a global change context (Virkkala et al., 2018).

The Zimov hypothesis suggests that large herbivores can increase the net carbon uptake of tundra ecosystems, and there is recent evidence that herbivory-induced replacement of deciduous shrubs by graminoids can increase soil carbon sequestration (Ylänne et al., 2018). This increased net flow of carbon into the soil in grassland-dominated ecosystems results from lower soil temperatures, due to the lack of snow-trapping by shrubs and trees, and the deep, diffused roots of graminoids, which add more carbon to the first 1 m of soil than the shallow root systems of tundra shrubs (Macias-Fauria et al., 2020). Higher evapotranspiration rates of graminoids also may result in drier soils, leading to a higher ratio of CO_2 to CH_4 in emissions (Zimov et al., 2012). Conversely, studies measuring fluxes have found that systems were weaker carbon sinks when large herbivores were present, even though herbivory maintained graminoid-dominated vegetation and prevented shrub growth. Cahoon et al. (2012) showed that exclusion of reindeer and muskoxen in Greenland over eight years led to dramatic increases in CO_2 uptake, linked primarily to increases in photosynthesis. Experimental warming further increased CO_2 uptake, but only when herbivores were excluded. Limited differences in respiration were observed in any of these comparisons. Väisänen et al. (2014) also found that areas under heavy grazing, this time due to 50 years of reindeer pressure after the establishment of a pasture rotation fence in northern Norway, were weaker carbon sinks. However, in contrast to the findings of Cahoon et al. (2012), the effect was driven by higher respiration, likely due to enhanced soil respiration. These results do not support the Zimov hypothesis, but this discrepancy may be partially due to the lack of permafrost in the latter study and the short-term nature of the exclusion in the former study. In another experiment in the same study area used by Väisänen et al. (2014), Ylänne & Stark (2019) compared areas with herbivory-induced, decades-old graminoid dominance to areas where this vegetation shift had happened recently. Both areas had similar carbon sink strength, lower than the lightly grazed area, but both photosynthesis and ecosystem respiration were higher in the long-term graminoid vegetation. Thus, ecosystem processes driving carbon cycle feedbacks can continue to develop over time, even after a major change in the vegetation community has already occurred.

In exclosure experiments that excluded either just reindeer or reindeer and small rodents, herbivory again reduced net carbon uptake but with little difference measured between the two exclosure types (Metcalfe & Olofsson, 2015; Min et al., 2021). In fact, Metcalfe & Olofsson (2015) found that photosynthesis was slightly higher when small rodents were present than when all herbivores were excluded in Sweden, and Min et al. (2021) measured

higher net uptake in the same treatment type in Alaska. Although neither of these results were statistically significant, they occurred even though vascular plant biomass was highest without herbivores in both studies. The explanation for this pattern remains unclear, but it suggests that the impacts of the herbivore assemblage are not cumulative and more complex than just the consequences of biomass removal. This complexity may be especially relevant to small rodent impacts, as exclusion of lemmings for over 50 years in Alaska significantly decreased CO_2 uptake, although only in some habitat types (Lara et al., 2017). Other studies have also highlighted the importance of habitat type in mediating the impact of herbivory on carbon fluxes (e.g., Sjögersten et al., 2008). Therefore, the influence of herbivory on Arctic carbon fluxes depends on temporal elements, the diversity of the herbivore assemblage, and the environmental context, as well as the interactions between these factors. Much more evidence is needed to improve our mechanistic understanding and to add nuance to the Zimov hypothesis.

2.4 Remote sensing of herbivore impacts in the Arctic

2.4.1 Satellite-based detection of herbivore impacts

There is increasing recognition that herbivory in the tundra may not just be relevant for local ecosystem dynamics but also have implications beyond the Arctic (Malhi et al., 2022). Yet, to establish the importance of herbivory and characterise its consequences within the Earth system, analyses detecting the impacts of herbivory over large spatial scales are needed. Satellite remote sensing has been employed for this purpose, and some of the clearest findings have included a reduction in NDVI over a 770 km^2 area in the year immediately following small rodent peaks (Olofsson et al., 2012) and a progressive loss of vegetated area ultimately totalling 350 km^2, classified based on changes in NDVI, with increasing numbers of lesser snow geese over time (Jefferies et al., 2006).

Although reindeer are the most widespread large herbivores in the Arctic and local-scale observations have attributed vegetation transformations to their influence, satellite remote sensing often has not shown significant vegetation responses to reindeer herbivory. Fauchald et al. (2017), using time series of monthly NDVI over a large area of North America, found that reindeer abundance was not linked to plant biomass, but rather increases in plant biomass led to unanticipated declines in caribou populations. They speculated that this result may be explained by an expansion of shrub species with strong antibrowsing defences. Yet, the NDVI product used in their analysis had a very coarse spatial grain (1/12°, or ~8 km pixels),

and the summer herd ranges of the animals were uncertain and variable over the study period. The lack of precise data on spatial variability in reindeer herbivory pressure has limited other regional-scale studies as well, such as prior work in Yamal that could not conclusively detect reindeer impacts (Verma et al., 2020; Walker et al., 2009). The work of Campeau et al. (2019) and Rickbeil et al. (2015) benefitted from data generated with satellite-tracking collars, and while both studies found evidence of negative effects of herd density on vegetation productivity over time, there were unexplained patterns in which this relationship was weakest where reindeer densities were highest. Moreover, the satellite telemetry data used to characterise the animal movements had location errors on the order of hundreds of metres, which is much greater than the metre-scale uncertainty in some recent applications of the technology (e.g., Jung et al., 2018) and may have contributed to their inconsistent findings. Due to the migratory nature of reindeer, spatial variability in reindeer pressure has been difficult to accurately map, potentially explaining why studies have struggled to detect regional-scale reindeer herbivory impacts.

The use of NDVI or other similar spectral proxies for vegetation productivity as the primary response variable also may have limited prior studies' detection of reindeer herbivory. As I have described, the main impact of reindeer is often a shift in vegetation composition, which cannot be identified by analysing only NDVI. For example, Kolari et al. (2019) did not find clear differences in NDVI between grazed and ungrazed areas at the border of Finland and Norway even though reindeer herbivory had reduced the abundance and height of the dominant shrub *Salix lapponum* L. Rees et al. (2003) instead created land cover classifications using 1988 and 2000 satellite imagery over a 600 km^2 area in the Russian Arctic and observed a notable transformation from shrub- to graminoid-dominated tundra. They could not definitively link this impact to reindeer herbivory, but it was recognised as the most likely driver. Another study combined a land cover classification with satellite-derived snow and albedo products in northern Fennoscandia, finding that herbivory-induced vegetation change had resulted in later snowmelt, which had significant implications for the energy balance due to the increased surface albedo (Cohen et al., 2013). These results suggest that reindeer may have a regional-scale impact on ecosystem structure and functioning in the Arctic, but the responses to their herbivory are complex and not clearly observed as trends in NDVI, the common approach applied in studies of Arctic greening. Further work incorporating the recent developments in high resolution mapping of tundra ecosystems,

combined with more accurate data on spatial variation in reindeer pressure, can improve our understanding of the influence of reindeer herbivory at scales relevant to the Earth system.

2.4.2 Application of UAVs for studying herbivory

Whereas satellite data provides the opportunity to observe the broad-scale impacts of herbivory, data acquired using UAVs can reveal the factors mediating responses to herbivory at the landscape scale. These spatially continuous insights at centimetre-scale resolutions can enhance our mechanistic understanding of top-down regulation in the Arctic. Mapping herbivory impacts is a new application of UAV technology in the Arctic that has been explored recently by Siewert & Olofsson (2021). They used repeated UAV flights to detect the impacts of voles and lemmings at four ~20 ha sites in northernmost Sweden, each covering a range of habitat types. The effects of small rodents were substantial but highly heterogeneous and depended strongly upon differences in average snow depth both within and between sites. These results relied on a strong relationship found between a field inventory of rodent impacts and reductions in NDVI.

The potential for using UAVs to study Arctic herbivory is not limited to surveys using multispectral sensors. Other sensors, such as thermal cameras and spectroradiometers, have been deployed with UAVs to identify plant species, measure plant traits, and assess surface properties such as the land-surface temperature, all of which may be affected by herbivory (Yang et al., 2022). Structural variables such as canopy height and biomass are also relevant and can be measured with airborne LiDAR or even optical RGB cameras by applying SfM techniques (Alonzo et al., 2020). Thus, the application of UAV remote sensing to study the interactions between Arctic herbivory, landscape variables, and vegetation in spatially continuous analyses represents a promising but so far unexplored research area. Within the rapidly evolving Arctic, where there are major biome-wide changes as well as high spatial heterogeneity, a focus on mechanisms and the spatial and temporal dimensions of impacts is necessary to advance our understanding of these complex systems.

2.5 References

Alonzo, M., Dial, R. J., Schulz, B. K., Andersen, H.-E., Lewis-Clark, E., Cook, B. D., & Morton, D. C. (2020). Mapping tall shrub biomass in Alaska at landscape scale using structure-from-motion photogrammetry and lidar. *Remote Sensing of Environment*, *245*(May 2019), 111841. https://doi.org/10.1016/j.rse.2020.111841

Assmann, J. J., Myers-Smith, I. H., Kerby, J. T., Cunliffe, A. M., & Daskalova, G. N. (2020).

Drone data reveal heterogeneity in tundra greenness and phenology not captured by satellites. *Environmental Research Letters*, *15*(12), 125002. https://doi.org/10.1088/1748-9326/abbf7d

Barrio, I. C., Lindén, E., Te Beest, M., Olofsson, J., Rocha, A., Soininen, E. M., Alatalo, J. M., Andersson, T., Asmus, A., Boike, J., Bråthen, K. A., Bryant, J. P., Buchwal, A., Bueno, C. G., Christie, K. S., Denisova, Y. V., Egelkraut, D., Ehrich, D., Fishback, L., … Kozlov, M. V. (2017). Background invertebrate herbivory on dwarf birch (Betula glandulosa-nana complex) increases with temperature and precipitation across the tundra biome. *Polar Biology*, *40*(11), 2265–2278. https://doi.org/10.1007/s00300-017-2139-7

Barthelemy, H., Stark, S., & Olofsson, J. (2015). Strong Responses of Subarctic Plant Communities to Long-Term Reindeer Feces Manipulation. *Ecosystems*, *18*(5), 740–751. https://doi.org/10.1007/s10021-015-9856-y

Bartsch, A., Widhalm, B., Leibman, M., Ermokhina, K., Kumpula, T., Skarin, A., Wilcox, E. J., Jones, B. M., Frost, G. V., Höfler, A., & Pointner, G. (2020). Feasibility of tundra vegetation height retrieval from Sentinel-1 and Sentinel-2 data. *Remote Sensing of Environment*, *237*(December 2019), 111515. https://doi.org/10.1016/j.rse.2019.111515

Bartsch, A., Widhalm, B., Pointner, G., Ermokhina, K., Leibman, M., & Heim, B. (2019). *Landcover derived from Sentinel-1 and Sentinel-2 satellite data (2015-2018) for subarctic and arctic environments*. PANGAEA. https://doi.org/10.1594/PANGAEA.897916

Beer, C., Zimov, N., Olofsson, J., Porada, P., & Zimov, S. (2020). Protection of Permafrost Soils from Thawing by Increasing Herbivore Density. *Scientific Reports*, *10*(1), 4170. https://doi.org/10.1038/s41598-020-60938-y

Berner, L. T., Jantz, P., Tape, K. D., & Goetz, S. J. (2018). Tundra plant above-ground biomass and shrub dominance mapped across the North Slope of Alaska. *Environmental Research Letters*, *13*, 035002.

Berner, L. T., Massey, R., Jantz, P., Forbes, B. C., Macias-Fauria, M., Myers-Smith, I., Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B. V., Burns, P., Zetterberg, P., D'Arrigo, R., & Goetz, S. J. (2020). Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature Communications*, *11*(1), 4621. https://doi.org/10.1038/s41467-020-18479-5

Bernes, C., Bråthen, K. A., Forbes, B. C., Speed, J. D. M., & Moen, J. (2015). What are the impacts of reindeer/caribou (Rangifer tarandus L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, *4*(4). https://doi.org/10.1186/s13750-014-0030-3

Bhatt, U. S., Walker, D. A., Raynolds, M. K., Bieniek, P. A., Epstein, H. E., Comiso, J. C., Pinzon, J. E., Tucker, C. J., Steele, M., Ermold, W., & Zhang, J. (2017). Changing seasonality of panarctic tundra vegetation in relationship to climatic variables. *Environmental Research Letters*, *12*(5). https://doi.org/10.1088/1748-9326/aa6b0b

Bhatt, U. S., Walker, D. A., Raynolds, M. K., Comiso, J. C., Epstein, H. E., Jia, G., Gens, R., Pinzon, J. E., Tucker, C. J., Tweedie, C. E., & Webber, P. J. (2010). Circumpolar Arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions*, *14*(8). https://doi.org/10.1175/2010EI315.1

Bonfils, C. J. W., Phillips, T. J., Lawrence, D. M., Cameron-Smith, P., Riley, W. J., & Subin, Z. M. (2012). On the influence of shrub height and expansion on northern high latitude climate. *Environmental Research Letters*, *7*(1). https://doi.org/10.1088/1748-9326/7/1/015503

Bråthen, K. A., Ravolainen, V. T., Stien, A., Tveraa, T., & Ims, R. A. (2017). Rangifer management controls a climate-sensitive tundra state transition. *Ecological Applications*, *27*(8), 2416–2427. https://doi.org/10.1002/eap.1618

Cahoon, S. M. P., Sullivan, P. F., Post, E., & Welker, J. M. (2012). Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology*, *18*(2), 469–479. https://doi.org/10.1111/j.1365-2486.2011.02528.x

Campeau, A. B., Rickbeil, G. J. M., Coops, N. C., & Côté, S. D. (2019). Long-term changes in the primary productivity of migratory caribou (Rangifer tarandus) calving grounds and summer pasture on the Quebec-Labrador Peninsula (Northeastern Canada): the mixed influences of climate change and caribou herbivory. *Polar Biology*, *42*(5), 1005–1023. https://doi.org/10.1007/s00300-019-02492-6

Chapin III, F. S. (1980). Nutrient Allocation and Responses to Defoliation in Tundra Plants. *Arctic and Alpine Research*, *12*(4), 553. https://doi.org/10.2307/1550500

Chapin III, F. S., Johnson, D. A., & McKendrick, J. D. (1980). Seasonal Movement of Nutrients in Plants of Differing Growth Form in an Alaskan Tundra Ecosystem: Implications for Herbivory. *The Journal of Ecology*, *68*(1), 189. https://doi.org/10.2307/2259251

Cohen, J., Pulliainen, J., Ménard, C. B., Johansen, B., Oksanen, L., Luojus, K., & Ikonen, J. (2013). Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. *Remote Sensing of Environment*, *135*, 107–117. https://doi.org/10.1016/j.rse.2013.03.029

Cunliffe, A. M., J Assmann, J., N Daskalova, G., Kerby, J. T., & Myers-Smith, I. H. (2020). Aboveground biomass corresponds strongly with drone-derived canopy height but weakly with greenness (NDVI) in a shrub tundra landscape. *Environmental Research Letters*, *15*(12), 125004. https://doi.org/10.1088/1748-9326/aba470

Duncan, B. N., Ott, L. E., Abshire, J. B., Brucker, L., Carroll, M. L., Carton, J., Comiso, J. C., Dinnat, E. P., Forbes, B. C., Gonsamo, A., Gregg, W. W., Hall, D. K., Ialongo, I., Jandt, R., Kahn, R. A., Karpechko, A., Kawa, S. R., Kato, S., Kumpula, T., … Wu, D. L. (2019). Space-Based Observations for Understanding Changes in the Arctic-Boreal Zone. *Reviews of Geophysics*, 2019RG000652. https://doi.org/10.1029/2019RG000652

Egelkraut, D., Aronsson, K.-Å., Allard, A., Åkerholm, M., Stark, S., & Olofsson, J. (2018). Multiple Feedbacks Contribute to a Centennial Legacy of Reindeer on Tundra Vegetation. *Ecosystems*, *21*(8), 1545–1563. https://doi.org/10.1007/s10021-018-0239-z

Egelkraut, D., Barthelemy, H., & Olofsson, J. (2020). Reindeer trampling promotes vegetation changes in tundra heathlands: Results from a simulation experiment. *Journal of Vegetation Science*, *31*(3), 476–486. https://doi.org/10.1111/jvs.12871

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., … Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. In *Ecology Letters* (Vol. 15, Issue 2, pp. 164–175). https://doi.org/10.1111/j.1461-0248.2011.01716.x

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Dorrepaal, E., Elumeeva, T. G., Gill, M., Gould, W. A., Harte, J., Hik, D. S., Hofgaard, A., Johnson, D. R., Johnstone, J. F., Jónsdóttir, I. S., Jorgenson, J. C., … Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, *2*(6), 453–457. https://doi.org/10.1038/nclimate1465

Epstein, H. E., Raynolds, M. K., Walker, D. A., Bhatt, U. S., Tucker, C. J., & Pinzon, J. E. (2012). Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters*, *7*(1), 015506. https://doi.org/10.1088/1748-9326/7/1/015506

Fauchald, P., Park, T., Tømmervik, H., Myneni, R., & Hausner, V. H. (2017). Arctic greening from warming promotes declines in caribou populations. *Science Advances*, *3*(4). https://doi.org/10.1126/sciadv.1601365

Fischer, W., Thomas, C. K., Zimov, N., & Göckede, M. (2022). Grazing enhances carbon cycling but reduces methane emission during peak growing season in the Siberian Pleistocene Park tundra site. *Biogeosciences*, *19*(6), 1611–1633. https://doi.org/10.5194/bg-19-1611-2022

Forbes, B. C., Macias-Fauria, M., & Zetterberg, P. (2010). Russian Arctic warming and "greening" are closely tracked by tundra shrub willows. *Global Change Biology*, *16*(5), 1542–1554. https://doi.org/10.1111/j.1365-2486.2009.02047.x

Forbes, B. C., & Stammler, F. (2009). Arctic climate change discourse: The contrasting politics of research agendas in the West and Russia. *Polar Research*, *28*(1), 28–42. https://doi.org/10.1111/j.1751-8369.2009.00100.x

Forbes, B. C., Stammler, F., Kumpula, T., Meschtyb, N., Pajunen, A., & Kaarlejärvi, E. (2009). High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences*, *106*(52), 22041–22048. https://doi.org/10.1073/pnas.0908286106

Fraser, R. H., Olthof, I., Carrière, M., Deschamps, A., & Pouliot, D. (2011). Detecting long-term changes to vegetation in northern Canada using the Landsat satellite image archive. *Environmental Research Letters*, *6*(4). https://doi.org/10.1088/1748-9326/6/4/045502

Fraser, R. H., Olthof, I., Lantz, T. C., & Schmitt, C. (2016). UAV photogrammetry for mapping vegetation in the low-Arctic. *Arctic Science*, *2*(3), 79–102. https://doi.org/10.1139/as-2016-0008

Frost, G. V., & Epstein, H. E. (2014). Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology*, *20*(4), 1264–1277. https://doi.org/10.1111/gcb.12406

Frost, G. V, Epstein, H. E., Walker, D. A., Matyshak, G., & Ermokhina, K. (2013). Patterned-ground facilitates shrub expansion in Low Arctic tundra. *Environmental Research Letters*, *8*(1). https://doi.org/10.1088/1748-9326/8/1/015035

Fufachev, I. A., Ehrich, D., Sokolova, N. A., Sokolov, V. A., & Sokolov, A. A. (2019). Flexibility in a changing arctic food web: Can rough-legged buzzards cope with changing small rodent communities? *Global Change Biology*, *25*(11), 3669–3679. https://doi.org/10.1111/gcb.14790

Hofhuis, S. P., Ehrich, D., Sokolova, N. A., van Hooft, P., & Sokolov, A. A. (2021). Breeding den selection by Arctic foxes (Vulpes lagopus) in southern Yamal Peninsula, Russia. *Polar Biology*, *44*(12), 2307–2319. https://doi.org/10.1007/s00300-021-02962-w

Jefferies, R. L., Jano, A. P., & Abraham, K. F. (2006). A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, *94*(1), 234–242. https://doi.org/10.1111/j.1365-2745.2005.01086.x

Jia, G. J., Epstein, H. E., & Walker, D. A. (2003). Greening of arctic Alaska, 1981-2001. *Geophysical Research Letters*, *30*(20). https://doi.org/10.1029/2003GL018268

Ju, J., & Masek, J. G. (2016). The vegetation greenness trend in Canada and US Alaska from 1984-2012 Landsat data. *Remote Sensing of Environment*, *176*, 1–16. https://doi.org/10.1016/j.rse.2016.01.001

Jung, T. S., Hegel, T. M., Bentzen, T. W., Egli, K., Jessup, L., Kienzler, M., Kuba, K., Kukka, P. M., Russell, K., Suitor, M. P., & Tatsumi, K. (2018). Accuracy and performance of low-feature GPS collars deployed on bison Bison bison and caribou Rangifer tarandus. *Wildlife Biology*, *2018*(1), 1–11. https://doi.org/10.2981/wlb.00404

Kaarlejärvi, E., Eskelinen, A., & Olofsson, J. (2017). Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nature Communications*,

8(1), 419. https://doi.org/10.1038/s41467-017-00554-z

Kaarlejärvi, E., Hoset, K. S., & Olofsson, J. (2015). Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. *Global Change Biology*, *21*(9), 3379–3388. https://doi.org/10.1111/gcb.12970

Keenan, T. F., & Riley, W. J. (2018). Greening of the land surface in the world's cold regions consistent with recent warming. *Nature Climate Change*, *8*(September), 825–828. https://doi.org/10.1038/s41558-018-0258-y

Kennedy, R. E. (2012). New views on changing Arctic vegetation. *Environmental Research Letters*, *7*(1). https://doi.org/10.1088/1748-9326/7/1/011001

Kitti, H., Forbes, B. C., & Oksanen, J. (2009). Long- and short-term effects of reindeer grazing on tundra wetland vegetation. *Polar Biology*, *32*(2), 253–261. https://doi.org/10.1007/s00300-008-0526-9

Kolari, T. H. M., Kumpula, T., Verdonen, M., Forbes, B. C., & Tahvanainen, T. (2019). Reindeer grazing controls willows but has only minor effects on plant communities in Fennoscandian oroarctic mires. *Arctic, Antarctic, and Alpine Research*, *51*(1), 506–520. https://doi.org/10.1080/15230430.2019.1679940

Lara, M. J., Johnson, D. R., Andresen, C., Hollister, R. D., & Tweedie, C. E. (2017). Peak season carbon exchange shifts from a sink to a source following 50+ years of herbivore exclusion in an Arctic tundra ecosystem. *Journal of Ecology*, *105*(1), 122–131. https://doi.org/10.1111/1365-2745.12654

Lindén, E., Gough, L., & Olofsson, J. (2021). Large and small herbivores have strong effects on tundra vegetation in Scandinavia and Alaska. *Ecology and Evolution*, *11*(17), 12141–12152. https://doi.org/10.1002/ece3.7977

Loranty, M. M., & Goetz, S. J. (2012). Shrub expansion and climate feedbacks in Arctic tundra. *Environmental Research Letters*, *7*(1), 011005. https://doi.org/10.1088/1748-9326/7/1/011005

Lucht, W., Prentice, I. C., Myneni, R. B., Sitch, S., Friedlingstein, P., Cramer, W., Bousquet, P., Buermann, W., & Smith, B. (2002). Climatic Control of the High-Latitude Vegetation Greening Trend and Pinatubo Effect. *Science*, *296*(5573), 1687–1689. https://doi.org/10.1126/science.1071828

Macias-Fauria, M., Forbes, B. C., Zetterberg, P., & Kumpula, T. (2012). Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nature Climate Change*, *2*, 613–618. https://doi.org/10.1038/nclimate1558

Macias-Fauria, M., Jepson, P., Zimov, N., & Malhi, Y. (2020). Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190122. https://doi.org/10.1098/rstb.2019.0122

Macias-Fauria, M., Karlsen, S. R., & Forbes, B. C. (2017). Disentangling the coupling between sea ice and tundra productivity in Svalbard. *Scientific Reports*, *7*(1), 8586. https://doi.org/10.1038/s41598-017-06218-8

Malhi, Y., Lander, T., le Roux, E., Stevens, N., Macias-Fauria, M., Wedding, L., Girardin, C., Kristensen, J. Å., Sandom, C. J., Evans, T. D., Svenning, J.-C., & Canney, S. (2022). The role of large wild animals in climate change mitigation and adaptation. *Current Biology*, *32*(4), R181–R196. https://doi.org/10.1016/j.cub.2022.01.041

Martin, A. C., Jeffers, E. S., Petrokofsky, G., Myers-Smith, I., & MacIas-Fauria, M. (2017). Shrub growth and expansion in the Arctic tundra: An assessment of controlling factors using an evidence-based approach. *Environmental Research Letters*, *12*(8). https://doi.org/10.1088/1748-9326/aa7989

Martin, A. C., Macias-Fauria, M., Bonsall, M. B., Forbes, B. C., Zetterberg, P., & Jeffers, E. S. (2022). Common mechanisms explain nitrogen-dependent growth of Arctic shrubs

over three decades despite heterogeneous trends and declines in soil nitrogen availability. *New Phytologist*, *233*(2), 670–686. https://doi.org/10.1111/nph.17529

Metcalfe, D. B., & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO 2 exchange during the peak of the growing season. *Oikos*, *124*(12), 1632–1638. https://doi.org/10.1111/oik.02085

Miles, V. V., & Esau, I. (2016). Spatial heterogeneity of greening and browning between and within bioclimatic zones in northern West Siberia. *Environmental Research Letters*, *11*(11). https://doi.org/10.1088/1748-9326/11/11/115002

Min, E., Wilcots, M. E., Naeem, S., Gough, L., McLaren, J. R., Rowe, R. J., Rastetter, E. B., Boelman, N. T., & Griffin, K. L. (2021). Herbivore absence can shift dry heath tundra from carbon source to sink during peak growing season. *Environmental Research Letters*, *16*(2), 024027. https://doi.org/10.1088/1748-9326/abd3d0

Monteath, A. J., Gaglioti, B. V., Edwards, M. E., & Froese, D. (2021). Late Pleistocene shrub expansion preceded megafauna turnover and extinctions in eastern Beringia. *Proceedings of the National Academy of Sciences*, *118*(52), e2107977118. https://doi.org/10.1073/pnas.2107977118

Mosbacher, J. B., Michelsen, A., Stelvig, M., Hjermstad-Sollerud, H., & Schmidt, N. M. (2019). Muskoxen Modify Plant Abundance, Phenology, and Nitrogen Dynamics in a High Arctic Fen. *Ecosystems*, *22*(5), 1095–1107. https://doi.org/10.1007/s10021-018-0323-4

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., Speed, J. D. M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N. M., Baittinger, C., Trant, A. J., Hermanutz, L., Collier, L. S., … Vellend, M. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, *5*(9), 887–891. https://doi.org/10.1038/nclimate2697

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., MacIas-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4). https://doi.org/10.1088/1748-9326/6/4/045509

Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A., Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., … Wipf, S. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, *10*(2), 106–117. https://doi.org/10.1038/s41558-019-0688-1

Myers-Smith, I. H., Grabowski, M. M., Thomas, H. J. D., Angers-Blondin, S., Daskalova, G. N., Bjorkman, A. D., Cunliffe, A. M., Assmann, J. J., Boyle, J. S., McLeod, E., McLeod, S., Joe, R., Lennie, P., Arey, D., Gordon, R. R., & Eckert, C. D. (2019). Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change. *Ecological Monographs*, *89*(2), e01351. https://doi.org/10.1002/ecm.1351

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., & Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, *386*(6626), 698–702. https://doi.org/10.1038/386698a0

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., & Oksanen, L. (2001). Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, *24*(1), 13–24. https://doi.org/10.1034/j.1600-0587.2001.240103.x

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009).

Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*(11), 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x

Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761). https://doi.org/10.1098/rstb.2017.0437

Olofsson, J., Stark, S., & Oksanen, L. (2004). Reindeer influence on ecosystem processes in the tundra. *Oikos*, *105*(2), 386–396. https://doi.org/10.1111/j.0030-1299.2004.13048.x

Olofsson, J., te Beest, M., & Ericson, L. (2013). Complex biotic interactions drive long-term vegetation dynamics in a subarctic ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624), 20120486. https://doi.org/10.1098/rstb.2012.0486

Olofsson, J., Tommervik, H., & Callaghan, T. V. (2012). Vole and lemming activity observed from space. *Nature Climate Change*, *2*(12), 880–883. https://doi.org/10.1038/nclimate1537

Orndahl, K. M., Ehlers, L. P. W., Herriges, J. D., Pernick, R. E., Hebblewhite, M., & Goetz, S. J. (2022). Mapping tundra ecosystem plant functional type cover, height and aboveground biomass in Alaska and northwest Canada using unmanned aerial vehicles. *Arctic Science*, *1180*, 1165–1180. https://doi.org/10.1139/as-2021-0044

Orndahl, K. M., Macander, M. J., Berner, L. T., & Goetz, S. J. (2022). Plant functional type aboveground biomass change within Alaska and northwest Canada mapped using a 35-year satellite time series from 1985 to 2020. *Environmental Research Letters*, *17*(11), 115010. https://doi.org/10.1088/1748-9326/ac9d50

Pajunen, A. M. (2009). Environmental and Biotic Determinants of Growth and Height of Arctic Willow Shrubs along a Latitudinal Gradient. *Arctic, Antarctic, and Alpine Research*, *41*(4), 478–485. https://doi.org/10.1657/1938-4246-41.4.478

Park, T., Ganguly, S., Tømmervik, H., Euskirchen, E. S., Høgda, K. A., Karlsen, S. R., Brovkin, V., Nemani, R. R., & Myneni, R. B. (2016). Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environmental Research Letters*, *11*(8). https://doi.org/10.1088/1748-9326/11/8/084001

Petit Bon, M., Inga, K. G., Jónsdóttir, I. S., Utsi, T. A., Soininen, E. M., & Bråthen, K. A. (2020). Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities. *Oikos*, *April*, 1–14. https://doi.org/10.1111/oik.07074

Phoenix, G. K., & Bjerke, J. W. (2016). Arctic browning: extreme events and trends reversing arctic greening. *Global Change Biology*, *22*(9), 2960–2962. https://doi.org/10.1111/gcb.13261

Piao, S., Nan, H., Huntingford, C., Ciais, P., Friedlingstein, P., Sitch, S., Peng, S., Ahlström, A., Canadell, J. G., Cong, N., Levis, S., Levy, P. E., Liu, L., Lomas, M. R., Mao, J., Myneni, R. B., Peylin, P., Poulter, B., Shi, X., … Chen, A. (2014). Evidence for a weakening relationship between interannual temperature variability and northern vegetation activity. *Nature Communications*, *5*, 1–7. https://doi.org/10.1038/ncomms6018

Post, E., Cahoon, S. M. P., Kerby, J. T., Pedersen, C., & Sullivan, P. F. (2021). Herbivory and warming interact in opposing patterns of covariation between arctic shrub species at large and local scales. *Proceedings of the National Academy of Sciences*, *118*(6), e2015158118. https://doi.org/10.1073/pnas.2015158118

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(34), 12353–12358. https://doi.org/10.1073/pnas.0802421105

Post, E., Steinman, B. A., & Mann, M. E. (2018). Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports*, *8*(1), 1–8. https://doi.org/10.1038/s41598-018-22258-0

Pouliot, D., Latifovic, R., & Olthof, I. (2008). Trends in vegetation NDVI from 1 km AVHRR data over Canada for the period 1985-2006. *International Journal of Remote Sensing*, *30*(1), 149–168. https://doi.org/10.1080/01431160802302090

Räsänen, A., Juutinen, S., Aurela, M., & Virtanen, T. (2018). Predicting aboveground biomass in Arctic landscapes using very high spatial resolution satellite imagery and field sampling. *International Journal of Remote Sensing*. https://doi.org/10.1080/01431161.2018.1524176

Räsänen, A., & Virtanen, T. (2019). Data and resolution requirements in mapping vegetation in spatially heterogeneous landscapes. *Remote Sensing of Environment*, *230*(May), 111207. https://doi.org/10.1016/j.rse.2019.05.026

Raynolds, M. K., Comiso, J. C., Walker, D. A., & Verbyla, D. (2008). Relationship between satellite-derived land surface temperatures, arctic vegetation types, and NDVI. *Remote Sensing of Environment*, *112*, 1884–1894. https://doi.org/10.1016/j.rse.2007.09.008

Raynolds, M. K., Walker, D. A., Balser, A., Bay, C., Campbell, M., Cherosov, M. M., Daniëls, F. J. A., Eidesen, P. B., Ermokhina, K. A., Frost, G. V., Jedrzejek, B., Jorgenson, M. T., Kennedy, B. E., Kholod, S. S., Lavrinenko, I. A., Lavrinenko, O. V., Magnússon, B., Matveyeva, N. V., Metúsalemsson, S., … Troeva, E. (2019). A raster version of the Circumpolar Arctic Vegetation Map (CAVM). *Remote Sensing of Environment*, *232*(January). https://doi.org/10.1016/j.rse.2019.111297

Rees, W. G., Williams, M., & Vitebsky, P. (2003). Mapping land cover change in a reindeer herding area of the Russian arctic using Landsat TM and ETM+ imagery and indigenous knowledge. *Remote Sensing of Environment*, *85*(4), 441–452. https://doi.org/10.1016/S0034-4257(03)00037-3

Rheubottom, S. I., Barrio, I. C., Kozlov, M. V., Alatalo, J. M., Andersson, T., Asmus, A. L., Baubin, C., Brearley, F. Q., Egelkraut, D. D., Ehrich, D., Gauthier, G., Jónsdóttir, I. S., Konieczka, S., Lévesque, E., Olofsson, J., Prevéy, J. S., Slevan-Tremblay, G., Sokolov, A., Sokolova, N., … Hik, D. S. (2019). Hiding in the background: community-level patterns in invertebrate herbivory across the tundra biome. *Polar Biology*, *42*(10), 1881–1897. https://doi.org/10.1007/s00300-019-02568-3

Ricca, M. A., Miles, A. K., Van Vuren, D. H., & Eviner, V. T. (2016). Impacts of introduced Rangifer on ecosystem processes of maritime tundra on subarctic islands. *Ecosphere*, *7*(3). https://doi.org/10.1002/ecs2.1219

Rickbeil, G. J. M., Coops, N. C., & Adamczewski, J. (2015). The grazing impacts of four barren ground caribou herds (Rangifer tarandus groenlandicus) on their summer ranges: An application of archived remotely sensed vegetation productivity data. *Remote Sensing of Environment*, *164*, 314–323. https://doi.org/10.1016/j.rse.2015.04.006

Siewert, M. B., & Olofsson, J. (2020). Scale-dependency of Arctic ecosystem properties revealed by UAV. *Environmental Research Letters*, *15*(9), 094030. https://doi.org/10.1088/1748-9326/aba20b

Siewert, M. B., & Olofsson, J. (2021). UAV reveals substantial but heterogeneous effects of herbivores on Arctic vegetation. *Scientific Reports*, *11*(1), 19468. https://doi.org/10.1038/s41598-021-98497-5

Sitters, J., Cherif, M., Egelkraut, D., Giesler, R., & Olofsson, J. (2019). Long-term heavy reindeer grazing promotes plant phosphorus limitation in arctic tundra. *Functional Ecology*, *33*(7), 1233–1242. https://doi.org/10.1111/1365-2435.13342

Sjögersten, S., van der Wal, R., Loonen, M. J. J. E., & Woodin, S. J. (2011). Recovery of ecosystem carbon fluxes and storage from herbivory. *Biogeochemistry*, *106*(3), 357–

370. https://doi.org/10.1007/s10533-010-9516-4
Sjögersten, S., van der Wal, R., & Woodin, S. J. (2012). Impacts of Grazing and Climate Warming on C Pools and Decomposition Rates in Arctic Environments. *Ecosystems*, *15*(3), 349–362. https://doi.org/10.1007/s10021-011-9514-y
Sjögersten, S., Van Der Wal, R., & Woodin, S. J. (2008). Habitat Type Determines Herbivory Controls Over Co2 Fluxes in a Warmer Arctic. *Ecology*, *89*(8), 2103–2116.
Speed, J. D. M., Woodin, S. J., Tømmervik, H., & van der Wal, R. (2010). Extrapolating herbivore-induced carbon loss across an arctic landscape. *Polar Biology*, *33*(6), 789–797. https://doi.org/10.1007/s00300-009-0756-5
Sturm, M., Racine, C., & Tape, K. (2001). Increasing shrub abundance in the Arctic. *Nature*, *411*(6837), 546–547. https://doi.org/10.1038/35079180
Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J., & Romanovsky, V. E. (2005). Winter Biological Processes Could Help Convert Arctic Tundra to Shrubland. *BioScience*, *55*(1), 17. https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2
Sundqvist, M. K., Moen, J., Björk, R. G., Vowles, T., Kytöviita, M. M., Parsons, M. A., & Olofsson, J. (2019). Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. *Journal of Ecology*, *April*, 1–13. https://doi.org/10.1111/1365-2745.13201
Suvanto, S., Le Roux, P. C., & Luoto, M. (2014). Arctic-alpine vegetation biomass is driven by fine-scale abiotic heterogeneity. *Geografiska Annaler: Series A, Physical Geography*, *96*(4), n/a-n/a. https://doi.org/10.1111/geoa.12050
Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, *12*(4), 686–702. https://doi.org/10.1111/j.1365-2486.2006.01128.x
Thomson, E. R., Spiegel, M. P., Althuizen, I. H. J., Bass, P., Chen, S., Chmurzynski, A., Halbritter, A. H., Henn, J. J., Jónsdóttir, I. S., Klanderud, K., Li, Y., Maitner, B. S., Michaletz, S. T., Niittynen, P., Roos, R. E., Telford, R. J., Enquist, B. J., Vandvik, V., Macias-Fauria, M., & Malhi, Y. (2021). Multiscale mapping of plant functional groups and plant traits in the High Arctic using field spectroscopy, UAV imagery and Sentinel-2A data. *Environmental Research Letters*, *16*(5). https://doi.org/10.1088/1748-9326/abf464
Treharne, R., Bjerke, J. W., Tømmervik, H., Stendardi, L., & Phoenix, G. K. (2019). Arctic browning: Impacts of extreme climatic events on heathland ecosystem CO 2 fluxes. *Global Change Biology*, *25*(2), 489–503. https://doi.org/10.1111/gcb.14500
Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., & Stark, S. (2014). Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, *4*(5), 384–388. https://doi.org/10.1038/nclimate2147
van der Wal, R., & Brooker, R. W. (2004). Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, *18*(1), 77–86. https://doi.org/10.1111/j.1365-2435.2004.00820.x
van Der Wal, R., Sjögersten, S., Woodin, S. J., Cooper, E. J., Jónsdóttir, I. S., Kuijper, D., Fox, T. A. D., & Huiskes, A. D. (2007). Spring feeding by pink-footed geese reduces carbon stocks and sink strength in tundra ecosystems. *Global Change Biology*, *13*(2), 539–545. https://doi.org/10.1111/j.1365-2486.2006.01310.x
Verdonen, M., Berner, L. T., Forbes, B. C., & Kumpula, T. (2020). Periglacial vegetation dynamics in Arctic Russia: decadal analysis of tundra regeneration on landslides with time series satellite imagery. *Environmental Research Letters*, *15*(10), 105020. https://doi.org/10.1088/1748-9326/abb500

Verma, M., Schulte to Bühne, H., Lopes, M., Ehrich, D., Sokovnina, S., Hofhuis, S. P., & Pettorelli, N. (2020). Can reindeer husbandry management slow down the shrubification of the Arctic? *Journal of Environmental Management*, *267*(April), 110636. https://doi.org/10.1016/j.jenvman.2020.110636

Virkkala, A., Virtanen, T., Lehtonen, A., Rinne, J., & Luoto, M. (2018). The current state of CO2 flux chamber studies in the Arctic tundra: A review. *Progress in Physical Geography*, *42*(2), 162–184. https://doi.org/10.1177/0309133317745784

Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Raynolds, M. K., Comiso, J. C., Gubarkov, A. A., Khomutov, A. V., Jia, G. J., Kaarlejärvi, E., Kaplan, J. O., Kumpula, T., Kuss, P., Matyshak, G., Moskalenko, N. G., Orekhov, P., Romanovsky, V. E., Ukraientseva, N. G., & Yu, Q. (2009). Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index. *Environmental Research Letters*, *4*(4), 045004. https://doi.org/10.1088/1748-9326/4/4/045004

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & The other members of the CAVM Team. (2005). The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, *16*(3), 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x

Wang, J. A., & Friedl, M. A. (2019). The role of land cover change in Arctic-Boreal greening and browning trends. *Environmental Research Letters*, *14*(12), 125007. https://doi.org/10.1088/1748-9326/ab5429

Wang, J. A., Sulla-Menashe, D., Woodcock, C. E., Sonnentag, O., Keeling, R. F., & Friedl, M. A. (2020). Extensive land cover change across Arctic–Boreal Northwestern North America from disturbance and climate forcing. *Global Change Biology*, *26*(2), 807–822. https://doi.org/10.1111/gcb.14804

Windirsch, T., Grosse, G., Ulrich, M., Forbes, B. C., Göckede, M., Wolter, J., Macias-Fauria, M., Olofsson, J., Zimov, N., & Strauss, J. (2022). Large herbivores on permafrost— a pilot study of grazing impacts on permafrost soil carbon storage in northeastern Siberia. *Frontiers in Environmental Science*, *10*(August), 1–17. https://doi.org/10.3389/fenvs.2022.893478

Yang, D., Morrison, B. D., Davidson, K. J., Lamour, J., Li, Q., Nelson, P. R., Hantson, W., Hayes, D. J., Swetnam, T. L., McMahon, A., Anderson, J., Ely, K. S., Rogers, A., & Serbin, S. P. (2022). Remote sensing from unoccupied aerial systems: Opportunities to enhance Arctic plant ecology in a changing climate. *Journal of Ecology*, *110*(12), 2812–2835. https://doi.org/10.1111/1365-2745.13976

Yang, D., Morrison, B. D., Hantson, W., Breen, A. L., McMahon, A., Li, Q., Salmon, V. G., Hayes, D. J., & Serbin, S. P. (2021). Landscape-scale characterization of Arctic tundra vegetation composition, structure, and function with a multi-sensor unoccupied aerial system. *Environmental Research Letters*, *16*(8), 085005. https://doi.org/10.1088/1748-9326/ac1291

Ylänne, H., Olofsson, J., Oksanen, L., & Stark, S. (2018). Consequences of grazer-induced vegetation transitions on ecosystem carbon storage in the tundra. *Functional Ecology*, *32*(4), 1091–1102. https://doi.org/10.1111/1365-2435.13029

Ylänne, H., & Stark, S. (2019). Distinguishing Rapid and Slow C Cycling Feedbacks to Grazing in Sub-arctic Tundra. *Ecosystems*, *22*(5), 1145–1159. https://doi.org/10.1007/s10021-018-0329-y

Zhou, L., Tucker, C. J., Kaufmann, R. K., Slayback, D., Shabanov, N. V., & Myneni, R. B. (2001). Variations in northern vegetation activity inferred from satellite data of

vegetation index during 1981 to 1999. *Journal of Geophysical Research: Atmospheres*, *106*(D17), 20069–20083. https://doi.org/10.1029/2000JD000115

Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., Ciais, P., Sitch, S., Friedlingstein, P., Arneth, A., Cao, C., Cheng, L., Kato, E., Koven, C., Li, Y., Lian, X., Liu, Y., Liu, R., Mao, J., … Zeng, N. (2016). Greening of the Earth and its drivers. *Nature Climate Change*, *6*(8), 791–795. https://doi.org/10.1038/nclimate3004

Zimov, S. A. (2005). Pleistocene Park: Return of the Mammoth's Ecosystem. *Science*, *308*(5723), 796–798. https://doi.org/10.1126/science.1113442

Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., Reynolds, J. F., & Chapin, M. C. (1995). Steppe-Tundra Transition: A Herbivore-Driven Biome Shift at the End of the Pleistocene. *The American Naturalist*, *146*(5), 765–794. https://doi.org/10.1086/285824

Zimov, S. A., Zimov, N. S., Tikhonov, A. N., & Chapin, I. S. (2012). Mammoth steppe: A high-productivity phenomenon. *Quaternary Science Reviews*, *57*, 26–45. https://doi.org/10.1016/j.quascirev.2012.10.005

Chapter 3:
Methods and study area



3.1 Overview

To achieve the objectives presented in **Chapter 1**, I designed three separate studies that analysed the impacts of reindeer herbivory at different spatial scales using methods that were informed by the literature outlined in **Chapter 2**. The research focused on the Yamal Peninsula and involved remote sensing data and field-based data collection. In this chapter, I first provide some background on Yamal before describing in more detail the areas delineated for regional-scale analysis and the site where I conducted fieldwork. I then discuss the methods that were used to measure responses to herbivory at each of the different scales while highlighting how these approaches were enabled by the long-term, stable reindeer herd migration patterns on Yamal and my colleagues' relationships with local herders. In this section, I present the theoretical background behind the key methods employed in the DPhil research, as well as methodological details not covered in the research chapters. Full descriptions of the methodology used in each study are provided in the relevant research chapters (see **Chapters 4**, **5**, and **6**).

3.2 Study area

3.2.1 The Yamal Peninsula

As I described in **Chapter 1**, the Yamal Peninsula comprises a social-ecological system where Indigenous Nenets mobile pastoralists migrate up to 1,200 km annually with their reindeer herds within a region that is experiencing rapid environmental change and industrial development. The peninsula covers 700 km from south to north between the northern terminus of the Polar Urals and the Kara Sea and encompasses a biogeographic gradient from the forest-tundra ecotone to the high Arctic (**Figure 3.1**) (Walker et al., 2009). This gradient supports a large variation in plant communities, which decrease in productivity, height, and diversity from south to north. Tall shrubs, primarily *Salix* spp., have increased notably due to climate change in the southern half of the peninsula (Frost & Epstein, 2014). Regarding the animal community, some latitudinal gradients include a northwards decrease in diversity of passerine birds and a northward shift in small rodents towards more lemmings and fewer voles (V. Sokolov et al., 2012; Sokolova et al., 2014). Climate change is causing animal species' ranges to shift northward, resulting in the expansion of boreal species such as red fox and Hooded Crow into local food webs (A. A. Sokolov et al., 2016).

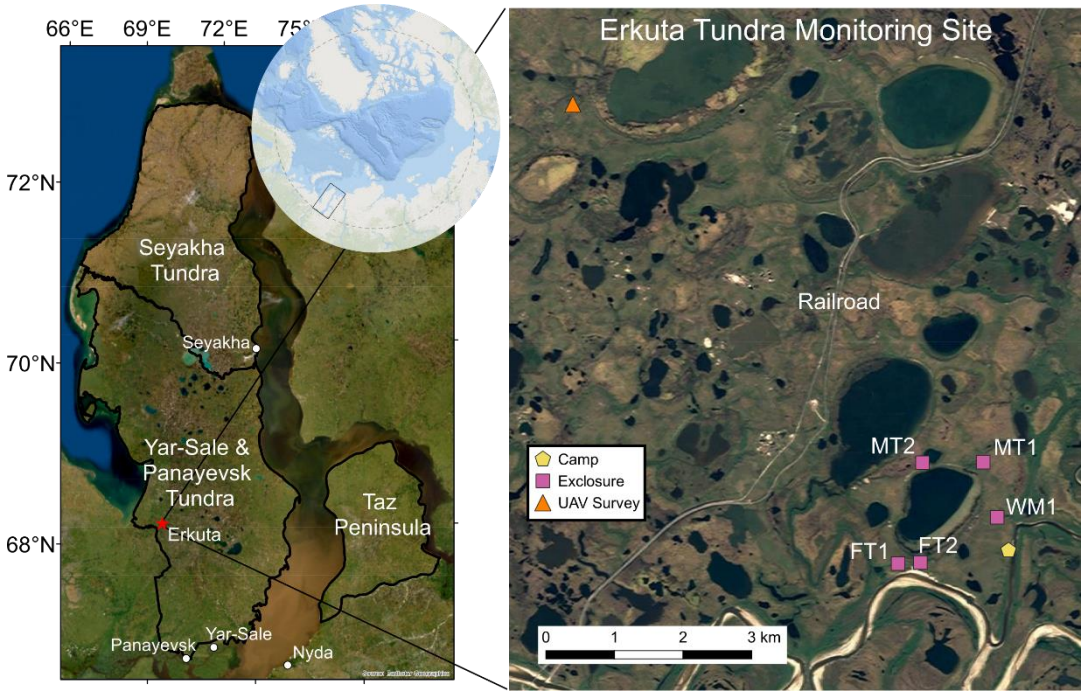


Figure 3.1: The study areas within the Yamal Peninsula. The regional-scale analysis in **Chapter 4** involves comparisons within the Yar-Sale & Panayevsk tundra and between this region and the Taz Peninsula. Reindeer herding centres – Yar-Sale, Panayevsk, Seyakha, and Nyda – are also displayed. The remaining research chapters present studies that were conducted at the Erkuta Tundra Monitoring Site, where there is an established research camp. The site is indicated where repeated UAV surveys were flown to detect landscape-scale change in **Chapter 5** and the locations of exclosures, established since 2014, are shown where carbon fluxes were measured as part of the study presented in **Chapter 6**. The base maps are from ESRI and Earthstar Geographics.

The nomadic population on Yamal presently includes ~5,500 people (~1,000 families) with ~225,000 reindeer (Terekhina & Volkovitskiy, 2020). Reindeer herding collectives are organised either as private households or brigades of reindeer herding enterprises – the remnants from Soviet-era state-owned *sovkhozy* – even though most of the reindeer in these enterprises are now privately owned. The herds are each associated with one of the villages serving as reindeer herding centres on the peninsula (Yar-Sale, Panayevsk, and Seyakha), which are linked to the territory that is used during the migrations (**Figure 3.1**). The industrial development in the region has posed challenges for the Nenets herders, including obstacles to their movement, but also opportunities, such as increased access to markets and use of the train (Forbes et al., 2009; Stammler, 2005). Yet, in the past decade, several crisis phenomena have emerged that have had more sudden impacts on reindeer herding. Rain-on-snow events have become more frequent, which has led to mass mortality of reindeer when the icing of pastures has made their winter forage inaccessible (Forbes et al., 2016). There was also an outbreak of anthrax on the peninsula in 2016, triggering discussions about both

the economics and environmental consequences of reindeer management practices (Golovnev, 2017). These stressors are only starting to cause major changes in herding on Yamal, which include, for example, herders choosing to remain year-round in the forest-tundra zone, but may soon have ecological implications related to changes in the timing and amount of reindeer herbivory pressure (Volkovitskiy & Terekhina, 2020).

3.2.2 Yar-Sale & Panayevsk tundra and Taz Peninsula

The regional-scale analysis in **Chapter 4** focusses on the southern part of the Yamal Peninsula where the territory is associated with the Yar-Sale and Panayevsk brigades (**Figure 3.1**). The majority of reindeer, approximately 160,000 out of the 225,000 total, are found on this part of the peninsula in the summer. Obtaining reindeer numbers on Yamal is not straightforward due to the lack of centralisation with both private households and enterprise brigades as well as herders' reticence to share the number of animals in their herd. Our efforts to map the herds and their sizes is described in **Section 3.3.1**. Whereas herd movements are often shorter and circular on the Seyakha tundra to the north, the migrations on the Yar-Sale and Panayevsk tundra are typically long and linear, with herds moving northwest towards the Kara Sea coast in the summer and returning south to the treeline for the winter while remaining at each campsite for 3-5 days on average (Degteva & Nellemann, 2013). These long migration patterns have been followed relatively consistently for many decades, inherited from past generations of Nenets nomads (Evladov, 1992). This consistency enables spatial comparisons of the vegetation within this region across variation in the density and intra-annual timing of reindeer pressure.

The Taz Peninsula was chosen as a region for broad-scale comparison against Yar-Sale/Panayevsk due to its proximity but much lower reindeer numbers. A more detailed description of the similarities between the vegetation, climate, geography, and geology of these regions is presented in **Chapter 4**, but both areas are dominated by shrubby and mossy tundra interspersed with sedge-dominated wetlands within low and flat topography shaped by meandering rivers and thermokarst lakes (Esau et al., 2016; Raynolds et al., 2019; Walker et al., 2009). There has been extensive greening in both regions accompanied by observations of tall shrub expansion (Berner et al., 2020; Esau et al., 2016). Although there is reindeer herding in Taz, with Nyda serving as the reindeer herding centre in the region, the numbers of reindeer in the tundra zone of Taz are very low compared to Yamal, estimated to be

approximately 10,000 animals (i.e., at least one order of magnitude less), due to the longer history of hydrocarbon development in the area acting as an obstacle to migrations (Kvashnin, 2009).

3.2.3 Erkuta Tundra Monitoring Site

The data collection for the landscape- and plot-scale studies was conducted at the Erkuta Tundra Monitoring Site near the confluence of the Payutayakha and Erkutayaha Rivers (68.2˚ N, 69.2˚ E; **Figure 3.1**). Long-term ecological monitoring, particularly of animal population dynamics, has been ongoing in Erkuta for decades (e.g., Fufachev et al., 2019; V. Sokolov et al., 2012; Sokolova et al., 2014), and there is a camp at the site used by researchers in all seasons (**Figure 3.2**). Erkuta is accessible by train on the Obskaya–Bovanenkovo railway line, the northernmost railway in the world which was opened by Gazprom in 2010 to support their hydrocarbon operations.



Figure 3.2: The research camp in Erkuta on the Payutayakha River. Image captured by Aleksandr Sokolov flying a Mavic 2 Pro (DJI, Shenzhen, China) UAV.



Figure 3.3: Marcus Spiegel conducting allometry measurements in a willow thicket. Summer 2021. Photo credit: Kirill Shklyar.



Figure 3.4: Teatime in the *chum* (nomadic tent) of Nenets herders. Summer 2021. Photo credit: Alexandra Terekhina.

The topography is especially flat in Erkuta within a dense network of streams and lakes that are used by the local Indigenous people (and researchers) for navigation. Vegetation is mostly dominated by mosses and dwarf shrubs in habitat types that are classified as mesic tundra, but tall thickets of willow (*Salix* spp.) and sometimes alder (*Alnus fruticosa*) reaching more than 2 m height (**Figure 3.3**) grow in concavities and along the banks of waterways (Baubin et al., 2016; Ehrich et al., 2012). Predators in Erkuta include the Arctic fox, weasel, stoat, wolverine, gyrfalcon, peregrine falcon, rough-legged buzzard, and several species of jaegers, whereas the herbivores include voles, lemmings, ptarmigans, the mountain hare, and reindeer (Fufachev et al., 2019; A. A. Sokolov et al., 2016; Sokolova et al., 2014).

Reindeer herds are present in Erkuta during all seasons, but since the area is not along a major migration corridor, the number of reindeer varies from year to year. Some herds come to the area in the summer, whereas others are only based there during the snow season, as families that live in Erkuta year-round often give their reindeer to relatives to herd. In summer 2021, when I conducted my fieldwork, the area was visited by a large herd of approximately 2,000 reindeer, the largest herd that had passed through Erkuta in several years (A. A. Sokolov, pers. comm.). My collaborators have developed strong relationships with the local herders during their many years of working in the area (**Figure 3.4**), which has enabled many research activities such as the collaring of reindeer (Terekhina et al., 2022) and the establishment of herbivore exclosures (Baubin et al., 2016).

3.3 Data collection, processing, and analysis

3.3.1 Regional scale

The study at the regional scale involved comparisons of two remotely sensed variables – the proportions of different landcover types and the vegetation sensitivity index (VSI, after Seddon & Macias-Fauria et al. (2016)) – across spatial variations in reindeer pressure. This analysis compared Yar-Sale/Panayevsk and Taz, but also utilised new maps of reindeer herd sizes and movements contributed by my co-authors (see **Chapter 4**). They developed these maps by compiling official statistics and conducting interviews and participatory mapping with Indigenous experts. The data collection included a visit to Yar-Sale, where they retrieved the official numbers of animals based on corral (round-up) calculations and mapped the migration routes of the enterprise brigades. Although they were not able to travel to Panayevsk, they met with a former employee of the enterprise, as well as zootechnicians, who are experts that are consulted on matters such as reindeer breeding and seasonal

movements, and employees of the Kharp *obshchina*, which is a community structure facilitating the cooperation of private reindeer herders. The Kharp *obshchina* is the largest in Yamal and includes more than 60,000 reindeer owned by several hundred families. Based on their interviews, the researchers found that the corridors travelled by the herds are rather permanent, although the exact timings of movements can vary each year depending on variables such as the thaw of rivers and condition of the animals. They estimated the monthly locations from June to August and mapped them together on printed GGTS (State GIS Center) maps (1:200,000). To ensure that their data were comprehensive, they independently determined that the total number of reindeer on Yamal was 225,000, of which 160,000 were on Yar-Sale/Panayevsk, during 2019-2020 based on interviews with veterinarians working as part of the annual anthrax vaccination campaigns. Then they calculated the total number of reindeer that were included in the results of this mapping exercise and found that only ~8,500 (~5%) were missing. These missing animals are likely spread throughout the region, as all large herds were mapped.

Due to the stability of reindeer herding on Yamal, we were able to use these new maps to test for correspondence between herbivory pressure and vegetation variables. The landcover product was produced by Bartsch et al. (2019) using optical bands from Sentinel-2 and C-band SAR from Sentinel-1. The classification approach first used a k-means unsupervised classification to segment the area and then these classes were used as training areas in a supervised classification. The supervised classification was performed by local experts who then refined the set of classes, ultimately achieving an accuracy of 83%. The final list of classes includes three aquatic classes and 18 terrestrial classes that are defined both by the vegetation and the moisture level, following the style of the CAVM (Walker et al., 2005). I condensed these 18 classes into 6 broader classes to facilitate comparisons of the distribution of landcover pixels between different areas. While manipulating these classes, I consulted with the authors of the dataset and compared the landcover map visually against the CAVM to ensure that my descriptions of the condensed classes were accurate.

The other remote sensing variable compared was VSI, which maps variation over space in the sensitivity of vegetation productivity to variability in three climate variables – air temperature, water availability, and cloud cover (Seddon & Macias-Fauria et al., 2016). I computed the VSI using monthly time series of the variables from 2000-2019 at 1 km spatial resolution. For the response variable in the VSI algorithm, I used the enhanced vegetation

index (EVI), a proxy for vegetation productivity, from the moderate-resolution imaging spectroradiometer (MODIS) MOD13A3 version 6 monthly product at 1 km spatial resolution (Didan, 2015). I used the MOD16A2GF version 6 evapotranspiration product at 1 km resolution (Running et al., 2019) and calculated water availability as the ratio of actual to potential evapotranspiration (AET/PET) . This product was only available at 16-day intervals, so I computed a monthly time series by taking weighted averages of the measurements within each month. I used the MOD35L2 version 6.1 cloud mask product with daily data at 250 m resolution (Ackerman, 2015) to calculate the proportion of cloudy to clear-sky days each month as an index representing incoming radiation. Lastly, for temperature I chose not to use a MODIS product because the only air temperature product, which was used in the original implementation of the VSI, is only at 5 km resolution, so I instead used monthly temperature (mean daily maximum) at 1 km resolution from CHELSA version 2.1 (Karger et al., 2017, 2018).

The algorithm computes sensitivity by considering both the strength of the correlations between monthly EVI and the climate variables and the magnitude of the response in EVI compared to the variability in climate. The calculations proceeded pixel by pixel, and for each pixel, months were excluded where mean EVI fell below 0.1 or mean temperature was less than 0 °C. For each of the included months, all time series were transformed to z-score anomalies and a principal component regression (PCR) was performed. Although the original implementation also included the one-month-lagged EVI monthly anomalies as a fourth variable in the regression representing memory effects, I chose not to include it because otherwise it would rule out months, particularly June, since there were rarely EVI data available for May, which is usually still during the snow period for most of Yamal. PCRs were only performed if there were at least 6 years in which all variables had data. For the principal components that were statistically significant ($p < 0.1$, following Seddon & Macias-Fauria et al, 2016) in the regression, the coefficients were transformed back to compute coefficients for the climate variables. The mean, absolute value of the coefficients from all included months for each climate variable was then computed for each pixel. Across all pixels, the climate coefficients were rescaled between 0 and 1 (using the minimum and maximum coefficients across all three variables) to be used as the first factor in the VSI product. For each pixel, time series were constructed for each variable (climate and EVI) that had the mean monthly values subtracted (so the mean over each month was 0) and only included months that had significant PCRs. The variance was computed for each time series,

giving a single value for each variable for each pixel. To account for any relationship between mean and variance, the residuals of a quadratic linear model fitted to the mean-variance relationship for each variable were used rather than just the variance values. These residuals were then standardised to between 0 and 100 for each variable across all pixels, and the $\log_{10}$-transformed ratios of EVI variability and each climate variable were computed for each pixel. Finally, this ratio was multiplied by the corresponding climate coefficient (from the regression step) for each climate variable and the products were summed to represent the overall sensitivity of EVI to the three climate variables for each pixel. The final sums were rescaled to 0-100 to give the VSI.

I also considered the effect of topography in mediating the relationships between reindeer herbivory pressure and the vegetation responses. Topography was quantified by classifying digital elevation model (DEM) pixels into landforms by applying the Geomorphons algorithm (Jasiewicz & Stepinski, 2013) to the ArcticDEM v3.0 release (Porter et al., 2018). Rather than using a fixed-size neighbourhood, this algorithm uses the line-of-sight principle to determine how the elevation of each pixel relates to the profile of the topography in eight directions around it. Based on these eight assessments, the pixel is assigned to one of 10 landform elements (e.g., flat, peak, ridge, valley, footslope). In my adaptation of the algorithm, I also reclassified the flat landforms into flat uplands and flat lowlands based on the surrounding landforms since this distinction is relevant both for reindeer use of the landscape and the vegetation community. I categorised all of the landforms into uplands, slopes, or lowlands and used these classes to control for the role of topography in my comparisons of landcover and VSI.

3.3.2 Landscape scale

Data collection at the landscape scale also used remote sensing, but rather than satellite-derived products, this work used UAV imagery to capture data that were still spatially continuous but exchanged breadth for much finer spatial grain. The methodology was designed to quantify the immediate impact of a reindeer herd after they had camped in an area and then to assess the vegetation once more later in the growing season. My colleagues approached a private Nenets household with whom they have a strong relationship and discussed the possibility of conducting this study based on the location of their next campsite. This household has a herd of ~1,000 reindeer, 13 of which my colleagues equipped with GPS collars in June 2021 that were already making measurements by the time this study took

place. After receiving the approval of the herders and coordinating with them (**Figure 3.5**), I designed a UAV survey that was flown over an area adjacent to the herders' next campsite (**Figure 3.1**) just hours before they arrived and repeated the day after they had migrated onwards, and again one month later.

The full details of the UAV flights and data processing workflow are presented in **Chapter 5**, but here I introduce and discuss the principles behind the methodology. Rather than using the UAV imagery to compare changes in the spectral information (i.e., colour) between surveys, I reconstructed the 3-dimensional structure of the survey area with very fine detail to compare physical changes in the vegetation. This reconstruction technique is called structure-from-motion (SfM) and relies on very high-resolution images (centimetre-scale) acquired by a UAV flying at low altitude and capturing sharp images, ideally by hovering at each capture, that have very high overlap (>75%) (Dandois & Ellis, 2013). The reconstructions can be improved by capturing both nadir imagery with the camera pointing downwards and oblique imagery with the camera at an angle to further increase the number of surfaces visible in the imagery and the number of angles at which they are seen. Photogrammetry techniques are then used to first identify points in common between multiple images forming a "sparse point cloud", which enables calculation of the exact position of the camera when each image was taken. Based on the positions of the camera and the camera lens parameters, the locations of all the surfaces visible in the images are computed and a "dense point cloud" is generated that has multiple orders of magnitude more points than the sparse cloud and includes all sharp features identified in the images. The dense cloud can be rasterised into a digital surface model (DSM) for raster-based analyses.



Figure 3.5: Discussions with herders about their next campsite to coordinate the logistics for the UAV survey area. Summer 2021. Photo credit: Alexandra Terekhina.

Although SfM can produce very impressive, detailed results just from RGB images captured by a consumer-grade UAV, there are still uncertainties in the reconstruction that must be considered. For my application, the goal was to detect changes in canopy height representing vegetation growth or trampling, grazing, or browsing by reindeer by comparing different surveys. Yet, even without issues such as wind affecting the position of the vegetation or error in the overall alignment of the reconstructions, also called co-registration error, there is photogrammetric uncertainty stemming from the calculation of the positions of the camera, the determination of the lens parameters, and the rasterisation to retrieve DSMs with a common alignment. When detecting change, it is critical to determine which differences exceed a level giving confidence that the change is due to the processes of interest rather than noise. James et al. (2017) developed a methodology for geomorphological applications that calculates a spatially variable limit of detection (LOD) for the set of two compared reconstructions across the survey area based on the uncertainty in the location of the sparse cloud points given the computed camera positions and parameters. This methodology was adapted by Graham et al. (2021) specifically for detecting canopy height change, which can

be more challenging than geomorphological applications due to the intricate – and more mobile due to e.g. wind – nature of vegetation. Instead of the original point-based approach, which is susceptible to noisy differences in the photogrammetric reconstructions of vegetation that do not represent canopy height change, the method of Graham et al. (2021) sacrifices some of the detail by rasterising but accounts for the uncertainty generated in this step. I applied the workflow of Graham et al. (2021) to my survey comparisons and retained only changes in the DSMs that exceeded the spatially variable LOD to detect robust changes in canopy height immediately after the herbivory event and one month later.

Spatial heterogeneity in the significant changes was assessed across three variables. Reindeer herbivory pressure was quantified based on the GPS collar data. The collars recorded positions every 1.5 hours, and fixes were only retained that had Dilution of Precision (DOP) values implying an accuracy of 4-14 m (Jung et al., 2018). To transform the GPS locations into a measurement of herbivory pressure across the landscape, I computed a metric of integrated proximity to reindeer for each pixel within the study site as the sum of the reciprocal of Euclidean distance to all GPS locations within 100 m of the study site. Higher values of this metric occur near where GPS points are clustered, providing a proxy for herbivore activity. The study site was also divided into habitat types based on visual inspection of the UAV imagery and descriptions of the vegetation at 10 locations where a set of two adjacent point intercept measurements were made. These measurements included plant groups similar to those defined by Bråthen et al. (2007) and followed a similar methodology using a 50 x 50 cm frame with 25 pins. The habitat boundaries were drawn directly onto the co-registered orthomosaics from the three UAV surveys as a vector layer. Lastly, the initial vegetation height before change occurred was included as a variable by modelling vegetation canopy height as the difference between the elevation values within the digital surface model (DSM), which captures the contours of the objects present (i.e., vegetation), and a digital terrain model (DTM), which models the ground surface. The DTM was constructed from the dense point cloud from a survey date when we also measured elevation across the site using a centimetre-precision global navigation satellite system (GNSS) device. The cloth simulation filtering (CSF) algorithm (Zhang et al., 2016) was used to generate the DTM in an approach that turns the point cloud upside down and then drapes a cloth over the inverted surface to select points belonging to the terrain. I tuned and validated the DTM using the GNSS points and calculated the canopy height models by subtracting the DSM and DTM rasters.

3.3.3 Plot scale

Compared to the remote sensing methods employed at the regional and landscape scale, the plot-scale work relied on a more traditional ecological approach. In Erkuta, exclosures were established in 2014 that cumulatively exclude three size classes of herbivores (Baubin et al., 2016) (**Figure 3.6**). The outer fence excludes large herbivores (reindeer) but is elevated to allow other herbivores to enter beneath the fence. Cages with a coarse mesh size within the fence additionally exclude medium-sized herbivores (willow ptarmigans and mountain hares), but small rodents (lemmings and voles) can get through the mesh or dig under the cages. Lastly, cages with a fine mesh are dug 10 cm into the ground to exclude all herbivores. Each exclosure setup has two replicates of each type of exclosure plot as well as two control plots outside of the fence. There are two exclosure setups within each of three habitat types – mesic tundra, willow meadows, and forb tundra (see **Chapter 6** for descriptions) – for each block, and three blocks each separated by a few kilometres in Erkuta. In total there are 18 exclosure setups in this experiment (3 blocks x 3 habitat types x 2 replicates), five of which I used for carbon flux measurements (**Figure 3.1**). These five were part of the block closest to camp, but I was not able to make measurements in one of the willow meadow exclosures in the block, which had been too damaged by snow for us to remain confident it was still effective.

I measured CO_2 fluxes in the plots using a custom-built transparent Perspex chamber, which I designed to be 692 x 692 x 600 mm so that it could fit over the cages that are dug into the ground to exclude all herbivores. These dimensions are somewhat larger than most typical flux chambers used in similar studies and made it challenging to transport the chamber in the field. As a solution, we built a *nosilki*, or stretcher that allowed two people to carry the chamber together over long distances (**Figure 3.7**). The goal of CO_2 flux chamber measurements is to measure net ecosystem exchange (NEE), which is the net uptake or emission rate of CO_2 within the plot, and partition it between gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER). The measurement involves attaching a gas analyzer and recording the CO_2 fluxes inside the chamber for a period of time while battery-powered fans ensure the air is well-mixed. Light is a key variable that influences photosynthesis, so the measurement is repeated with the light level manipulated while photosynthetically active radiation (PAR) is measured by a sensor within the chamber. In my experiment, I draped up to three layers of mosquito netting over the chamber to vary the light level and then an opaque sheet to omit all light and measure dark respiration. Chamber flux measurements

commonly assume that the flux from dark respiration is equivalent to ER and is relatively constant regardless of light level (Hobbie & Chapin, 1998). The flux, or NEE, for each measurement is calculated based on the slope of the changes in CO_2 concentration over time, and the NEE measurements are converted to a standardized PAR value based on the light-response curves (Cahoon et al., 2012). The standardised GEP is then the difference between NEE and ER, and these fluxes can be compared across different treatments.



Figure 3.6: A set of exclosures and a researcher demonstrating how to enter underneath the fence. Summer 2021.Photo credit: Kirill Shklyar.



Figure 3.7: Carrying the chamber on the *nosilki*. Summer 2021. Photo credit: Alexandra Terekhina.

Chamber flux studies commonly also include point intercept measurements to non-destructively measure the biomass in the plots (e.g., Cahoon et al., 2012; Metcalfe & Olofsson, 2015). I was not able to perform these measurements during my fieldwork, but instead I took pictures of each plot after each set of measurements that could be later used to quantify the plant cover. I designed an approach for scoring the cover of seven different plant groups within the plot photos that included two metrics – an estimate of the overall cover of each group and the number of cells in a 5x5 grid in which each group was present. Cover of moss, lichens, and litter was also scored in addition to the plant groups. All scoring was done by one of my colleagues, Svetlana Abdulmanova, who has expertise on the plant species in the area. I assessed the consistency of the scoring by randomly duplicating 11 (~10%) of the photos without her knowledge so that these scores could be compared. The scores were used to test whether cover of plant groups and litter significantly explained differences in the fluxes measured.

3.4 References

Ackerman, S. (2015). MODIS Atmosphere L2 Cloud Mask Product. *NASA MODIS Adaptive Processing System, Goddard Space Flight Center, USA*. https://doi.org/10.5067/MODIS/MOD35_L2.061

Bartsch, A., Widhalm, B., Pointner, G., Ermokhina, K., Leibman, M., & Heim, B. (2019). *Landcover derived from Sentinel-1 and Sentinel-2 satellite data (2015-2018) for subarctic and arctic environments*. PANGAEA. https://doi.org/10.1594/PANGAEA.897916

Baubin, C., Ehrich, D., Ravolainen, V., Sokovina, S., Ektova, S., Sokolova, N., Ims, R. A., & Sokolov, A. (2016). First results from an experiment excluding three sizes classes of herbivores from tundra vegetation in southern Yamal, Russia. *Czech Polar Reports*, *6*(2), 132–140. https://doi.org/10.5817/CPR2016-2-12

Berner, L. T., Massey, R., Jantz, P., Forbes, B. C., Macias-Fauria, M., Myers-Smith, I., Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B. V., Burns, P., Zetterberg, P., D'Arrigo, R., & Goetz, S. J. (2020). Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature Communications*, *11*(1), 4621. https://doi.org/10.1038/s41467-020-18479-5

Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Fauchald, P., Tveraa, T., & Hausner, V. H. (2007). Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems*, *10*(5), 773–789. https://doi.org/10.1007/s10021-007-9058-3

Cahoon, S. M. P., Sullivan, P. F., Post, E., & Welker, J. M. (2012). Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology*, *18*(2), 469–479. https://doi.org/10.1111/j.1365-2486.2011.02528.x

Dandois, J. P., & Ellis, E. C. (2013). High spatial resolution three-dimensional mapping of vegetation spectral dynamics using computer vision. *Remote Sensing of Environment*, *136*, 259–276. https://doi.org/10.1016/j.rse.2013.04.005

Degteva, A., & Nellemann, C. (2013). Nenets migration in the landscape: impacts of industrial development in Yamal peninsula, Russia. *Pastoralism*, *3*(1), 1–21. https://doi.org/10.1186/2041-7136-3-15

Didan, K. (2015). MOD13A3 MODIS/Terra vegetation Indices Monthly L3 Global 1km SIN Grid V006 [Data set]. *NASA EOSDIS Land Processes DAAC*. https://doi.org/10.5067/MODIS/MOD13A3.006

Ehrich, D., Henden, J.-A., Ims, R. A., Doronina, L. O., Killengren, S. T., Lecomte, N., Pokrovsky, I. G., Skogstad, G., Sokolov, A. A., Sokolov, V. A., & Yoccoz, N. G. (2012). The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? *Oecologia*, *168*(1), 141–151. https://doi.org/10.1007/s00442-011-2059-0

Esau, I., Miles, V. V., Davy, R., Miles, M. W., & Kurchatova, A. (2016). Trends in normalized difference vegetation index (NDVI) associated with urban development in northern West Siberia. *Atmospheric Chemistry and Physics*, *16*(15), 9563–9577. https://doi.org/10.5194/acp-16-9563-2016

Evladov, V. P. (1992). *Through the Yamal tundra to the Belyi Island. Expedition to the Far North of the Yamal Peninsula in 1928-1929 (in Russian)*. Institute of the problems of Northern development, SB RAS.

Forbes, B. C., Kumpula, T., Meschtyb, N., Laptander, R., Macias-Fauria, M., Zetterberg, P., Verdonen, M., Skarin, A., Kim, K.-Y., Boisvert, L. N., Stroeve, J. C., & Bartsch, A. (2016). Sea ice, rain-on-snow and tundra reindeer nomadism in Arctic Russia. *Biology Letters*, *12*(11), 20160466. https://doi.org/10.1098/rsbl.2016.0466

Forbes, B. C., Stammler, F., Kumpula, T., Meschtyb, N., Pajunen, A., & Kaarlejärvi, E. (2009). High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences*, *106*(52), 22041–22048. https://doi.org/10.1073/pnas.0908286106

Frost, G. V., & Epstein, H. E. (2014). Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology*, *20*(4), 1264–1277. https://doi.org/10.1111/gcb.12406

Fufachev, I. A., Ehrich, D., Sokolova, N. A., Sokolov, V. A., & Sokolov, A. A. (2019). Flexibility in a changing arctic food web: Can rough-legged buzzards cope with changing small rodent communities? *Global Change Biology*, *25*(11), 3669–3679. https://doi.org/10.1111/gcb.14790

Golovnev, A. V. (2017). Challenges to Arctic Nomadism: Yamal Nenets Facing Climate Change Era Calamities. *Arctic Anthropology*, *54*(2), 40–51. https://doi.org/10.3368/aa.54.2.40

Graham, H., Benaud, P., Cunliffe, A., Puttock, A., Anderson, K., Chant, J., Elliott, M., & Brazier, R. (2021). *exeter-creww/SFM_Precision: SfM Precision and Workflow v0.2 (v0.2)*. Zenodo. https://doi.org/10.5281/zenodo.5760603

Hobbie, S. E., & Chapin, F. S. (1998). The response of tundra plant biomass, aboveground production, nitrogen, and CO2 flux to experimental warming. *Ecology*, *79*(5), 1526–1544. https://doi.org/10.2307/176774

James, M. R., Robson, S., & Smith, M. W. (2017). 3-D uncertainty-based topographic change detection with structure-from-motion photogrammetry: precision maps for ground control and directly georeferenced surveys. *Earth Surface Processes and Landforms*, *42*(12), 1769–1788. https://doi.org/10.1002/esp.4125

Jasiewicz, J., & Stepinski, T. F. (2013). Geomorphons - a pattern recognition approach to classification and mapping of landforms. *Geomorphology*, *182*, 147–156. https://doi.org/10.1016/j.geomorph.2012.11.005

Jung, T. S., Hegel, T. M., Bentzen, T. W., Egli, K., Jessup, L., Kienzler, M., Kuba, K., Kukka, P. M., Russell, K., Suitor, M. P., & Tatsumi, K. (2018). Accuracy and performance of low-feature GPS collars deployed on bison Bison bison and caribou Rangifer tarandus. *Wildlife Biology*, *2018*(1), 1–11. https://doi.org/10.2981/wlb.00404

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. ., Linder, H. P., & Kessler, M. (2018). Climatologies at high resolution for the earth's land surface areas. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.kd1d4

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 1–20. https://doi.org/10.1038/sdata.2017.122

Kvashnin, I. N. (2009). *The Nenets reindeer herding in the 20 c. - beginning of 21 c. (in Russian)*. Koleso.

Metcalfe, D. B., & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO 2 exchange during the peak of the growing season. *Oikos*, *124*(12), 1632–1638. https://doi.org/10.1111/oik.02085

Porter, C., Morin, P., Howat, I., Noh, M.-J., Bates, B., Peterman, K., Keesey, S., Schlenk, M., Gardiner, J., Tomko, K., Willis, M., Kelleher, C., Cloutier, M., Husby, E., Foga, S., Nakamura, H., Platson, M., Wethington, Michael, J., Williamson, C., … Bojesen, M. (2018). ArcticDEM. *Harvard Dataverse, V1*. https://doi.org/10.7910/DVN/OHHUKH

Raynolds, M. K., Walker, D. A., Balser, A., Bay, C., Campbell, M., Cherosov, M. M., Daniëls, F. J. A., Eidesen, P. B., Ermokhina, K. A., Frost, G. V., Jedrzejek, B., Jorgenson, M. T., Kennedy, B. E., Kholod, S. S., Lavrinenko, I. A., Lavrinenko, O. V., Magnússon, B., Matveyeva, N. V., Metúsalemsson, S., … Troeva, E. (2019). A raster version of the Circumpolar Arctic Vegetation Map (CAVM). *Remote Sensing of Environment*, *232*(January). https://doi.org/10.1016/j.rse.2019.111297

Running, S., Mu, Q., Zhao, M., & Moreno, A. (2019). MOD16A2GF MODIS/Terra Net Evapotranspiration Gap-Filled 8-Day L4 Global 500 m SIN Grid V006 [Data set]. *NASA EOSDIS Land Processes DAAC*. https://doi.org/doi.org/10.5067/MODIS/MOD16A2GF.006

Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, *531*(7593), 229–232. https://doi.org/10.1038/nature16986

Sokolov, A. A., Sokolova, N. A., Ims, R. A., Brucker, L., & Ehrich, D. (2016). Emergent Rainy Winter Warm Spells May Promote Boreal Predator Expansion into the Arctic. *ARCTIC*, *69*(2), 121–129. https://doi.org/10.14430/arctic4559

Sokolov, V., Ehrich, D., Yoccoz, N. G., Sokolov, A., & Lecomte, N. (2012). Bird Communities of the Arctic Shrub Tundra of Yamal: Habitat Specialists and Generalists. *PLoS ONE*, *7*(12), e50335. https://doi.org/10.1371/journal.pone.0050335

Sokolova, N. A., Sokolov, A. A., Ims, R. A., Skogstad, G., Lecomte, N., Sokolov, V. A., Yoccoz, N. G., & Ehrich, D. (2014). Small rodents in the shrub tundra of Yamal (Russia): Density dependence in habitat use? *Mammalian Biology*, *79*(5), 306–312. https://doi.org/10.1016/j.mambio.2014.04.004

Stammler, F. (2005). *Reindeer Nomads Meet the Market: Culture, Property and Globalisation at the `End of the Land'*. Lit.

Terekhina, A., Filippova, V., Volkovitskiy, A., Shklyar, K., Orekhov, P., Sokolova, N., Abdulmanova, S., & Sokolov, A. (2022). Influence of Indigenous Herding Activities on the Spatio-temporal Distribution of Reindeer during the Summer-Autumn Period: Case from Yamal, Russia. *Human Ecology*. https://doi.org/10.1007/s10745-022-00384-8

Terekhina, A., & Volkovitskiy, A. (2020). Patterns of resource use by the Yamal nomads: The micro-regions ethnography. In V. N. Davydov (Ed.), *Energy of the Arctic and Siberia: The Use of Resources in the Context of Socio-Economic Changes* (pp. 87–113). Izdatel'stvo vostochnoi literatury.

Volkovitskiy, A., & Terekhina, A. (2020). The contemporary issues of Yamal reindeer herding: discussions and perspectives (in Russian). *Etnografia*, *2*(8), 152–169.

Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Raynolds, M. K., Comiso, J. C., Gubarkov, A. A., Khomutov, A. V., Jia, G. J., Kaarlejärvi, E., Kaplan, J. O., Kumpula, T., Kuss, P., Matyshak, G., Moskalenko, N. G., Orekhov, P., Romanovsky, V. E., Ukraientseva, N. G., & Yu, Q. (2009). Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index. *Environmental Research Letters*, *4*(4), 045004. https://doi.org/10.1088/1748-9326/4/4/045004

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & The other members of the CAVM Team. (2005). The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, *16*(3), 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x

Zhang, W., Qi, J., Wan, P., Wang, H., Xie, D., Wang, X., & Yan, G. (2016). An Easy-to-Use Airborne LiDAR Data Filtering Method Based on Cloth Simulation. *Remote Sensing*, *8*(6), 501. https://doi.org/10.3390/rs8060501

Chapter 4:

Top-down regulation by a reindeer herding system limits climate-driven Arctic vegetation change at a regional scale

Marcus P. Spiegel[1], Alexander Volkovitskiy[2], Alexandra Terekhina[2], Bruce C. Forbes[3], Taejin Park[4,5], Marc Macias-Fauria[1]

[1]Biogeosciences Lab, School of Geography & the Environment, University of Oxford, Oxford, OX1 3QY, United Kingdom.

[2]Arctic Research Station of Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Zelenaya Gorka Str., 21, 629400 Labytnangi, Russia.

[3]Arctic Centre, University of Lapland, 96101, Rovaniemi, Finland.

[4]NASA Ames Research Center, Moffett Field, CA, 94035, USA.

[5]Bay Area Environmental Research Institute, Moffett Field, CA, 94035, USA.



Photo: Alexander Volkovitskiy

4.1 Chapter statement

The series of research articles in this thesis begins with a study at the regional scale testing whether reindeer herbivory is having extensive impacts on vegetation on the Yamal Peninsula. This work compared vegetation cover and the sensitivity of vegetation productivity to climate across variations in reindeer herbivory pressure over space, which have been consistent over time due to the stable migration patterns of reindeer herds in the region. The analysis used satellite remote sensing products in combination with a novel dataset mapping herd sizes and migration routes compiled by my collaborators.

This chapter has been submitted to *Earth's Future*. The work was presented as a poster at the American Geophysical Union Fall Meeting in December 2022 in Chicago, USA.

4.2 Author contributions

MPS and MM-F conceptualised the research and designed the study. AV and AT carried out the anthropological fieldwork to produce the reindeer herd maps. TP assisted with the processing of the remote sensing data. MPS analysed the data with input from MM-F and BCF. MPS wrote the manuscript with significant contributions from all authors.

4.3 Abstract

Warming-driven growth of tall woody vegetation in the Arctic has the potential to accelerate climate change through multiple positive feedbacks. Local-scale evidence suggests that large herbivores limit this vegetation shift, but there is uncertainty at larger, regional scales whether current herbivory pressure is a major top-down control on ecosystem structure and functioning. Across a 67,000 km^2 region of the Yamal Peninsula in West Siberia, we integrated satellite remote sensing with a novel dataset mapping the migrations of herds comprising 151,000 domesticated reindeer. Where reindeer numbers varied over space, higher reindeer herbivory pressure was consistently linked with lower coverage of tall woody vegetation. Within areas dominated by this vegetation type, productivity and climate were increasingly decoupled where reindeer density was higher. Our spaceborne fingerprint detection suggests that large herbivores, at current population densities, counteract Arctic vegetation responses to climate change over large spatial scales.

4.4 Plain language summary

Large herbivores influence tundra vegetation via their grazing, trampling, and nutrient inputs from faeces and urine. However, the extent of these impacts remains unclear as we seek to understand and predict the responses of Arctic ecosystems to climate change. Using maps we developed that record the annual summertime movements of herds comprising 151,000 domesticated reindeer managed by indigenous Nenets herders, we assessed whether reindeer had an effect on vegetation productivity and community composition across a 67,000 km^2 region of the Yamal Peninsula in West Siberia, an area about the size of the Republic of Ireland. Analyses of satellite data comparing areas varying in reindeer density consistently showed that higher reindeer herbivory pressure was limiting the coverage of tall woody vegetation and its expansion in response to warming. This effect had not been observed previously at such a large spatial scale and was significant enough to be detected from space. Our findings demonstrate that reindeer have a substantial impact on ecosystem structure and functioning, which likely has implications for the carbon cycle and energy balance within the Arctic and beyond.

4.5 Introduction

Large herbivores have significant impacts on ecosystem structure and functioning throughout Earth's biomes (Enquist et al., 2020; Kristensen et al., 2022; Lundgren et al., 2020). During the Pleistocene, land in the non-glaciated high latitudes supported a diverse assemblage of large herbivores, including mammoth, woolly rhino, and wild horse, that grazed on a productive graminoid- and forb-rich heterogeneous vegetation matrix and likely maintained it through selective foraging, increased nutrient cycling, bark-stripping, and trampling (Macias-Fauria et al., 2020; Olofsson & Post, 2018; Zimov et al., 2012). In the modern moss- and shrub-dominated Arctic tundra, reindeer (*Rangifer tarandus* L.) are the only remaining large herbivores still widespread (Olofsson & Post, 2018). Local-scale studies, utilising variations in grazing intensity due to the introduction of reindeer on islands (Klein, 1968; Ricca et al., 2016), different grazing regimes separated by management fences (Egelkraut et al., 2018; Olofsson et al., 2001, 2004; Ylänne et al., 2018), and exclosure experiments (Cahoon et al., 2012; Kolari et al., 2019; Metcalfe & Olofsson, 2015; Ylänne et al., 2020), consistently have found that reindeer cause declines in deciduous shrubs. These woody plants, especially willow and birch species, are highly palatable to reindeer, and are not as tolerant to repeated defoliation and trampling as graminoids (van der Wal, 2006). Thus, reindeer herbivory often drives transitions from shrub- to graminoid-dominated vegetation (Olofsson & Post, 2018).

The expansion of woody vegetation, especially tall shrubs, with climate change in the Arctic is well-documented (Myers-Smith et al., 2011). Studies have shown that, under observed and experimental warming, reindeer herbivory counteracts this vegetation shift, weakening or even negating the positive relationship between annual mean temperature and shrub growth and preventing the shrubline from advancing (Bråthen et al., 2017; Olofsson et al., 2009; Olofsson & Post, 2018; Post & Pedersen, 2008; Väisänen et al., 2014). Since the transition to more shrub-dominated tundra leads to lower albedo and increased permafrost thaw (Parker et al., 2021; Sturm et al., 2005), reindeer herbivory in the rapidly warming Arctic may have important Earth system implications by mitigating these positive climate change feedbacks.

Despite the strong evidence that reindeer herbivory acts as a significant top-down control when reindeer are concentrated over small areas, there is uncertainty over whether reindeer, at current population densities, have a substantial impact at larger spatial scales across the Arctic. Remote sensing is emerging as a tool for analysing Arctic herbivory impacts, and has been used, for example, to detect a reduction in the normalised difference vegetation index (NDVI), a spectral

reflectance metric for vegetation "greenness" (Raynolds et al., 2012), over a 770 km^2 area in the year after vole and lemming peaks (Olofsson et al., 2012). Several studies have found that reindeer reduce NDVI on summer pastures, but these effects were typically weak or inconsistent when comparing across differences in herd sizes or animal densities over space (Campeau et al., 2019; Newton et al., 2014; Rickbeil et al., 2015). Conversely, a study of migratory tundra caribou (same species as reindeer) herds in North America found that an increase in summer NDVI led to declines in caribou populations, likely related to the expansion of shrub species with strong antibrowsing defences (Fauchald et al., 2017). Their results showed no evidence of a top-down effect of caribou on the vegetation, but instead implied a bottom-up effect initiated by the warming-driven increases in plant biomass. Although testing the relationship between reindeer abundances and NDVI provides an indication of how reindeer grazing is linked with vegetation productivity, analyses relying on NDVI alone cannot detect differences in vegetation cover, the main impact of herbivory found in many field studies. A lack of spatially explicit reindeer data has thus far hindered large-scale comparisons of vegetation cover across variations in grazing pressure over space or time (e.g., Rees et al., 2003; Verma et al., 2020; Walker et al., 2009).

Here, we analyse the influence of reindeer on vegetation on the Yamal Peninsula in West Siberia, where indigenous Nenets nomads manage the world's largest domesticated reindeer herds (~225,000 animals in total) and migrate up to 1,200 km annually (Forbes et al., 2009; Stammler, 2005). As described in the Russian literature, the style of reindeer herding practised by tundra Nenets belongs to the so-called Samoyedic type – a tradition common in the tundra zone of Europe and West Siberia, where it was also adopted by several other ethnic groups, including the Khanty and Komi-Izhma (Habeck, 2007; Istomin & Dwyer, 2021; Jernsletten & Klokov, 2002). The defining features of Samoyedic reindeer herding, common to all the local variants, are the large herds of up to several thousand reindeer, extended migrations that enable the rotation of seasonal pastures, and herders' constant control over their herds (i.e., 24 hours a day, 7 days a week). The greatest attention is required during the summer, especially during periods of intense bloodsucking insect harassment in July. The emphasis on controlling animals dictates the nomadic lifestyle of the reindeer pastoralists of the Yamal Peninsula, who live year-round in the tundra in *chums* (mobile tents) and move on reindeer sledges and, in recent decades, on snowmobiles. Thus, analysis of the influence of reindeer on the ecosystem of Yamal must incorporate an understanding of the role of humans as actors directing and modifying reindeer movements in response to multiple factors (ecological, weather, social,

etc.) (Dwyer & Istomin, 2008). These features of herding in Yamal distinguish the reindeer herbivory patterns from those of both wild reindeer populations and free grazing semi-domestic reindeer in Fennoscandia.

Within the Yamal Peninsula, reindeer herding collectives are either private households (most local reindeer herders) or brigades of reindeer herding enterprises – the "heirs" of Soviet-era state-owned reindeer enterprises (*sovkhozy*). Both types of collectives have followed relatively stable patterns of seasonal movement, inherited largely from the routes of past generations of Nenets nomads, described since the 19th century (Evladov, 1992). Dozens of households migrate along the same "corridors" with consistent movement timings from year-to-year. Although the winter pasture locations of a certain Nenets household may vary within their corridor, the nomadic route and pasture areas visited in the summer months are more stable. In fact, the local identity of most Nenets is defined mainly by their summer pastures.

Given the intensity of reindeer herbivory on the Yamal Peninsula and the long-term stability of the seasonal migration patterns of the herds, we investigated whether variations in vegetation productivity and composition over space were linked to differences in the timing and density of reindeer pressure. Central to our analysis is a new dataset we present that maps the annual June-August migrations of all the herds on the southern and central parts of the peninsula encompassing the Yar-Sale and Panayevsk tundra (the territory of the Yarsalinskii and Panayevskii *sovkhozy*, **Figure 4.1**), which has the highest summer density of reindeer on Yamal. Prior depictions of herd migrations on the Yamal Peninsula have either focused on the specific routes of a small subset of herds or the general movement patterns within the different *sovkhozy* (Degteva & Nellemann, 2013; Golovnev et al., 2014; Stammler, 2005), making our dataset the first comprehensive map of reindeer numbers and summer ranges on an extensive region covering more than half of the Yamal Peninsula.

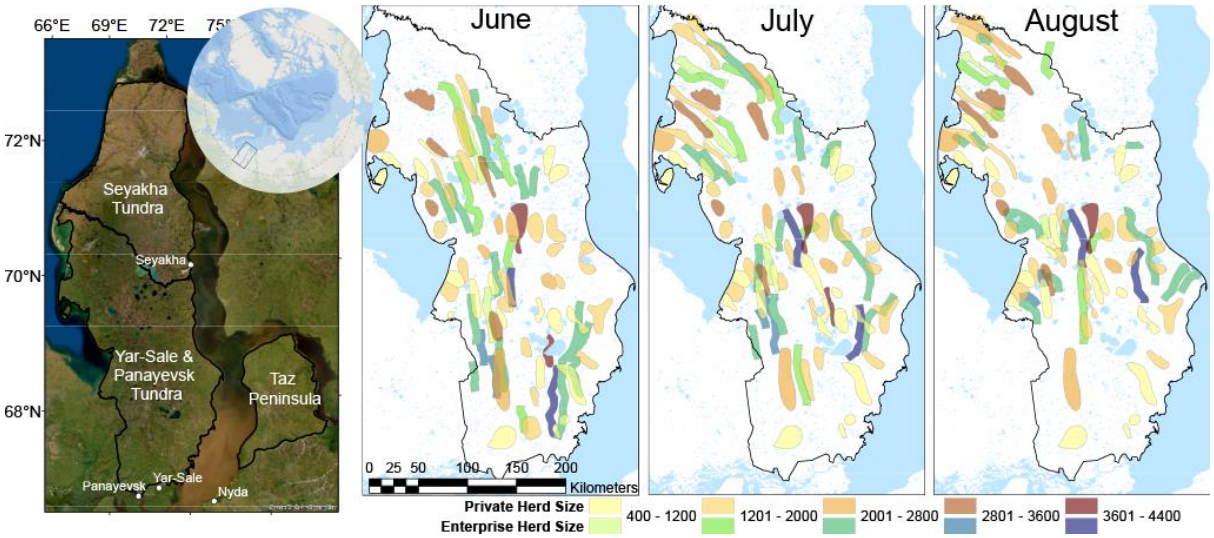


Figure 4.1: Reindeer herds and their summer migrations on the Yar-Sale and Panayevsk tundra. The majority of Yamal reindeer have summer pastures on the southern and central parts of the Peninsula, on the Yar-Sale and Panayevsk tundra, whereas the Taz Peninsula to the east has many fewer reindeer. The locations of towns and villages serving as reindeer herding centres, Panayevsk, Yar-Sale, Seyakha, and Nyda, are also shown. We present a new dataset of reindeer numbers and herd locations in June, July, and August for both the private and enterprise herds with summer pastures on the Yar-Sale and Panayevsk tundra. The imagery base map is from Esri and Earthstar Geographics, and the water bodies base map is derived from the MOD44W Land Water Mask product (Carroll et al., 2017).

We formulated two hypotheses that address whether the local impacts of reindeer found across the Arctic can be detected at much larger, regional scales. First, we hypothesised that reindeer herbivory would alter the distribution of landcover types, specifically linking lower coverage of tall woody vegetation with higher reindeer numbers. Second, we proposed that vegetation productivity in areas with higher reindeer numbers would be less responsive to climate variability, measured by the vegetation sensitivity index (VSI, after Seddon & Macias-Fauria et al. (2016)). Herbivory in the Arctic tends to have the strongest effect on the species expected to be favoured by warming (Olofsson & Post, 2018), so we anticipated that areas with higher herbivory pressure would have lower VSI, indicating that reindeer were constraining vegetation responses to climate change. Whereas differences in the proportions of landcover types present can be interpreted as the cumulative impacts of reindeer herbivory over time, differences in the VSI represent herbivory's effects on the responsiveness of vegetation to recent climate variability.

Experiments are not feasible at such large scales as the 67,000 km^2 Yar-Sale and Panayevsk tundra, and process-based models similar to those used in climate change attribution studies are rarely appropriate for biotic systems due to the need to incorporate myriad extrinsic factors

with complex interactions (Parmesan et al., 2013). Thus, our approach adopts a framework along the lines of "associative pattern attribution," a method that evaluates whether multiple lines of evidence point to a coherent and parsimonious conclusion in accordance with a predicted biotic response (Hegerl et al., 2009). We present a systematic analysis examining each of our hypotheses at three levels of spatial comparison using remotely sensed climate, vegetation, and topographic data. We compared differences in landcover and VSI: (*i*) between the Yar-Sale/Panayevsk tundra and the neighbouring Taz Peninsula, which has considerably fewer reindeer but otherwise resembles Yar-Sale/Panayevsk geographically, geologically, and climatically (see **Text S4.1** for a detailed comparison); (*ii*) between areas in Yar-Sale/Panayevsk that are within summer herd ranges and areas outside of the migrations; (*iii*) within the summer ranges, considering differences in the density of animals on different pasture land. In these comparisons, we divided the areas into upland, slope, and lowland landform units (see Materials and Methods, **Figure S4.2**). Despite the notably flat terrain of Yamal and Taz, which is mostly less than 70 m above sea level, landform is an important determinant of both vegetation cover in the region (Walker et al., 2009) and the amount of time reindeer spend on a given area. We expected the impacts of herbivory to be greatest in the uplands, which are preferred by herders for migrating and campsites because they provide greater insect relief for the reindeer, dry ground for the campsite, and an elevated view of the landscape (Degteva & Nellemann, 2013; Skarin et al., 2020). We also separated the grazing areas within Yar-Sale/Panayevsk depending on the month in which they were used and anticipated that the pastures used earlier in the growing season would be most affected by herbivory. Reindeer tend to prefer deciduous shrubs for their diet in the early growing season, at which point they are most vulnerable to herbivory, before the amount of nitrogen and phosphorus in their leaves declines rapidly at the end of June (Chapin III, 1980; Chapin III et al., 1980).

4.6 Materials and methods

4.6.1 Study area

The study area is located within the Yamal Peninsula and neighbouring Taz Peninsula in the Yamal-Nenets Autonomous Okrug (YNAO), West Siberia, Russia (**Figure 4.1**). The area within the Yamal Peninsula was confined to the territory of the Yar-Sale/Panayevsk tundra, where herd migrations are typically long and linear compared with the more circular migrations in the northern Seyakha tundra (Degteva & Nellemann, 2013). The area on the Taz Peninsula was delineated based on the extent included in the Circumpolar Arctic Vegetation Map (Walker et al., 2005).

A detailed comparison of the Yar-Sale/Panayevsk tundra and the Taz Peninsula based on topography (Porter et al., 2018), geology (Drozdov et al., 2005), and temperature (Karger et al., 2017, 2018) is presented in **Text S4.1**. Taz was chosen as a region for comparison with Yar-Sale/Panayevsk that differs mainly in the abundance of reindeer while having a similar physical environment. Overall, the whole study area is low and flat and traverses primarily bioclimate subzones D and E, although the northwest extent of Yar-Sale/Panayevsk is in subzone C (Walker et al., 2005). The land was unglaciated during the last glaciation and consists of sandy and clayey marine, alluvial and lacustrine sediments (Walker et al., 2009). The region is underlain by continuous, ice-rich permafrost, and the vegetation consists of a mosaic of tall woody shrub tundra (dominated by *Salix* spp., *Betula*), low stature shrub tundra (*Betula*, ericoids), and mires dominated by sedges (*Carex* spp., *Eriophorum* spp.) (Botch et al., 1971; Forbes et al., 2009). The geomorphology is shaped by big meandering rivers, thermokarst lakes, and frequent cryogenic landslides (Walker et al., 2009).

4.6.2 Mapping of reindeer herds and migrations

We recorded the number of reindeer in each herd on Yar-Sale/Panayevsk and mapped the extent of the area on which they graze annually in June, July, and August using official statistics, semi-structured interviews, and participatory mapping with indigenous experts. The official statistics for the Yar-Sale herding enterprise were based on corral (round-up) calculations of animals in the enterprise herds in 2019-2020. Interview participants included 'zootechnicians,' experts who are consulted on reindeer herding matters such as breeding and seasonal movements, from the Yar-Sale and Panayevsk herding enterprises as well as employees of the Kharp *obshchina*, a community structure facilitating the cooperation of private reindeer herders. The Kharp *obshchina* is the largest in Yamal, accounting for the ownership of more than 60,000 reindeer. All applicable international, national and/or institutional guidelines for the social research were followed. Interviewees consented to be interviewed and have approved the information and the sharing of it publicly.

We used printed GGTS (State GIS Center) maps (1:200,000) to mark the herd locations during the interviews. After separately recording the reindeer numbers for each herd, we checked their totals against the 2019-2020 reconstructed official estimate of all reindeer on Yar-Sale/Panayevsk (155,000-160,000 animals). We counted 37,747 reindeer in Yar-Sale brigades, 19,700 in Panayevsk brigades, and 94,000 in private herds, giving 151,447 total reindeer. Since

we mapped all major herds, we presume that the reindeer constituting the small discrepancy between our count and the reconstructed estimate are spread over the whole region.

After digitising the mapped routes into polygons for each herd's location in each month, we created monthly maps giving the number of reindeer across the Yar-Sale/Panayevsk tundra. Animal densities were calculated by dividing the number of reindeer by the amount of land area (excluding water bodies) within their respective range for each month based on the 20 m landcover classification of Bartsch et al. (2019). We dealt with overlapping polygons by adding the reindeer numbers and densities, but since this inflated the amount of reindeer pressure occurring within small intersecting areas at the edge of the ranges of multiple herds, we discarded any new polygons smaller than 10 km^2 (< 2% of the total pasture area in total) in subsequent analyses in which reindeer density was considered.

In comparison, many fewer reindeer graze on the Taz Peninsula compared with Yar-Sale/Panayevsk. The most recent published information on reindeer herds grazing in the summer on Taz within our study area estimated their numbers at ∼10,000, although this is reflective of the 1980-90's (Kvashnin, 2009). Our conversations with local people in Nyda, the reindeer herding centre in the region, confirmed that the number of reindeer in Taz is significantly lower than in any part of the Yamal Peninsula.

4.6.3 Landcover classification

To analyse the effect of reindeer herbivory on the distribution of landcover types, we used the landcover classification of Bartsch et al. (2019) (**Figure S4.1C**). This landcover product was developed using a supervised classification of Sentinel-1 and Sentinel-2 imagery from 2016-2018 and groundtruthed by local experts. It contains 18 terrestrial classes and three aquatic classes. We merged the terrestrial classes into six broad classes, including 'sparse vegetation', 'low stature shrub tundra', 'tall woody vegetation', 'meadow', 'inundated/landslides', and 'barren/rare vegetation'. The associations between the original class definitions and the landcover classes we used in our analysis are presented in **Table S4.1**. To facilitate our adaptation of the landcover classes, we compared the Bartsch et al. (2019) landcover map with the 1 km resolution Circumpolar Arctic Vegetation Map (Raynolds et al., 2019). This comparison helped us determine, for example, which classes aligned with our definition of tall shrubs as exceeding 0.4 m height.

'Low stature shrub tundra' includes areas with a mixture of graminoids, forbs, erect dwarf shrubs (0.1-0.4 m), and prostrate dwarf shrubs (<0.1 m) (Myers-Smith et al., 2011). This class is distinguished from 'tall woody vegetation', which consists of tall shrub tundra as well as deciduous, coniferous, and mixed forest, although tree-dominated pixels cover less than 4% of the study area and are exclusively concentrated in the far south of the area. The 'sparse vegetation' class describes land on mostly sandy soil with few shrubs and potentially dry biological crusts. The 'inundated/landslide' class consists of areas within disturbed habitats that are seasonally inundated or within landslide scars. Landslide scars are commonly found on Yamal, and landslides are increasing in frequency with ongoing rapid permafrost thaw (Leibman, 1995; Walker et al., 2009). In our analyses, we discarded pixels in the 'meadow' and 'barren/rare vegetation' classes because they represented no more than 8% of the total pixels within any comparison. The meadow pixels were primarily confined to riparian areas rather than occurring throughout the landscape where they might be indicative of herbivory-driven transitions from moss- and shrub-dominated tundra to grasslands (Forbes et al., 2009).

4.6.4 Landcover and landform analysis

We compared the proportions of pixels in the four selected landcover classes between regions (Yar-Sale/Panayevsk and Taz) and between different pasture areas within Yar-Sale/Panayevsk by calculating odds ratios. These comparisons were performed separately for pixels within 'upland', 'slope', or 'lowland' landforms. Our landform classification was performed by applying the Geomorphons algorithm (Jasiewicz & Stepinski, 2013) to the ArcticDEM v3.0 release (Porter et al., 2018) at 32 m resolution (**Figure S4.2**). The algorithm assigns each pixel to one of 10 common landform elements (e.g., ridge, pit) in a procedure that automatically chooses the most appropriate spatial scale for landform delineation at each location. We further divided the pixels assigned to the flat landform class into flat uplands and flat lowlands based on the gradient in their neighbouring pixels, and then reclassified the remaining landform pixels into 'uplands', 'slopes', and 'lowlands'.

We used log-linear modelling to test whether reindeer pressure (categorically differentiated by region or by pasture area), landform, and the interactions between them significantly affected the proportions of sparse vegetation and tall woody vegetation pixels. We tested a suite of possible models each representing different hypotheses regarding which factors were significant predictors using the glm function from the stats package (R Core Team, 2020) with

a poisson variance and log link function. We evaluated the fit of each model using the residual deviance statistic G^2.

For our analysis of the effect of reindeer density on landcover distributions, we computed the difference from the expected ratio of sparse vegetation to tall woody vegetation pixels within each pasture area with a given animal density. The ratio was calculated as the fraction of sparse vegetation pixels, (sparse/(sparse+tall woody)), and the expected ratio was based on the landforms present, calculated as a weighted average combining the number of pixels and the mean sparse fraction for each landform.

4.6.5 Vegetation sensitivity index (VSI)

We adapted the vegetation sensitivity index (VSI) from Seddon & Macias-Fauria et al. (2016) to quantify the sensitivity of vegetation productivity to variability in temperature, cloudiness, and water availability. We computed the VSI over the study area at 1 km resolution using monthly time series of remote sensing data from 2000-2019 (**Figure S4.1A**). The model used the moderate-resolution imaging spectroradiometer (MODIS) enhanced vegetation index (EVI) MOD13A3 version 6 product (Didan, 2015) as the response variable representing vegetation productivity. The three climate predictor variables were monthly maximum temperature (obtained from CHELSA version 2.1 (Karger et al., 2017, 2018)), ratio of actual to potential evapotranspiration (AET/PET) for water availability (obtained from MODIS MOD16A2GF version 6 (Running et al., 2019)), and cloudiness fraction (obtained from the MODIS MOD35L2 version 6.1 cloud mask product (Ackerman, 2015)). All time series were transformed to z-score anomalies using monthly means and standard deviations, and the months were filtered based on a minimum EVI (0.1) and temperature threshold (0°C) to identify the growing season for each pixel. Principal component regressions were used to identify the relative importance of the predictor variables in driving variations in EVI for each pixel, and these coefficients were multiplied by the $\log_{10}$-transformed ratios of EVI variability and variability in each climate time series to arrive at sensitivity. The sensitivity (VSI) is a relative metric, scaled from 0-100 over the study area, and was mapped in the MODIS sinusoidal projection.

4.6.6 VSI comparisons

The VSI map, at 1 km resolution, is much coarser than the landcover classification (20 m) or landform classification (32 m). To enable analysis at a common spatial scale, each VSI pixel

was assigned to a landcover class if that class covered at least half of the 1 km pixel and to a landform class if it covered at least 2/3 of the pixel. The higher threshold for landforms was chosen because of the fewer landform classes and to avoid potentially complex dynamics in more rugged terrain. Pixels that did not meet these thresholds were not used in the subsequent comparisons, but the classified pixels were well-distributed over the area with ample coverage (**Figure S4.3**).

Comparisons of VSI in which only two samples were compared (i.e., between Yar-Sale/Panayevsk and Taz within a common landform or landcover) used the Wilcoxon rank sum test (wilcox.test from stats (R Core Team, 2020)) to determine significance. Comparisons involving more than two samples or multiple categorical variables used one-way ANOVAs or multi-way ANOVAs with type II sum of squares (anova test from rstatix (Kassambara, 2020)). When the ANOVAs found significant differences, we evaluated the differences between pairs of samples using Tukey's test (TukeyHSD from stats (R Core Team, 2020)). To quantify the relationship between VSI and reindeer density within pasture areas, we performed linear regressions between these two variables (lm from stats (R Core Team, 2020)).

4.7 Results

4.7.1 Variation in landcover with reindeer herbivory pressure

In comparisons of the relative proportions of landcover types between the Yar-Sale/Panayevsk tundra, where reindeer numbers are highest on Yamal, and the Taz Peninsula, where there are considerably fewer reindeer (**Figure 4.2A,C,E**), and between areas with and without summer pastures within Yar-Sale/Panayevsk (**Figure 4.2B,D,F**), the areas with higher reindeer pressure consistently had higher coverage of sparse vegetation and lower coverage of tall woody vegetation than areas with fewer reindeer. This pattern occurred within all landform units, but in accordance with our hypothesis, the effect was greatest in the uplands, where reindeer spend the most time. Based on odds ratios, the ratio of tall woody vegetation area to sparse vegetation area was 4.0 times lower on the uplands, 3.6 times lower on the slopes, and 3.2 times lower on the lowlands of Yar-Sale/Panayevsk compared to Taz.

Also in accordance with our expectations, the pastures grazed in June, when deciduous shrubs are most vulnerable to herbivory, generally had the most sparse vegetation area and least tall woody vegetation within Yar-Sale/Panayevsk. This result would be surprising in the absence of herbivory, as especially for the enterprise herds, these pastures tend to be located farther

south in the low Arctic (**Figure 4.1**), where greater coverage of tall shrubs is expected (Myers-Smith et al., 2015). When comparing the June pastures to the no pastures area, the ratio of tall woody vegetation area to sparse vegetation area was 2.3 times lower on the uplands, 1.5 times lower on the slopes, and 1.2 times lower on the lowlands. Using a suite of log-linear models formulated to test the dependence of the proportions of landcover classes on categorical predictors, we found that both landforms and comparison areas (region in the first case, Yar-Sale/Panayevsk pasture areas in the second) significantly improved the model fit when their main effects and the interaction effects between them were included (see **Table S4.2** for deviance statistics).

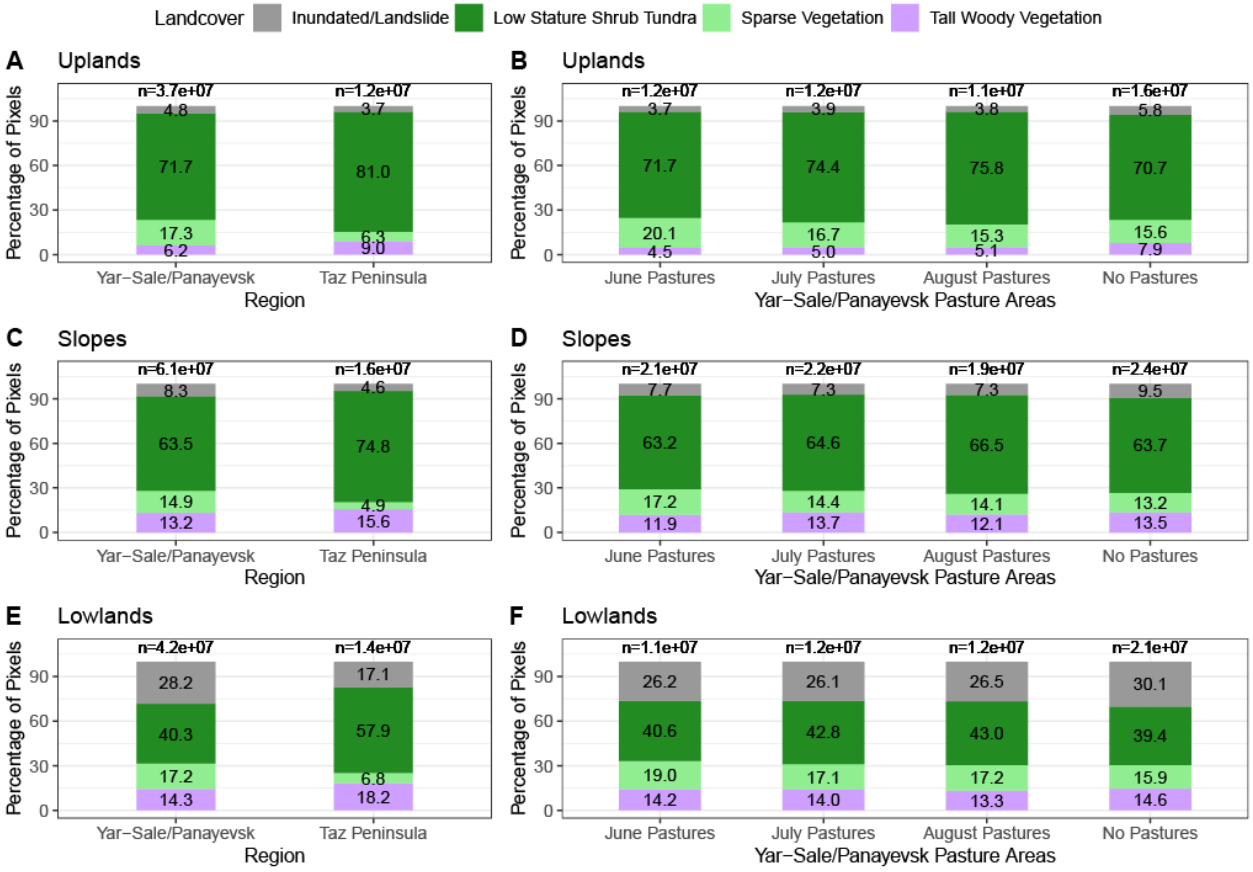


Figure 4.2: Distribution of 20 m resolution landcover pixels based on the classification of Bartsch et al. (2019). The distributions are compared by region (A,C,E) and by the different pasture areas used in the summer months by herds in the Yar-Sale/Panayevsk tundra (B,D,F). 'No pastures' represents areas without any known reindeer herds. The pixels are also divided topographically into landforms: uplands (A,B), slopes (C,D), and lowlands (E,F). The percentage of pixels within each landcover type is written inside the bar segments, and the total number of pixels in the specified area is given above the bar. Note that for each landform class, the sum of the number of pixels in the different pasture areas (B,D,F) exceeds the number of pixels in the Yar-Sale/Panayevsk region (A,C,E) because pixels may belong to multiple pasture areas (i.e., grazed in multiple months).

While there were also differences in the relative proportions of low stature shrub tundra and inundated/landslide area, they showed mixed responses to reindeer presence. These differences likely were not caused by variation in herbivory pressure, but potentially due to a higher density of rivers and lakes in Yar-Sale/Panayevsk (11.7% area covered by water, compared to 4.8% in Taz (Bartsch et al., 2019)), leading to greater coverage of inundated/landslide area than in Taz, and a tendency for reindeer herds to avoid landslide and mire areas (Skarin et al., 2020), resulting in lower coverage of this landcover in pasture areas within Yar-Sale/Panayevsk.

We also found that higher reindeer pressure remained linked to less tall woody vegetation and more sparse vegetation when considering variations in animal density across the pasture areas. Within each herd area of constant reindeer density, we calculated how the observed proportions of sparse vegetation and tall woody vegetation differed from the expectation based on the average coverage proportions associated with the landforms present (**Figure 4.3**). A positive value for this difference implies that the area contains more sparse vegetation and less tall woody vegetation than expected. The relationship between reindeer density and this difference was highly nonlinear, as the most pronounced effect occurred once the reindeer density exceeded a high threshold: 21 reindeer/km^2 on June pastures and 47.5 reindeer·months/km^2 when integrating over June-August. In all comparisons, points were mostly absent from the lower right of the plot area, representing high animal density and more tall woody vegetation than expected based on the landforms present. This tendency is highlighted by the contours, which display the results of 2D kernel density estimation. Especially when only considering the uplands (**Figure 4.3B,D**), the outermost contour lines slope upwards (from lower left to upper right in the plot), indicating a similar probability of pasture areas having low reindeer density with more tall woody vegetation than expected and high reindeer density with more sparse vegetation than expected.

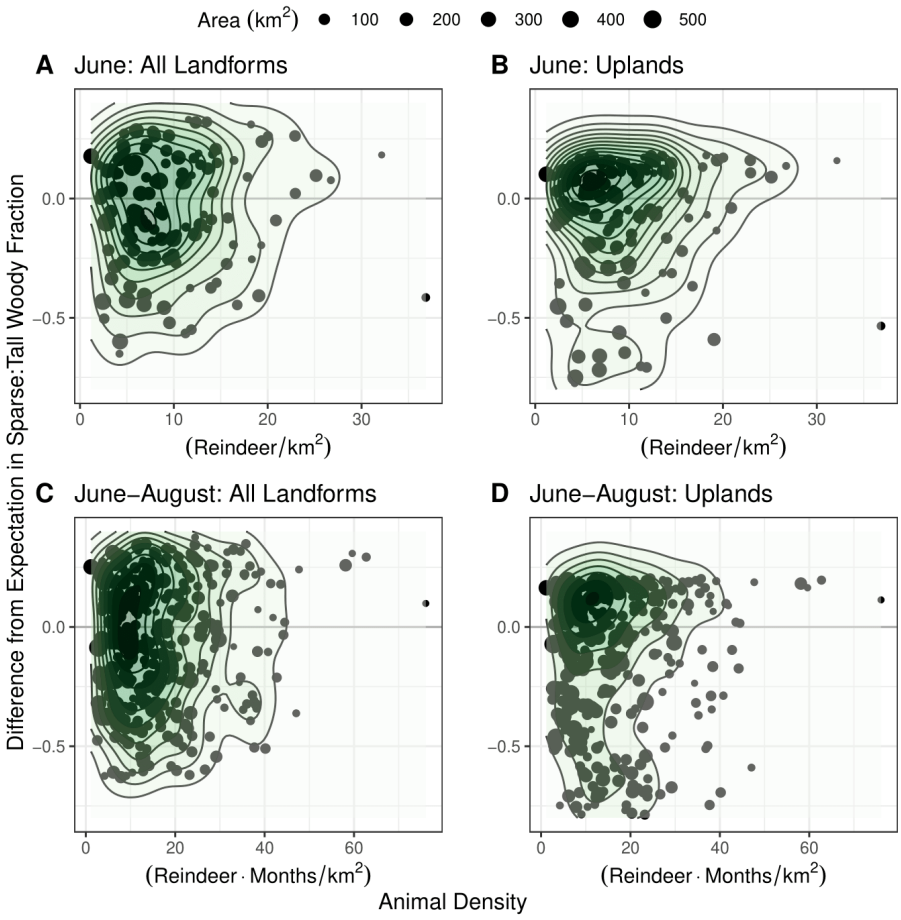


Figure 4.3: Link between reindeer density and the amount by which the ratio of sparse vegetation to tall woody vegetation differs from the ratio that would be expected based on the distribution of landforms in each herd area. Each point represents a continuous herd area with a given reindeer density in June (A,B) or density summed over June, July, and August (C,D). The difference from the expected ratio was calculated as (sparse fraction - expected sparse fraction), where the sparse fraction is (sparse/(sparse + tall woody)) and expected sparse fraction is a weighted average combining the number of pixels and the mean sparse fraction in each relevant landform class over all June pasture areas (A,B) or all summer pasture areas (C,D) in Yar-Sale/Panayevsk. The number of sparse vegetation and tall woody vegetation pixels on all landforms is included in A and C, while the sparse fractions are only calculated on upland pixels in B and D. The contour lines and shading display the results of 2D kernel density estimation.

4.7.2 Effect of reindeer herbivory on vegetation sensitivity to climate

Contrary to our hypothesis, VSI values were consistently greater in Yar-Sale/Panayevsk than in Taz, albeit by a small margin, despite the much greater herbivory pressure in Yar-Sale/Panayevsk (**Figure 4.4**). Paired comparisons of the VSI between regions using the Wilcoxon rank sum test indicated a significant difference for all comparisons within landforms and all comparisons within landcover, except within tall woody vegetation.

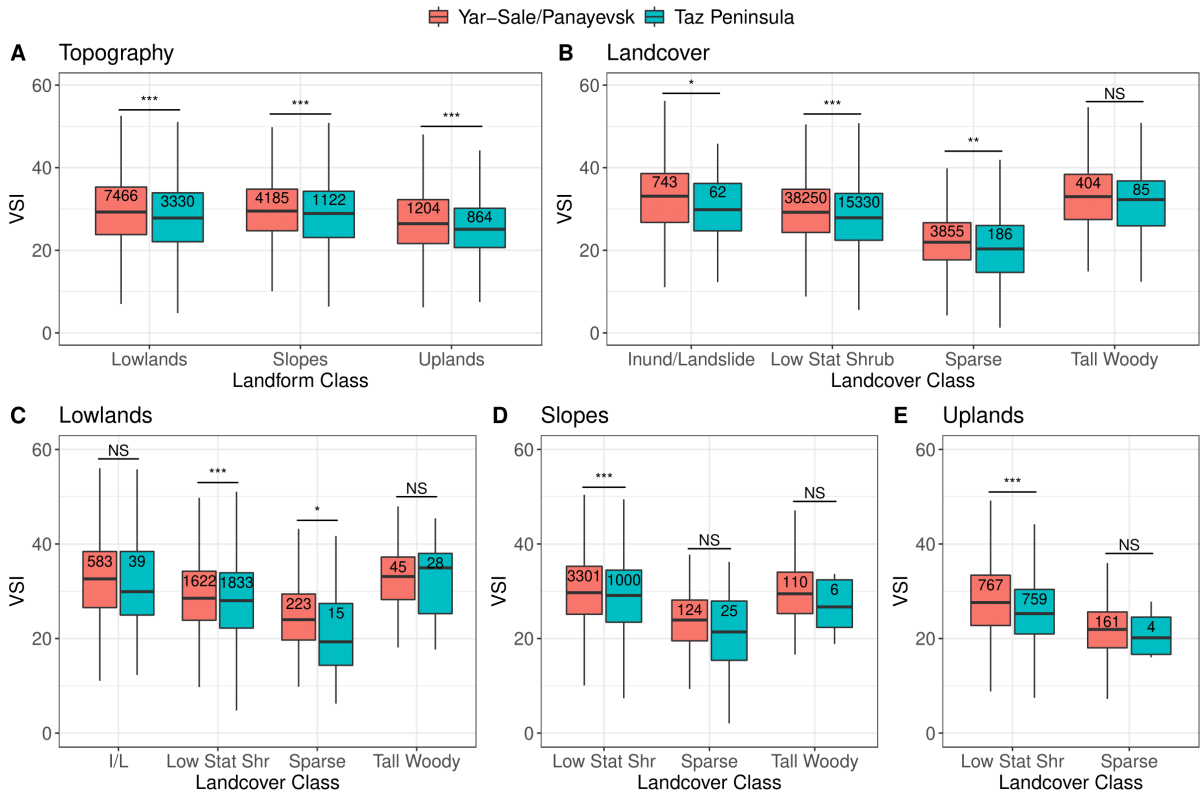


Figure 4.4: Comparisons of vegetation sensitivity index (VSI) values mediated by landforms (A), landcover (B), and the interactions between them (C-E). Landcover classes are excluded in D and E where there were fewer than three representative pixels in both regions. The lower and upper box boundaries correspond to the 25th and 75th percentiles, respectively, and the line inside the box gives the median. The number of 1 km pixels in each comparison is given in the boxes, and the significance level of the differences based on the Wilcoxon rank sum test is shown above them. NS indicates not significant, $p>0.05$; a single asterisk (*) indicates $p<0.05$; double asterisks (**) indicate $p<0.01$; and triple asterisks (***) indicate $p<0.001$.

When dividing Yar-Sale/Panayevsk into pasture areas, the VSI in each area remained slightly higher than in Taz within every landcover type except, notably, within tall woody vegetation. Whereas the mean VSI in tall woody vegetation still was higher in the no pasture area of Yar-Sale/Panayevsk than in Taz (+2.59), all reindeer pasture areas had a lower mean VSI (June: -1.38, July: -1.64, August: -0.533) (**Figure 4.5A**). A one-way ANOVA indicated significant differences in the mean VSI in the comparisons within tall woody vegetation ($F=4.728$, $p<0.001$), but Tukey's test showed a significant difference only in the comparison of no pasture area with July pastures ($p=0.002$). This finding suggests that reindeer herbivory does not have an extensive impact on vegetation sensitivity, but that it still has an observable effect in tall woody vegetation, where vegetation is otherwise most sensitive and where we would expect herbivory to counteract climate effects as drivers of vegetation change (Olofsson et al., 2009; Post & Pedersen, 2008). The higher climate sensitivity of vegetation observed in Yar-Sale/Panayevsk with respect to the Taz Peninsula is not explained by differences in landforms,

general relief, landcover, or substrate and occurs in both pastures and non-pastures (**Figures 4.4, 4.5, S4.4**). We speculate that this pattern might be driven by differences in growing season climate variability between both regions during the period 2000-2019 over which the VSI is computed.

The impact of reindeer herbivory on the sensitivity of tall woody vegetation to climate is further supported by the negative correlation between VSI and reindeer density within this landcover (**Figure 4.5B,C**). The estimated slope of the linear regression was -0.708 VSI/(reindeer/km^2) (p=0.0415) for June pastures and -0.268 VSI/(reindeer·months/km^2) (p=0.0155) for all pasture areas.

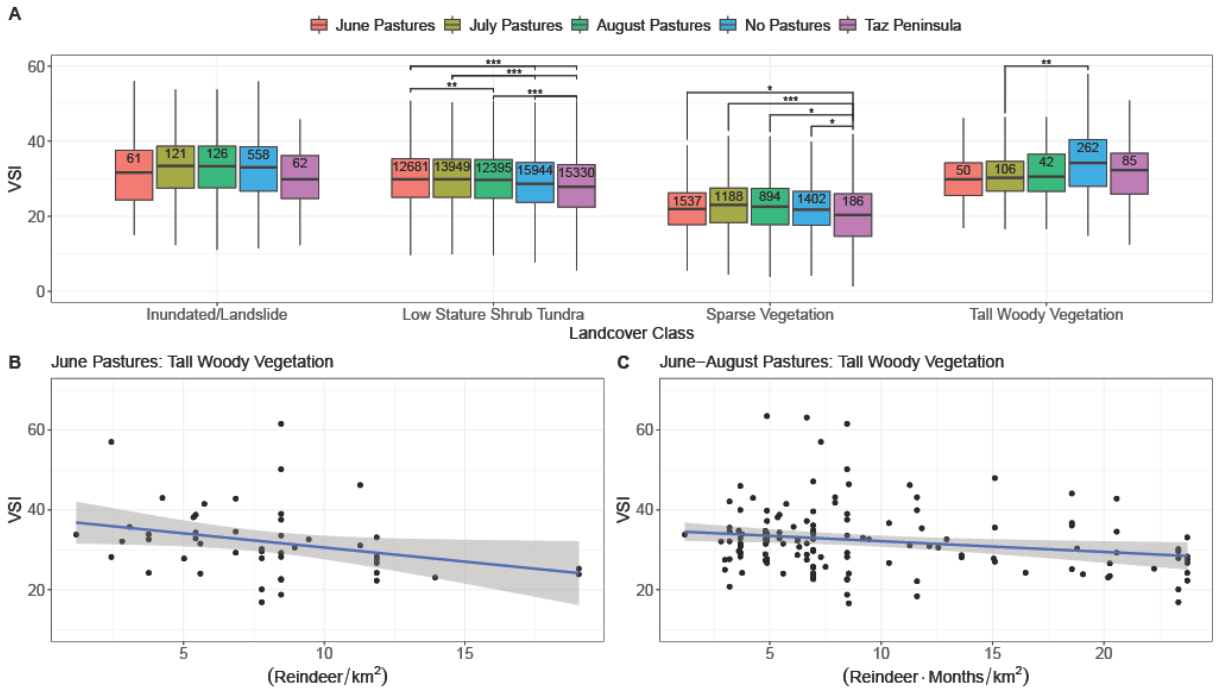


Figure 4.5: Comparison of vegetation sensitivity index (VSI) values between different pasture areas in Yar-Sale/Panayevsk and Taz (A), and the relationship between VSI and reindeer density within tall woody vegetation in June pastures (B) and all pasture areas (C). See the caption of **Figure 4.4** for the explanation of the boxes. Only significant differences based on Tukey's tests are annotated: a single asterisk (*) indicates p<0.05; double asterisks (**) indicate p<0.01; and triple asterisks (***) indicate p<0.001. Each point in B&C represents a 1 km VSI pixel within tall woody vegetation with a given June reindeer density (B) or density summed over June, July, and August (C). The linear least squares fits have a significant negative slope (-0.708 VSI/(reindeer/km2) (B), -0.268 VSI/(reindeer·months/km2) (C), p<0.05) and are displayed with shaded 95% confidence intervals.

4.8 Discussion

Our results suggest that reindeer herbivory on Yamal constrains the response of tall woody vegetation to warming and limits shrub expansion, shaping the landscape to consist of less tall woody vegetation and more sparse vegetation than it would have without the influence of animals. Using an associative pattern attribution approach, we evaluated six lines of evidence, which entailed comparing VSI and landcover distributions across three spatial contrasts in herbivory pressure. After considering all the evidence simultaneously, top-down control from reindeer herbivory emerged as the most parsimonious, consistent explanation for the observed patterns, which included both lower coverage of tall woody vegetation and lower climate sensitivity of vegetation within this landcover type at higher reindeer densities.

Our findings contrast with earlier regional-scale work concluding that bottom-up, climate-driven increases in unpalatable shrubs in North America contributed to declines in caribou abundance (Fauchald et al., 2017). However, our analysis benefitted from finer spatial grain – whereas Fauchald et al. (2017) used the GIMMS NDVI3g product at 1/12° resolution (~8 km), our coarsest remote sensing product was at 1 km resolution, ~60 times finer resolution – which enabled the pixel-based observations to better represent landscape-scale ecosystem structure and functioning. Additionally, the spatial comprehensiveness of the herd size and movement data provided a more accurate picture of the heterogeneity in herbivory pressure across the region, avoiding the implicit assumption often found within prior studies, including those in Yamal (e.g., Verma et al., 2020; Veselkin et al., 2021), that reindeer and changes in their population sizes are spread evenly over a region. The integration of high-resolution remote sensing products with spatially explicit reindeer population data provided the opportunity for multiple tests of our hypotheses, allowing us to carefully examine the competing effects of climate and herbivory on the vegetation on Yamal at a regional scale. The pattern-based methodology could be adapted for future studies testing whether, or the degree to which, large-scale ecosystem responses can be attributed to the influence of animals.

The magnitude of the vegetation response to herbivory detected in this study was relatively modest, observed as small percentage differences in VSI and landcover composition between the reindeer areas and their controls, and primarily in the areas with the strongest grazing pressure. This result evokes prior work which found that reindeer limited tall shrub expansion in Northern Norway but only when their densities exceeded approximately 5 animals/km2 (Bråthen et al., 2017). The threshold we found (i.e., 21 reindeer/km2 on June pastures, **Figure**

4.3) was higher than that observed in Northern Norway, but this disparity may be related to differences between the Nenets' reindeer herding in Yamal and the practices in Fennoscandia. Although Nenets herders are generally guided by the natural ecology of reindeer, at the regional scale, the seasonal choice of pastures and the timing of movements are determined entirely by herders. In the summer, Nenets on the Yar-Sale/Panayevsk tundra migrate every 3-5 days on average and even while a household remains in one place between movements, the herders try to direct reindeer to new areas as time passes. Thus, we hypothesise that a lower density of Fennoscandian free-grazing reindeer without constant human control could exert greater pressure on vegetation, especially the preferred shrub pastures in June, by remaining longer in certain areas. Within the Yamal Peninsula, the greater vegetation response we detected on June pastures may be not only due to the vulnerability of the vegetation to herbivory in the early growing season, but also because many households pass through the same areas as they migrate before dispersing to their July and August pastures. As a result, it is primarily the June pastures that exceed the threshold of reindeer density needed to cause significant impacts on the vegetation, despite the characteristic high rates of movement.

Furthermore, detecting the impacts of herbivory in an uncontrolled setting is complicated by challenges such as rapid vegetation recovery blurring the signal of the herbivory impact (Ravolainen et al., 2011) and uncertainty in the precise positioning and timing of animal movements. Thus, the true ecological magnitude of the herbivory impacts on Yamal may exceed our findings, and given the 67,000 km2 regional expanse over which we made our observations, there likely are implications for carbon storage and albedo relevant to Earth system functioning (Meredith et al., 2019).

Our observations represent a snapshot and do not inform whether the impact of reindeer on Yamal is changing over time nor the extent to which it may counteract climate-driven shrub growth in the future. Repeated monitoring of vegetation is needed to track and anticipate how the region will respond as the Arctic continues to warm. Our data on summer locations of reindeer herds and their migratory corridors reflect at least the last 30 years, but reindeer herding practices in the area are also changing, as herders adapt to infrastructure development for hydrocarbon extraction (Forbes et al., 2009) and climate change, which affects the timing of the freezing and thawing of rivers and has led to an increase in rain-on-snow events (Forbes et al., 2016, 2022). The latter cause the severe icing of pastures, leading to high reindeer mortality. There also have been calls from both biologists and administrators to reduce the

number of reindeer on Yamal and restrict their migrations in response to a recurring argument that the land is overgrazed, based primarily on a decline in lichen availability (Golovnev, 2017; Volkovitskiy & Terekhina, 2020). While the definition and perception of overgrazing is a complex, interdisciplinary topic, our findings can inform these discussions by providing empirical insights into the impact reindeer are having on the vegetation over a regional scale.

The potential for rewilding the Arctic with large herbivores to reduce the abundance of shrubs and slow climate change feedbacks has already drawn considerable attention, but questions remain as to how effectively such projects will provide these ecosystem services (Macias-Fauria et al., 2020; Olofsson & Post, 2018). Some of this discussion arises from uncertainty over whether Pleistocene megafauna had a large top-down role in maintaining the graminoid- and forb-rich vegetation, or whether they were a more passive element within a trophic chain in which vegetation cover was determined by climate as a bottom-up driver (Monteath et al., 2021). Our results support that herbivores, at current population densities, affect vegetation cover in the modern Arctic at a regional and potentially biome-wide scale. The domesticated reindeer herds of the Nenets are the largest in the world today, whereas estimates of past megafauna population sizes are highly uncertain (Monteath et al., 2021). The density of large herbivores across the Arctic historically may have been similar or likely much higher than the current reindeer density on Yamal (Zimov et al., 2012), and the modern perception of this density as high may be a case of 'shifting base-line syndrome' (Pauly, 1995) occurring over long periods of time. Thus, especially given the larger and more diverse Pleistocene herbivore assemblage (Olofsson & Post, 2018), it is likely that herbivory in the Arctic during the Pleistocene had even stronger impacts than what we have found here. Further work is necessary to translate the fingerprints of reindeer herbivory we detected into ecosystem variables and their quantitative estimates, but our findings demonstrate that top-down regulation by herbivory must be considered to understand how tundra ecosystems will respond to climate change.

4.9 Acknowledgments

We thank the employees of the Yar-Sale herding enterprise and Kharp *obshchina* for their expert insights into modern Yamal reindeer herding. This work was supported by the Clarendon Fund (to M.P.S.); the Russian Ministry of Science and Higher Education program "Terrestrial ecosystem of Northwestern Siberia: assessment of the modern transformation of the communities", No. 122021000089-9 (to A.V. & A.T.); the Russian Science Foundation

Project No. 22-24-00642 (to A.T.); the European Union's Horizon 2020 research and innovation programme under Grant Agreement No. 869471 (to B.C.F. & M.M.F.); Academy of Finland Decisions No. 256991 and JPI Climate No. 291581 (to B.C.F); and NASA Earth Science Directorate Grant NNX16AO34H (to T.P.).

4.10 Open research

The data used in this study are available in the Oxford University Research Archive via https://doi.org/10.5287/bodleian:E2x6bnggk under a Creative Commons license (CC BY 4.0) (Spiegel et al., 2022b). V1.0.0 of the code (Spiegel et al., 2022a) used in the pre-processing of the data, analysis, and figure generation is preserved at https://doi.org/10.5281/zenodo.7387883, available under a GNU General Public License v3.0 and developed openly using R version 4.0.0 (R Core Team, 2020).

4.11 References

Ackerman, S. (2015). MODIS Atmosphere L2 Cloud Mask Product. *NASA MODIS Adaptive Processing System, Goddard Space Flight Center, USA*. https://doi.org/10.5067/MODIS/MOD35_L2.061

Bartsch, A., Widhalm, B., Pointner, G., Ermokhina, K., Leibman, M., & Heim, B. (2019). *Landcover derived from Sentinel-1 and Sentinel-2 satellite data (2015-2018) for subarctic and arctic environments*. PANGAEA. https://doi.org/10.1594/PANGAEA.897916

Botch, M. C., Gerasimenko, T. V, & Tolchelnikov, Y. C. (1971). Mires of the Yamal Peninsula (in Russian with English summary). *Botanicheskii Zhurnal*, *56*, 1421–1435.

Bråthen, K. A., Ravolainen, V. T., Stien, A., Tveraa, T., & Ims, R. A. (2017). Rangifer management controls a climate-sensitive tundra state transition. *Ecological Applications*, *27*(8), 2416–2427. https://doi.org/10.1002/eap.1618

Cahoon, S. M. P., Sullivan, P. F., Post, E., & Welker, J. M. (2012). Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology*, *18*(2), 469–479. https://doi.org/10.1111/j.1365-2486.2011.02528.x

Campeau, A. B., Rickbeil, G. J. M., Coops, N. C., & Côté, S. D. (2019). Long-term changes in the primary productivity of migratory caribou (Rangifer tarandus) calving grounds and summer pasture on the Quebec-Labrador Peninsula (Northeastern Canada): the mixed influences of climate change and caribou herbivory. *Polar Biology*, *42*(5), 1005–1023. https://doi.org/10.1007/s00300-019-02492-6

Carroll, M. L., DiMiceli, C. M., Wooten, M. R., Hubbard, A. B., Sohlberg, R. A., & Townshend, J. R. G. (2017). MOD44W MODIS/Terra Land Water Mask Derived from MODIS and SRTM L3 Global 250m SIN Grid V006 [Data set]. *NASA EOSDIS Land Processes DAAC*.

Chapin III, F. S. (1980). Nutrient Allocation and Responses to Defoliation in Tundra Plants. *Arctic and Alpine Research*, *12*(4), 553. https://doi.org/10.2307/1550500

Chapin III, F. S., Johnson, D. A., & McKendrick, J. D. (1980). Seasonal Movement of Nutrients in Plants of Differing Growth Form in an Alaskan Tundra Ecosystem: Implications for Herbivory. *The Journal of Ecology*, *68*(1), 189.

https://doi.org/10.2307/2259251
Degteva, A., & Nellemann, C. (2013). Nenets migration in the landscape: impacts of industrial development in Yamal peninsula, Russia. *Pastoralism*, *3*(1), 1–21. https://doi.org/10.1186/2041-7136-3-15
Didan, K. (2015). MOD13A3 MODIS/Terra vegetation Indices Monthly L3 Global 1km SIN Grid V006 [Data set]. *NASA EOSDIS Land Processes DAAC*. https://doi.org/10.5067/MODIS/MOD13A3.006
Drozdov, D. S., Rivkin, F. M., Rachold, V., Ananjeva-Malkova, G. V., Ivanova, N. V., Chehina, I. V., Koreisha, M. M., Korostelev, Y. V., & Melnikov, E. S. (2005). Electronic atlas of the Russian Arctic coastal zone. *Geo-Marine Letters*, *25*(2–3), 81–88. https://doi.org/10.1007/s00367-004-0189-7
Dwyer, M. J., & Istomin, K. V. (2008). Theories of Nomadic Movement: A New Theoretical Approach for Understanding the Movement Decisions of Nenets and Komi Reindeer Herders. *Human Ecology*, *36*(4), 521–533. https://doi.org/10.1007/s10745-008-9169-2
Egelkraut, D., Aronsson, K.-Å., Allard, A., Åkerholm, M., Stark, S., & Olofsson, J. (2018). Multiple Feedbacks Contribute to a Centennial Legacy of Reindeer on Tundra Vegetation. *Ecosystems*, *21*(8), 1545–1563. https://doi.org/10.1007/s10021-018-0239-z
Enquist, B. J., Abraham, A. J., Harfoot, M. B. J., Malhi, Y., & Doughty, C. E. (2020). The megabiota are disproportionately important for biosphere functioning. *Nature Communications*, *11*(1), 1–11. https://doi.org/10.1038/s41467-020-14369-y
Evladov, V. P. (1992). *Through the Yamal tundra to the Belyi Island. Expedition to the Far North of the Yamal Peninsula in 1928-1929 (in Russian)*. Institute of the problems of Northern development, SB RAS.
Fauchald, P., Park, T., Tømmervik, H., Myneni, R., & Hausner, V. H. (2017). Arctic greening from warming promotes declines in caribou populations. *Science Advances*, *3*(4). https://doi.org/10.1126/sciadv.1601365
Forbes, B. C., Kumpula, T., Meschtyb, N., Laptander, R., Macias-Fauria, M., Zetterberg, P., Verdonen, M., Skarin, A., Kim, K.-Y., Boisvert, L. N., Stroeve, J. C., & Bartsch, A. (2016). Sea ice, rain-on-snow and tundra reindeer nomadism in Arctic Russia. *Biology Letters*, *12*(11), 20160466. https://doi.org/10.1098/rsbl.2016.0466
Forbes, B. C., Kumpula, T., Meschtyb, N., Laptander, R., Macias-Fauria, M., Zetterberg, P., Verdonen, M., Skarin, A., Kim, K.-Y., Boisvert, L. N., Stroeve, J. C., & Bartsch, A. (2022). Coping with a Warming Winter Climate in Arctic Russia: Patterns of Extreme Weather Affecting Nenets Reindeer Nomadism. In *Resilience Through Knowledge Co-Production* (pp. 217–232). Cambridge University Press. https://doi.org/10.1017/9781108974349.017
Forbes, B. C., Stammler, F., Kumpula, T., Meschtyb, N., Pajunen, A., & Kaarlejärvi, E. (2009). High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences*, *106*(52), 22041–22048. https://doi.org/10.1073/pnas.0908286106
Golovnev, A. V. (2017). Challenges to Arctic Nomadism: Yamal Nenets Facing Climate Change Era Calamities. *Arctic Anthropology*, *54*(2), 40–51. https://doi.org/10.3368/aa.54.2.40
Golovnev, A. V, Lezova, S. V, Abramov, I. V, Belorussova, S. Y., & Babenkova, N. A. (2014). *Ethno-expertise on Yamal: Nenets routes and gas fields (in Russian)*. AMB Press.
Habeck, J. O. (2007). *What it Means to be a Herdsman: The Practice and Image of Reindeer Husbandry*. Lit Verlag.
Hegerl, G. C., Hoegh-Guldberg, O., Casassa, G., Hoerling, M., Kovats, S., Parmesan, C., Pierce, D., & Stott, P. (2009). IPCC Expert Meeting on Detection and Attribution

Related to Anthropogenic Climate Change The World Meteorological Organization Good Practice Guidance Paper on Detection and Attribution Related to Anthropogenic Climate Change Good Practice Guidance Paper o. In T. Stocker, C. Field, Q. Dahe, V. Barros, G.-K. Plattner, M. Tignor, P. Midgley, & K. Ebi (Eds.), *IPCC Expert Meeting on Detection and Attribution Related to Anthropogenic Climate Change*.

Istomin, K., & Dwyer, M. (2021). *Reindeer herder's thinking: A comparative research on relations between economy, cognition, and way of life*. Verlag der Kulturstiftung Sibirien.

Jasiewicz, J., & Stepinski, T. F. (2013). Geomorphons - a pattern recognition approach to classification and mapping of landforms. *Geomorphology*, *182*, 147–156. https://doi.org/10.1016/j.geomorph.2012.11.005

Jernsletten, J.-L. L., & Klokov, K. (2002). *Sustainable Reindeer Husbandry*.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. ., Linder, H. P., & Kessler, M. (2018). Climatologies at high resolution for the earth's land surface areas. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.kd1d4

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 1–20. https://doi.org/10.1038/sdata.2017.122

Kassambara, A. (2020). *rstatix: Pipe-Friendly Framework for Basic Statistical Tests*. https://cran.r-project.org/package=rstatix

Klein, D. R. (1968). The Introduction, Increase, and Crash of Reindeer on St. Matthew Island. *The Journal of Wildlife Management*, *32*(2), 350. https://doi.org/10.2307/3798981

Kolari, T. H. M., Kumpula, T., Verdonen, M., Forbes, B. C., & Tahvanainen, T. (2019). Reindeer grazing controls willows but has only minor effects on plant communities in Fennoscandian oroarctic mires. *Arctic, Antarctic, and Alpine Research*, *51*(1), 506–520. https://doi.org/10.1080/15230430.2019.1679940

Kristensen, J. A., Svenning, J.-C., Georgiou, K., & Malhi, Y. (2022). Can large herbivores enhance ecosystem carbon persistence? *Trends in Ecology & Evolution*, *37*(2), 117–128. https://doi.org/10.1016/j.tree.2021.09.006

Kvashnin, I. N. (2009). *The Nenets reindeer herding in the 20 c. - beginning of 21 c. (in Russian)*. Koleso.

Leibman, M. O. (1995). Cryogenic landslides on the Yamal Peninsula, Russia: Preliminary observations. *Permafrost and Periglacial Processes*, *6*, 259–264. https://doi.org/10.1002/ppp.3430060307

Lundgren, E. J., Ramp, D., Rowan, J., Middleton, O., Schowanek, S. D., Sanisidro, O., Carroll, S. P., Davis, M., Sandom, C. J., Svenning, J.-C., & Wallach, A. D. (2020). Introduced herbivores restore Late Pleistocene ecological functions. *Proceedings of the National Academy of Sciences*, *117*(14), 7871–7878. https://doi.org/10.1073/pnas.1915769117

Macias-Fauria, M., Jepson, P., Zimov, N., & Malhi, Y. (2020). Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190122. https://doi.org/10.1098/rstb.2019.0122

Meredith, M., Sommerkorn, M., Cassotta, S., Derksen, C., Ekaykin, A., Hollowed, A., Kofinas, G., Mackintosh, A., Melbourne-Thomas, J., Muelbert, M. M. C., Ottersen, G., Pritchard, H., & Schuur, E. A. G. (2019). Polar Regions. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A.

Alegria, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. M. Weyer (Eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*.

Metcalfe, D. B., & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO 2 exchange during the peak of the growing season. *Oikos*, *124*(12), 1632–1638. https://doi.org/10.1111/oik.02085

Monteath, A. J., Gaglioti, B. V., Edwards, M. E., & Froese, D. (2021). Late Pleistocene shrub expansion preceded megafauna turnover and extinctions in eastern Beringia. *Proceedings of the National Academy of Sciences*, *118*(52), e2107977118. https://doi.org/10.1073/pnas.2107977118

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., Speed, J. D. M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N. M., Baittinger, C., Trant, A. J., Hermanutz, L., Collier, L. S., … Vellend, M. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, *5*(9), 887–891. https://doi.org/10.1038/nclimate2697

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., MacIas-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4). https://doi.org/10.1088/1748-9326/6/4/045509

Newton, E. J., Pond, B. A., Brown, G. S., Abraham, K. F., & Schaefer, J. A. (2014). Remote sensing reveals long-term effects of caribou on tundra vegetation. *Polar Biology*, *37*(5), 715–725. https://doi.org/10.1007/s00300-014-1472-3

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., & Oksanen, L. (2001). Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, *24*(1), 13–24. https://doi.org/10.1034/j.1600-0587.2001.240103.x

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*(11), 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x

Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761). https://doi.org/10.1098/rstb.2017.0437

Olofsson, J., Stark, S., & Oksanen, L. (2004). Reindeer influence on ecosystem processes in the tundra. *Oikos*, *105*(2), 386–396. https://doi.org/10.1111/j.0030-1299.2004.13048.x

Olofsson, J., Tommervik, H., & Callaghan, T. V. (2012). Vole and lemming activity observed from space. *Nature Climate Change*, *2*(12), 880–883. https://doi.org/10.1038/nclimate1537

Parker, T. C., Thurston, A. M., Raundrup, K., Subke, J., Wookey, P. A., & Hartley, I. P. (2021). Shrub expansion in the Arctic may induce large-scale carbon losses due to changes in plant-soil interactions. *Plant and Soil*, *463*(1–2), 643–651. https://doi.org/10.1007/s11104-021-04919-8

Parmesan, C., Burrows, M. T., Duarte, C. M., Poloczanska, E. S., Richardson, A. J., Schoeman, D. S., & Singer, M. C. (2013). Beyond climate change attribution in conservation and ecological research. *Ecology Letters*, *16*, 58–71. https://doi.org/10.1111/ele.12098

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, *10*(10), 430. https://doi.org/10.1016/S0169-5347(00)89171-5

Porter, C., Morin, P., Howat, I., Noh, M.-J., Bates, B., Peterman, K., Keesey, S., Schlenk, M., Gardiner, J., Tomko, K., Willis, M., Kelleher, C., Cloutier, M., Husby, E., Foga, S.,

Nakamura, H., Platson, M., Wethington, Michael, J., Williamson, C., … Bojesen, M. (2018). ArcticDEM. *Harvard Dataverse, V1*. https://doi.org/10.7910/DVN/OHHUKH

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(34), 12353–12358. https://doi.org/10.1073/pnas.0802421105

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. https://www.r-project.org/

Ravolainen, V. T., Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Henden, J.-A., & Killengreen, S. T. (2011). Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. *Basic and Applied Ecology*, *12*(8), 643–653. https://doi.org/10.1016/j.baae.2011.09.009

Raynolds, M. K., Walker, D. A., Balser, A., Bay, C., Campbell, M., Cherosov, M. M., Daniëls, F. J. A., Eidesen, P. B., Ermokhina, K. A., Frost, G. V., Jedrzejek, B., Jorgenson, M. T., Kennedy, B. E., Kholod, S. S., Lavrinenko, I. A., Lavrinenko, O. V., Magnússon, B., Matveyeva, N. V., Metúsalemsson, S., … Troeva, E. (2019). A raster version of the Circumpolar Arctic Vegetation Map (CAVM). *Remote Sensing of Environment*, *232*(January). https://doi.org/10.1016/j.rse.2019.111297

Raynolds, M. K., Walker, D. A., Epstein, H. E., Pinzon, J. E., & Tucker, C. J. (2012). A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. *Remote Sensing Letters*, *3*, 403–411. https://doi.org/10.1080/01431161.2011.609188

Rees, W. G., Williams, M., & Vitebsky, P. (2003). Mapping land cover change in a reindeer herding area of the Russian arctic using Landsat TM and ETM+ imagery and indigenous knowledge. *Remote Sensing of Environment*, *85*(4), 441–452. https://doi.org/10.1016/S0034-4257(03)00037-3

Ricca, M. A., Miles, A. K., Van Vuren, D. H., & Eviner, V. T. (2016). Impacts of introduced Rangifer on ecosystem processes of maritime tundra on subarctic islands. *Ecosphere*, *7*(3). https://doi.org/10.1002/ecs2.1219

Rickbeil, G. J. M., Coops, N. C., & Adamczewski, J. (2015). The grazing impacts of four barren ground caribou herds (Rangifer tarandus groenlandicus) on their summer ranges: An application of archived remotely sensed vegetation productivity data. *Remote Sensing of Environment*, *164*, 314–323. https://doi.org/10.1016/j.rse.2015.04.006

Running, S., Mu, Q., Zhao, M., & Moreno, A. (2019). MOD16A2GF MODIS/Terra Net Evapotranspiration Gap-Filled 8-Day L4 Global 500 m SIN Grid V006 [Data set]. *NASA EOSDIS Land Processes DAAC*. https://doi.org/doi.org/10.5067/MODIS/MOD16A2GF.006

Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, *531*(7593), 229–232. https://doi.org/10.1038/nature16986

Skarin, A., Verdonen, M., Kumpula, T., Macias-Fauria, M., Alam, M., Kerby, J., & Forbes, B. C. (2020). Reindeer use of low Arctic tundra correlates with landscape structure. *Environmental Research Letters*, *15*(11), 115012. https://doi.org/10.1088/1748-9326/abbf15

Spiegel, M. P., Volkovitskiy, A., Terekhina, A., Forbes, B. C., Park, T., & Macias-Fauria, M. (2022a). *marcusspiegel/yamal_rs: yamal_rs v1.0.0*. https://doi.org/10.5281/zenodo.7387883

Spiegel, M. P., Volkovitskiy, A., Terekhina, A., Forbes, B. C., Park, T., & Macias-Fauria, M. (2022b). *Top-down regulation by a reindeer herding system limits climate-driven Arctic vegetation change at a regional scale: data*. Oxford University Research Archive. https://doi.org/10.5287/bodleian:E2x6bnggk

Stammler, F. (2005). *Reindeer Nomads Meet the Market: Culture, Property and*

Globalisation at the `End of the Land'. Lit.

Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J., & Romanovsky, V. E. (2005). Winter Biological Processes Could Help Convert Arctic Tundra to Shrubland. *BioScience*, *55*(1), 17. https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., & Stark, S. (2014). Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, *4*(5), 384–388. https://doi.org/10.1038/nclimate2147

van der Wal, R. (2006). Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, *114*(1), 177–186. https://doi.org/10.1111/j.2006.0030-1299.14264.x

Verma, M., Schulte to Bühne, H., Lopes, M., Ehrich, D., Sokovnina, S., Hofhuis, S. P., & Pettorelli, N. (2020). Can reindeer husbandry management slow down the shrubification of the Arctic? *Journal of Environmental Management*, *267*(April), 110636. https://doi.org/10.1016/j.jenvman.2020.110636

Veselkin, D. V., Morozova, L. M., & Gorbunova, A. M. (2021). Decrease of NDVI values in the southern tundra of Yamal in 2001–2018 correlates with the size of domesticated reindeer population. *Sovremennye Problemy Distantsionnogo Zondirovaniya Zemli Iz Kosmosa*, *18*(2), 143–155. https://doi.org/10.21046/2070-7401-2021-18-2-143-155

Volkovitskiy, A., & Terekhina, A. (2020). The contemporary issues of Yamal reindeer herding: discussions and perspectives (in Russian). *Etnografia*, *2*(8), 152–169.

Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Raynolds, M. K., Comiso, J. C., Gubarkov, A. A., Khomutov, A. V., Jia, G. J., Kaarlejärvi, E., Kaplan, J. O., Kumpula, T., Kuss, P., Matyshak, G., Moskalenko, N. G., Orekhov, P., Romanovsky, V. E., Ukraientseva, N. G., & Yu, Q. (2009). Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index. *Environmental Research Letters*, *4*(4), 045004. https://doi.org/10.1088/1748-9326/4/4/045004

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & The other members of the CAVM Team. (2005). The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, *16*(3), 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x

Ylänne, H., Kaarlejärvi, E., Väisänen, M., Männistö, M. K., Ahonen, S. H. K., Olofsson, J., & Stark, S. (2020). Removal of grazers alters the response of tundra soil carbon to warming and enhanced nitrogen availability. *Ecological Monographs*, *90*(1), 1–13. https://doi.org/10.1002/ecm.1396

Ylänne, H., Olofsson, J., Oksanen, L., & Stark, S. (2018). Consequences of grazer-induced vegetation transitions on ecosystem carbon storage in the tundra. *Functional Ecology*, *32*(4), 1091–1102. https://doi.org/10.1111/1365-2435.13029

Zimov, S. A., Zimov, N. S., Tikhonov, A. N., & Chapin, I. S. (2012). Mammoth steppe: A high-productivity phenomenon. *Quaternary Science Reviews*, *57*, 26–45. https://doi.org/10.1016/j.quascirev.2012.10.005

4.12 Supplementary material

Text S4.1:

Comparison of Yar-Sale and Panayevsk Tundra and Taz Peninsula

The northern Taz Peninsula was chosen as a comparison area for the Yar-Sale and Panayevsk tundra due to its similar physical geography and contrasting reindeer density. Both areas are within the low Arctic tundra zone with landscapes of low plains created mainly by recent submergence (Drozdov et al., 2005). The most common lithology within each area is clay/silt and sand, accounting for between 40% and 45% of the land area (**Figure S4.4A**). Whereas sand and clay/silt is the second most prominent lithology class in Yar-Sale/Panayevsk, the second most prominent class in Taz is peat, sand, and clay/silt. Although otherwise similar, the substrate of Taz seems to be more peat-dominated.

The topography in both areas is low and flat with valleys created by meandering rivers and lowlands with thaw lakes and drained thaw-lake basins (Walker et al., 2009). The average land elevation calculated from ArcticDEM (Porter et al., 2018) is 16.2 m in Yar-Sale/Panayvesk and 16.3 m in Taz. In the summer months, the average monthly maximum temperature calculated from the CHELSA v2.1 monthly time series (Karger et al., 2017, 2018) over the VSI analysis period, 2000-2019, in Yar-Sale/Panayevsk was 10.4°C with a standard deviation of 3.77°C, and 11.5°C with a standard deviation of 4.05°C in Taz.

The main text and figures depict the extensive reindeer herding activity on the Yar-Sale and Panayevsk tundra, whereas Taz has considerably fewer reindeer. One main reason for this is that the Yamburg settlement near the western coast of the Taz Peninsula within the study area has been a major centre for hydrocarbon extraction since the Yamburg gas field was discovered in 1969. Yamburg is a closed town and acts as a major obstacle for migrations. Although the current number of reindeer grazing within our study area on Taz in the summer is uncertain, our interactions with local people in Nyda, the reindeer herding centre in the region, make us confident that the contrast in herbivory pressure between Taz and Yar-Sale/Panayevsk is sufficiently large.

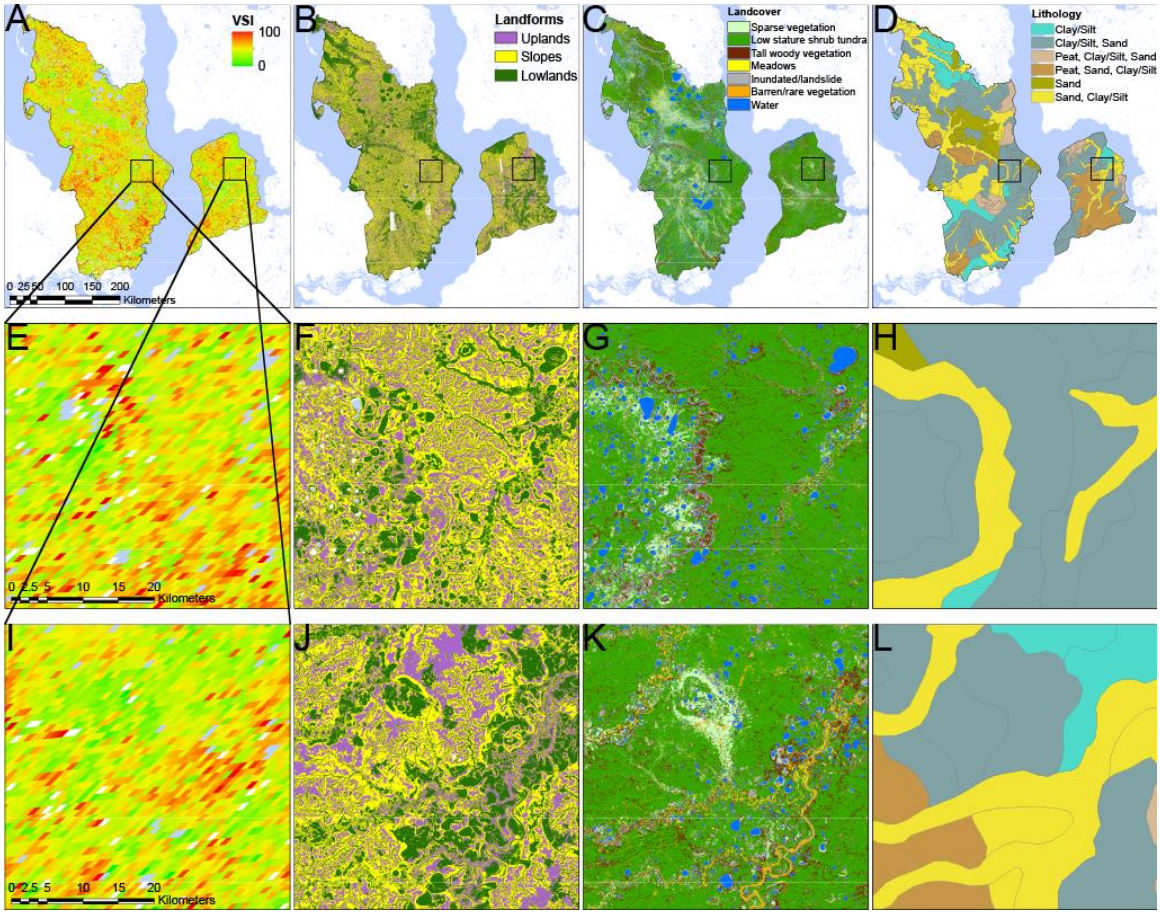


Figure S4.1: Spatially continuous variables used in the analysis mapped over the Yar-Sale and Panayevsk tundra and Taz Peninsula. (A,E,I) The vegetation sensitivity index (VSI), adapted from Seddon & Macias-Fauria et al. (2016), depicting the sensitivity of vegetation productivity to climate variability over 2000-2019 at 1 km resolution. (B,F,J) Landform classification applying the Geomorphons algorithm (Jasiewicz & Stepinski, 2013) to the ArcticDEM (Porter et al., 2018) at 32 m resolution. See **Figure S4.2** for an illustration of the steps in the classification. (C,G,K) Landcover classification at 20 m resolution adapted from the landcover product of Bartsch et al. (2019), which was developed using a supervised classification of Sentinel-1 and Sentinel-2 imagery from 2016-2018. **Table S4.1** shows the associations between the landcover classes and the original data codes. (D,H,L) Lithology characterisation based on maps of the Russian Arctic coastal zone (Drozdov et al., 2005). Where multiple soil textures are listed in a single lithology unit, they are in descending order of prominence. Areas in Yar-Sale/Panayevsk (E-H) and Taz (I-L) are enlarged to show the variables in greater detail. All panels are displayed in the WGS84 UTM 42N projection. The landform, landcover, and lithology maps were also provided in or converted to this local projection for analysis, whereas the VSI was calculated and analysed in the MODIS sinusoidal projection, matching the native projection of the MODIS vegetation and climate variables used as inputs in the algorithm.

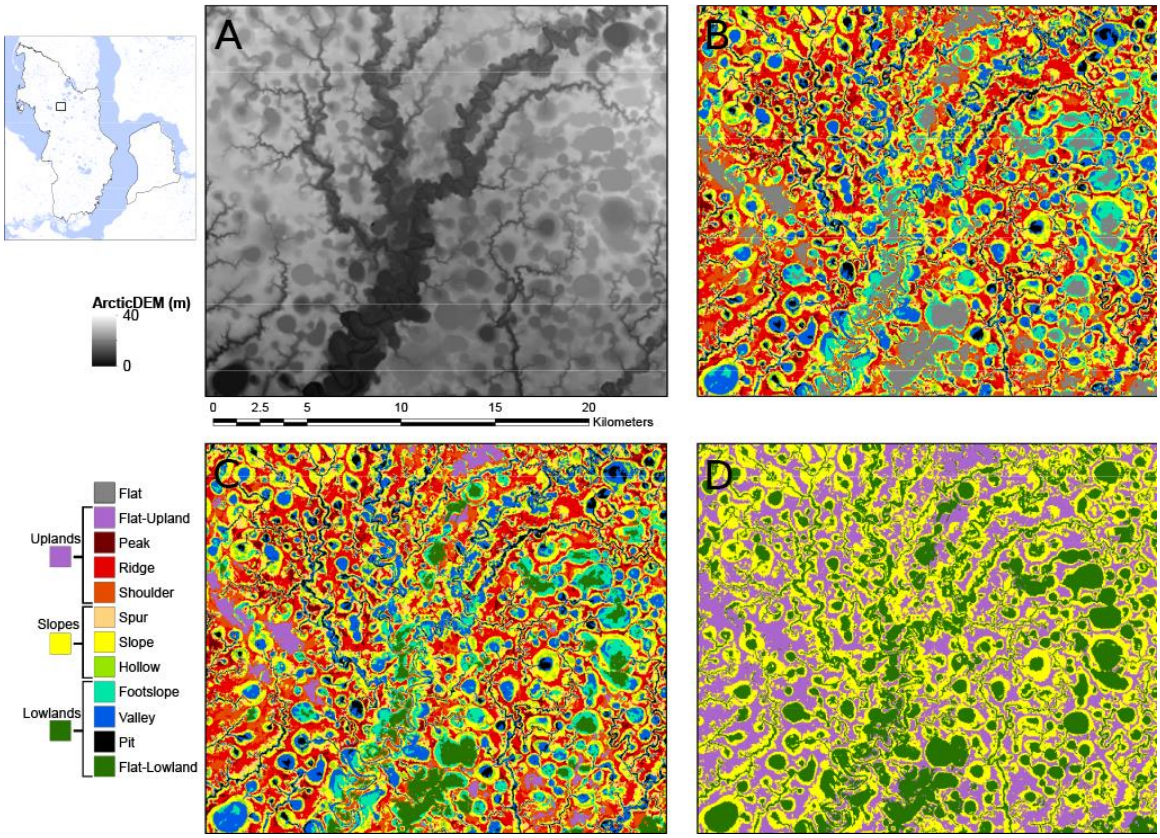


Figure S4.2: Demonstration of the steps used to generate the landform classification. (A) Digital surface model (DSM) from ArcticDEM (Porter et al., 2018) at 32 m resolution. (B) Classification of the DSM pixels into 10 common landform elements by applying the Geomorphons algorithm (Jasiewicz & Stepinski, 2013) with a 50 cell lookup distance and 0.5° flatness threshold. (C) Reclassification of the pixels determined to be flat into flat uplands and flat lowlands based on the progression of landforms in their neighbouring pixels. (D) Landform elements merged into uplands, slopes, and lowlands.

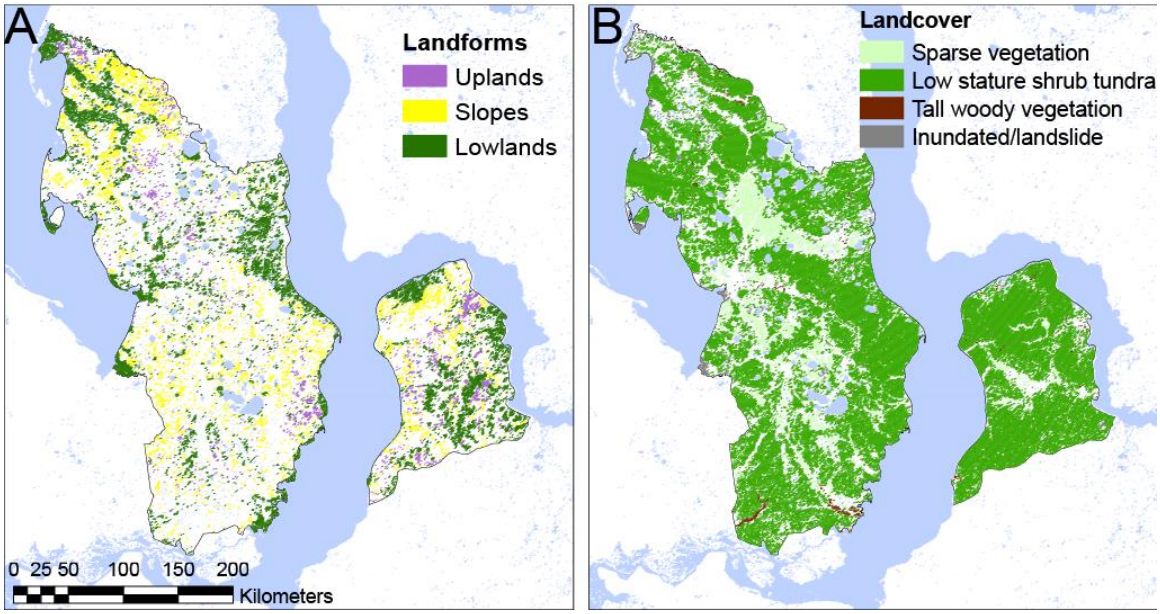


Figure S4.3: Assignment of 1 km pixels from the VSI map (**Figure S4.1A**) to landform and landcover classes. (A) Pixels were assigned to a landform class if at least two-thirds of the 1 km pixel footprint was covered by a single class based on the 32 m resolution landform map (**Figure S4.1B**). (B) Pixels were assigned to a landcover class if at least half of the 1 km pixel footprint was covered by a single class based on the 20 m resolution landcover map (**Figure S4.1C**). Only the classes used in the VSI comparison analyses (**Figures 4.4, 4.5**) are displayed.

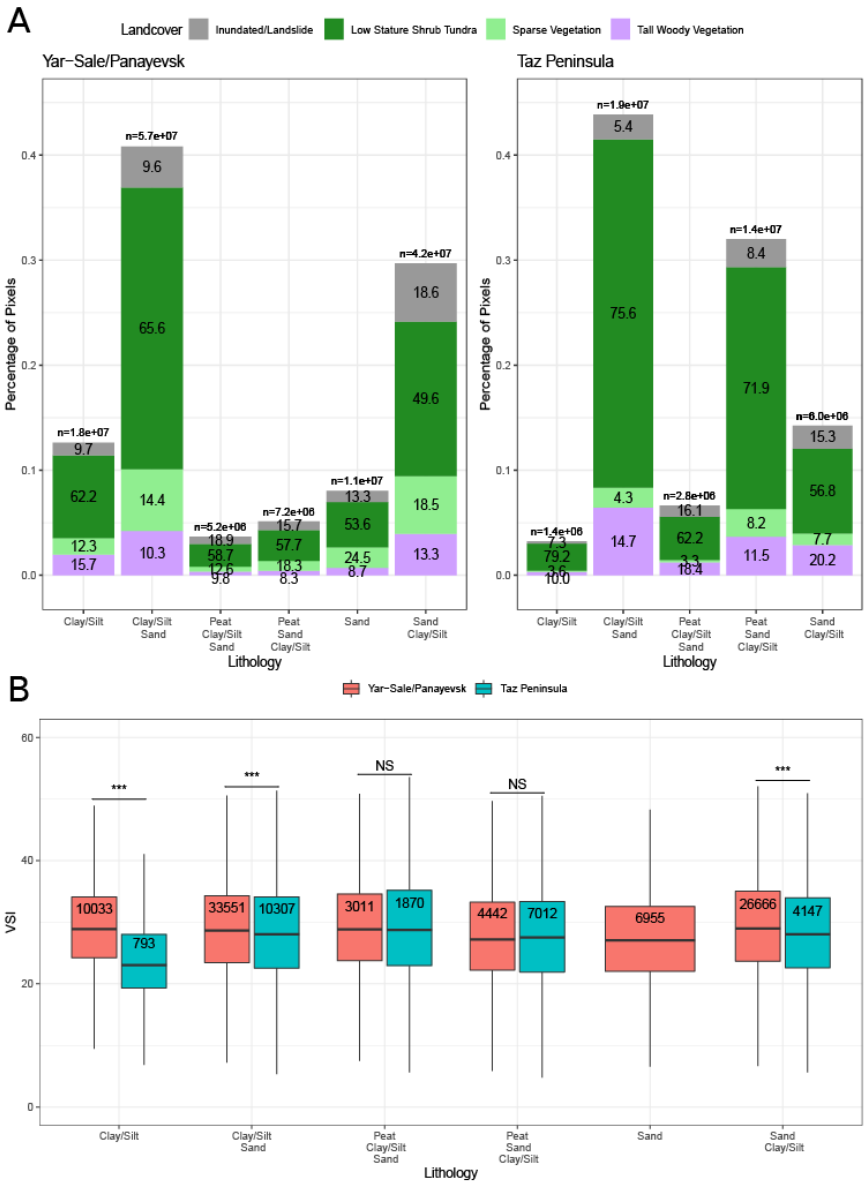


Figure S4.4: Variation in landcover composition and VSI values depending on lithology in Yar-Sale/Panayevsk and Taz. The lithology characterisation is based on maps of the Russian Arctic coastal zone (Drozdov et al., 2005) (**Figure S4.1D**). (A) Distribution of 20-m resolution landcover pixels based on the classification of Bartsch et al. (2019) (**Figure S4.1C**) within lithology units in both regions. The total number of pixels in the specified lithology unit is given above the bar, and the percentage of pixels within each landcover class is written inside the bar segments. All lithology units are shared between both regions, except sand, which is only present in Yar-Sale/Panayevsk. (B) Comparison of vegetation sensitivity index (VSI, **Figure S4.1A**) values within lithology units in Yar-Sale/Panayevsk and the Taz Peninsula. The number of 1 km pixels in each comparison are given in the boxes, and the significance level of the differences based on the Wilcoxon rank sum test are shown above them. NS indicates not significant, $p>0.05$; a single asterisk (*) indicates $p<0.05$; double asterisks (**) indicate $p<0.01$; and triple asterisks (***) indicate $p<0.001$.

Table S4.1: Landcover classes derived by merging the classes from Bartsch et al. (2019).

	Bartsch et al. (41) data codes	
Class	ID	Description
Sparse vegetation	1	Sparse vegetation (without shrubs), mostly sandy soil; flood plains, recent landslides, also within fire scars
	2	Dry cryptogamic-crust or sparse vegetation
Low stature shrub tundra	3	Graminoid, prostrate dwarf shrub, patterned ground, partially bare
	4	Dry to moist prostrate to erect dwarf shrub tundra
	5	Moist to wet graminoid prostrate to erect dwarf shrub tundra
Tall woody vegetation	6	Wet to waterlogged graminoid prostrate to low shrub tundra
	7	Moist low dense shrubs
	8	Tall shrubs, deciduous forest
	9	Mixed forest
	10	Coniferous (partially mixed) forest
Meadows	11	Meadows, grass and herb-dominated
Inundated/landslide	12	Wet ecotops, especially in floodplains
	13	Disturbed, including forest fire scars, seasonally inundated areas and landslide scars
	14	Floodplain, mostly fluvial
	15	Floodplain, mostly lacustrine
	16	Seasonally inundated
Barren/rare vegetation	17	Barren, rare vegetation (petrophytes and psammophytes)
	18	Barren, including articficial surfaces
Water	19	Water (shallow or high sediment yield)
	20	Water (medium depth or medium sediment yield)
	21	Water (low sediment yield)

Table S4.2: Deviance statistics for log-linear models evaluating possible explanations for the differences in the proportions of tall woody vegetation and sparse vegetation landcover pixels (see **Figure 4.2**). One set of models evaluates differences in landcover between Yar-Sale/Panayevsk and Taz ('Regions'), while the other set evaluates differences between June pastures, July pastures, August pastures, and land not used for summer pastures in Yar-Sale/Panayevsk ('Pasture Areas'). For each model, df represents the degrees of freedom and G^2 gives the residual deviance comparing the fitted model against the saturated model with all possible effects including interactions.

Comparison	Assumption	Predictors	df	G^2
Regions	Joint Independence	None	5	3798785
	Conditional Independence	Only Region	4	1334717
	Conditional Independence	Only Landform	3	2533505
	Homogeneous Association	Region & Landform	2	9034.8
Pasture Areas	Joint Independence	None	11	2062131
	Conditional Independence	Only Pasture Area	8	1782651
	Conditional Independence	Only Landform	9	383104
	Homogeneous Association	Pasture Area & Landform	6	95499

Chapter 5:

Heterogeneity in immediate and lagged effects of reindeer herbivory over spatially comprehensive fine scales

Marcus P. Spiegel[1], Jeffrey T. Kerby[2,3], Dorothée Ehrich[4], Alexander Volkovitskiy[5], Alexandra Terekhina[5], Violetta Filippova[5], Kirill Shklyar[5], Natalia Sokolova[5], Aleksandr A. Sokolov[5], Marc Macias-Fauria[1]

[1]Biogeosciences Lab, School of Geography & the Environment, University of Oxford, Oxford, OX1 3QY, United Kingdom.

[2]Aarhus Institute of Advanced Studies, Aarhus University, Aarhus 8000, Denmark

[3]Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus 8000, Denmark

[4]UiT - The Arctic University of Norway, Department of Arctic and Marine Biology, 9019 Tromsø, Norway

[5]Arctic Research Station of Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Labytnangi, Russia, 629400, Zelenaya Gorka Str., 21



Photo: Alexandra Terekhina

5.1 Chapter statement

This chapter employed unmanned aerial vehicle (UAV) surveys to map canopy height changes across a landscape immediately before and after a week-long reindeer herbivory event as well as one month after the event. UAVs have been frequently used to map vegetation in the Arctic but rarely in studies of the effects of herbivory. Whereas the satellite-based analysis in **Chapter 4** aimed to detect the regional-scale impacts of reindeer, this research was designed to investigate fine-scale spatial heterogeneity in the immediate and lagged effects stemming from an herbivory event.

This chapter has been submitted to *Journal of Ecology*. The work was presented online in a seminar organized by the Plant Functional Trait Courses in November 2022.

5.2 Author contributions

MPS conceptualised the research and designed the study together with DE, AV, AT, AAS, and MMF. DE, AV, and AT coordinated the logistics. MPS, DE, and AV performed the data collection in the field. VF and KS contributed the GPS collar data. MPS processed the imagery with significant guidance from JTK. MPS analysed the data with input from JTK and MMF. NS and AAS provided additional logistical support. MPS wrote the manuscript with significant contributions from all authors.

5.3 Abstract

1. Reindeer influence ecosystem structure and functioning in the Arctic via their grazing, browsing, trampling, and nutrient inputs from faeces and urine. The combination of these activities can promote a shift from moss- and shrub-dominated tundra towards graminoid-dominated vegetation with potential implications for carbon cycling and the energy balance.
2. The impacts of reindeer herbivory vary depending on the animal density, the environmental context, and the duration of and time since the herbivory event. Remote sensing provides the opportunity to analyse these factors and their interactions at ecologically appropriate scales by assessing spatial heterogeneity in vegetation responses at the fine grains and landscape extents inherent to these interactions.
3. We conducted unmanned aerial vehicle (UAV) surveys at a site on the Yamal Peninsula, West Siberia next to a campsite of Indigenous Nenets mobile pastoralists managing a reindeer herd. The surveys mapped the landscape immediately before the herd arrived, immediately after they had left the site, and one month after the herd's activity. Using structure-from-motion (SfM) photogrammetry in a novel workflow that accounts for spatially variable uncertainty in the SfM reconstructions, we detected significant decreases in canopy height over 0.4% of the site after the herbivory event and significant growth over 3% of the site one month later.
4. We evaluated how the significant changes varied spatially depending on the habitat type, initial canopy height, and amount of herbivory pressure, determined based on reindeer collar GPS data. In areas with higher reindeer activity, there were initial decreases in canopy height both in low-lying vegetation, likely trampling, and taller vegetation, representing reindeer browsing around the edges of erect shrubs, and subsequent growth predominantly in low-lying vegetation one month later. Areas with lower herbivory pressure within the same habitat types showed strikingly little change throughout the study period.
5. *Synthesis*. High-resolution mapping of the physical changes in vegetation structure through time and across the landscape can disentangle the factors mediating variation in plant responses to herbivory. Our results demonstrate that reindeer browsing of erect shrubs and trampling of low-lying vegetation within a single growing season limits Arctic shrub expansion and enhances grasslands.

5.4 Introduction

Vegetation cover and biomass in the Arctic are heterogeneous across fine scales due to localised variability in abiotic determinants (Elmendorf et al., 2012; Niittynen et al., 2020; Räsänen & Virtanen, 2019; Suvanto et al., 2014). Biotic factors, including competition, mycorrhizal symbioses, and trophic dynamics, also exert important controls on tundra vegetation (Wookey et al., 2009), and recent work has highlighted the substantial effects of herbivores, which vary spatially within landscapes, mediated by abiotic conditions and the vegetation (Olofsson et al., 2013). Within the extant community of large herbivores in the Arctic, only reindeer (*Rangifer tarandus*) remain widespread, but their influence on vegetation has potentially broad-scale consequences for ecosystem structure and functioning throughout the tundra biome with climate feedbacks to the Earth system (Olofsson & Post, 2018; Väisänen et al., 2014). The impact of reindeer is more complex than just their consumption of aboveground biomass, as the combination of their defoliation, trampling, and nutrient inputs from faeces/urine has been shown to promote the growth of graminoids at the expense of deciduous shrubs, which are otherwise becoming taller and more abundant in response to climate warming (Bråthen et al., 2017; Egelkraut et al., 2018; Kaarlejärvi et al., 2015; Olofsson et al., 2009). Yet, these impacts are not spread uniformly across the Arctic or even within landscapes, and uncertainty remains regarding how vegetation responses vary over space, at different timescales following herbivory events, and as a function of the density of animals (Siewert & Olofsson, 2021).

In a systematic review of the impacts of reindeer on vegetation, the meta-analysis found only weak or non-significant effects on vascular plants despite many individual studies showing clear effects, but explanations for this context dependence were unclear (Bernes et al., 2015). Remote sensing provides an opportunity to tease apart this context dependence by evaluating variation in vegetation responses to herbivory between and within landscapes. Broad-scale and spatially continuous observations enable both analysis of the factors regulating herbivory over space and determination of the dominant impacts relevant for incorporation into ecosystem models (Siewert & Olofsson, 2021). Most prior work using remote sensing to study herbivory in the Arctic has relied on satellite measurements of the normalised difference vegetation index (NDVI), a metric of vegetation greenness that is calculated using spectral reflectance data and broadly related to productivity and aboveground biomass (Raynolds et al., 2012). For example, reductions in plant biomass the year after vole and lemming peaks were visible as a decrease in NDVI over a 770 km^2 area (Olofsson et al., 2012), and similar relationships between changes

in reindeer abundance and NDVI on reindeer summer pastures have also been observed (Campeau et al., 2019; Newton et al., 2014). Approaches employing remote sensing products other than NDVI have found changes in albedo and the energy balance (Cohen et al., 2013) and land cover transformation (Rees et al., 2003) as a result of reindeer herbivory, but these observations are also at the coarse resolution of satellite images and unable to evaluate landscape-scale heterogeneity.

Unmanned aerial vehicles (UAVs) provide the opportunity to map the impacts of herbivory at a resolution comparable to the scale at which these ecological changes occur. UAVs can capture centimetre-resolution imagery, which has been used successfully to distinguish plant functional groups and predict plant chemistry based on spectral reflectance values in the Arctic (Thomson et al., 2021). This spatial grain is necessary to evaluate how the impact of herbivory within a landscape might vary depending on animal density, topography, habitat type, vegetation productivity, and other ecosystem variables that are likely spatially variable within satellite pixels (Assmann et al., 2020; Siewert & Olofsson, 2020). Using an approach with repeated UAV flights, one study, leveraging a strong correspondence observed between NDVI decreases and ground truth field inventory counts of rodent impacts, found that these impacts varied between four different sites and between habitat types within each site, mediated largely by snow conditions (Siewert & Olofsson, 2021). Very high resolution imagery can also be used to quantify plant and community level responses and further explore their context dependencies, such as a recent finding that higher reindeer densities were linked to decreased plant species richness in low-productive sites and increased species richness in more productive sites (Sundqvist et al., 2019).

In addition to observations based on spectral reflectance measurements, remote sensing also provides the capability to measure three-dimensional plant structure. Light detection and ranging (LiDAR) is an active remote sensing technology that has been widely used to quantify vegetation structure and biomass (e.g., Goetz & Dubayah, 2011; Greaves et al., 2015), but the high cost of LiDAR sensors can be a barrier and limit the temporal and spatial scales at which this technology is deployed (Cunliffe et al., 2016). As an alternative, structure-from-motion (SfM) can generate comparable 3D models using imagery captured with consumer-grade cameras by applying photogrammetry techniques to overlapping images capturing objects from many angles (Dandois & Ellis, 2013). Compared to the point clouds generated by LiDAR, which can include sub-canopy vegetation or terrain beneath dense canopy cover, SfM can only

characterise the outer canopy surface, and the point clouds can have large uncertainties and processing artefacts depending on the survey quality (Alonzo et al., 2020; James, Robson, d'Oleire-Oltmanns, et al., 2017). Yet, with very high resolution imagery and high overlap, SfM point clouds can be 10x as dense as LiDAR point clouds, and SfM is well-suited to the open cover in most Arctic environments, where there is limited need for canopy penetration (Alonzo et al., 2020; Fraser et al., 2016). Studies in the Arctic have shown very high accuracy when comparing shrub vegetation heights derived from SfM point clouds against ground measurements (Fraser et al., 2016), and the accuracy of SfM-modelled biomass was found to be equivalent to LiDAR models, even in the highest biomass areas (Alonzo et al., 2020), and higher than NDVI-based models (Cunliffe et al., 2020).

Conducting repeated SfM-based surveys is thus a promising approach for measuring precise changes in tundra vegetation height and biomass over time. SfM surveys before and after an herbivory event can reveal where vegetation change occurred within a landscape and the magnitude of the change. However, simply subtracting digital surface models (DSMs) derived from the point clouds yields a noisy change product due to small differences between the DSMs caused by both physical differences, such as branch and leaf movements in the wind, and differences in the photogrammetric reconstructions, including registration errors between the point clouds and uncertainties inherent in photo-based surveys (Fraser et al., 2016; James, Robson, & Smith, 2017). Using this approach together with a shrub cutting experiment, Fraser et al. (2016) found that the change product accurately captured the extent of the cutting, but there was a nonsignificant relationship between the change in the DSMs and the amount trimmed. Furthermore, differences were detected outside the area of shrub cutting that were likely just noise.

To identify only robust change between SfM surveys, James, Robson & Smith (2017) developed a method for topographic change detection that accounts for the spatially variable precision within SfM reconstructions and computes a variable 'level (or limit) of detection' (LoD) over space. Their LoD calculation incorporates 3D photogrammetric and georeferencing uncertainty, such that changes of a smaller magnitude than the value of the LoD at a given location are deemed not to satisfy the specified confidence level and can be discarded. Although the intricate structure of vegetation makes robust change detection of canopy height more challenging than in the geomorphological applications for which this approach was developed, here we have followed a workflow developed by Graham et al. (2021) and adapted

from the methodology of James, Robson & Smith (2017) to quantify vegetation change in an Arctic landscape after a reindeer herbivory event.

Our study included UAV surveys repeated three times in summer 2021 over an area in the Yamal Peninsula, West Siberia immediately before the arrival of a reindeer herd, soon after they had left the site and migrated onwards, and again one month after the herbivory event. We coordinated the timing of our surveys and the location of the study area with the Indigenous Nenets herders managing the reindeer, 13 of which had been fitted with GPS collars. Using our SfM workflow, we quantified centimetre-resolution changes in canopy height across the landscape while assessing how this change varied with spatial differences in reindeer activity, habitat type, and initial canopy height, as well as the interactions between these variables. Our analysis examined the factors contributing to spatial heterogeneity in the response of vegetation to reindeer herbivory both in the immediate aftermath of the herbivory event and later within the same growing season.

5.5 Material and methods

5.5.1 Study area

We conducted our study near the Erkuta Tundra Monitoring Site in the southern part of the Yamal Peninsula, West Siberia, Russia (68.3° N, 69.0° E, **Figure 5.1**). The vegetation cover in the area is mostly characterised as erect dwarf shrub tundra and low shrub tundra, and although the topography is generally flat, landforms such as slopes and ridges influence the vegetation height and community composition (Walker et al., 2005). Tall thickets of willow (*Salix* spp.) and sometimes alder (*Alnus fruticosa*) reaching more than 2 m height grow in concavities and along rivers and lakes, which form a dense network subdividing the land (Ehrich et al., 2012; Hofhuis et al., 2021; V. Sokolov et al., 2012; Sokolova et al., 2014). The area is underlain by continuous permafrost (Walker et al., 2009). The mean annual precipitation is 488 mm, and mean daily maximum temperature ranges from -19.7°C in January to 16.0°C in July (2000-2019 averages, CHELSA v2.1; Karger et al. 2017, 2018).

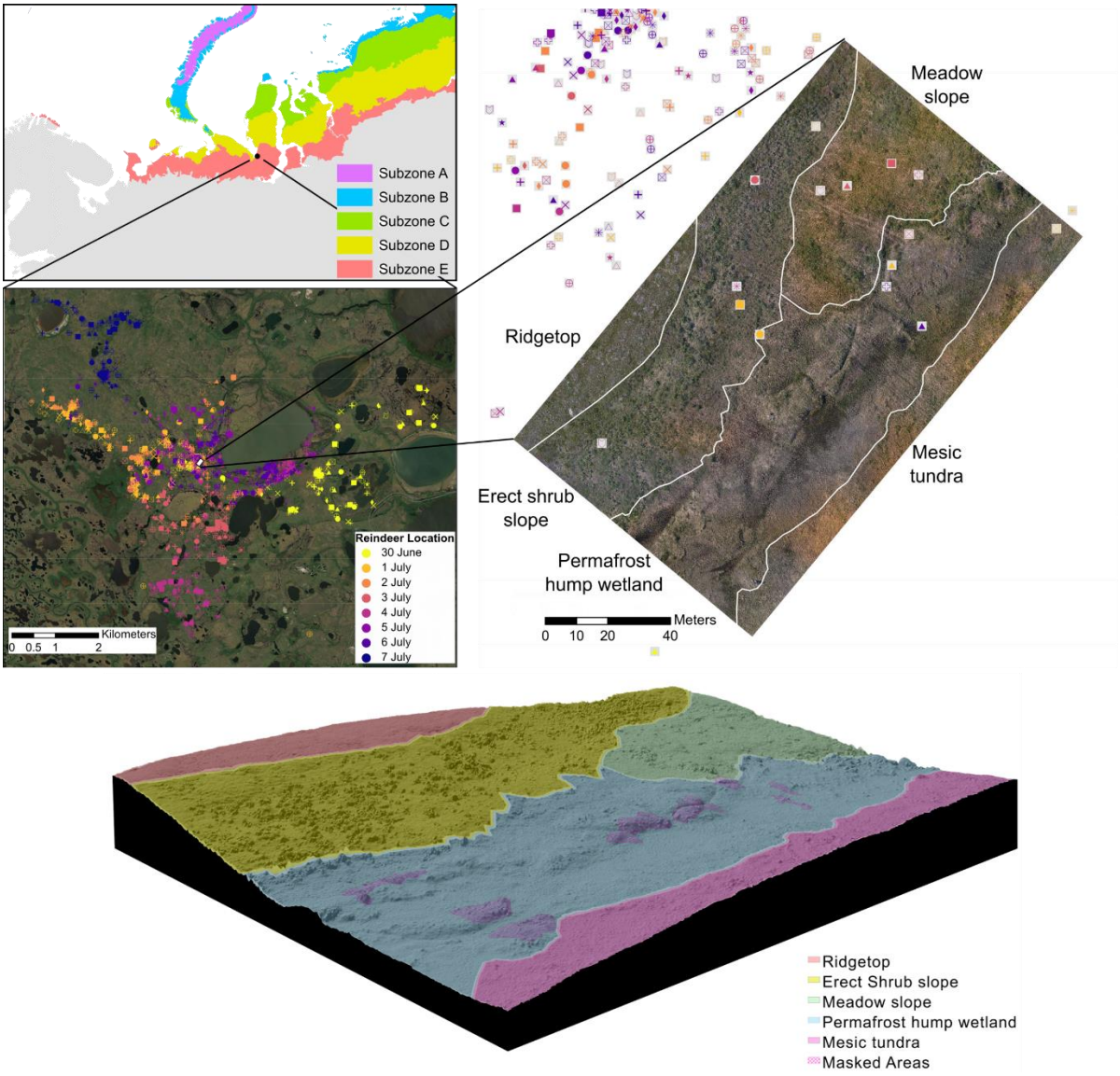


Figure 5.1: The location of the study site within the Yamal Peninsula and the reindeer GPS collar locations showing animal movements around the site from 30 June-7 July. The colour of the GPS points represents the date whereas a unique shape denotes each of the 13 collared reindeer. Polygons delineate broad habitat classes (see **Table S5.2** for descriptions) overlaid on the 30 June orthomosaic. The 3D panel shows a representation of the land surface based on the 30 June DSM and includes hatched polygons showing the areas within the permafrost hump wetland that were masked from the canopy height model. The imagery base map is from Esri and Earthstar Geographics, and the bioclimatic subzones are from the Circumpolar Arctic Vegetation map (Walker et al., 2005).

In Yamal, Indigenous Nenets herders manage the world's largest domesticated reindeer herds (~225,000 animals in total) while migrating up to 1,200 km annually (Forbes et al., 2009; Stammler, 2005; Terekhina & Volkovitskiy, 2020). The Nenets herding tradition belongs to the so-called Samoyedic type, which is common in the tundra zone of Europe and West Siberia and practised by several other ethnic groups including the Khanty and Komi-Izhma (Habeck, 2007; Istomin & Dwyer, 2021; Jernsletten & Klokov, 2002). Within the Samoyedic type,

reindeer herds are large with up to several thousand animals, and herders maintain constant control over their herds. The Nenets on the southern Yamal tundra migrate every 3-5 days on average throughout the summer, which enables the rotation of seasonal pastures. While a household stays in place between movements, the herders guide the reindeer to different areas around the camp on different days (**Figure 5.1**), but the use of the landscape within these areas is determined by the reindeer and influenced by the forage quality and landscape structure (e.g., wind-exposed areas on ridges provide insect relief) (Skarin et al., 2020).

In the area of our study site, reindeer herds are present in all seasons (A. A. Sokolov et al., 2016). Some herds come to the area during the summer, often along long-distance migrations, whereas others are based there in the snow season. Other herbivores in the area include lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*), voles (*Lasiopodomys gregalis, Alexandromy middendorffii, Myodes rutilus, Arvicola amphibius*), willow ptarmigan (*Lagopus lagopus*), mountain hare (*Lepus timidus*), and muskrat (*Ondatra zibethicus*) (Ehrich et al., 2012; Hofhuis et al., 2021; Sokolova et al., 2014). We chose our specific ~1.7 ha site where we conducted our UAV surveys to be adjacent to a planned campsite of a large reindeer herd passing through the area. Our team has built a relationship with the herders over the past years, and we discussed their planned movements with them while designing our study. To the best of our knowledge, no other reindeer passed through the site within the period of our study, although we identified grazing marks during our initial visit indicating that some herbivory had occurred earlier in the growing season. Additionally, multiple vehicles drove through after the herd had migrated onwards to collect velvet antlers from the reindeer. The site includes a range of habitat types within a landscape that progresses from a ridgetop with bare ground and a mixture of very low stature prostrate shrubs and graminoids, down a slope with meadow vegetation and erect dwarf birch and willow shrubs, to a sedge wetland interspersed with permafrost humps, and finally mesic tundra with dwarf shrubs, sedges, and a thick moss layer (**Figure 5.1**). The elevation of the study site varies from 8-17 m.a.s.l.

5.5.2 UAV surveys

In summer 2021, we conducted UAV surveys on three dates: 30 June, before the herd migrated to the site; 7 July, just after the herd had migrated onwards; and 5 August, approximately one month after the herd had been there (**Table 5.1**). We used a DJI Phantom 4 (DJI, Shenzhen, China), a consumer-grade quadcopter with a 12.4 Megapixel RGB camera. An automated flight mission was planned using the DJI Ground Station Pro app, and the same mission was flown

each time. The mission was repeated twice on each date, first to obtain nadir imagery and then with the camera angle 20° off nadir, following the protocol of Cunliffe et al. (2020). The UAV flew at a nominal 25 m AGL with 75% image overlap, such that at least 10 overlapping images captured every part of the study site, including the edges, and the ground resolution was ~1 cm. To ensure the sharpness of the images, the "Capture Mode" was set to hover and capture at each waypoint.

We also set out 60 cm x 60 cm ground control markers, which were visible from the air and used to constrain the photogrammetric modelling. The markers were geolocated to centimetre-level precision using an RTK-GNSS survey instrument (Emlid Reach+, Emlid, Hong Kong). Five markers (one in each corner and one in the centre) were used on 30 June and four markers (one in each corner) on 7 July. Due to equipment malfunction, we were not able to geolocate ground control markers on 5 August, but instead, we found four clear features (large rocks, logs) within the photographs that had not moved over the duration of the study and used them as markers with their precise position taken from the photogrammetric models of the earlier surveys.

Table 5.1: Description of drone surveys and their photogrammetric models. Each survey included a flight obtaining nadir imagery and a second flight obtaining oblique (20° from nadir) imagery. The flights all followed the same mission plan with prescribed waypoints, but differences in the launch point affected the true flying altitude, leading to slight variation in resolution. The automatic camera triggering during the mission skipped a waypoint or took an extra photograph in rare instances, causing small differences in the number of images captured.

Date	Local time (UTC+5)	No. of images	Ground resolution [cm/pixel]	Point density [points/cm²]	No. of dense cloud points	Reprojection error [pixels]
30 June 2021	16:49	365	0.939	1.13	350,365,588	0.278
7 July 2021	12:39	362	1.06	0.896	284,981,730	0.295
5 August 2021	14:24	363	1.09	0.849	280,955,358	0.283

5.5.3 Imagery processing

The UAV images were initially processed in Agisoft Metashape Professional (v1.7.1) using an SfM workflow following the recommendations of Over et al. (2021). For each date, all images from both the nadir and oblique flights were imported into Metashape and converted into the WGS 84 UTM zone 42N (EPSG:32642) coordinate reference system. Photos were aligned using the highest quality setting, a key point limit of 60,000, and unlimited tie points. For each survey, the alignment produced a sparse point cloud consisting of at least 1.3 million tie points representing points found in common between multiple images.

Ground control markers were added as control points to supply georeferencing information and constrain the subsequent error reduction phase of the workflow. The error reduction involves iteratively deleting low-quality tie points from the sparse point cloud and optimising the camera model, commonly known in photogrammetry as a "bundle adjustment" (Over et al., 2021). The optimisation process is sensitive to three settings used to weigh the influence of the tie points and control points: marker location accuracy, marker projection accuracy, and tie point accuracy (James, Robson, d'Oleire-Oltmanns, et al., 2017). Marker location accuracy was set to 0.02 m to account for the uncertainty in the GNSS measurements, and marker projection accuracy and tie point accuracy were initially left at the default values of 0.5 pixels and 1 pixel, respectively. Points were removed based on their reconstruction uncertainty, projection accuracy, and reprojection error, and optimisation after each removal used the following lens parameters: focal length (f), principal point (cx,cy), radial distortion (k1, k2, k3), and tangential distortion (p1, p2). For each survey, after the last point removal iteration, the standard error of unit weight (SEUW) for bundle adjustment had deviated from unity, an indication of inconsistency between the error in the results and initial estimates of precision (James et al., 2020). To resolve this issue, the tie point accuracy was changed to 0.18 pixels, resulting in near-unity SEUW in each case. After completing this process, the unweighted root mean square reprojection error, a measure of tie point quality, for all surveys was below 0.3 pixels (Table 1), which is considered ideal (Over et al., 2021).

The final optimised model contained precise estimates of the position of the camera during each image capture and the camera lens parameters. Depth maps were generated for all camera positions and a dense point cloud containing hundreds of millions of points representing all sharp features identified within each individual image was produced using the ultra high quality setting and mild depth filtering. The dense point clouds were edited by hand to remove

unrealistically high and low points displaced from the land surface, termed “flyers” and “sinkers”, and exported in the .laz format.

5.5.4 Robust change maps

The approach used to identify significant changes in canopy height between the survey dates was based on the methodology developed by James, Robson & Smith (2017) for detecting topographic change and the raster-based adaptation for detecting vegetation change created by Graham et al. (2021) in the *sfm_gridz* package of the *SFM_Precision* repository. The procedure allows for the propagation of uncertainty in the SfM model, quantified by estimates of the precision in the tie points in the sparse point cloud, and rasterisation uncertainty, based on surface roughness.

Although the digital surface models (DSMs) used in the change calculations (i.e., the subtraction of DSMs produced after and before a given event) are based on the dense point clouds, the dense matching process does not alter the optimised image network, so the precision of the surface model is mainly derived from the tie point precision (James, Robson, & Smith, 2017). Both James, Robson & Smith (2017) and Graham et al. (2021) used a Monte Carlo procedure to obtain the precision estimates, but more recent versions of Metashape enable precision estimates to be calculated directly from the bundle adjustment within the software (James et al., 2020). When rasterising the dense point clouds into DSMs and the sparse point cloud precision estimates into precision rasters, pixel resolution was chosen to be fine enough to retain the detailed spatial variation captured by the points, but not so fine that the rasters would be noisy and require extensive gap filling. This resulted in the rasterisation of the DSMs at 5 cm pixel resolution, compared to the ~1 cm ground resolution of the surveys, using the mean point height within each pixel. The standard deviation of point heights within each pixel was taken as the DSM roughness. The precision rasters were calculated at 10 cm resolution, and gaps were filled by the maximum (worst) precision estimate within each point cloud, providing a conservative estimate of the uncertainty in the photogrammetric reconstruction in these areas (**Figure S5.1**). Each 10 cm pixel within a precision raster covered four 5 cm pixels within the associated DSM to quantify the uncertainty at that location within the reconstruction rather than one value characterising the overall reconstruction uncertainty.

The spatially variable limit of detection (LoD) for significant changes between two repeated surveys was calculated at 5 cm resolution as:

$$LoD = t\sqrt{{R_1}^2 + {P_1}^2 + {R_2}^2 + {P_2}^2 + reg^2} \quad (1)$$

where t is an appropriate scalar value for the required confidence level, R_1 and R_2 are the DSM roughness rasters, P_1 and P_2 are the precision rasters, and reg is the overall registration error between surveys (**Figure S5.2**). Based on the t distribution, we chose t=1.96 to represent a 95% confidence level, and *reg* was taken as 0, as all surveys were defined from the same datum and georeferencing uncertainty is included within P_1 and P_2 (James, Robson, & Smith, 2017). The robust canopy height change maps were produced by subtracting the DSMs, but only retaining differences exceeding the LoD at the location of the change.

5.5.5 Habitat delineation

We divided the study site into broad habitat classifications based on habitat descriptions while in the field and visual inspection of the orthomosaics and DSMs (**Figure 5.1**, 3D panel). At 10 locations chosen across the study site to cover a variety of vegetation communities, we described the habitat type and noted the dominant species or plant groups using groups similar to the plant functional types defined by Bråthen et al. (2007) (**Figure S5.3**, **Table S5.1**). Six of the locations were described on 30 June and four on 7 July, and each was geolocated precisely using the GNSS. We compared our field observations with the UAV-derived products and delineated five broad habitats characterised by their landscape position and vegetation: ridgetop, erect shrub slope, meadow slope, permafrost hump wetland, and mesic tundra (**Figure 5.1**, see **Table S5.2** for descriptions). These habitat classifications were used to identify where canopy change was occurring in the landscape and to evaluate the spatial heterogeneity in plant responses within similar vegetation communities.

5.5.6 Canopy height modelling

To compute vegetation canopy height, we took the difference between the elevation values within the DSM from each survey date and a digital terrain model (DTM) that we generated from the dense point cloud from the 7 July survey. This survey was chosen as the basis for the DTM because on this date, we also walked transects across the study site with the GNSS, recording terrain points approximately every 10 m to give a total of 162 points for validation of the DTM (**Figure S5.4**). We derived the DTM using the cloth simulation filtering (CSF) algorithm implemented in the LidR package in R (Roussel et al., 2020; Roussel & Auty, 2021),

which turns the original point cloud upside down and then drapes a cloth over the inverted surface from above to distinguish which points belong to the terrain (Zhang et al., 2016). The algorithm relies on the choice of three parameters that govern how the cloth interacts with the point cloud: "class_threshold," "cloth_resolution," and "rigidness." To choose these parameters, we first coarsely tuned the values while visually assessing the resulting DTM, and then fine-tuned the values while calculating the root-mean-square error (RMSE) and mean error using the GNSS points for validation. We found a tradeoff between minimising these two errors, indicating that a model that fit the points better (lower RMSE) would have higher bias (i.e., mean error was always positive, so higher values implied that the DTM tended to be further above the true terrain). We selected a Pareto-optimal combination of parameters (class_threshold=0.01 [m], cloth_resolution=0.45 [m], rigidness=3) that produced a reasonable DTM upon visual inspection with an RMSE of 11 cm and mean error of 2.5 cm (**Figure S5.4**). The canopy height models (CHM) were computed as the difference between the DSM for each survey and this DTM, but we found that some permafrost humps, rather than the vegetation on them, were characterised as part of the canopy due to their anomalous geomorphology within the landscape. For analyses incorporating the CHMs, we masked out these areas to avoid introducing any error (**Figures 5.1, S5.4**); in any case, they include very little area with robust change (0.15 m^2 after herbivory, 2.8 m^2 one month later).

5.5.7 GPS collars

We estimate that there were roughly 1,000 reindeer in the herd passing through our study site over the course of six days. Thirteen of these animals had been fitted with Lotek Litetrack Iridium 420 GPS collars (Lotek Wireless Inc., Newmarket, ON, Canada), which recorded their positions every 1.5 hours from 30 June to 7 July 2021. The collar weighs 400-450 g depending on the length of the strap, making up less than 1% of animal body weight. The accuracy of each fix was assessed using the dilution of precision (DOP). DOP is an indicator of the quality of a GPS position and is based on the number of satellites used, each satellite's location relative to the other satellites in the constellation, and their geometry in relation to the GPS receiver. All GPS fixes we received had DOP values lower than 7, implying an accuracy of 4-14 m (Jung et al., 2018). The GPS data show that the herd moved to their campsite adjacent to our study site on 30 June in the late evening after we had visited the site, remained there until 6 July, and by 7 July, had moved onto their next campsite (**Figure 5.1**).

To quantify the spatial variation in the reindeer activity across the study site, we calculated the integrated proximity of each pixel *i* showing significant canopy height change to the *n*=212 reindeer collar points within 100 m of the study site as:

$$Integrated\ proximity_i = \sum_{j=1}^{n} \frac{1}{(Euclidean\ distance)_{ij}} \quad (2)$$

We also computed how the integrated proximity to reindeer varies over the whole study site (**Figure S5.5**) to enable comparison between the distribution in this metric within the change pixels and the wider distribution.

5.6 Results

5.6.1 Maps of significant canopy height change

Significant canopy height changes (i.e., differences exceeding the LoD) occurred only within specific areas of the site, while large swathes showed no significant change (**Figure 5.2**). Comparing the observations immediately before and after the herd was present on the site, the total area of significant change was 66.6 m^2 (0.403% of the study site), of which 60.8 m^2 showed height decreases. One month later, canopy height had changed significantly across 489 m^2 (2.96% of the study site), of which 462 m^2 increased in height since immediately after the herd had left. Assessed visually, the most concentrated changes observed immediately after the reindeer herbivory event were significant decreases in the height of both erect shrubs and low-lying graminoids and forbs in the habitats on the sloped area, primarily towards the northeast and closer to the campsite. The height decreases detected on the erect shrubs were often only around their lateral extents, appearing doughnut-shaped in the change map (**Figure 5.2**). Large stretches of vegetation, mostly sedges, within the wet topographic lows showed significant increases in height one month later, but there was also significant growth in the same sloped area where decreases were observed immediately after the herd had left, primarily where there was low-lying vegetation around the erect shrubs (i.e., not in the same pixels where a height loss was detected immediately after the herbivory event).

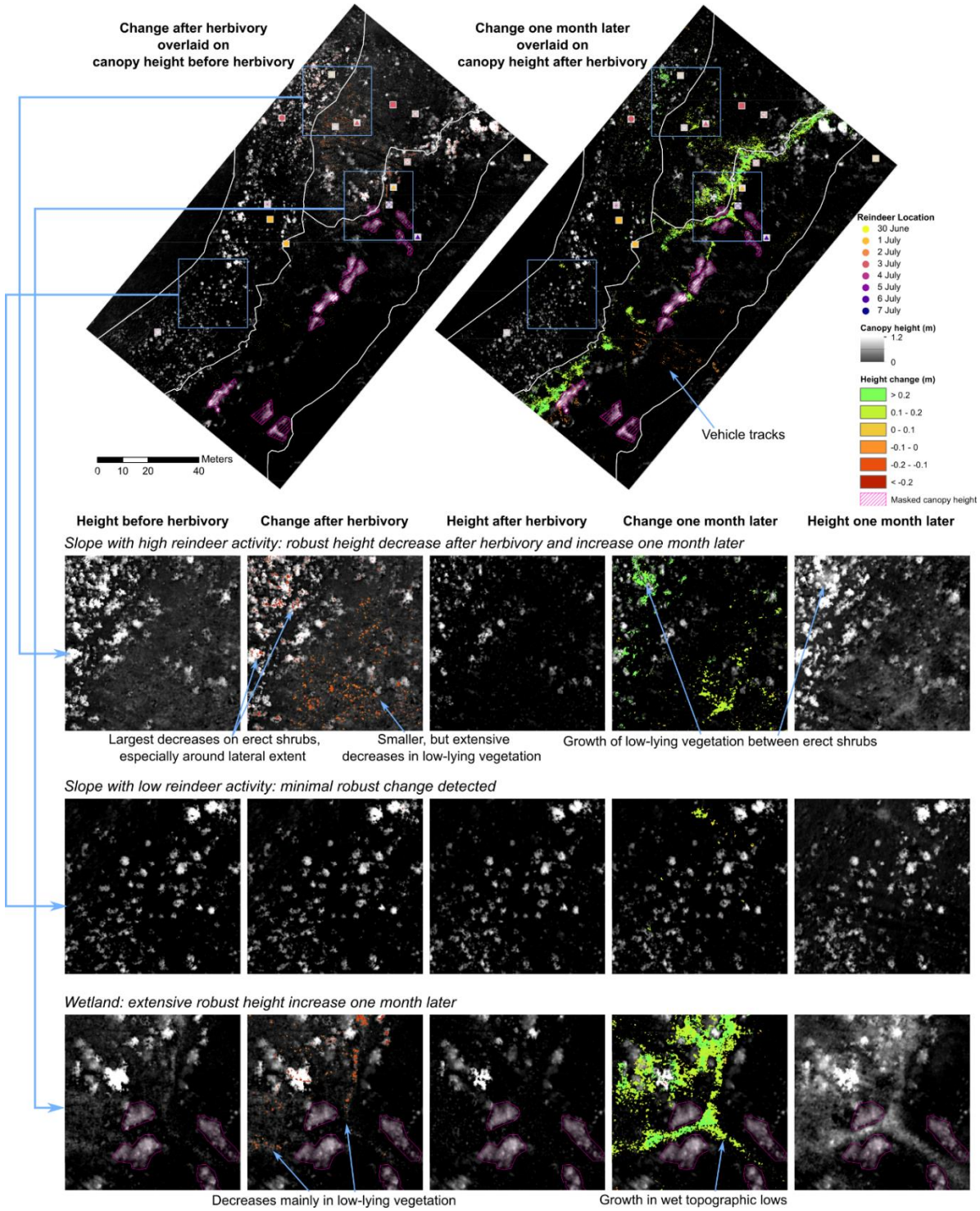


Figure 5.2: Maps showing the significant changes in canopy height detected immediately after the herd had left the site and one month later. The changes are overlaid on the canopy height model from the UAV survey preceding the change. Reindeer collar GPS points within the study site are displayed with the colour representing the date between 30 June and 7 July and the shape denoting different animals. Hatched polygons show areas that were masked out in analyses involving canopy height due to mischaracterisation of permafrost humps as part of the vegetation canopy. Vehicle tracks that were identified as significant decreases in canopy height one month later are indicated in the full map of change one month later. Three areas within the site are enlarged and annotated for more detailed comparison of the products from the UAV surveys at these locations.

5.6.2 Comparison between habitat types

The significant canopy change was distributed unevenly between habitat types (**Figure 5.3**). The meadow slope had the most area (29.3 m^2, 1.1% of habitat area) where canopy height decreased after the herbivory event, but the average magnitude of that change was only 14.0 ± 9.1 cm (± SD). Significant decreases also occurred over a substantial area on the erect shrub slope and permafrost hump wetland, 15.5 m^2 (0.34% of habitat) and 15.7 m^2 (0.25% of habitat), respectively, with the largest average decrease of 32.7 ± 10.7 cm on the erect shrub slope. Only the permafrost hump wetland had more than 1 m^2 significantly increase in height, showing an average increase of 8.19 ± 2.4 cm over 5.57 m^2 (0.089% of habitat).

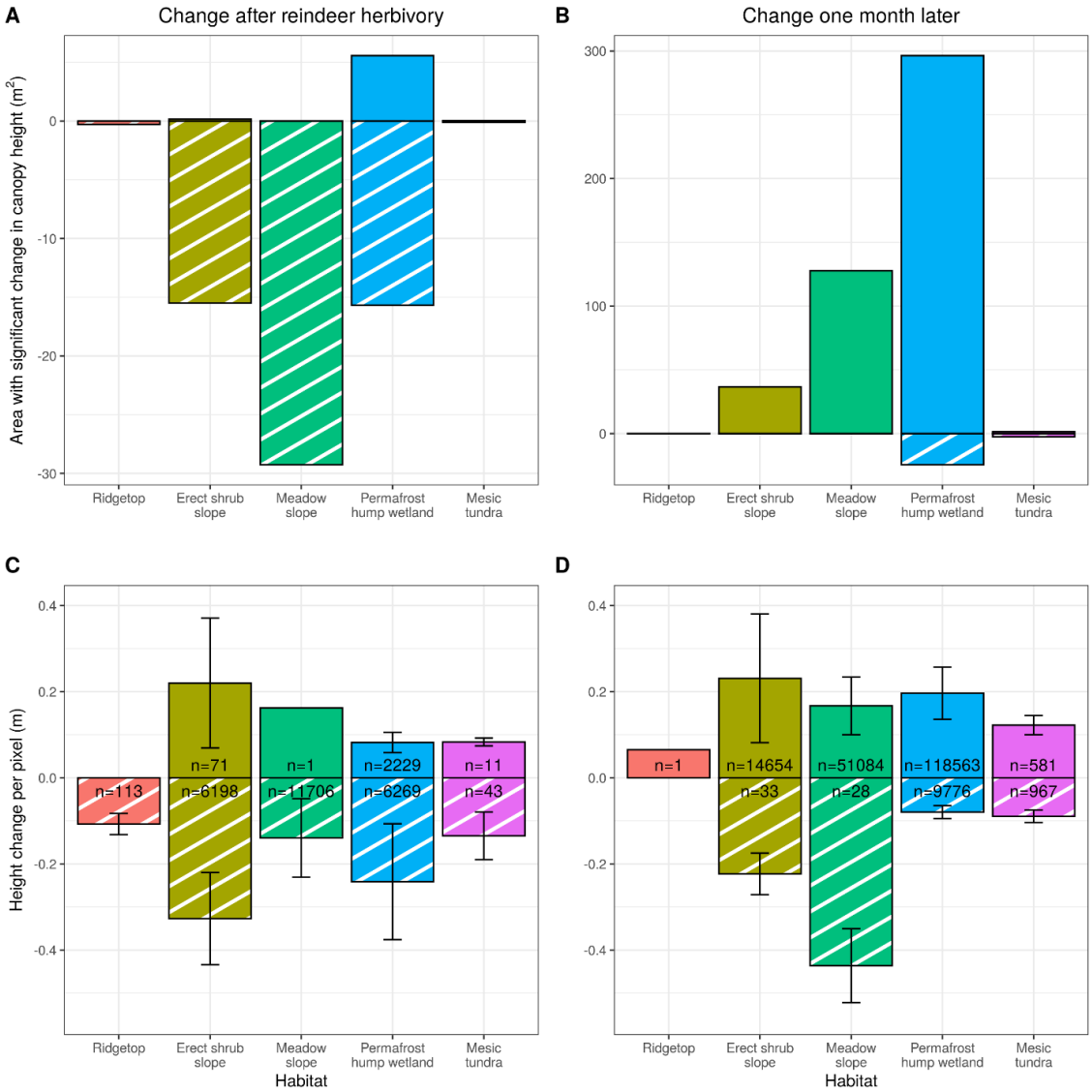


Figure 5.3: Area of significant change (**A,B**) and mean height change per pixel with significant change **(C,D)** within different habitat types. Change is separated into height increases (solid) and decreases (white stripes). Error bars represent ± standard deviation, and the number of change pixels is given within the bars.

One month later, the majority of significant increase, 296 m^2 (4.8% of habitat), was on the permafrost wetland, followed by 128 m^2 (4.7% of habitat) on the meadow slope and 36.6 m^2 (0.80% of habitat) on the erect shrub slope (**Figure 5.3B**). The average magnitude of the growth was similar in each of these three habitat types, 23.1 ± 14.9 cm, 16.7 ± 6.7 cm, and 19.6 ± 6.1 cm on the erect shrub slope, meadow slope, and permafrost hump wetland, respectively. Significant decreases were primarily detected on the permafrost hump wetland and mesic tundra, both with an average magnitude less than 10 cm. These decreases were mostly in the tracks of the vehicles that drove through the study site to collect reindeer antlers (**Figure 5.2**).

5.6.3 Distribution of canopy heights where significant change occurred

The distribution of initial canopy heights varied between habitat types (**Figure 5.4**). Within the erect shrub slope, the median canopy height of all pixels with positive (non-zero) canopy heights before the herd arrived was 4.02 ± 9.23 cm, whereas the median initial canopy height in the meadow slope and permafrost hump wetland was 5.27 ± 6.29 cm and 2.31 ± 11.0 cm, respectively (**Figure 5.4A**). There was also variation between the habitat types in how the initial canopy heights in the areas where significant decreases were detected compared with the overall distribution within each habitat type. In essence, on the erect shrub slope, significant height decreases detected after the herbivory event occurred predominantly in the taller vegetation within the habitat type, whereas the height decreases were spread more evenly over the range of canopy heights within the other habitat types. Within the erect shrub slope, the median initial canopy height in the pixels with a significant decrease was 33.2 ± 12.3 cm, compared to 10.2 ± 10.3 cm in the meadow slope and 24.4 ± 20.3 cm in the permafrost hump wetland (**Figure 5.4C**). Of the significant decreases immediately after herbivory in vegetation initially shorter than 20 cm, 72.8% occurred within the meadow slope. Conversely, 50.6% of the decreases in vegetation taller than 20 cm were in the erect shrub slope.

After the herd had left, the distribution of canopy heights had shifted toward lower heights (**Figure 5.4B**). Across all habitat types, the pixels showing a significant increase one month later were predominantly in low-lying vegetation. Over 52% of these pixels had an initial canopy height of 0, indicating that their elevation was taken as the level of the terrain in the generation of the DTM. The tendency for the significant height increases to be disproportionately within the low stature vegetation was most pronounced, again, in the erect shrub slope. Although the erect shrub slope had the highest percentage of its area, 7.26%, covered by vegetation with a canopy height greater than 10 cm, only 2.39% of its area that

showed significant increases in height one month later were in vegetation taller than 10 cm (**Figure 5.4D**). In contrast, 5.08% of the meadow slope had a canopy height above 10 cm, and nearly that percentage, 3.90%, of the area that increased significantly in height in the meadow slope had an initial height above 10 cm. Thus, whereas significant decreases in the erect shrub slope immediately after the herbivory event tended to occur in the taller vegetation, one month later, significant height increases occurred predominantly where the vegetation had been shorter initially.

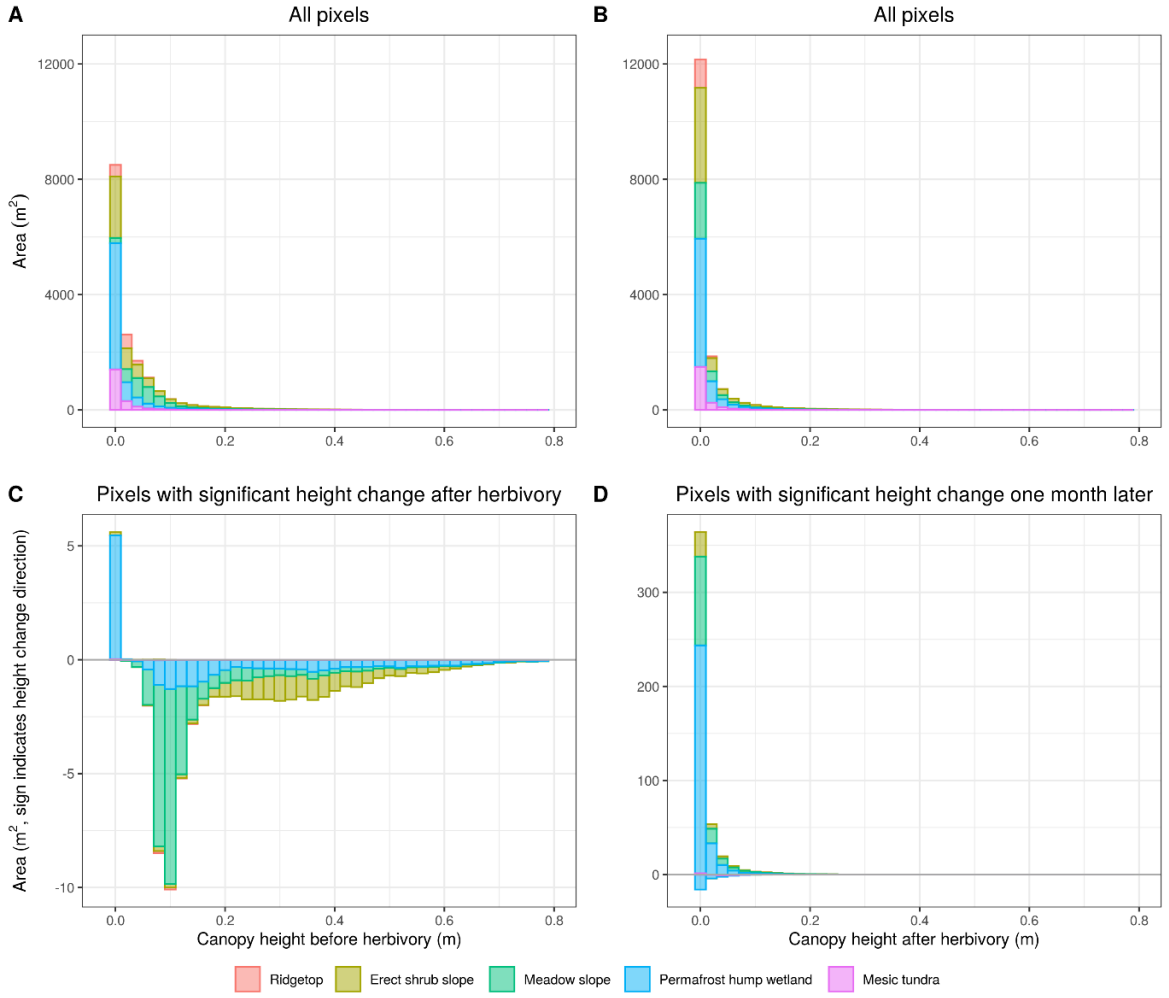


Figure 5.4: Comparison between the distribution of initial canopy height in pixels with significant canopy height change and the full distribution of canopy height within each habitat type. All pixels in the study site are categorised by habitat type and binned by canopy height before the herbivory event in **A** and after the herd had left in **B**. The subset of pixels in **A** with significant canopy height change detected after herbivory are shown in **C**, and the subset of pixels in **B** with significant change one month later are shown in **D**. The sign of the bars in **C** and **D** divides the area with significant increase in canopy height from the area with significant decrease.

5.6.4 Influence of reindeer activity within habitat types

The significant height changes varied in the strength of their association with the activity of the reindeer herd. After the herbivory event, the height decreases that were detected in the erect shrub slope were especially concentrated where the integrated proximity to reindeer was higher, typically above 3 m^{-1} (**Figure 5.5B**), even though much of the erect shrub slope had lower reindeer activity (**Figure 5.5A**, integrated proximity around 2 m^{-1}). Significant decreases also tended to occur where there was higher reindeer activity within the meadow slope and, to some extent, within the permafrost hump wetland.

The influence of the reindeer herd was less clear in the significant growth observed one month later. Here, the changes in the permafrost hump wetland and the meadow slope did not seem to be predominantly in the areas with higher reindeer activity, as the distributions of integrated proximity for the change pixels (**Figure 5.5C**) resembled the full distributions over the habitat types (**Figure 5.5A**). Although there were fewer pixels showing significant increases in the erect shrub slope, these were concentrated again in areas with higher integrated proximity. Where reindeer activity was higher with integrated proximity above 3 m^{-1} in the erect shrub slope, the median height increase was 23.4 cm, but a substantial proportion of the detected growth, 35.3%, was less than 10 cm. Given that the LoD was typically higher than 10 cm for the erect shrubs (**Figure S5.2**), this small magnitude growth likely represents the fine-scale detection of increases where there was low-lying vegetation.

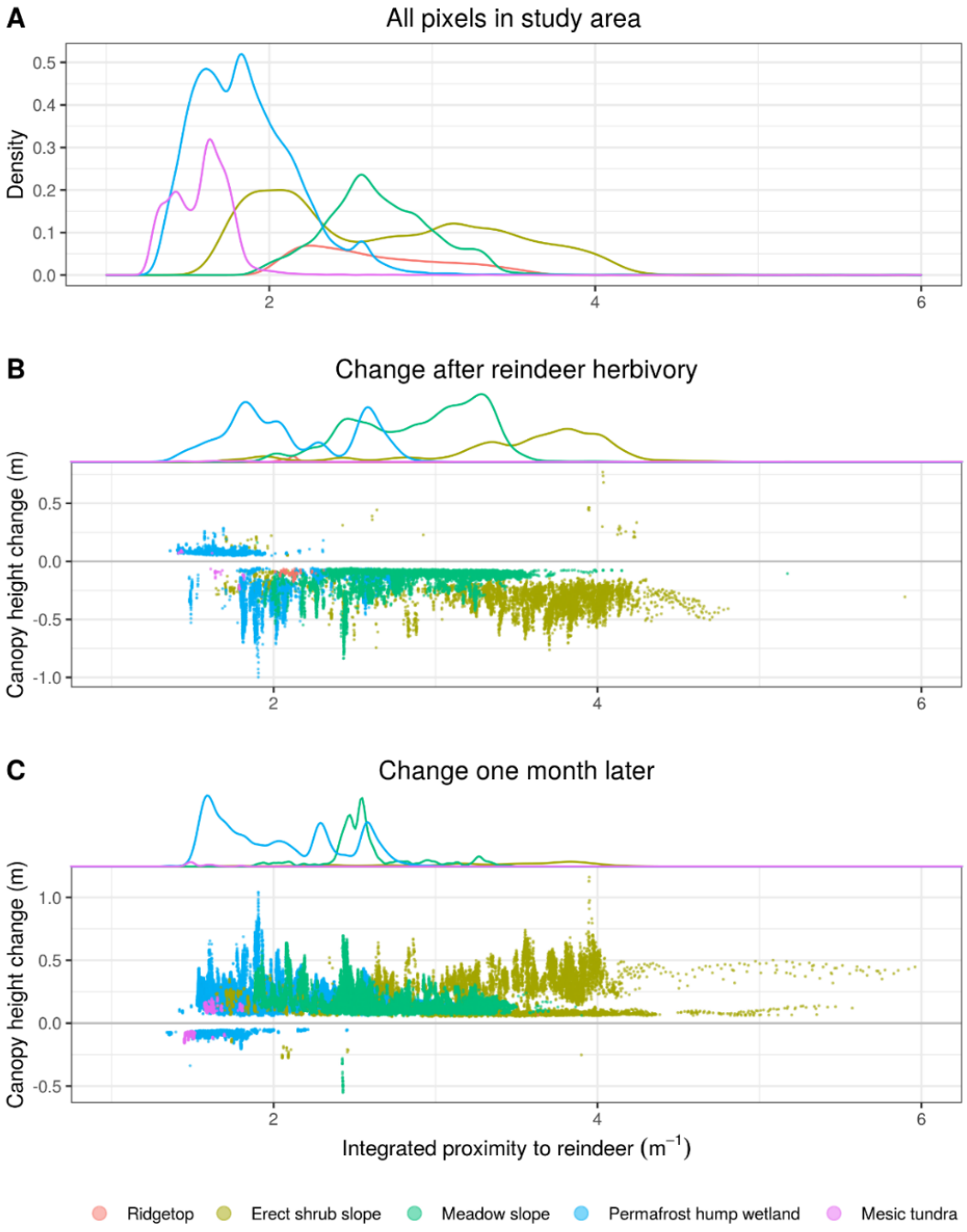


Figure 5.5: Variation in canopy height change within habitat types depending on the level of reindeer herbivory pressure. The density plot in **A** depicts the distribution of values for each habitat type over the whole study site for comparison, plotted along a gradient of increasing integrated proximity to reindeer metric (closer to reindeer presence with higher x-axis values). The canopy height change for each pixel showing significant change after the herbivory event (**B**) and one month later (**C**) is plotted against integrated proximity to reindeer, and density plots above the scatterplots show how the significant change pixels are distributed within this metric. The comparison of the overall distributions in **A** against the distributions where significant changes were detected in **B** and **C** enables analysis of the tendency of detected changes in vegetation height to occur in association with higher reindeer pressure.

5.7 Discussion

We examined spatial heterogeneity in vegetation change after a reindeer herd remained in a tundra environment for a week using a novel photogrammetric approach. Although this methodology for robust change detection has been used successfully in geomorphological applications (James et al., 2020; James, Robson, & Smith, 2017), its adaptation for detecting vegetation change is new (Graham et al., 2021). Our analysis showed significant changes over a small fraction of the study site, less than 1% immediately after reindeer herbivory and less than 3% one month later. Yet, as expected, nearly all the changes in the week between the first two surveys were significant height decreases linked to reindeer activity, and then there was predominantly significant growth over the month between the second and third surveys covering the peak of the growing season. This result, combined with our visual inspection, provides confidence that all the canopy height differences we mapped were robust rather than noise resulting from the intricate nature of the vegetation or photogrammetric error (Fraser et al., 2016).

The area and magnitude of change varied substantially across the study site. Even within the same habitat type, some areas exhibited extensive change whereas others showed almost no change and were nearly indistinguishable in the DSMs of the three surveys (**Figure 5.2**). We assessed how the habitat type interacted with reindeer herbivory pressure and the initial canopy height of the vegetation in driving this spatial heterogeneity in responses. Although only 13 of the roughly 800 reindeer in the herd were collared, reindeer are a highly gregarious species, especially when domesticated, and animals within a group typically show highly synchronous behaviour (Colman et al., 2004). Therefore, the 15 collar GPS points falling within our study site (**Figure 5.1**) likely each represent considerably more herbivory pressure than just a single reindeer. These points were recorded from seven different reindeer on four different dates from 1 July to 6 July, indicating that there was likely substantial pressure from the herd throughout the period between our first two surveys. Accordingly, on our second visit we saw clear signs of recent presence of a considerable number of reindeer in the form of fresh faeces, hoofprints in humid places, trampled vegetation, and shed hair.

The significant decreases in canopy height after the herbivory event were found in the erect shrub slope, meadow slope, and permafrost hump wetland. Within each of these habitat types, the change predominantly occurred in areas in closer proximity to reindeer activity (**Figure 5.5**). The greatest area of change was in the meadow slope, where the decreases in canopy

height were typically of small magnitude and affecting vegetation that was already low-lying (**Figures 5.3, 5.4**). These changes were likely the result of reindeer trampling, an important component of the impact of large herbivores that can cause shifts in vegetation community composition by damaging plants, creating gaps for seedling establishment, and altering soil properties (Egelkraut et al., 2020; Olofsson et al., 2001; Tuomi et al., 2020; van der Wal, 2006). Moreover, Nenets herders typically direct their reindeer so that grazing and browsing primarily take place not in the immediate vicinity of the campsite. Where our site was located adjacent to the campsite, trampling is expected to be the main physical impact from the reindeer's activities, such as the daily corrals (round-ups) of all reindeer to rotate draft animals.

In contrast, the significant decreases in canopy height in the erect shrub slope covered a smaller area and were primarily larger changes in initially taller vegetation (**Figures 5.3, 5.4**). These changes likely represent reindeer browsing around the edges of erect shrubs, illustrating how reindeer herbivory can prevent shrub infilling via lateral growth, one of the ways in which shrub expansion is occurring across the Arctic (Myers-Smith et al., 2011). While these shrubs are small enough, reindeer can keep them in a browse trap and limit their growth, maintaining the open state of the vegetation (Bråthen et al., 2017). This reindeer effect works towards counteracting the likely tendency for shrub expansion at our study site, as predicted especially in the low Arctic and observed elsewhere in the region (Epstein et al., 2004; Macias-Fauria et al., 2012; Myers-Smith et al., 2015), although our study cannot determine by how much.

One limitation of our raster-based approach is that it does not indicate whether the decreases in canopy height represent the vegetation initially present becoming shorter or the contraction of the crown of a plant revealing the terrain or understory below. We believe that the significant height decreases we detected include both types of changes, primarily contraction of the crown in the taller vegetation and height reduction of the low-lying vegetation itself, but regardless, they have the same implications for calculating overall changes in vegetation volume. Classifying vegetation into functional types based on point clouds and/or by incorporating additional spectral information has been achieved with high accuracy in the Arctic (e.g., Orndahl et al., 2022; Thomson et al., 2021; Yang et al., 2021) and could be incorporated into the workflow to differentiate between these changes.

This issue is also relevant to the significant height increases we detected one month after the herd had left. In the erect shrub slope, again in areas in closer proximity to reindeer activity,

there was growth, but now where there was initially low-lying vegetation. Some of the larger magnitude growth was likely from the lateral expansion of the crowns of erect shrubs, some of which may have recovered from browsing and continued to grow, as has been observed previously in deciduous shrubs following defoliation (Chapin III, 1980; Chapin III et al., 1980). Yet, a substantial portion of this growth was in the low-lying vegetation itself, which was clear because the change was of a low magnitude that would not have exceeded the higher LoD in areas where erect shrubs were present in either of the surveys compared (**Figures 5.5, S5.2**). One potential caveat is that some component of these detected height increases may not have been entirely due to vegetation growth but may instead represent physical vegetation rebound after trampling. The trampling may have also initially compressed the active layer, amplifying the rebound effect. However, our observations in the field and of the RGB imagery showed only sparse vegetation between the erect shrubs before the reindeer arrival in June and abundant graminoids during our final visit in August, indicating that substantial vegetation growth did occur in these areas where our modelling detected significant change. Notably, this growth occurred only where there was higher reindeer activity, whereas no significant change was detected in other areas of the erect shrub slope (**Figures 5.2, 5.5**), demonstrating that reindeer activity can prevent the infilling of shrubs and promote grassland vegetation, even within a single growing season. Although our study covers just one site that was directly adjacent to a campsite, it provides an evidence point supporting that reindeer are ecosystem engineers in the region, as similar densities of reindeer are present within comparable landscapes across Yamal during the growing season. Our findings also highlight that the impact of reindeer is not confined to their consumption, but that their trampling and nutrient inputs via faeces and urine can have significant effects on plant growth and community composition (Forbes et al., 2009; Olofsson et al., 2004).

Our methodology can be developed further not only to quantify changes in canopy height, but also to derive measurements of biomass change. There is a strong, linear relationship between canopy height and aboveground biomass in non-forest ecosystems that is consistent within but different between plant functional types (Cunliffe et al., 2022). Thus, converting canopy height estimates into biomass would require additionally mapping plant functional types, as described above, and ideally site-specific calibration of linear models using vegetation harvests and/or the point intercept method (Bråthen & Hagberg, 2004). This approach would also benefit from precise measurement of the terrain elevation using LiDAR to derive more reliable canopy height models (Alonzo et al., 2020). To quantify all biomass change, the LoD needs to be

minimised across the study area to maximise the fine-scale changes that can be incorporated without capturing differences due to uncertainties stemming from the SfM processing. A larger quantity of precisely located ground control points or the use of UAVs with an onboard GNSS RTK receiver would better constrain the photogrammetric modelling, and higher-resolution surveys capturing the vegetation from many angles in still conditions would enable rasterisation at finer resolution, reducing the DSM roughness (Graham et al., 2021; James et al., 2020). These improvements in survey quality would minimise the LoD, and the subsequent biomass calculations could then be used to determine, for example, the amount of biomass removed by grazing and browsing during an herbivory event.

Combining this measurement of animals' consumption with data on their movements opens the possibility for developing a more complete understanding of reindeer energetics (Trondrud et al., 2021). In this study, we used GPS collar data, which provide the opportunity to study animals' resource use, home range, and dispersal (Cagnacci et al., 2010) and has been employed to analyse, for example, reindeer summer habitat preferences and responses to built infrastructure (Skarin et al., 2008, 2018). However, limited prior work has used GPS collar data to quantify reindeer herbivory impacts over space, and the precision of the GPS locations in these studies was worse than 100 m (e.g., Campeau et al., 2019; Rickbeil et al., 2015). GPS measurements with metre-level precision, as we have used here, are necessary to assess vegetation responses to herbivory at the landscape scale and link reindeer consumption with energy expenditure.

Our findings are consistent with the widely observed tendency for reindeer herbivory to limit deciduous shrub growth and maintain or enhance grasslands (Olofsson & Post, 2018). This effect was visible within a single growing season, but only where there was high reindeer activity and evidence of reindeer browsing and trampling following the herd's departure. By mapping vegetation responses continuously over space and integrating precise measurements of both biotic and abiotic elements, we were able to differentiate between the impacts of reindeer within different habitat and vegetation types, as well as identify where changes were likely unrelated to the herbivory event and instead likely driven by water availability (**Figures 5.2, 5.5**). Whereas prior studies of top-down impacts on vegetation in the Arctic have employed remote sensing primarily to assess broader scale responses (e.g., Fauchald et al., 2017; Jefferies et al., 2006; Newton et al., 2014; Olofsson et al., 2012), our work demonstrates the value of very high-resolution, spatially continuous observations at the landscape scale for understanding

the heterogeneity that is often present but difficult to characterise in traditional plot-based studies. Our study design and processing workflows can be adapted to analyse vegetation change in a wide range of settings, including experiments such as those incorporating exclosures, but also with other drivers, such as fires, if they can be mapped precisely over space. When combined with spatially explicit measurements, fine-scale remote sensing opens the opportunity to disentangle the interacting mechanisms controlling vegetation responses across different ecosystems at ecologically relevant scales.

5.8 References

Alonzo, M., Dial, R. J., Schulz, B. K., Andersen, H.-E., Lewis-Clark, E., Cook, B. D., & Morton, D. C. (2020). Mapping tall shrub biomass in Alaska at landscape scale using structure-from-motion photogrammetry and lidar. *Remote Sensing of Environment*, *245*(May 2019), 111841. https://doi.org/10.1016/j.rse.2020.111841

Assmann, J. J., Myers-Smith, I. H., Kerby, J. T., Cunliffe, A. M., & Daskalova, G. N. (2020). Drone data reveal heterogeneity in tundra greenness and phenology not captured by satellites. *Environmental Research Letters*, *15*(12), 125002. https://doi.org/10.1088/1748-9326/abbf7d

Bernes, C., Bråthen, K. A., Forbes, B. C., Speed, J. D. M., & Moen, J. (2015). What are the impacts of reindeer/caribou (Rangifer tarandus L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, *4*(4). https://doi.org/10.1186/s13750-014-0030-3

Bråthen, K. A., & Hagberg, O. (2004). More efficient estimation of plant biomass. *Journal of Vegetation Science*, *15*(5), 653–660. https://doi.org/10.1111/j.1654-1103.2004.tb02307.x

Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Fauchald, P., Tveraa, T., & Hausner, V. H. (2007). Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems*, *10*(5), 773–789. https://doi.org/10.1007/s10021-007-9058-3

Bråthen, K. A., Ravolainen, V. T., Stien, A., Tveraa, T., & Ims, R. A. (2017). Rangifer management controls a climate-sensitive tundra state transition. *Ecological Applications*, *27*(8), 2416–2427. https://doi.org/10.1002/eap.1618

Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2157–2162. https://doi.org/10.1098/rstb.2010.0107

Campeau, A. B., Rickbeil, G. J. M., Coops, N. C., & Côté, S. D. (2019). Long-term changes in the primary productivity of migratory caribou (Rangifer tarandus) calving grounds and summer pasture on the Quebec-Labrador Peninsula (Northeastern Canada): the mixed influences of climate change and caribou herbivory. *Polar Biology*, *42*(5), 1005–1023. https://doi.org/10.1007/s00300-019-02492-6

Chapin III, F. S. (1980). Nutrient Allocation and Responses to Defoliation in Tundra Plants. *Arctic and Alpine Research*, *12*(4), 553. https://doi.org/10.2307/1550500

Chapin III, F. S., Johnson, D. A., & McKendrick, J. D. (1980). Seasonal Movement of Nutrients in Plants of Differing Growth Form in an Alaskan Tundra Ecosystem: Implications for Herbivory. *The Journal of Ecology*, *68*(1), 189. https://doi.org/10.2307/2259251

Cohen, J., Pulliainen, J., Ménard, C. B., Johansen, B., Oksanen, L., Luojus, K., & Ikonen, J. (2013). Effect of reindeer grazing on snowmelt, albedo and energy balance based on

satellite data analyses. *Remote Sensing of Environment*, *135*, 107–117. https://doi.org/10.1016/j.rse.2013.03.029

Colman, J. E., Eidesen, R., Hjermann, D., Gaup, M. A., Holand, Ø., Moe, S. R., & Reimers, E. (2004). Reindeer 24-hr within and between group synchronicity in summer versus environmental variables. *Rangifer*, *24*(1), 25–30. https://doi.org/10.7557/2.24.1.298

Cunliffe, A. M., Anderson, K., Boschetti, F., Brazier, R. E., Graham, H. A., Myers-Smith, I. H., Astor, T., Boer, M. M., Calvo, L. G., Clark, P. E., Cramer, M. D., Encinas-Lara, M. S., Escarzaga, S. M., Fernández-Guisuraga, J. M., Fisher, A. G., Gdulová, K., Gillespie, B. M., Griebel, A., Hanan, N. P., … Wojcikiewicz, R. (2022). Global application of an unoccupied aerial vehicle photogrammetry protocol for predicting aboveground biomass in non-forest ecosystems. *Remote Sensing in Ecology and Conservation*, *8*(1), 57–71. https://doi.org/10.1002/rse2.228

Cunliffe, A. M., Brazier, R. E., & Anderson, K. (2016). Ultra-fine grain landscape-scale quantification of dryland vegetation structure with drone-acquired structure-from-motion photogrammetry. *Remote Sensing of Environment*, *183*, 129–143. https://doi.org/10.1016/j.rse.2016.05.019

Cunliffe, A. M., J Assmann, J., N Daskalova, G., Kerby, J. T., & Myers-Smith, I. H. (2020). Aboveground biomass corresponds strongly with drone-derived canopy height but weakly with greenness (NDVI) in a shrub tundra landscape. *Environmental Research Letters*, *15*(12), 125004. https://doi.org/10.1088/1748-9326/aba470

Dandois, J. P., & Ellis, E. C. (2013). High spatial resolution three-dimensional mapping of vegetation spectral dynamics using computer vision. *Remote Sensing of Environment*, *136*, 259–276. https://doi.org/10.1016/j.rse.2013.04.005

Egelkraut, D., Aronsson, K.-Å., Allard, A., Åkerholm, M., Stark, S., & Olofsson, J. (2018). Multiple Feedbacks Contribute to a Centennial Legacy of Reindeer on Tundra Vegetation. *Ecosystems*, *21*(8), 1545–1563. https://doi.org/10.1007/s10021-018-0239-z

Egelkraut, D., Barthelemy, H., & Olofsson, J. (2020). Reindeer trampling promotes vegetation changes in tundra heathlands: Results from a simulation experiment. *Journal of Vegetation Science*, *31*(3), 476–486. https://doi.org/10.1111/jvs.12871

Ehrich, D., Henden, J.-A., Ims, R. A., Doronina, L. O., Killengren, S. T., Lecomte, N., Pokrovsky, I. G., Skogstad, G., Sokolov, A. A., Sokolov, V. A., & Yoccoz, N. G. (2012). The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? *Oecologia*, *168*(1), 141–151. https://doi.org/10.1007/s00442-011-2059-0

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., … Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. In *Ecology Letters* (Vol. 15, Issue 2, pp. 164–175). https://doi.org/10.1111/j.1461-0248.2011.01716.x

Epstein, H. E., Beringer, J., Gould, W. A., Lloyd, A. H., Thompson, C. D., Chapin, F. S., Michaelson, G. J., Ping, C. L., Rupp, T. S., & Walker, D. A. (2004). The nature of spatial transitions in the Arctic. *Journal of Biogeography*, *31*(12), 1917–1933. https://doi.org/10.1111/j.1365-2699.2004.01140.x

Fauchald, P., Park, T., Tømmervik, H., Myneni, R., & Hausner, V. H. (2017). Arctic greening from warming promotes declines in caribou populations. *Science Advances*, *3*(4). https://doi.org/10.1126/sciadv.1601365

Forbes, B. C., Stammler, F., Kumpula, T., Meschtyb, N., Pajunen, A., & Kaarlejärvi, E. (2009). High resilience in the Yamal-Nenets social-ecological system, West Siberian

Arctic, Russia. *Proceedings of the National Academy of Sciences*, *106*(52), 22041–22048. https://doi.org/10.1073/pnas.0908286106

Fraser, R. H., Olthof, I., Lantz, T. C., & Schmitt, C. (2016). UAV photogrammetry for mapping vegetation in the low-Arctic. *Arctic Science*, *2*(3), 79–102. https://doi.org/10.1139/as-2016-0008

Goetz, S., & Dubayah, R. (2011). Advances in remote sensing technology and implications for measuring and monitoring forest carbon stocks and change. *Carbon Management*, *2*(3), 231–244. https://doi.org/10.4155/cmt.11.18

Graham, H., Benaud, P., Cunliffe, A., Puttock, A., Anderson, K., Chant, J., Elliott, M., & Brazier, R. (2021). *exeter-creww/SFM_Precision: SfM Precision and Workflow v0.2 (v0.2)*. Zenodo. https://doi.org/10.5281/zenodo.5760603

Greaves, H. E., Vierling, L. A., Eitel, J. U. H., Boelman, N. T., Magney, T. S., Prager, C. M., & Griffin, K. L. (2015). Estimating aboveground biomass and leaf area of low-stature Arctic shrubs with terrestrial LiDAR. *Remote Sensing of Environment*, *164*, 26–35. https://doi.org/10.1016/j.rse.2015.02.023

Habeck, J. O. (2007). *What it Means to be a Herdsman: The Practice and Image of Reindeer Husbandry*. Lit Verlag.

Hofhuis, S. P., Ehrich, D., Sokolova, N. A., van Hooft, P., & Sokolov, A. A. (2021). Breeding den selection by Arctic foxes (Vulpes lagopus) in southern Yamal Peninsula, Russia. *Polar Biology*, *44*(12), 2307–2319. https://doi.org/10.1007/s00300-021-02962-w

Istomin, K., & Dwyer, M. (2021). *Reindeer herder's thinking: A comparative research on relations between economy, cognition, and way of life*. Verlag der Kulturstiftung Sibirien.

James, M. R., Antoniazza, G., Robson, S., & Lane, S. N. (2020). Mitigating systematic error in topographic models for geomorphic change detection: accuracy, precision and considerations beyond off-nadir imagery. *Earth Surface Processes and Landforms*, *45*(10), 2251–2271. https://doi.org/10.1002/esp.4878

James, M. R., Robson, S., d'Oleire-Oltmanns, S., & Niethammer, U. (2017). Optimising UAV topographic surveys processed with structure-from-motion: Ground control quality, quantity and bundle adjustment. *Geomorphology*, *280*, 51–66. https://doi.org/10.1016/j.geomorph.2016.11.021

James, M. R., Robson, S., & Smith, M. W. (2017). 3-D uncertainty-based topographic change detection with structure-from-motion photogrammetry: precision maps for ground control and directly georeferenced surveys. *Earth Surface Processes and Landforms*, *42*(12), 1769–1788. https://doi.org/10.1002/esp.4125

Jefferies, R. L., Jano, A. P., & Abraham, K. F. (2006). A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, *94*(1), 234–242. https://doi.org/10.1111/j.1365-2745.2005.01086.x

Jernsletten, J.-L. L., & Klokov, K. (2002). *Sustainable Reindeer Husbandry*.

Jung, T. S., Hegel, T. M., Bentzen, T. W., Egli, K., Jessup, L., Kienzler, M., Kuba, K., Kukka, P. M., Russell, K., Suitor, M. P., & Tatsumi, K. (2018). Accuracy and performance of low-feature GPS collars deployed on bison Bison bison and caribou Rangifer tarandus. *Wildlife Biology*, *2018*(1), 1–11. https://doi.org/10.2981/wlb.00404

Kaarlejärvi, E., Hoset, K. S., & Olofsson, J. (2015). Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. *Global Change Biology*, *21*(9), 3379–3388. https://doi.org/10.1111/gcb.12970

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. ., Linder, H. P., & Kessler, M. (2018). Climatologies at high resolution for the earth's land surface areas. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.kd1d4

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 1–20. https://doi.org/10.1038/sdata.2017.122

Macias-Fauria, M., Forbes, B. C., Zetterberg, P., & Kumpula, T. (2012). Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nature Climate Change*, *2*, 613–618. https://doi.org/10.1038/nclimate1558

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., Speed, J. D. M., Boulanger-Lapointe, N., Rixen, C., Lévesque, E., Schmidt, N. M., Baittinger, C., Trant, A. J., Hermanutz, L., Collier, L. S., … Vellend, M. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, *5*(9), 887–891. https://doi.org/10.1038/nclimate2697

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., MacIas-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4). https://doi.org/10.1088/1748-9326/6/4/045509

Newton, E. J., Pond, B. A., Brown, G. S., Abraham, K. F., & Schaefer, J. A. (2014). Remote sensing reveals long-term effects of caribou on tundra vegetation. *Polar Biology*, *37*(5), 715–725. https://doi.org/10.1007/s00300-014-1472-3

Niittynen, P., Heikkinen, R. K., Aalto, J., Guisan, A., Kemppinen, J., & Luoto, M. (2020). Fine-scale tundra vegetation patterns are strongly related to winter thermal conditions. *Nature Climate Change*, *10*(12), 1143–1148. https://doi.org/10.1038/s41558-020-00916-4

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., & Oksanen, L. (2001). Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography*, *24*(1), 13–24. https://doi.org/10.1034/j.1600-0587.2001.240103.x

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*(11), 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x

Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761). https://doi.org/10.1098/rstb.2017.0437

Olofsson, J., Stark, S., & Oksanen, L. (2004). Reindeer influence on ecosystem processes in the tundra. *Oikos*, *105*(2), 386–396. https://doi.org/10.1111/j.0030-1299.2004.13048.x

Olofsson, J., te Beest, M., & Ericson, L. (2013). Complex biotic interactions drive long-term vegetation dynamics in a subarctic ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624), 20120486. https://doi.org/10.1098/rstb.2012.0486

Olofsson, J., Tommervik, H., & Callaghan, T. V. (2012). Vole and lemming activity observed from space. *Nature Climate Change*, *2*(12), 880–883. https://doi.org/10.1038/nclimate1537

Orndahl, K. M., Ehlers, L. P. W., Herriges, J. D., Pernick, R. E., Hebblewhite, M., & Goetz, S. J. (2022). Mapping tundra ecosystem plant functional type cover, height and aboveground biomass in Alaska and northwest Canada using unmanned aerial vehicles. *Arctic Science*, *1180*, 1165–1180. https://doi.org/10.1139/as-2021-0044

Over, J.-S. R., Ritchie, A. C., Kranenburg, C. J., Brown, J. A., Buscombe, D. D., Noble, T., Sherwood, C. R., Warrick, J. A., & Wernette, P. A. (2021). Processing coastal imagery

with Agisoft Metashape Professional Edition, version 1.6—Structure from motion workflow documentation. In *U.S. Geological Survey Open-File Report*. https://doi.org/10.3133/ofr20211039

Räsänen, A., & Virtanen, T. (2019). Data and resolution requirements in mapping vegetation in spatially heterogeneous landscapes. *Remote Sensing of Environment*, *230*(May), 111207. https://doi.org/10.1016/j.rse.2019.05.026

Raynolds, M. K., Walker, D. A., Epstein, H. E., Pinzon, J. E., & Tucker, C. J. (2012). A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. *Remote Sensing Letters*, *3*, 403–411. https://doi.org/10.1080/01431161.2011.609188

Rees, W. G., Williams, M., & Vitebsky, P. (2003). Mapping land cover change in a reindeer herding area of the Russian arctic using Landsat TM and ETM+ imagery and indigenous knowledge. *Remote Sensing of Environment*, *85*(4), 441–452. https://doi.org/10.1016/S0034-4257(03)00037-3

Rickbeil, G. J. M., Coops, N. C., & Adamczewski, J. (2015). The grazing impacts of four barren ground caribou herds (Rangifer tarandus groenlandicus) on their summer ranges: An application of archived remotely sensed vegetation productivity data. *Remote Sensing of Environment*, *164*, 314–323. https://doi.org/10.1016/j.rse.2015.04.006

Roussel, J.-R., & Auty, D. (2021). *Airborne LiDAR Data Manipulation and Visualization for Forestry Applications*. https://cran.r-project.org/package=lidR

Roussel, J.-R., Auty, D., Coops, N. C., Tompalski, P., Goodbody, T. R. H., Meador, A. S., Bourdon, J.-F., de Boissieu, F., & Achim, A. (2020). lidR: An R package for analysis of Airborne Laser Scanning (ALS) data. *Remote Sensing of Environment*, *251*, 112061. https://doi.org/10.1016/j.rse.2020.112061

Siewert, M. B., & Olofsson, J. (2020). Scale-dependency of Arctic ecosystem properties revealed by UAV. *Environmental Research Letters*, *15*(9), 094030. https://doi.org/10.1088/1748-9326/aba20b

Siewert, M. B., & Olofsson, J. (2021). UAV reveals substantial but heterogeneous effects of herbivores on Arctic vegetation. *Scientific Reports*, *11*(1), 19468. https://doi.org/10.1038/s41598-021-98497-5

Skarin, A., Danell, Ö., Bergström, R., & Moen, J. (2008). Summer habitat preferences of GPS-collared reindeer Rangifer tarandus tarandus. *Wildlife Biology*, *14*(1), 1–15. https://doi.org/10.2981/0909-6396(2008)14[1:SHPOGR]2.0.CO;2

Skarin, A., Sandström, P., & Alam, M. (2018). Out of sight of wind turbines—Reindeer response to wind farms in operation. *Ecology and Evolution*, *8*(19), 9906–9919. https://doi.org/10.1002/ece3.4476

Skarin, A., Verdonen, M., Kumpula, T., Macias-Fauria, M., Alam, M., Kerby, J., & Forbes, B. C. (2020). Reindeer use of low Arctic tundra correlates with landscape structure. *Environmental Research Letters*, *15*(11), 115012. https://doi.org/10.1088/1748-9326/abbf15

Sokolov, A. A., Sokolova, N. A., Ims, R. A., Brucker, L., & Ehrich, D. (2016). Emergent Rainy Winter Warm Spells May Promote Boreal Predator Expansion into the Arctic. *ARCTIC*, *69*(2), 121–129. https://doi.org/10.14430/arctic4559

Sokolov, V., Ehrich, D., Yoccoz, N. G., Sokolov, A., & Lecomte, N. (2012). Bird Communities of the Arctic Shrub Tundra of Yamal: Habitat Specialists and Generalists. *PLoS ONE*, *7*(12), e50335. https://doi.org/10.1371/journal.pone.0050335

Sokolova, N. A., Sokolov, A. A., Ims, R. A., Skogstad, G., Lecomte, N., Sokolov, V. A., Yoccoz, N. G., & Ehrich, D. (2014). Small rodents in the shrub tundra of Yamal (Russia): Density dependence in habitat use? *Mammalian Biology*, *79*(5), 306–312. https://doi.org/10.1016/j.mambio.2014.04.004

Stammler, F. (2005). *Reindeer Nomads Meet the Market: Culture, Property and*

Globalisation at the `End of the Land'. Lit.

Sundqvist, M. K., Moen, J., Björk, R. G., Vowles, T., Kytöviita, M. M., Parsons, M. A., & Olofsson, J. (2019). Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. *Journal of Ecology*, *April*, 1–13. https://doi.org/10.1111/1365-2745.13201

Suvanto, S., Le Roux, P. C., & Luoto, M. (2014). Arctic-alpine vegetation biomass is driven by fine-scale abiotic heterogeneity. *Geografiska Annaler: Series A, Physical Geography*, *96*(4), n/a-n/a. https://doi.org/10.1111/geoa.12050

Terekhina, A., & Volkovitskiy, A. (2020). Patterns of resource use by the Yamal nomads: The micro-regions ethnography. In V. N. Davydov (Ed.), *Energy of the Arctic and Siberia: The Use of Resources in the Context of Socio-Economic Changes* (pp. 87–113). Izdatel'stvo vostochnoi literatury.

Thomson, E. R., Spiegel, M. P., Althuizen, I. H. J., Bass, P., Chen, S., Chmurzynski, A., Halbritter, A. H., Henn, J. J., Jónsdóttir, I. S., Klanderud, K., Li, Y., Maitner, B. S., Michaletz, S. T., Niittynen, P., Roos, R. E., Telford, R. J., Enquist, B. J., Vandvik, V., Macias-Fauria, M., & Malhi, Y. (2021). Multiscale mapping of plant functional groups and plant traits in the High Arctic using field spectroscopy, UAV imagery and Sentinel-2A data. *Environmental Research Letters*, *16*(5). https://doi.org/10.1088/1748-9326/abf464

Trondrud, L. M., Pigeon, G., Albon, S., Arnold, W., Evans, A. L., Irvine, R. J., Król, E., Ropstad, E., Stien, A., Veiberg, V., Speakman, J. R., & Loe, L. E. (2021). Determinants of heart rate in Svalbard reindeer reveal mechanisms of seasonal energy management. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1831), 20200215. https://doi.org/10.1098/rstb.2020.0215

Tuomi, M., Väisänen, M., Ylänne, H., Brearley, F. Q., Barrio, I. C., Anne Bråthen, K., Eischeid, I., Forbes, B. C., Jónsdóttir, I. S., Kolstad, A. L., Macek, P., Petit Bon, M., Speed, J. D. M., Stark, S., Svavarsdóttir, K., Thórsson, J., & Bueno, C. G. (2020). Stomping in silence: Conceptualizing trampling effects on soils in polar tundra. *Functional Ecology*, *February*, 1365-2435.13719. https://doi.org/10.1111/1365-2435.13719

Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., & Stark, S. (2014). Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, *4*(5), 384–388. https://doi.org/10.1038/nclimate2147

van der Wal, R. (2006). Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, *114*(1), 177–186. https://doi.org/10.1111/j.2006.0030-1299.14264.x

Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Raynolds, M. K., Comiso, J. C., Gubarkov, A. A., Khomutov, A. V., Jia, G. J., Kaarlejärvi, E., Kaplan, J. O., Kumpula, T., Kuss, P., Matyshak, G., Moskalenko, N. G., Orekhov, P., Romanovsky, V. E., Ukraientseva, N. G., & Yu, Q. (2009). Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index. *Environmental Research Letters*, *4*(4), 045004. https://doi.org/10.1088/1748-9326/4/4/045004

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & The other members of the CAVM Team. (2005). The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, *16*(3), 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x

Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K., Cornelissen, J. H. C., Gough, L., Hartley, I. P., Hopkins, D. W., Lavorel, S., & Shaver, G. R. (2009). Ecosystem feedbacks and cascade processes: Understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, *15*(5), 1153–1172. https://doi.org/10.1111/j.1365-2486.2008.01801.x

Yang, D., Morrison, B. D., Hantson, W., Breen, A. L., McMahon, A., Li, Q., Salmon, V. G., Hayes, D. J., & Serbin, S. P. (2021). Landscape-scale characterization of Arctic tundra vegetation composition, structure, and function with a multi-sensor unoccupied aerial system. *Environmental Research Letters*, *16*(8), 085005. https://doi.org/10.1088/1748-9326/ac1291

Zhang, W., Qi, J., Wan, P., Wang, H., Xie, D., Wang, X., & Yan, G. (2016). An Easy-to-Use Airborne LiDAR Data Filtering Method Based on Cloth Simulation. *Remote Sensing*, *8*(6), 501. https://doi.org/10.3390/rs8060501

5.9 Supplementary material

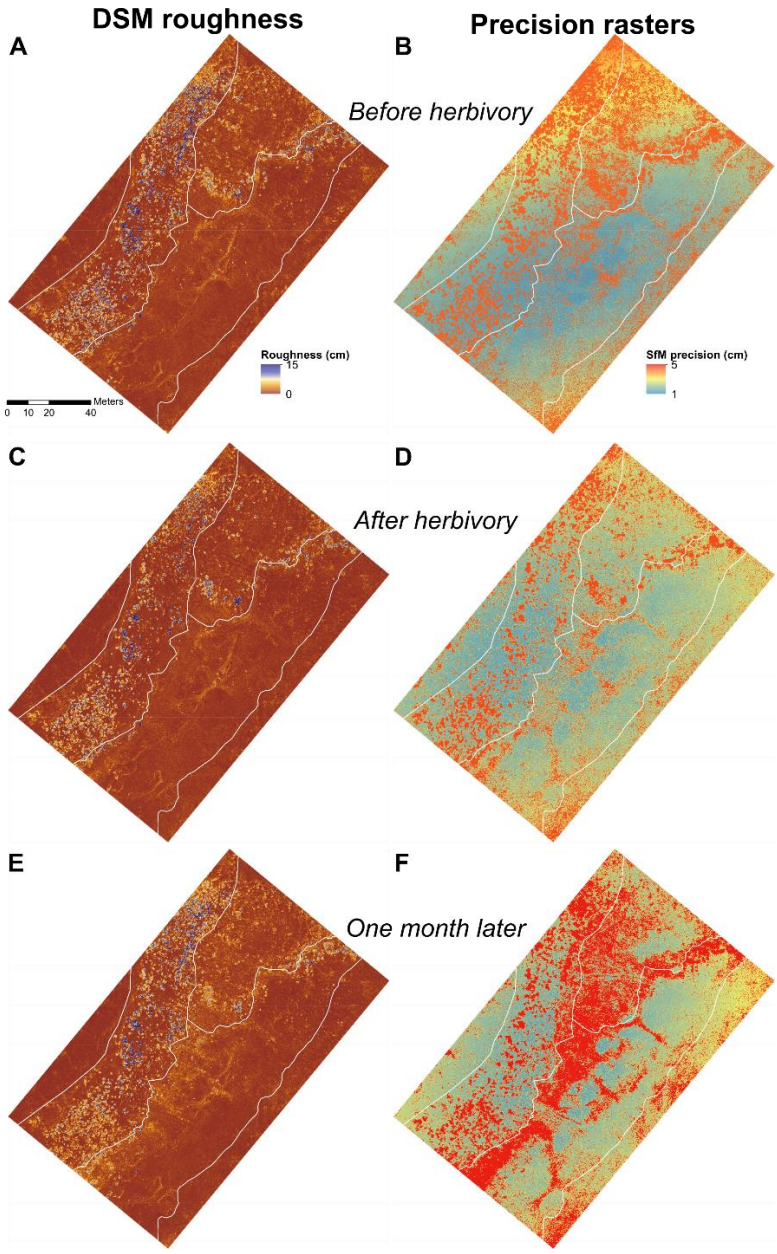


Figure S5.1: Rasters used in the calculation of the limit of detection (LoD). The DSM roughness maps (**A,C,E**) were rasterised at 5 cm resolution from the dense point clouds as the standard deviation of the point elevations within each pixel. The precision rasters (**B,D,F**) were rasterised at 10 cm resolution from the precision estimates of the tie points in the sparse point cloud. Gaps were filled with the lowest precision estimate from the survey.

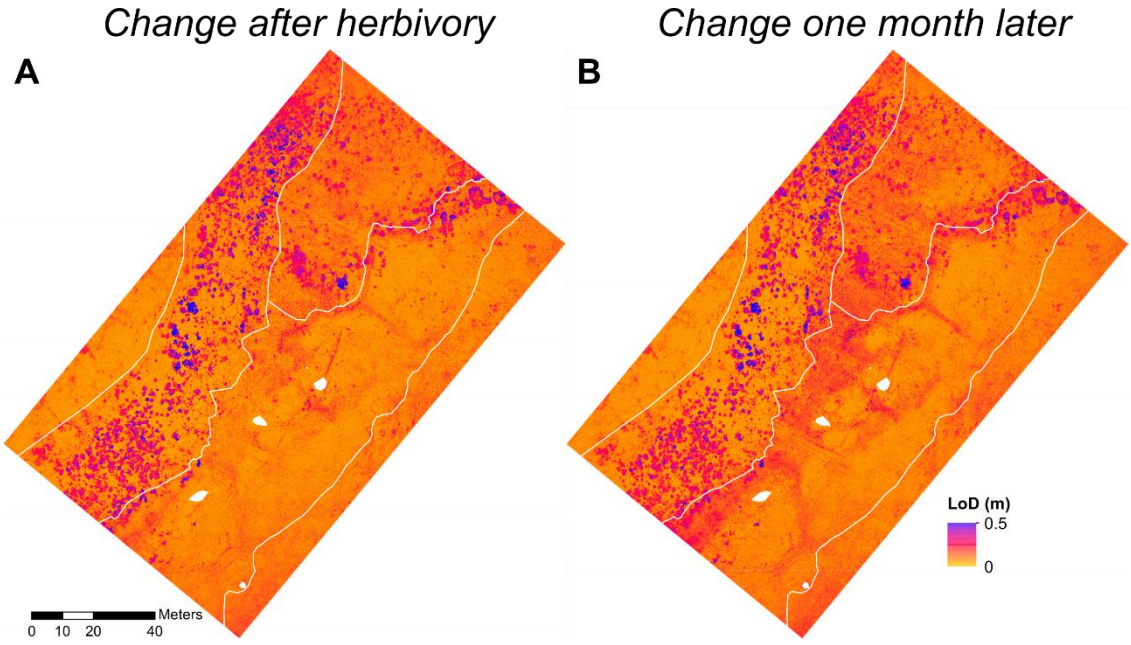


Figure S5.2: Rasters depicting the spatially variable limit of detection (LoD) across the study area calculated based on uncertainty in the photogrammetric reconstructions and rasterisation uncertainty. The areas with no data were masked out due to humans or equipment present there during the UAV flights on one of the collection dates.

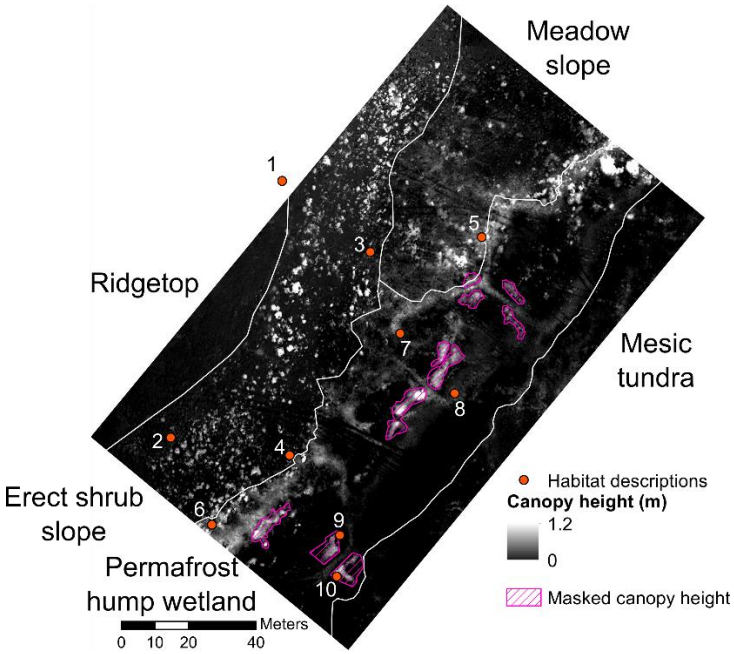


Figure S5.3: The locations of the habitat descriptions used to inform the habitat delineation overlaid on the canopy height model from 5 August (one month after the herd was at the site). The hatched polygons show where the canopy height raster was masked from the analysis due to misidentification of permafrost humps as part of the canopy. The habitat descriptions at the 10 locations are given in **Table S5.1** and the five broad habitat classes are described in **Table S5.2**.

Table S5.1: Habitat descriptions for selected points across the study site. The number in the first column corresponds to the numbered points in **Figure S5.3**, and the date indicates when (during which survey) we made the description. The points and their elevations were precisely located with a GNSS. The habitat types over the whole study site were delineated based on these descriptions and visual assessment of the UAV survey products.

No.	Date	Elevation [m]	Habitat type	Description
1	30 June	16.1	Ridgetop	Very low vegetation on the ridgetop under 10 cm in height consisting of primarily *Betula nana* and *Vaccinium vitis-idaea*, but also *Ledum palustre*, *Empetrum nigrum*, and *Equisetum arvense*.
2	7 July	14.8	Erect shrub slope	Upper part of the slope. Forb-rich tundra up to 20 cm in height with species in the Fabaceae family as well as *Vaccinium uliginosum*, *Betula nana*, and many narrow-leaved graminoids.
3	30 June	12.3	Erect shrub slope	Dry with erect *Salix* spp. (willow) shrubs up to 60 cm tall and *Carex* and *Eriophorum* spp. All willows have grazing marks, both new and older, and some graminoids have grazing marks as well.
4	30 June	11.9	Erect shrub slope	Very grazed willow shrubs up to 40 cm tall surrounded by narrow-leaved grasses.
5	7 July	10.3	Meadow slope	Meadow with a mixture of erect *Betula nana* and *Salix* shrubs up to 60 cm tall. Graminoids, mainly *Eriophorum* spp. Are quite trampled.
6	7 July	11.3	Permafrost hump wetland	Dry area upslope from wetland with vegetation up to 40 cm in height including *Veratrum lobelianum*, *Rubus chamaemorus*, graminoids, and small erect willow shrubs.
7	7 July	11.1	Permafrost hump wetland	Sedge wetland up to 60 cm in height with large *Carex* spp. (mainly *Carex aquatilis*) and some narrow-leaved grasses and *Comarum palustre*.
8	30 June	10.0	Permafrost hump wetland	*Eriophorum* wetland up to 30 cm in height with some *Carex* spp. and *Comarum palustre*.
9	30 June	10.3	Permafrost hump wetland	Meadow wetland under 30 cm in height. A mixture of sedges, narrow-leaved grasses, forbs, and low erect *Betula nana* and *Salix* shrubs
10	30 June	10.4	Permafrost hump wetland	On big permafrost hump in the wetland with vegetation rarely over 10 cm in height. Mostly *Vaccinium vitis-idaea* and lots of moss with *Rubus chamaemorus* and *Empetrum nigrum* at the edge of the hump.

Table S5.2: Descriptions of the habitat types which we delineated over the study site. The descriptions were made based on observations in the field, particularly those at points listed in **Table S5.1**, and visual assessment of the UAV survey products. Although no specific habitat descriptions were made within mesic tundra, this area was noted in the field as belonging to this habitat type, which is very common around the study area and described by Hofhuis et al. (2021). The elevation is given as the mean ± standard deviation computed from the DTM (**Figure S5.4**) over the area covered by the habitat type.

Habitat type	Area [m^2]	Elevation [m]	Description
Ridgetop	1057	16.5 ± 0.32	Open patches mixed with very low stature vegetation (<10 cm), mostly shrubs, especially *Vaccinium vitis-idaea*, but also small forbs and graminoids.
Erect shrub slope	4557	13.5 ± 1.09	Rather dry part of the slope with erect willow shrubs, some taller than 50 cm, throughout the area. Graminoids *(*especially *Carex* spp. and *Eriophorum* spp.) are consistently found around the willow shrubs, while small forbs and *Betula nana* become more common at the top of the slope.
Meadow slope	2711	11.2 ± 0.85	Meadow with a mixture of erect *Betula nana* and willow shrubs, although in lower abundance than within the erect shrub slope. Graminoids, especially *Eriophorum* spp., become more dense towards the bottom of the slope.
Permafrost hump wetland	6278	10.2 ± 0.80	Wetland with dense graminoids interspersed with dry permafrost hump features with very low stature vegetation. Dominant graminoid vegetation varies between *Carex* spp. and *Eriophorum* spp. The large forb *Comarum palustre* is also abundant.
Mesic tundra	1941	9.7 ± 0.72	Very common habitat type in the area with a thick moss layer, tussocks of *Eriophorum vaginatum*, and abundant, low stature dwarf shrubs (Ericaceae, *Betula nana*, and willows) (<25 cm).

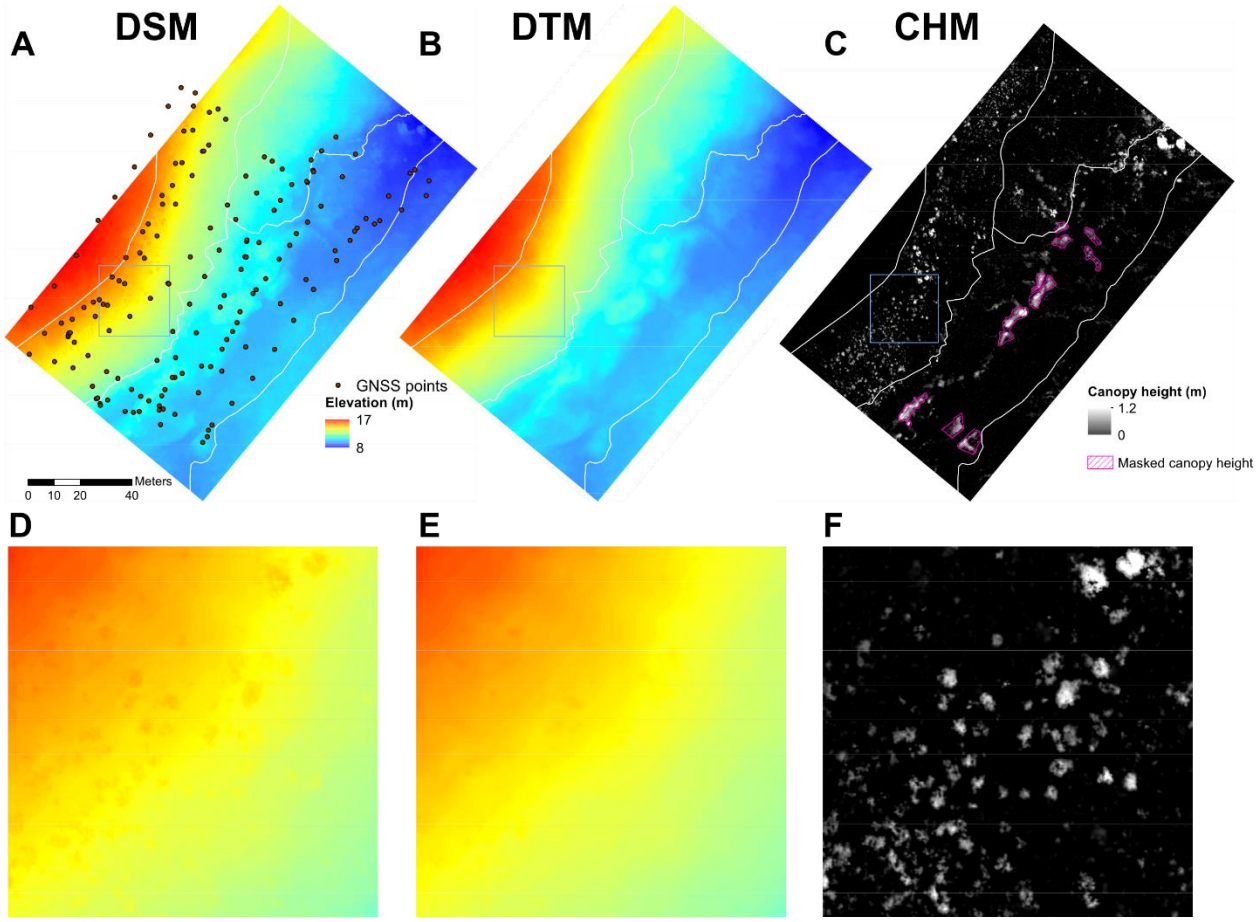


Figure S5.4: Digital surface model (DSM), digital terrain model (DTM), and resulting canopy height model (CHM). Both the DSM (**A,D**) and CHM (**C,F**) were constructed from the 7 July survey (after herbivory), when the displayed GNSS points were also taken and used to validate the DTM (**B,E**). The DTM was also derived from 7 July dense point cloud, but it is used to represent the terrain for the study site for all survey dates. The CHM (**C**) also displays as hatched polygons the areas where the canopy height was masked in analyses due to mischaracterisation of the permafrost humps as canopy.

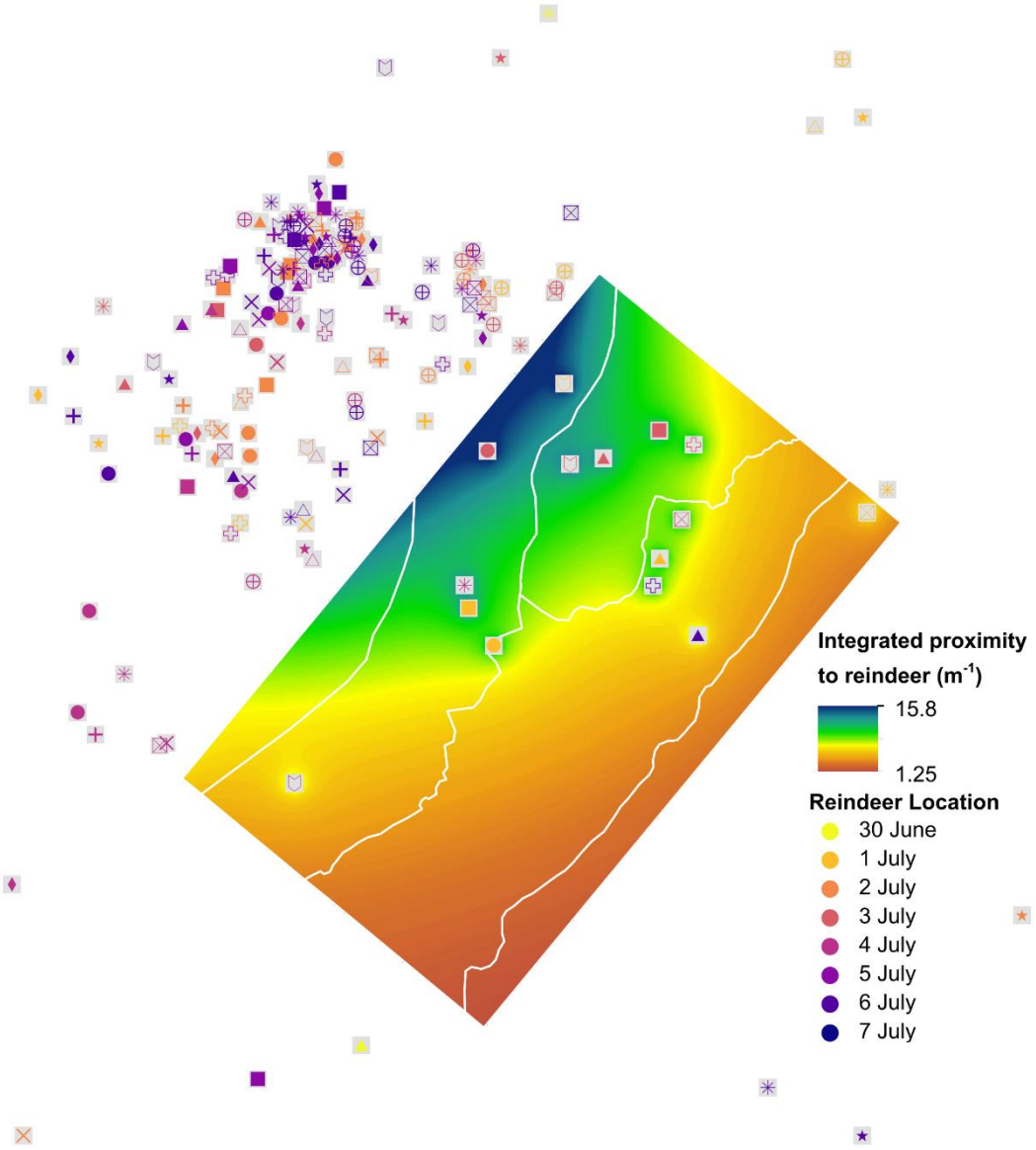


Figure S5.5: The metric for quantifying spatial variation in reindeer activity across the study site, calculated as the integrated proximity to the reindeer collar points. All reindeer collar points within 100 m of the study site are included, and different shapes are used to represent the 13 collared reindeer whereas the colours represent the date when each point was recorded.

Chapter 6:

Offsetting impacts of different size classes of herbivores on CO_2 uptake in a tundra ecosystem

Marcus P. Spiegel[1], Svetlana Abdulmanova[2], Dorothée Ehrich[3], Alexander Volkovitskiy[2], Natalia Sokolova[2], Aleksandr A. Sokolov[2], Marc Macias-Fauria[1]

[1]Biogeosciences Lab, School of Geography & the Environment, University of Oxford, Oxford, OX1 3QY, United Kingdom.

[2]Arctic Research Station of Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Labytnangi, Russia, 629400, Zelenaya Gorka Str., 21

[3]UiT - The Arctic University of Norway, Department of Arctic and Marine Biology, 9019 Tromsø, Norway



Photo: Dorothée Ehrich

6.1 Chapter statement

The final research article included in this thesis assessed the influence of different size classes of herbivores on CO_2 fluxes in a tundra ecosystem using an exclosure experiment. Building on the work in **Chapters 4 & 5** that detected the effects of reindeer on vegetation at the regional and landscape scales, this study examined the implications for the carbon cycle at a local scale. By comparing the impacts of different size classes of herbivores, this chapter aimed to tease apart the various mechanisms by which different herbivores affect ecosystem processes and quantify the aggregate impact on the carbon balance.

This chapter has been submitted to *Oikos*.

6.2 Author contributions

MPS conceptualised the research and designed the study with input from DE, AAS, and MM-F. SA, DE, NS, and AAS made the exclosure experiment available for data collection. MPS performed the flux measurements with the help of AV. SA analysed the vegetation photographs. MPS analysed the data with input from DE and MM-F. MPS wrote the manuscript with significant contributions from all authors.

6.3 Abstract

Herbivory exerts an important control on ecosystem structure and functioning in the Arctic, yet the implications for the carbon cycle are complex and vary with landscape heterogeneity as well as the herbivore assemblage that is present. We measured CO_2 fluxes in a unique experimental design that has cumulatively excluded large-, medium-, and small-sized herbivores within three different Arctic habitat types for seven years. Whereas plots that excluded only reindeer had significantly higher CO_2 uptake than the controls, the additional exclusion of medium-sized herbivores and small rodents consistently had progressively lower photosynthesis than exclusion of reindeer alone. We propose that the most likely explanation for these dynamics is that they stem from a combination of defoliation from reindeer and nutrient inputs from smaller herbivores. The responses in photosynthesis were greater than effects on respiration and varied between habitat types, as exclusion of both large and smaller herbivores had a significant role within forb tundra, while only large herbivores had a significant impact in willow meadows, and limited differences from the controls were observed in mesic tundra. Our findings suggest that scaled-up estimates of CO_2 exchange across the Arctic need to account for the diversity of impacts from herbivore assemblages within different habitat types.

6.4 Introduction

Rapid warming in the Arctic is driving carbon cycle feedbacks to climate change, notably causing increases in permafrost thaw (Schuur et al., 2015) and vegetation productivity (Berner et al., 2020). These bottom-up processes are mediated to a yet largely unconstrained extent by the top-down impacts of herbivores, which ultimately affect both aboveground and belowground carbon stocks and fluxes (Olofsson, E. Hulme, et al., 2004; Schmitz et al., 2018; Ylänne et al., 2020). Herbivores affect the carbon balance most directly by consuming photosynthetically active plant tissue, reducing carbon uptake in grazed areas (Tanentzap & Coomes, 2012). However, over time, the combined impacts of herbivores' grazing, browsing, trampling, and addition of faeces and urine cause shifts in plant community composition and the soil environment, which have further implications for ecosystem functioning (Egelkraut et al., 2020; Olofsson & Post, 2018; Tanentzap & Coomes, 2012). Thus, the responses of Arctic ecosystems to herbivory are complex, and it is uncertain to what degree and in which contexts herbivory may mitigate or exacerbate climate warming feedbacks.

The mechanisms by which herbivory affects the carbon balance depend on the assemblage of herbivores and their functional diversity (Bardgett & Wardle, 2003). Although both large (>10 kg) and small mammalian herbivores in tundra ecosystems commonly reduce the abundance of shrubs while promoting graminoids (e.g., Forbes et al., 2009; Kaarlejärvi et al., 2015; Olofsson et al., 2013; Post & Pedersen, 2008), previous work has shown that reindeer limit the expansion of taller shrubs (>0.3m), whereas microtine rodents only reduce the abundance of dwarf shrubs (<0.3 m) (Lindén et al., 2021; Olofsson et al., 2009). Even among large herbivores, bovids and equids that have been introduced into the Pleistocene Park experiment in northeastern Siberia have primarily complementary rather than overlapping impacts, as bovids are able to digest cellulose whereas equids consume less fibrous vegetation (Macias-Fauria et al., 2020). Consequently, the presence of additional herbivore species within an assemblage does not necessarily imply an amplified effect, but instead could contribute to a larger diversity of ecosystem responses which may have conflicting impacts on the carbon balance. Measurements in northern Sweden found that excluding reindeer increased ecosystem CO_2 uptake compared to the grazed controls, but the plots additionally excluding small mammals had lower CO_2 uptake, although the difference between these treatments was not significant (Metcalfe & Olofsson, 2015). This finding occurred despite a greater increase in aboveground vascular plant biomass when small mammals were additionally excluded,

suggesting that even though the effects on aboveground plant biomass were cumulative, other herbivore-induced changes contributed to the differences in photosynthesis.

Landscape heterogeneity is also an important source of variation in carbon cycle dynamics, as although the Arctic is generally a net sink of CO_2, different landcover types vary substantially in their magnitude as a sink and some landcovers, such as dry lichen tundra, can even be a net source (Treat et al., 2018). The impact of herbivores on ecosystem carbon fluxes depends on the vegetation cover and soil characteristics, which form distinct habitat types across the landscape (Kelsey et al., 2016; Sjögersten et al., 2008). This interaction arises due to herbivores' preferential usage and foraging within certain habitat types (Skarin et al., 2020; Sokolova et al., 2014), as well as differences in how habitat types respond to herbivore pressure. For example, in productive riparian tundra on sediment plains, herbivore exclusion resulted in rapid changes in the abundance of different plant growth forms, whereas responses within less productive habitat types have taken multiple years to manifest (Ravolainen et al., 2011). In another experiment involving the introduction of captive Barnacle Geese in Svalbard, grazing reduced the sink strength of a mesic heath, whereas a wet meadow became a weaker source of CO_2 (Sjögersten et al., 2008). Consequently, scaled-up predictions of carbon cycle feedbacks in the Arctic must incorporate knowledge of how common habitat types in the Arctic differ in their responses depending on the herbivores present in the area (Virkkala et al., 2021).

Here, we used a unique experimental setup that cumulatively excluded three different size classes of herbivores for seven years to measure the impact of different herbivore assemblages on ecosystem carbon fluxes. This experimental design was replicated across three distinct habitat types: forb tundra (FT), mesic tundra (MT), and willow meadows (WM) (see Material and methods for a description of the different habitat types). Early results from this experiment reported that after one year, the biomass of most plant functional groups did not differ significantly between the exclosures and the controls, although total biomass was significantly greater in the plots excluding only large herbivores in WM, primarily due to an increase in forb biomass, and in the plots excluding all herbivores in FT (Baubin et al., 2016). We hypothesised that given the relatively recent establishment of the exclosures, differences in carbon fluxes would be driven mostly by the immediate effects of plant consumption by herbivores, thereby leading to greater gross ecosystem photosynthesis (GEP) where herbivores were excluded and limited differences in ecosystem respiration (ER), as found in similar studies elsewhere (Cahoon et al., 2012; Metcalfe & Olofsson, 2015; Ylänne & Stark, 2019). We anticipated that

the importance of the herbivore assemblage excluded would differ depending on the habitat type. Based on the focal habitats of the different herbivore species and evidence from the initial results from the experiment (Baubin et al., 2016; Sokolova et al., 2014), we expected exclusion of large herbivores to have the greatest effect in WM, all size classes of herbivores to be similarly important in FT, and limited responses in MT.

6.5 Material and methods

6.5.1 Site description

The study was conducted at the Erkuta Tundra Monitoring Site in the southern part of the Yamal Peninsula, West Siberia, Russia (68.2° N, 69.2° E). The area is mostly flat with hills up to 40 m high and is underlain by continuous permafrost (Walker et al., 2009). Vegetation cover is mostly characterised as erect dwarf shrub tundra and low shrub tundra, and willow thickets are common in concavities formed by a dense network of rivers and lakes (Ehrich et al., 2012; Walker et al., 2005). The mean daily maximum temperature ranges from -19.7°C in January to 16.0°C in July, and mean annual precipitation is 488 mm (2000-2019 averages, CHELSA v2.1; Karger et al. 2017, 2018).

Whereas the small rodents in the region include lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*), the present community is dominated by voles (*Lasiopodomys gregalis, Alexandromy middendorffii*, *Myodes rutilus, Arvicola amphibius*) (Sokolova et al., 2014). Vole abundance fluctuates in multi-annual population cycles and peaked in summer 2021 (Ehrich, Sokolova, and Sokolov unpubl.), the season during which we made the carbon flux measurements. Medium-sized herbivores include willow ptarmigans (*Lagopus lagopus*) and mountain hares (*Lepus timidus*), and the only large herbivores present are reindeer (*Rangifer tarandus*) (Baubin et al., 2016). Domesticated reindeer, in herds managed by Indigenous Nenets mobile pastoralists, graze year-round in the region, some visiting the area during the summer along long-distance migrations whereas others are based there in the snow season. From 3 July to 7 July 2021, a group of herders with approximately 2,000 reindeer camped in the area, constituting a large pulse of grazing pressure within the timespan of our measurements. A visit from such a large herd only occurs once every few growing seasons in Erkuta and likely had not happened more than twice previously since the exclosures had been established.

6.5.2 Experimental design

Details of the herbivore exclusion experiment are reported by Baubin et al. (2016) and summarised here. In summer 2014, exclosures were erected that consisted of six 0.6 x 0.6 m plots: two excluding only reindeer (EX_L), two additionally excluding hares and ptarmigans (EX_M), and two excluding all herbivores including small rodents (EX_S). Two control plots (C) were also randomly chosen outside but nearby each exclosure, giving a total of eight plots associated with each established exclosure. The exclosures were placed within each of three habitat types: forb tundra (FT), mesic tundra (MT), and willow meadows (WM). FT, typically found on upper slopes and on top of sandy hills, consists mainly of short stature plants belonging to the Fabaceae family, and is a focal habitat for all the herbivores present. MT, a very common habitat type in the low Arctic, is dominated by low stature dwarf shrubs (Ericaceae, *Betula nana*, and willows) and sedges with a thick moss layer. WM was defined as the sloped areas adjacent to willow thickets consisting of a mixture of graminoids, forbs, and shorter stature willows. Between 2014 and 2016, analysis of faeces counts and automatic camera photographs confirmed that the expected herbivore assemblage was present in (or absent from) each plot, although the evidence of ptarmigans was substantially smaller than that of hares among the medium-sized herbivores (Baubin et al., 2016). Additionally, in 2021 after the arrival of the herd of 2,000 reindeer, there was evidence, via automatic camera and/or the presence of fresh fur, that they had grazed in the immediate vicinity of each exclosure used in this study (M. P. Spiegel, pers. obs.). Five exclosures were used in this study, including two in FT (FT1, FT2), two in MT (MT1, MT2), and one in WM (WM1), each with two sets of plots consisting of a control and three herbivore exclusion treatments. A summary of the exclosure and habitat types and their abbreviations is presented in **Table 6.1**.

Table 6.1: The independent variables in the experimental design.

Variable	Values	Abbreviations
Herbivory exclusion	Control	C
	Large herbivores excluded	EX_L
	Large and medium-sized herbivores excluded	EX_M
	All herbivores excluded including small rodents	EX_S
Habitat type	Forb tundra	FT
	Mesic tundra	MT
	Willow meadows	WM

6.5.3 CO_2 flux measurements and calculations

We measured ecosystem CO_2 fluxes using a custom-built transparent Perspex chamber (692 x 692 x 600 mm) and a Picarro GasScouter G4301 Mobile Gas Concentration Analyzer (Picarro, Inc., Santa Clara, CA, USA) in a closed-loop configuration. The chamber was designed so that it could be placed over the cages in EX_S, which are buried in the ground and cannot be temporarily removed. We attached a plastic skirt to the bottom of the sides of the chamber, which we weighed down with a heavy chain during measurements to prevent leakage. Two battery-powered fans circulated air continuously within the chamber.

Between 23 June and 12 August 2021, we conducted flux measurements at each exclosure either two or three times. When possible, all plots at an exclosure were measured within a single day, but due to constraints stemming from the weather and equipment, two exclosure measurements (out of 14 total) were conducted over two or three consecutive days. All fluxes were measured within six hours of solar noon. For each plot, we repeated the flux measurement five times: once with the clear chamber, three times with increasing levels of shade produced by draping mosquito netting over the chamber, and finally with the chamber beneath an opaque sheet to estimate ecosystem dark respiration (ER). CO_2 concentration was logged at 1 s intervals for at least 120 s during each measurement, and between measurements, we lifted the chamber to restore the CO_2 concentration to a basal level. While lifting the chamber, we monitored the live readings of CO_2 concentration and only replaced it once the concentration had restabilised at ambient conditions. Photosynthetically active radiation (PAR) within the chamber was logged every 10 s using an LI-190R Quantum Sensor (LI-COR Biosciences, Cambridge, UK), and air temperature in the chamber was recorded every 2 minutes using an iButton device (model DS1923, Maxim Integrated, San Jose, CA, USA) placed beneath a fan to avoid direct sunlight.

To determine the net ecosystem exchange (NEE) of CO_2 from the temporal change in CO_2 concentrations, we first calculated the slope of the CO_2 concentrations during the 60 s of each measurement with the strongest linear fit (defined as the highest r^2 value). Measurements without a clear linear fit indicate outliers or signs of leakage and were discarded. We calculated NEE (µmol CO_2 m^{-2} s^{-1}) using the following formula:

$$\mathrm{NEE} = \frac{\frac{\mathrm{d}CO_2}{\mathrm{d}t} \times P \times V}{R \times A \times T},$$

where dCO_2/dt is the slope of CO_2 concentration against time, P is pressure, V is the chamber volume, R is the universal gas constant, A is the surface area covered by the chamber, and T is air temperature in the chamber, taken from the iButton. A negative NEE value indicates uptake of CO_2. Photosynthesis does not occur during the dark measurements, implying NEE=ER.

To control for the confounding effect of variable light levels, we modelled our CO_2 fluxes at a common irradiance. For each plot on each date, we fit a rectangular hyperbola to our NEE values and the associated average PAR during the measurements under varying shade levels using the *nls* function in R version 4.0.3 (R Core Team, 2020):

$$NEE = ER - \frac{A_{max} \times PAR}{k + PAR},$$

where A_{max} is the light-saturated photosynthetic rate (µmol CO_2 m^{-2} s^{-1}) and k is the half-saturation constant (µmol photons m^{-2} s^{-1}). When the data did not conform to a rectangular hyperbola and the model failed to converge, we discarded the measurements for that plot under light conditions (Min et al., 2021). The modelled NEE for at least one of the two plots converged for all controls and treatments at each exclosure on each date, except for WM1, where NEE measurements under light conditions (but not ER) were discarded for all plots during the first visit on 23-24 June, likely due to the low levels of photosynthesis in this habitat type this early in the growing season. The relationship between all predicted NEE values, calculated using the measured PAR and the fitted values of A_{max} and k, and the observed NEE values was highly linear with a slope near unity (r^2=0.95, y = 0.95x – 0.13, Supplementary material **Figure S6.1**). Using the fitted parameter values, we predicted estimates of NEE (NEE_{400}) at a standardised PAR value of 400 µmol m^{-2} s^{-1}. This light level was chosen to maximise the number of plot measurements for which the standardised light level was within the range of the measured PAR values during the clear and shaded measurements. An estimate for GEP at this same light level for each plot on each date was then calculated as GEP_{400} = NEE_{400} – ER.

6.5.4 Plot photographs

For every set of flux measurements at a plot, we photographed the plot so that we could later characterise and compare plant cover. Each plot was photographed using a Google Pixel 3a smartphone camera first from a consistent chest height and then from a lower height to provide a second image at finer resolution. Based on the spatial resolution of the chest-height photograph, a rectangle matching the size of the plot (0.6 x 0.6 m) and a corresponding 5x5 grid were first placed on that photograph and then placed on the finer resolution photograph to cover the identical area (**Figure S6.2**). Each photograph was scored to measure the cover of seven plant groups (or common species within the study area) that were distinguishable within the photographs, varied between plots, and contained plants thought to have a relatively similar influence on the CO_2 fluxes. These groups included evergreen ericoids/*Dryas octopetala*, erect *Salix* spp., *Betula nana*, small deciduous shrubs, graminoids, forbs, and *Veratrum lobelianum*, which was separated from the other forbs due to its large leaf area. Litter within each plot was also scored to determine whether litter had accumulated within the plots due to the cages and fences in the exclosure experiment. Two metrics were scored – the number of grid cells (out of the 25) in the photograph annotation in which the group was visible (hereafter 'presence') and an estimate of the overall percent cover of each group. The total percent cover within a plot can exceed 100% as even within the 2D photographs, we were able to infer when multiple groups were present at a plot location.

6.5.5 Supplementary measurements

Immediately after the flux measurements, we also measured soil temperature and soil moisture within each plot. Soil temperature was measured using a FieldScout Direct Soil EC Meter (Model: 2265FS; Spectrum Technologies, Aurora IL, USA) at 10 cm and 20 cm depth at two corners of each plot. Soil moisture was measured using an ML3-ThetaProbe soil moisture sensor (10 cm depth) connected to an HH2 moisture meter (Delta-T Devices, Burwell, UK) at all four corners of each plot. Since the cages could not be temporarily removed from EX_S, soil temperature and moisture measurements were taken just outside of rather than within these plots. Due to equipment malfunction, we were unable to take soil moisture measurements during the last visit to each exclosure. Throughout summer 2021, air temperature was measured at 5-minute intervals by a HOBO temperature logger installed on a U30 Weather Station (Onset Computer Corporation, Bourne MA, USA) less than 2 km away from each exclosure.

6.5.6 Statistical analyses

Plots of the same treatment within each exclosure and the associated controls are not likely to be independent replicates due to spatial autocorrelation and the high likelihood that both plots are affected by any chance events (Metcalfe & Olofsson, 2015). Therefore, for our flux comparisons, we pooled these plots prior to statistical analysis and used the means, which should be more robust and representative of the effects of the treatments. We used linear mixed effects models with herbivore exclusion treatment and habitat type as fixed effects and measurement date nested within exclosure as the random effect. Response variables were NEE_{400}, GEP_{400}, ER, soil temperature at 10 and 20 cm, and soil moisture. Where significant effects were found, we used Bonferroni corrected post hoc comparisons to identify significant differences among treatments.

In our analysis of the plot photographs, 10% (11 out of 112) were randomly duplicated before the cover of the plant groups was scored to test the consistency of our scoring. Both the presence and percent cover were consistently recorded ($r^2 > 0.9$) with no groups showing consistent discrepancies (**Figure S6.3**). We also examined the correspondence between our two scoring metrics and found that higher values for percent cover were found only with high presence, but low percent cover values were possible across values for presence (**Figure S6.4**). This makes sense, as it is possible for a group to cover a small proportion of the plot despite appearing sparsely across the whole plot. Litter, for example, was present in all 25 grid cells in most plots but with a range of percent cover. For the analysis of the photograph scores and CO_2 fluxes, data were used from each plot only on one date (consistent within exclosures), chosen towards the beginning of August near the time when maximum photosynthesis was measured. The relationship between the CO_2 fluxes and each metric of vegetation cover was analysed for the plant groups (i.e., excluding litter) using stepwise regressions including both forward and backward selection with the best model chosen by Akaike information criterion (AIC). Relationships between the CO_2 fluxes and litter were assessed using linear regression. Regressions were performed separately for different habitat types due to differences in the plant groups present in each (e.g., FT and MT did not have *Veratrum lobelianum,* WM did not have *Betula nana*). The regressions with litter were repeated both including all plots and with the control plots excluded to specifically test across differences in litter within the exclosure plots. All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020) using the 'lme4' (Bates et al., 2015), 'emmeans' (Lenth, 2022), and 'MASS' (Venables & Ripley, 2002) packages.

6.6 Results

Over the course of the growing season, CO_2 fluxes varied depending on the habitat type and the measurement date, but flux values measured within a span of a few days within replicate exclosures of the same habitat type were similar (**Figures 6.1, S6.5**). Measurements of both FT1 and FT2, separated by ~300 m in space, were taken on either the same day or within two consecutive days on two occasions in August, and after averaging over treatments, the mean of the standard deviations of the fluxes from the two exclosures on each occasion (NEE_{400}: 0.382, ER: 0.065, GEP_{400}: 0.266 μmol CO_2 m^{-2} s^{-1}) was smaller than the standard deviation over all four measurements (NEE_{400}: 0.476, ER: 0.376, GEP_{400}: 0.569 μmol CO_2 m^{-2} s^{-1}). This was also true of the measurements in MT1 and MT2, separated by ~900 m in space, for which the mean value of the standard deviations on three occasions (NEE_{400}: 0.449, ER: 0.484, GEP_{400}: 0.267 μmol CO_2 m^{-2} s^{-1}) was smaller than the standard deviations over all six measurements (NEE_{400}: 1.005, ER: 1.168, GEP_{400}: 0.948 μmol CO_2 m^{-2} s^{-1}). This similarity in fluxes within habitat types occurred despite large differences in air temperature between measurements (**Figure S6.6**).

Although the measurements throughout the growing season are too sparse to observe clear seasonal patterns in the fluxes within different habitat types, high ER, 31.5% greater than the next largest value, was measured in FT in early July, and high GEP, 48.2% greater in magnitude than the next largest value, was measured in WM in late July (**Figure 6.1**). These peaks in values of photosynthesis and respiration are not explained by air temperature, soil temperature or soil moisture (**Figures S6.6, S6.7**), so they likely reflect seasonal patterns in soil respiration and vegetation productivity that may be distinct in the different habitat types.

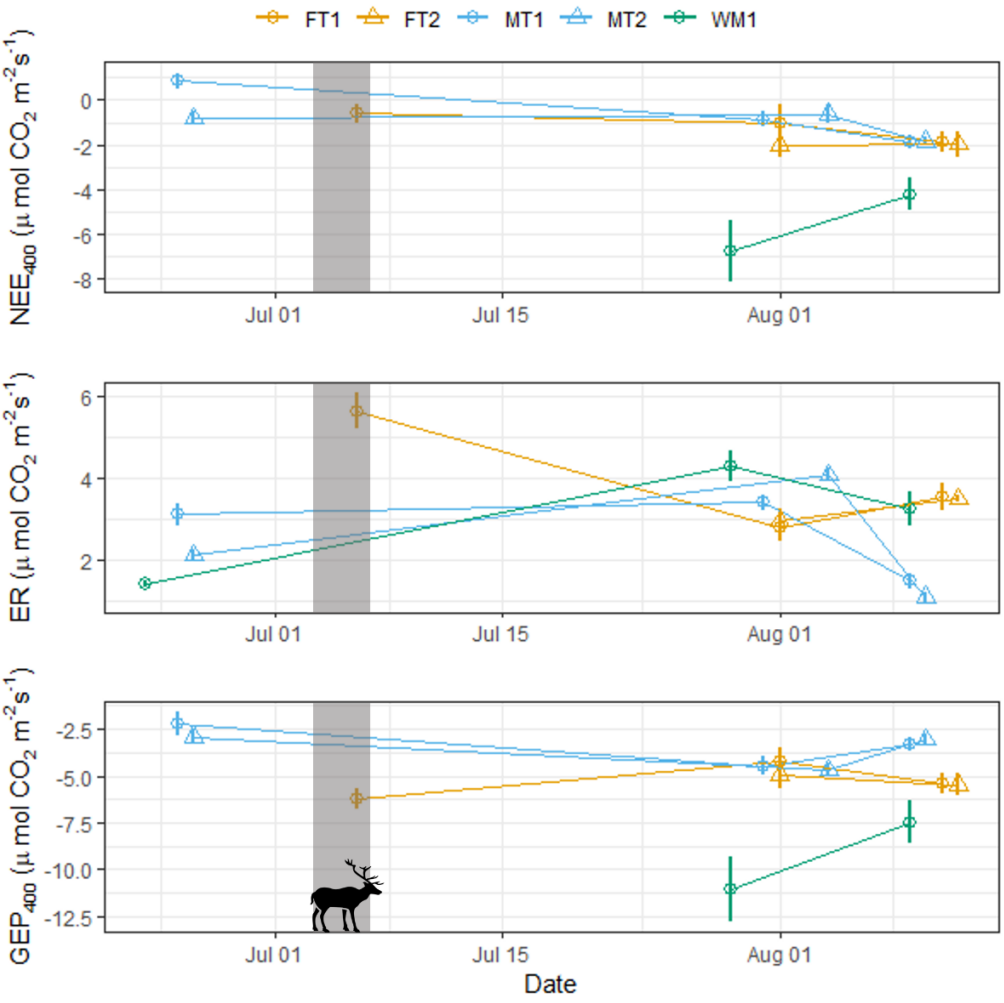


Figure 6.1: Variation in ecosystem carbon fluxes within different habitat types over multiple measurements during the 2021 growing season. Negative values indicate uptake of CO_2 from the atmosphere, whereas positive values indicate emission of CO_2. The legend labels display the identifiers given to each exclosure, which indicate the habitat type (matching colours) and the replicate number of the habitat type within the block. Each point represents the mean of the pooled measurements for the treatments and control (n = 4) within the exclosure, and error bars are standard errors. The shaded area indicates the period when a herd of ~2,000 reindeer camped in the study area.

Herbivory exclusion and habitat type, as well as the interaction between them, had significant effects on NEE_{400} and GEP_{400}, whereas only herbivory exclusion and the interaction between herbivory exclusion and habitat type were significant for ER (**Table 6.2**). Across habitat types, the most consistent finding after averaging over measurement dates was a progressive decrease in GEP_{400} with additional exclusion of herbivore classes among the plots within the exclosures (excluding controls), although these differences were not always significant (**Figure 6.2**). The control plots (C) typically had the lowest value for GEP_{400}, which was significantly different from photosynthesis in the plots excluding only reindeer (EX_L) in all habitat types. GEP_{400} was 44.6% greater in FT, 58.1% greater in MT, and 124% greater in WM in EX_L compared to C.

ER generally followed the same pattern as GEP_{400}, decreasing with additional exclusion of smaller herbivores while lowest in the controls, although ER was greatest in the controls in FT (**Figure 6.2**). These results include some measurements of ER where the corresponding flux measurements under light conditions were discarded, and thus estimation of NEE_{400} was not possible, but these ER values have a negligible impact on the overall patterns (**Figures S6.8, S6.9**). The magnitude of fluxes was larger in GEP_{400} than ER, causing all combinations of habitat types and herbivory treatments to have net uptake of CO_2 at PAR levels of 400 µmol photons m^{-2} s^{-1}. Furthermore, the magnitude of the differences between herbivory treatments was larger in GEP_{400}, such that the variation in fluxes across treatments in NEE_{400} resembled that of GEP_{400} (**Figure 6.2**). In all habitat types, the controls had the lowest net CO_2 uptake, and for all treatments, net uptake was largest in WM and smallest in MT.

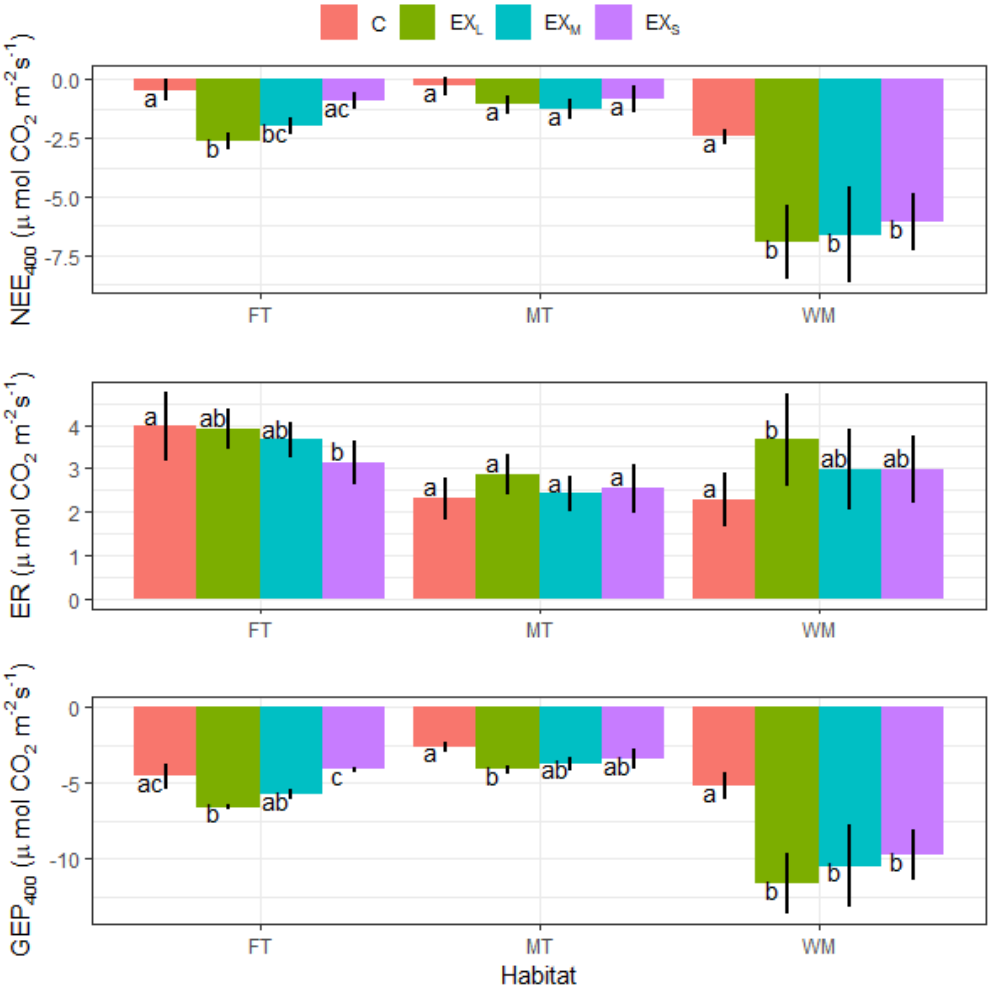


Figure 6.2: Effect of cumulative exclusion of three different size classes of herbivores on ecosystem carbon fluxes within three different habitat types. Flux values represent averages over exclosures and sampling dates, and error bars are standard errors. Different letters atop bars denote significant differences (p<0.05) determined from Bonferroni corrected post hoc comparisons following linear mixed effects modelling (i.e., responses were not significantly different within a habitat if bars share the same letter).

Table 6.2: Statistical summary of the results of a linear mixed effects model testing the effects of herbivory exclusion, habitat type, and the interaction between them on light-standardised net ecosystem exchange (NEE_{400}) and its component fluxes: GEP_{400} and ER.

	NEE_{400}			GEP_{400}			ER		
Effect	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Herbivory exclusion	3, 30	30.8	<0.001	3, 30	37.5	<0.001	3, 33	5.4	0.004
Habitat type	2, 10	16.7	<0.001	2, 10	19.5	<0.001	2, 11	1.2	0.343
Herbivory + Habitat	6, 30	6.2	<0.001	6, 30	8.8	<0.001	6, 33	2.8	0.026

Within the different habitat types, the magnitude and significance of the differences in fluxes between herbivore exclusion treatments varied. In FT, the findings of significance differed depending on the flux, but in NEE_{400}, both EX_L and EX_M had significantly greater net uptake than C, while EX_L also had significantly greater uptake than EX_S. There were no significant differences between treatments in MT, except for the increase in GEP_{400} in EX_L compared to C. In WM¸ C was clearly distinct from the exclosure plots in GEP_{400} and NEE_{400}, but only C and EX_L were significantly different in ER. Although soil moisture and soil temperature varied during the growing season (**Figure S6.7**), they did not differ significantly ($p<0.05$) between herbivory treatments (**Table S6.1**). The regression analyses between the CO_2 fluxes and the photograph-derived cover of different vegetation groups or litter also did not produce statistically significant models, except in some cases where ER was the response variable (**Tables S6.2, S6.3**). Variations in photosynthesis and net uptake were not significantly explained by the litter or plant cover.

6.7 Discussion

6.7.1 The effects of excluding large, medium, and small herbivores

Our results indicate that after 7 years of an experiment excluding different size classes of herbivores, the exclusion of reindeer led to larger values of net CO_2 uptake measured during growing season, but the additional cumulative exclusion of medium- and then small-sized herbivores weakened this effect. This finding supports our hypothesis with respect to large herbivores, as the primary impact of exclusion of reindeer was an increase in GEP, but the absence of a further increase with the elimination of consumption from additional classes of herbivores was unexpected. Whereas the difference in GEP_{400} between the grazed controls and EX_L was significant regardless of habitat, the differences between the exclosure treatments were consistent but not significant except in FT, where EX_S had significantly lower GEP_{400} than EX_M and EX_L (**Figure 6.2**). However, this effect of additional exclusion of smaller

herbivores on carbon fluxes is consistent with findings from similar experiments in northern Sweden and Alaska (Metcalfe & Olofsson, 2015; Min et al., 2021). In northern Sweden, when large and small mammals were excluded, GPP_{600} was reduced, albeit insignificantly, compared to when only large mammals were excluded, despite a 25% increase in aboveground plant biomass (Metcalfe & Olofsson, 2015). Although GPP_{600} was almost identical between these same two treatments in Alaska, leaf area index and vascular plant abundance were still higher when large and small herbivores were excluded (Min et al., 2021). Additionally, another tundra ecosystem in Alaska shifted from a net sink of CO_2 to a source after 50 years of exclusion of lemmings (Lara et al., 2017). Thus, the impact of small herbivores on carbon fluxes cannot be fully explained by their consumption of plant material. Given the evidence provided by these previous studies and our findings, which suggested a similar effect with the intermediate exclusion of medium-sized herbivores as well, the mechanisms responsible warrant further investigation. Here, we discuss three possible explanations for these results:

Increased litter in medium and small herbivore exclosures: one possible explanation could be related to the amount of litter remaining in the plots, which has been observed to increase within exclosures in past experiments (e.g. Virtanen 2000, van der Wal and Brooker 2004, Falk et al. 2015). The litter accumulation may be due to the lack of grazing, but it could also be an artefact from the experimental design, as the exclosure fencing traps the litter and prevents it from being blown away. Regardless of the source, a more substantial litter layer can create shading and the need for physiological adaptions by plants, such as longer tillers in graminoids, which can reduce photosynthesis (Falk et al., 2015). However, based on the analysis of the plot photographs, litter cover did not vary substantially between the treatments and was a poor explanatory variable for the differences in CO_2 fluxes, including when only considering the exclosure plots where litter trapping may occur (**Table S6.3**).

Changes in vegetation cover: since Metcalfe & Olofsson (2015) and Min et al. (2021) found that CO_2 uptake was similar or higher with small herbivores present despite lower overall aboveground plant biomass and abundance, differences in the community composition might explain the flux patterns. In essence, this potential explanation suggests that small herbivores reduce the amount of vegetation present but shift the community to more productive species. Large and small mammalian herbivores have been observed to shift tundra communities towards greater species diversity (Lindén et al., 2021; Sundqvist et al., 2019), and evidence exists that herbivore-driven transitions towards more graminoid-dominated vegetation can

enhance primary production (Olofsson, Stark, et al., 2004; Zimov et al., 2012). Yet, our analysis of the plant groups in the plot photographs did not indicate that differences in the cover of these groups was significantly linked to variations in photosynthesis (**Table 6.2**). Comparisons of the biomass, in addition to the cover, of the different plant groups within each plot may better explain the fluxes, but deriving biomass is not possible due to the lack of structure visible in the photographs. Still, the lack of a significant relationship between community composition and CO_2 fluxes in our analysis suggests that the mechanism behind the patterns we observed likely was not species shifts.

Changes in nutrient cycling: the greater GEP in plots accessible to small- and medium-sized herbivores may also be due to differences in nutrient cycle dynamics. Although changes in nutrients may cause changes in the community composition (Olofsson, Stark, et al., 2004) linking to the previous, discarded explanation, they may also have intraspecific effects on plant traits (Bjorkman et al., 2018). Herbivores promote nutrient cycling via the addition of faeces and urine, which can be important in nutrient-limited tundra ecosystems (Egelkraut et al., 2020; Tanentzap & Coomes, 2012). In a comparison of nutrient levels in grassland plant communities depending on disturbance by small rodents and reindeer, winter disturbance by small rodents led to significantly higher nutrient content in forbs and grasses that persisted over the entirety of the next growing season (Petit Bon et al., 2020). This effect was stronger than the effect of summer reindeer herbivory on nutrient content and greater when reindeer were excluded. These results support a possible explanation that in our experiment, the primary impact of reindeer was defoliation, which reduced photosynthesis in the controls compared to the exclosure plots, but within the exclosures, plant productivity in plots with small- and medium-sized herbivores was progressively higher due to enhanced nutrient availability. Formally testing this hypothesis would entail measuring nutrient content in leaves sampled from the plots or in the soil, but it is supported by our field observations, as well as those of Baubin et al. (2016), of high presence of faeces in exclosure plots, particularly hare faeces in FT where the effect of small and medium-sized herbivores was largest. We propose that it is the most likely explanation for the offsetting effects of the different size classes of herbivores after ruling out explanations related to litter and the cover of different plant groups.

6.7.2 Effects of peaks in herbivore abundance at the time of measurements

Although there was a rodent peak in our study area during the 2021 growing season, there is usually a one-year lag between changes in rodent density and plant biomass because rodents

have the largest effect on the plants they forage during the winter (Olofsson et al., 2012). Consumption by lemmings has been shown to reduce CO_2 uptake, but this impact is transient and limited to a single growing season (Plein et al., 2022). Thus, it is likely that the effect of rodent consumption on CO_2 fluxes stemming from the rodent peak would have only emerged in the year after our flux measurements, so our findings, which instead showed increased uptake, likely are unrelated to the peak. Instead, attributing the impacts of small- and medium-sized herbivores to greater nutrient inputs, which would be a more stable effect over time, is further supported by their prominence in FT. Additionally, whereas differences between treatments were similar for both GEP_{400} and ER in WM and MT, in FT, the control plots had the greatest ER despite having significantly lower GEP_{400} than EX_L (**Figure 6.2**), implying the importance of ecosystem functions besides those arising directly from differences in plant cover. The significance of differences occurring in all treatments in FT agrees with our hypothesis that all size classes of herbivores would affect carbon fluxes in this habitat type, although the effect of small- and medium-sized herbivores was opposite to our expectations.

The impact of reindeer consumption in the control plots was likely amplified by the arrival of a herd of 2,000 reindeer during the study period. Only two sets of measurements of NEE_{400} and GEP_{400}, one in each of the MT exclosures, occurred before their arrival. In MT2, the grazed control had lower GEP_{400} compared to the treatments, but in MT1, GEP_{400} was larger in the controls than in EX_S and the differences between the control and any of the treatments were within the standard errors (**Figure S6.2**). However, MT was the habitat type where the differences between treatments were least significant, also in accordance with our hypothesis. Consequently, it is unclear whether the differences in fluxes between the controls and the plots excluding reindeer would have occurred without the disturbance from the large herd, but there will likely be a lasting impact on the vegetation, as legacy effects from reindeer herbivory have been observed to persist long after the disturbance (Egelkraut et al., 2018; Walker et al., 2009).

6.7.3 The need to consider herbivory when considering carbon cycling in the tundra

Since we only took two or three sets of flux measurements at each exclosure, we were unable to extrapolate our results to determine the cumulative photosynthesis and ecosystem respiration as well as the differences between treatments over the whole growing season. However, the differences we measured in instantaneous ecosystem CO_2 exchange related to habitat type and herbivore exclusion likely persisted over the season and scaled up to affect the net carbon balance. Although we were only able to compare fluxes from multiple different exclosures

within the same habitat type on a few occasions, the consistency between these measurements suggests that efforts to scale up carbon fluxes may reasonably assume that a significant portion of the variation is captured by landscape heterogeneity and the assemblage of herbivores present, at least within our study region. Still, more carbon flux measurements, either from eddy covariance or chamber measurements, are needed, especially from understudied regions such as the Siberian Arctic (Virkkala et al., 2018), where this study took place, to constrain the uncertainty in upscaled statistical models (Virkkala et al., 2021).

MT was included as a habitat type in the experimental design used here because it is common in the low Arctic and therefore contributes substantially to the overall carbon balance of the region. We found a smaller impact of herbivory in MT compared to the other habitat types, but as the Arctic warms, the distribution of landcover is changing as well. Shrubs, especially tall shrubs such as the *Salix* species found in WM, are expanding, and their encroachment could transform areas that are currently within MT (Myers-Smith et al., 2011). However, large herbivores limit this shrub expansion (Olofsson et al., 2009; Olofsson & Post, 2018) due to their strong effects within habitat types similar to WM, as we hypothesized and found here. Our results demonstrate that to predict carbon cycle feedbacks in the Arctic as rapid warming continues, the top-down role of herbivory must be considered jointly with bottom-up abiotic factors.

6.8 References

Bardgett, R. D., & Wardle, D. A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, *84*(9), 2258–2268. https://doi.org/10.1890/02-0274

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using {lme4}. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Baubin, C., Ehrich, D., Ravolainen, V., Sokovina, S., Ektova, S., Sokolova, N., Ims, R. A., & Sokolov, A. (2016). First results from an experiment excluding three sizes classes of herbivores from tundra vegetation in southern Yamal, Russia. *Czech Polar Reports*, *6*(2), 132–140. https://doi.org/10.5817/CPR2016-2-12

Berner, L. T., Massey, R., Jantz, P., Forbes, B. C., Macias-Fauria, M., Myers-Smith, I., Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B. V., Burns, P., Zetterberg, P., D'Arrigo, R., & Goetz, S. J. (2020). Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature Communications*, *11*(1), 4621. https://doi.org/10.1038/s41467-020-18479-5

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Thomas, H. J. D., Alatalo, J. M., Alexander, H., Anadon-Rosell, A., Angers-Blondin, S., Bai, Y., Baruah, G., te Beest, M., Berner, L., Björk, R. G., Blok, D., Bruelheide, H., Buchwal, A., Buras, A., Carbognani, M., … Zamin, T. (2018). Tundra Trait Team: A database of plant traits

spanning the tundra biome. *Global Ecology and Biogeography*, *27*(12), 1402–1411. https://doi.org/10.1111/geb.12821

Cahoon, S. M. P., Sullivan, P. F., Post, E., & Welker, J. M. (2012). Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global Change Biology*, *18*(2), 469–479. https://doi.org/10.1111/j.1365-2486.2011.02528.x

Egelkraut, D., Aronsson, K.-Å., Allard, A., Åkerholm, M., Stark, S., & Olofsson, J. (2018). Multiple Feedbacks Contribute to a Centennial Legacy of Reindeer on Tundra Vegetation. *Ecosystems*, *21*(8), 1545–1563. https://doi.org/10.1007/s10021-018-0239-z

Egelkraut, D., Barthelemy, H., & Olofsson, J. (2020). Reindeer trampling promotes vegetation changes in tundra heathlands: Results from a simulation experiment. *Journal of Vegetation Science*, *31*(3), 476–486. https://doi.org/10.1111/jvs.12871

Ehrich, D., Henden, J.-A., Ims, R. A., Doronina, L. O., Killengren, S. T., Lecomte, N., Pokrovsky, I. G., Skogstad, G., Sokolov, A. A., Sokolov, V. A., & Yoccoz, N. G. (2012). The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? *Oecologia*, *168*(1), 141–151. https://doi.org/10.1007/s00442-011-2059-0

Falk, J. M., Schmidt, N. M., Christensen, T. R., & Ström, L. (2015). Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. *Environmental Research Letters*, *10*(4). https://doi.org/10.1088/1748-9326/10/4/045001

Forbes, B. C., Stammler, F., Kumpula, T., Meschtyb, N., Pajunen, A., & Kaarlejärvi, E. (2009). High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences*, *106*(52), 22041–22048. https://doi.org/10.1073/pnas.0908286106

Kaarlejärvi, E., Hoset, K. S., & Olofsson, J. (2015). Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. *Global Change Biology*, *21*(9), 3379–3388. https://doi.org/10.1111/gcb.12970

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. ., Linder, H. P., & Kessler, M. (2018). Climatologies at high resolution for the earth's land surface areas. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.kd1d4

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 1–20. https://doi.org/10.1038/sdata.2017.122

Kelsey, K. C., Leffler, A. J., Beard, K. H., Schmutz, J. A., Choi, R. T., & Welker, J. M. (2016). Interactions among vegetation, climate, and herbivory control greenhouse gas fluxes in a subarctic coastal wetland. *Journal of Geophysical Research: Biogeosciences*, *121*(12), 2960–2975. https://doi.org/10.1002/2016JG003546

Lara, M. J., Johnson, D. R., Andresen, C., Hollister, R. D., & Tweedie, C. E. (2017). Peak season carbon exchange shifts from a sink to a source following 50+ years of herbivore exclusion in an Arctic tundra ecosystem. *Journal of Ecology*, *105*(1), 122–131. https://doi.org/10.1111/1365-2745.12654

Lenth, R. V. (2022). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. https://cran.r-project.org/package=emmeans

Lindén, E., Gough, L., & Olofsson, J. (2021). Large and small herbivores have strong effects on tundra vegetation in Scandinavia and Alaska. *Ecology and Evolution*, *11*(17), 12141–12152. https://doi.org/10.1002/ece3.7977

Macias-Fauria, M., Jepson, P., Zimov, N., & Malhi, Y. (2020). Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190122.

https://doi.org/10.1098/rstb.2019.0122
Metcalfe, D. B., & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO 2 exchange during the peak of the growing season. *Oikos*, *124*(12), 1632–1638. https://doi.org/10.1111/oik.02085
Min, E., Wilcots, M. E., Naeem, S., Gough, L., McLaren, J. R., Rowe, R. J., Rastetter, E. B., Boelman, N. T., & Griffin, K. L. (2021). Herbivore absence can shift dry heath tundra from carbon source to sink during peak growing season. *Environmental Research Letters*, *16*(2), 024027. https://doi.org/10.1088/1748-9326/abd3d0
Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., MacIas-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4). https://doi.org/10.1088/1748-9326/6/4/045509
Olofsson, J., E. Hulme, P., Oksanen, L., & Suominen, O. (2004). Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, *106*(2), 324–334. https://doi.org/10.1111/j.0030-1299.2004.13224.x
Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, *15*(11), 2681–2693. https://doi.org/10.1111/j.1365-2486.2009.01935.x
Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761). https://doi.org/10.1098/rstb.2017.0437
Olofsson, J., Stark, S., & Oksanen, L. (2004). Reindeer influence on ecosystem processes in the tundra. *Oikos*, *105*(2), 386–396. https://doi.org/10.1111/j.0030-1299.2004.13048.x
Olofsson, J., te Beest, M., & Ericson, L. (2013). Complex biotic interactions drive long-term vegetation dynamics in a subarctic ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624), 20120486. https://doi.org/10.1098/rstb.2012.0486
Olofsson, J., Tommervik, H., & Callaghan, T. V. (2012). Vole and lemming activity observed from space. *Nature Climate Change*, *2*(12), 880–883. https://doi.org/10.1038/nclimate1537
Petit Bon, M., Inga, K. G., Jónsdóttir, I. S., Utsi, T. A., Soininen, E. M., & Bråthen, K. A. (2020). Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities. *Oikos*, *April*, 1–14. https://doi.org/10.1111/oik.07074
Plein, J., Clark, R. W., Arndt, K. A., Oechel, W. C., Stow, D., & Zona, D. (2022). Response of vegetation and carbon fluxes to brown lemming herbivory in northern Alaska. *Biogeosciences*, *19*(11), 2779–2794. https://doi.org/10.5194/bg-19-2779-2022
Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(34), 12353–12358. https://doi.org/10.1073/pnas.0802421105
R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. https://www.r-project.org/
Ravolainen, V. T., Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Henden, J.-A., & Killengreen, S. T. (2011). Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. *Basic and Applied Ecology*, *12*(8), 643–653. https://doi.org/10.1016/j.baae.2011.09.009
Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M., Davies, A. B., & Goetz, S. J. (2018). Animals and the zoogeochemistry of the carbon

cycle. *Science*, *362*(6419), eaar3213. https://doi.org/10.1126/science.aar3213

Schuur, E. A. G., McGuire, A. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., Hugelius, G., Koven, C. D., Kuhry, P., Lawrence, D. M., Natali, S. M., Olefeldt, D., Romanovsky, V. E., Schaefer, K., Turetsky, M. R., Treat, C. C., & Vonk, J. E. (2015). Climate change and the permafrost carbon feedback. *Nature*, *520*(7546), 171–179. https://doi.org/10.1038/nature14338

Sjögersten, S., Van Der Wal, R., & Woodin, S. J. (2008). Habitat Type Determines Herbivory Controls Over Co2 Fluxes in a Warmer Arctic. *Ecology*, *89*(8), 2103–2116.

Skarin, A., Verdonen, M., Kumpula, T., Macias-Fauria, M., Alam, M., Kerby, J., & Forbes, B. C. (2020). Reindeer use of low Arctic tundra correlates with landscape structure. *Environmental Research Letters*, *15*(11), 115012. https://doi.org/10.1088/1748-9326/abbf15

Sokolova, N. A., Sokolov, A. A., Ims, R. A., Skogstad, G., Lecomte, N., Sokolov, V. A., Yoccoz, N. G., & Ehrich, D. (2014). Small rodents in the shrub tundra of Yamal (Russia): Density dependence in habitat use? *Mammalian Biology*, *79*(5), 306–312. https://doi.org/10.1016/j.mambio.2014.04.004

Sundqvist, M. K., Moen, J., Björk, R. G., Vowles, T., Kytöviita, M. M., Parsons, M. A., & Olofsson, J. (2019). Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. *Journal of Ecology*, *April*, 1–13. https://doi.org/10.1111/1365-2745.13201

Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: Do browsing and grazing herbivores matter? *Biological Reviews*, *87*(1), 72–94. https://doi.org/10.1111/j.1469-185X.2011.00185.x

Treat, C. C., Marushchak, M. E., Voigt, C., Zhang, Y., Tan, Z., Zhuang, Q., Virtanen, T. A., Räsänen, A., Biasi, C., Hugelius, G., Kaverin, D., Miller, P. A., Stendel, M., Romanovsky, V., Rivkin, F., Martikainen, P. J., & Shurpali, N. J. (2018). Tundra landscape heterogeneity, not interannual variability, controls the decadal regional carbon balance in the Western Russian Arctic. *Global Change Biology*, *24*(11), 5188–5204. https://doi.org/10.1111/gcb.14421

van der Wal, R., & Brooker, R. W. (2004). Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, *18*(1), 77–86. https://doi.org/10.1111/j.1365-2435.2004.00820.x

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (Fourth). Springer. http://www.stats.ox.ac.uk/pub/MASS4/

Virkkala, A., Aalto, J., Rogers, B. M., Tagesson, T., Treat, C. C., Natali, S. M., Watts, J. D., Potter, S., Lehtonen, A., Mauritz, M., Schuur, E. A. G., Kochendorfer, J., Zona, D., Oechel, W., Kobayashi, H., Humphreys, E., Goeckede, M., Iwata, H., Lafleur, P. M., … Luoto, M. (2021). Statistical upscaling of ecosystem CO 2 fluxes across the terrestrial tundra and boreal domain: Regional patterns and uncertainties. *Global Change Biology*, *27*(17), 4040–4059. https://doi.org/10.1111/gcb.15659

Virkkala, A., Virtanen, T., Lehtonen, A., Rinne, J., & Luoto, M. (2018). The current state of CO2 flux chamber studies in the Arctic tundra: A review. *Progress in Physical Geography*, *42*(2), 162–184. https://doi.org/10.1177/0309133317745784

Virtanen, R. (2000). Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland. *Oikos*, *90*(2), 295–300. https://doi.org/10.1034/j.1600-0706.2000.900209.x

Walker, D. A., Leibman, M. O., Epstein, H. E., Forbes, B. C., Bhatt, U. S., Raynolds, M. K., Comiso, J. C., Gubarkov, A. A., Khomutov, A. V., Jia, G. J., Kaarlejärvi, E., Kaplan, J. O., Kumpula, T., Kuss, P., Matyshak, G., Moskalenko, N. G., Orekhov, P., Romanovsky, V. E., Ukraientseva, N. G., & Yu, Q. (2009). Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and

social factors affecting the Arctic normalized difference vegetation index. *Environmental Research Letters*, *4*(4), 045004. https://doi.org/10.1088/1748-9326/4/4/045004

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A., & The other members of the CAVM Team. (2005). The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, *16*(3), 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x

Ylänne, H., Kaarlejärvi, E., Väisänen, M., Männistö, M. K., Ahonen, S. H. K., Olofsson, J., & Stark, S. (2020). Removal of grazers alters the response of tundra soil carbon to warming and enhanced nitrogen availability. *Ecological Monographs*, *90*(1), 1–13. https://doi.org/10.1002/ecm.1396

Ylänne, H., & Stark, S. (2019). Distinguishing Rapid and Slow C Cycling Feedbacks to Grazing in Sub-arctic Tundra. *Ecosystems*, *22*(5), 1145–1159. https://doi.org/10.1007/s10021-018-0329-y

Zimov, S. A., Zimov, N. S., Tikhonov, A. N., & Chapin, I. S. (2012). Mammoth steppe: A high-productivity phenomenon. *Quaternary Science Reviews*, *57*, 26–45. https://doi.org/10.1016/j.quascirev.2012.10.005

6.9 Supplementary material

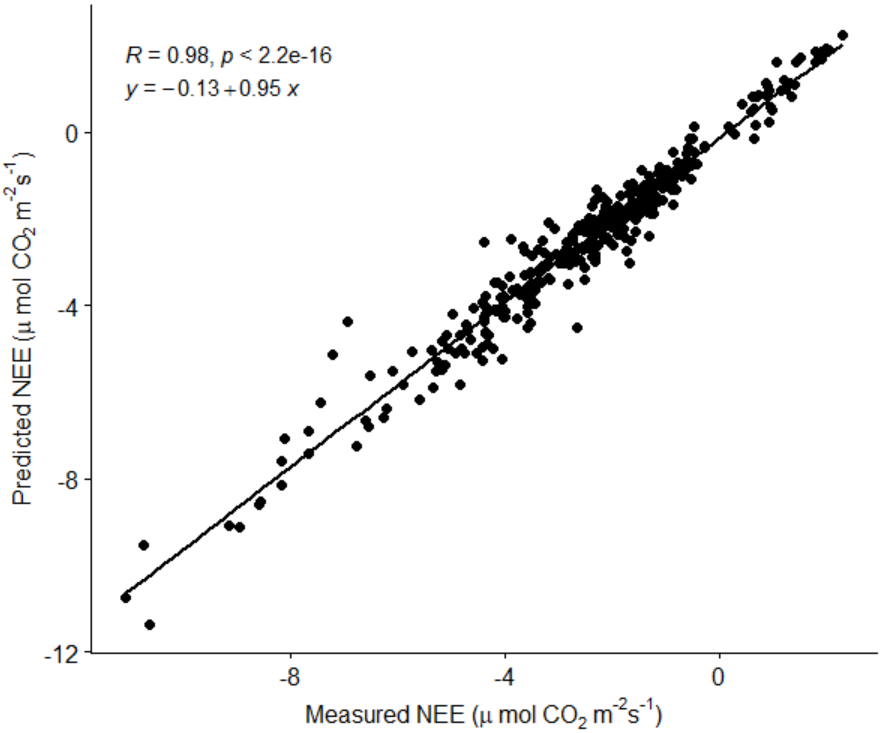


Figure S6.1: Relationship between the predicted and measured NEE values for the carbon flux measurements (excluding dark respiration measurements). The predicted values were determined by fitting a rectangular hyperbola to the measured NEE values under varying light conditions for each plot on each date. A negative value of NEE indicates uptake of CO_2 from the atmosphere, whereas positive values indicate net emission of CO_2.



Figure S6.2: Example of a set of annotated plot photographs used to score the presence and percent cover of seven plant groups as well as litter. This plot, photographed during the flux measurements on 1 August 2021, excludes only reindeer (EX_L) and is within the forb tundra habitat type. The top photograph was taken from chest height, and the bottom photograph was taken from lower height to capture the vegetation more clearly. The rectangle (left) and grid (right) were first placed on the top photograph to include the correct plot area (0.6 x 0.6 m), and then they were matched to cover the same area in the bottom photograph.

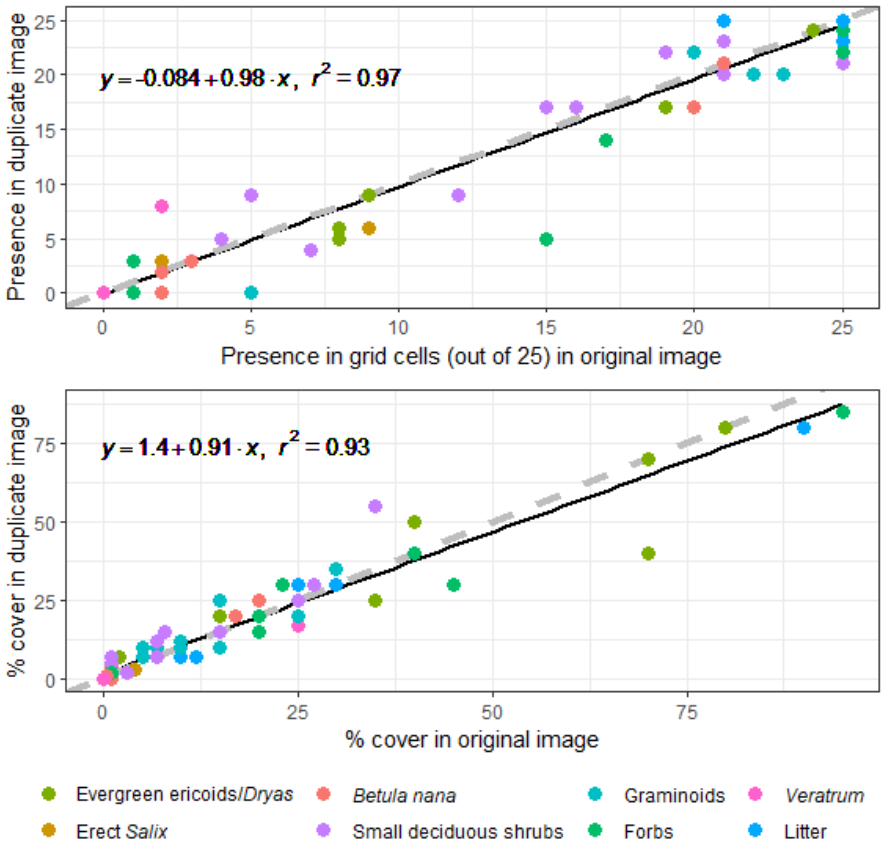


Figure S6.3: Comparison of the scoring of plot photographs between duplicates (*n*=11) that were randomly included in the dataset. The top panel shows the recorded presence, and the bottom panel shows percent cover. The dashed grey line is a one-to-one line, whereas the solid black line is the linear least-squares line. The estimated scores for litter are included in addition to the seven plant groups/species used to categorise the vegetation.

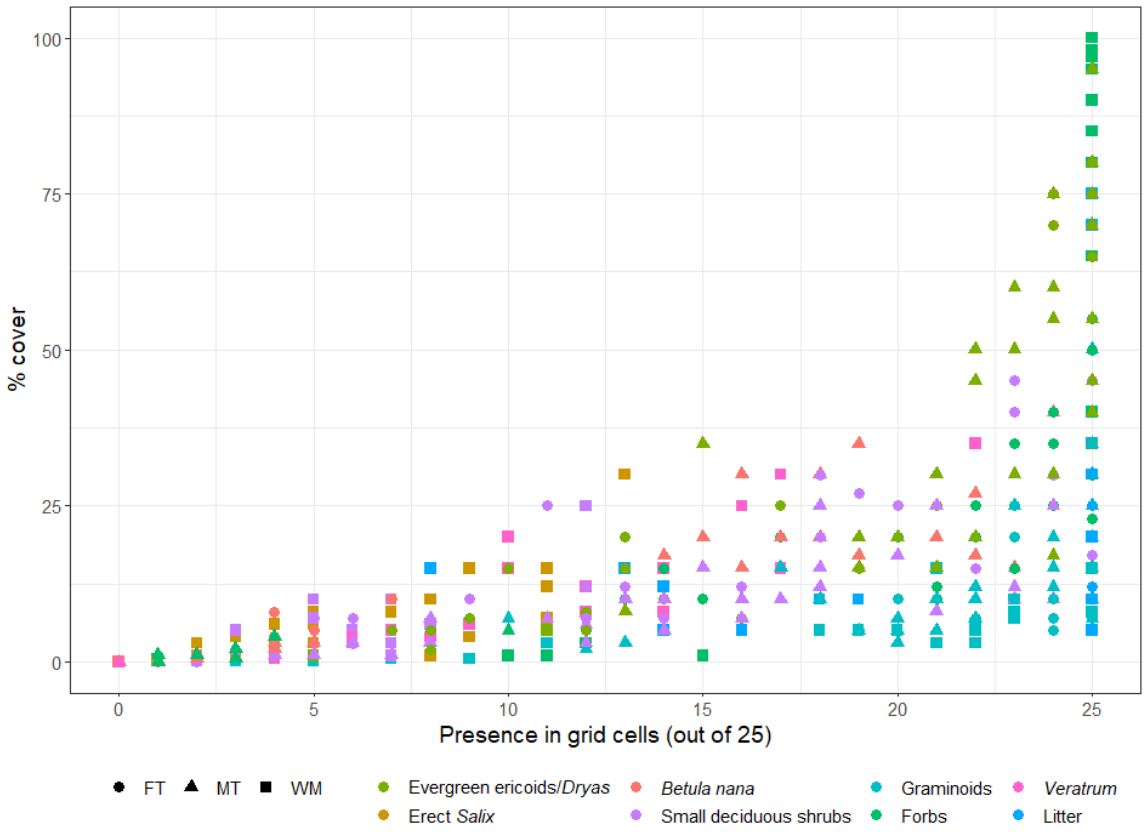


Figure S6.4: Correspondence between the percent cover and presence scores for all plot photos (disregarding duplicates, *n*=112). The estimated scores for litter are included in addition to the seven plant groups/species as different coloured points. The point shape depicts the habitat type (FT=forb tundra, MT=mesic tundra, WM=willow meadows).



Figure S6.5: Carbon flux measurements for each exclosure on each measurement date. Error bars show standard errors for the two plots of the same treatment within an exclosure or are missing when measurements for only one plot were retained. In some instances, more measurements were retained for ER than for NEE_{400} due to a lack of linear relationships found with CO_2 concentration over time or failure of the measured fluxes to fit a rectangular hyperbola, preventing prediction at a standardised PAR value. In these cases, GEP_{400} was calculated only for the plots with a value for NEE_{400}.

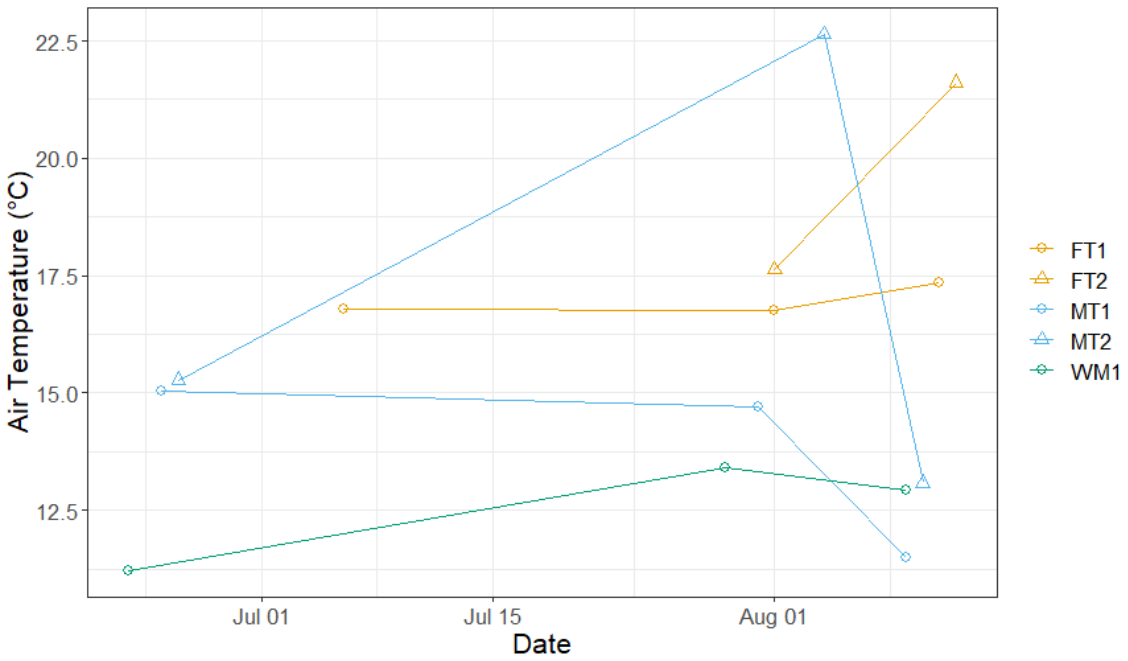


Figure S6.6: Average air temperature during the carbon flux measurements at each exclosure on each measurement date. Air temperature was logged at 5-minute intervals by a weather station at the study site less than 2 km away from each exclosure.



Figure S6.7: Soil moisture and soil temperature at 10 cm and 20 cm depths measured by handheld probes in each plot directly after carbon flux measurements. Soil moisture measurements were not possible during the last set of measurements in each exclosure in early August due to equipment malfunction, and soil temperature was only measured at 20 cm during the first measurements in K-WM1.

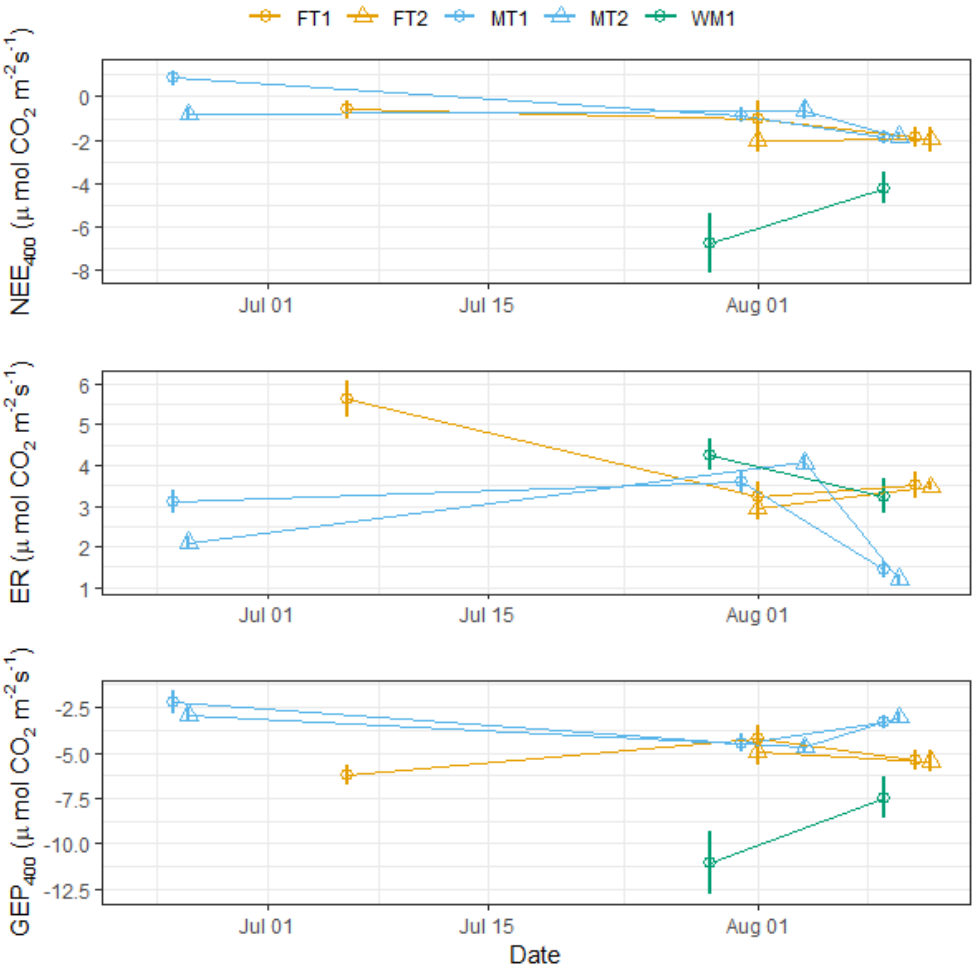


Figure S6.8: Variation in ecosystem carbon fluxes over multiple measurements during the 2021 growing season, excluding any ER measurements for which the associated NEE measurements were discarded. The panels for NEE_{400} and GEP_{400} are unchanged from **Figure 6.1**.

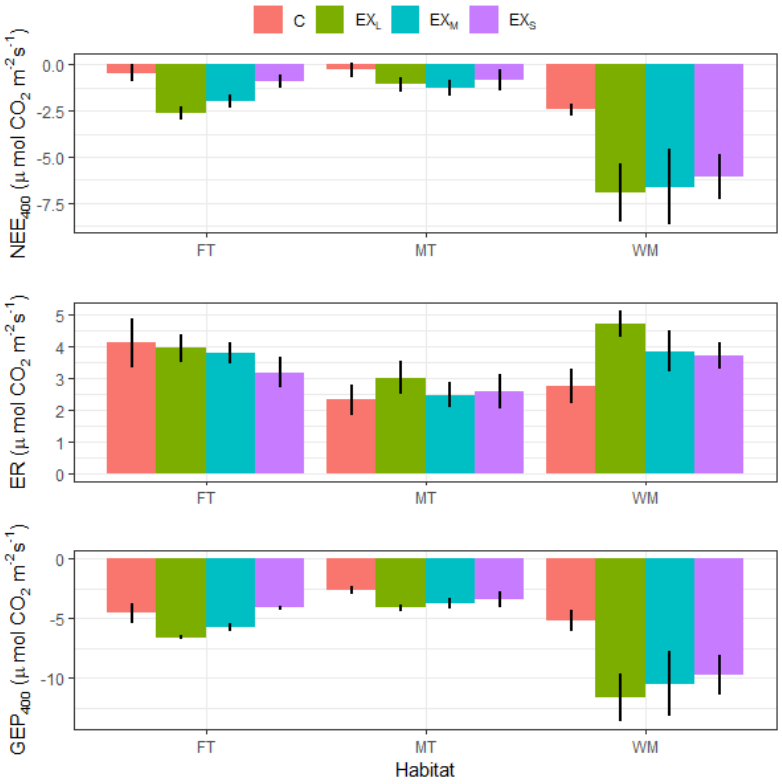


Figure S6.9: Effect of cumulative exclusion of three different size classes of herbivores on ecosystem carbon fluxes within three different habitat types, excluding any ER measurements for which the associated NEE measurements were discarded. The panels for NEE_{400} and GEP_{400} are unchanged from **Figure 6.2**.

Table S6.1: Statistical summary of the results of a linear mixed effects model testing the effects of herbivory exclusion, habitat type, and the interaction between them on soil moisture and soil temperature at 10 and 20 cm. The only significant effect (p<0.05) was that of habitat type on soil temperature at 10 cm, but no significant differences were subsequently found using Bonferroni corrected post hoc comparisons.

	Soil Moisture			Soil T at 10 cm			Soil T at 20 cm		
Effect	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Herbivory exclusion	3, 18	2.32	0.110	3, 30	2.73	0.061	3, 33	0.87	0.466
Habitat type	2, 2	2.91	0.254	2, 10	8.48	0.007	2, 11	1.82	0.207
Herbivory + Habitat	6, 18	1.48	0.239	6, 30	1.29	0.292	6, 33	2.13	0.076

Table S6.2: Results from the stepwise regression models between the plot CO_2 fluxes and the presence and percent cover of the seven vegetation groups interpreted from the plot photographs. Separate models were created for each habitat type (FT=forb tundra, MT=mesic tundra, WM=willow meadow) and the two vegetation metrics. Statistics are reported for the overall best model for each stepwise regression (R^2 is adjusted R-squared) as well as the variables (vars) included in that best model and their coefficient values (est.). The sign of the carbon fluxes is consistent with how they are presented throughout, such that a negative coefficient in the GEP model indicates that higher levels of the plant group are linked with higher CO_2 uptake, or more negative GEP. Plant groups/species abbreviations: *Betula*=*Betula nana*, Evergr.=Evergreen ericoids/*Dryas octopetala*, Decid.=Small deciduous shrubs, Gram.=Graminoids, *Salix*=Erect *Salix*, *Verat*.=*Veratrum lobelianum*.

		NEE					ER					GEP				
		Model		Coefficients			Model		Coefficients			Model		Coefficients		
Habitat	Measure	R^2	*p*	vars	est.	*p*	R^2	*p*	vars	est.	*p*	R^2	*p*	vars	est.	*p*
FT	Presence	0.06	0.19	Forbs	-0.14	0.19	0.22	0.04	*Betula*	-0.11	0.04	—	—	—	—	—
n=16	% cover	—	—	—	—	—	0.19	0.14	Evergr.	-0.01	0.19	—	—	—	—	—
									Betula	-0.11	0.05					
									Forbs	-0.02	0.15					
MT	Presence	0.19	0.06	Gram.	0.55	0.06	0.12	0.11	Decid.	0.04	0.11	0.18	0.07	Gram.	0.57	0.07
n=16	% cover	0.24	0.08	Evergr.	-0.02	0.21	0.10	0.12	Decid.	0.04	0.12	0.19	0.06	Evergr.	-0.03	0.06
				Gram.	0.06	0.16										
WM	Presence	0.43	0.07	*Verat.*	-0.37	0.07	0.32	0.08	*Verat.*	0.10	0.08	0.44	0.06	*Verat.*	-0.46	0.06
n=8	% cover	0.63	0.41	*Salix*	-0.11	0.66	0.67	0.06	Decid.	-0.17	0.02	0.86	0.26	*Salix*	-0.21	0.38
				Decid.	0.21	0.51			Gram.	0.40	0.02			Decid.	0.44	0.23
				Gram.	-0.79	0.42			*Verat.*	0.08	0.02			Gram.	-1.43	0.20
				Forbs	-0.13	0.40								Forbs	-0.14	0.30
				Verat.	-0.25	0.29								*Verat.*	-0.37	0.16

Table S6.3: Results of linear regression between plot CO_2 fluxes and the litter cover interpreted from plot photographs. The regressions were run separately for each habitat type (FT=forb tundra, MT=mesic tundra, WM=willow meadow) as well as for two separate combinations of plots: all plots or just exclosure plots (excluding controls). The coefficient for litter cover is reported in addition to the r-squared and p-value for the regression model. The sign of the carbon fluxes is consistent with how they are presented throughout, such that a negative coefficient in the GEP model indicates that higher litter cover is linked with higher CO_2 uptake, or more negative GEP.

		NEE			ER			GEP		
Habitat	Plots	Coeff.	r^2	p	Coeff.	r^2	p	Coeff.	r^2	p
FT	All	0.01	<0.01	0.85	-0.04	0.27	0.04	0.05	0.06	0.35
	Only EX	0.03	0.03	0.57	-0.04	0.29	0.07	0.07	0.11	0.28
MT	All	0.04	0.17	0.13	-0.01	0.02	0.65	0.05	0.20	0.09
	Only EX	<0.01	<0.01	0.93	-0.03	0.17	0.18	0.03	0.08	0.41
WM	All	-0.12	0.04	0.69	0.14	0.44	0.07	-0.25	0.09	0.51
	Only EX	-0.07	0.06	0.65	0.12	0.43	0.16	-0.19	0.23	0.34

Chapter 7:
Synthesis and conclusion


Photo: Marcus Spiegel

7.1 Summary

This doctoral thesis aimed to advance our understanding of the influence of top-down regulation by herbivores in tundra ecosystems. I set out to detect how the broad-scale impacts of herbivory interact with warming-driven Arctic vegetation trends and to explain the spatial heterogeneity in the effects of herbivory. In **Chapter 1**, I presented the following four key research objectives:

1. Does reindeer herbivory have a regional-scale effect on tundra vegetation that can be detected using space-borne satellite imagery?
2. How does vegetation change across a landscape after the area is used for pastures along the migration route of a large reindeer herd?
3. What is the resultant effect on ecosystem functioning when reindeer herbivory interacts with the effects of other herbivores within the local assemblage?
4. How do landcover and topography mediate ecosystem responses to reindeer herbivory?

I addressed these four objectives through a series of three research chapters, which progressed from the regional to plot scale. I review the main findings from each chapter below and then synthesise the ways in which the research advanced our knowledge of ecological dynamics and developed methodological innovations. I conclude with a discussion of implications and potential future research directions.

7.2 Main findings

Comparisons in **Chapter 4** provided evidence that reindeer have had a regional-scale influence on shrub growth and expansion in Yar-Sale/Panayevsk in south-central Yamal. Where reindeer herbivory pressure was higher, there was lower coverage of tall woody vegetation and less sensitivity of productivity to climate exclusively within this vegetation type. The differences in the landcover distributions and VSI attributed to herbivory were relatively small but consistent across six different spatial comparisons. The consistency of the story told by these different lines of evidence provided confidence in our conclusion that we had detected the influence of the world's largest domesticated reindeer herds by employing space-borne imagery. The findings suggest that while reindeer are not having an extensive impact on vegetation across the tundra, their top-down influence mitigates shrub growth and expansion in response to climate change, causing lower coverage of tall shrubs than there would be otherwise. These differences in vegetation cover are likely relevant for the Earth system due to their effect on carbon cycling and the energy balance.

In **Chapter 5**, I focused on the landscape scale and used repeated UAV surveys to detect significant changes in canopy height within a single growing season in an area adjacent to where a herd of ~1,000 reindeer had camped. As in **Chapter 4**, there was a clear effect of herbivory on the tall shrubs. Immediately after the herd had migrated onwards, detection of canopy height changes revealed a decrease in the lateral extent of tall vegetation likely resulting from reindeer browsing. This change was accompanied by more evenly spread, lower magnitude decreases in the height of low-lying vegetation appearing to represent reindeer trampling. Both changes happened in the part of the landscape where reindeer GPS collar data showed high reindeer activity, whereas areas with few or no GPS points showed strikingly little change even within the same habitat types. One month later, there was growth primarily in the low-lying vegetation, but again exclusively in the part of the landscape disturbed by reindeer. These results suggest that reindeer can limit shrub expansion and promote graminoid growth within a growing season after one week-long herbivory event. This transition to more graminoid-dominated vegetation has been frequently observed in past studies (**Chapter 2**) and seems to be driven especially by a combination of reindeer trampling and fertilisation with faeces and urine. Thus, our study demonstrated the application of UAV surveys to detect both immediate and lagged effects of herbivory on vegetation resulting from multiple reindeer activities. The fine grain of the imagery allowed us to observe high spatial heterogeneity in vegetation change across the landscape, which we found was related to the habitat type, the initial canopy height of the vegetation, and the amount of herbivory pressure.

Whereas **Chapters 4** and **5** evaluated responses in the plant community composition and vegetation structure to reindeer herbivory, **Chapter 6** measured ecosystem function. I compared CO_2 fluxes in plots in a 7-year exclosure experiment that cumulatively excluded three different size classes of herbivores. The smallest carbon sink generally was found when all herbivores were present, but the effect of excluding herbivore groups was not cumulative. Within the treatments excluding reindeer, the smallest carbon sink was typically found where no herbivores were present, followed by where there were only small rodents, and the largest carbon sink occurred where small rodents and medium-sized herbivores – hares and ptarmigans – were permitted. In summary, reindeer herbivory reduced the carbon sink, but the other herbivores promoted higher CO_2 uptake. This pattern was driven primarily by differences in photosynthesis (GEP) rather than respiration (ER) and was consistent across habitat types. Reindeer caused a significant reduction in photosynthesis in all habitat types, but especially in the willow meadows, whereas the increase in photosynthesis linked to small

rodents was significant and most pronounced in forb tundra. Thus, as in **Chapters 4** and **5**, the impact of reindeer herbivory was mediated by the vegetation cover and was strongest where tall shrubs were growing. The reduction in photosynthesis caused by reindeer was expected, as a large herd of ~2,000 animals visited the area for 5 days towards the start of measurements and left much of the vegetation defoliated. Yet, the offsetting effect of both small- and medium-sized herbivores suggests that their main impact likely was not grazing or damage to the vegetation, but promotion of plant growth, most likely related to enhanced nutrient levels as found by Petit Bon et al. (2020). These findings reveal that ecosystem functioning in the Arctic is dependent on the assemblage of herbivores that is present and the complex interactions between their varied activities.

7.3 Synthesis

7.3.1 Top-down control of shrub growth by reindeer

All three research chapters provided lines of evidence demonstrating that reindeer limit shrub growth and expansion. In **Chapter 4**, I detected a pattern which suggested that reindeer reduced the cover of tall woody vegetation and constrained its productivity in response to climate at the regional scale. The repeated UAV surveys in **Chapter 5** depicted how reindeer browsing around the edges of shrubs and trampling of the area between them prevented their infilling and establishment, leaving the shrubs in a browse trap, as theorised by Bråthen et al. (2017). Further, reindeer presence seemed to enhance graminoid growth. Lastly, the carbon flux measurements in **Chapter 6** showed that reindeer substantially reduced the photosynthesis where willow shrubs were a dominant species such that the productivity of the willow meadow habitat type was similar to that of mesic tundra or forb tundra. In the absence of reindeer herbivory, net uptake in the willow meadow was more than double what it was in the other habitat types. Although the influence of reindeer herbivory on shrubs in tundra ecosystems has been widely observed in prior studies (Olofsson & Post, 2018), my work demonstrates that the impact is occurring at a regional scale, emerges within a single growing season following a week-long herbivory event, and has landcover-dependent consequences for ecosystem functioning, namely carbon cycling.

The magnitude of the change in community composition resulting from reindeer herbivory has not transformed tundra ecosystems on Yamal so that they resemble the mammoth steppe, which likely would require much higher density and diversity of large herbivores (Macias-Fauria et al., 2020; Zimov et al., 1995). Yet, our evidence that reindeer are affecting shrub

cover and productivity is unprecedented in its spatial extent and further justifies calls for inclusion of Arctic herbivory into global ecosystem models (e.g., Metcalfe & Olofsson, 2015; Väisänen et al., 2014). Whereas our UAV observations in **Chapter 5** also showed the promotion of graminoids, this impact was not possible to detect in our regional-scale study given the spatial grain of our remote sensing products and the response variables chosen. Future applications of remote sensing for monitoring herbivory impacts can leverage higher resolution data to observe the plant community composition in greater detail (**Section 7.4**).

7.3.2 Importance of environmental context

Another common theme emerging from my research was the importance of environmental context in mediating the effects of herbivory. In **Chapter 6**, the carbon fluxes as well as how they responded to exclusion of herbivores varied markedly between habitat types but were comparable within replicates measured with no more than a few days in between. The topic of replication has received attention recently in field ecology, as lack of repetition has reduced confidence in findings, leading some to question whether there is a "reproducibility crisis" in the discipline (Filazzola & Cahill, 2021). However, replicating plots in traditional field ecology setups is challenging because no two areas or points in time have identical environmental conditions. With enough replicates in a randomised design, ideally the signal from the variables of interest should exceed the noise, but spatial heterogeneity can be considerable, especially in the Arctic. During my fieldwork with the exclosures, I often speculated that the carbon fluxes would likely vary substantially if the grazed controls, which could occur anywhere in the vicinity of the exclosures, were shifted even by metres.

I advocate for more studies that measure response variables continuously over space that strive not just to control for varying environmental contexts but to observe their role in the outcomes. In the remote sensing work in **Chapters 4** and **5**, I detected that the impacts of reindeer herbivory tended to appear within upland terrain and where erect shrubs were present bud did not occur uniformly in these areas. Limited sample sizes could have missed or overrepresented areas where the effects of reindeer herbivory were pronounced, yet spatially continuous measurements can provide insights into the likelihood of effects given an environmental variable and can reveal unexpected drivers, such as the clear influence of topography and moisture on sedge growth late in the growing season observed in the study site in **Chapter 5**. Although remote sensing techniques cannot be used to directly measure many variables of interest, in many cases they can be used to scale up field measurements to

extend predictions of these variables beyond the ecological plot (e.g., Orndahl et al., 2022; Siewert & Olofsson, 2020; Thomson et al., 2021).

7.3.3 Complexity of multiple herbivory activities

As Tanentzap & Coomes (2012) suggest, it is naïve to assume that the impacts of herbivores follow just from their consumption of biomass. In **Chapter 5**, the comparisons of UAV reconstructions immediately before and after an herbivory event showed the separate effects of reindeer browsing and trampling, whereas the growth in low-lying vegetation that had occurred exclusively in the disturbed area one month later was likely an emergent consequence of multiple activities including faeces and urine deposition. The responses became even more complex when multiple groups of herbivores were compared. Similarly to the finding of Petit Bon et al. (2020) that reindeer weakened the positive effects of small rodents on nutrient levels, I found in **Chapter 6** that small- and medium-sized herbivores offset the reduction in CO_2 uptake caused by reindeer herbivory.

I argue that to understand the impacts of herbivory, more focus is needed specifically on the mechanisms by which herbivores affect ecosystem structure and functioning. In **Chapter 6**, the large reduction in CO_2 uptake due to reindeer was likely primarily driven by the defoliation event that occurred earlier in the growing season. This effect on the aboveground biomass was dominant in the short term, but over longer timescales, changes in the vegetation community or belowground processes could have a larger impact on carbon cycling. Since the analysis of plant cover in **Chapter 6** did not show a strong link with carbon fluxes, intraspecific variation in plant traits such as nutrient levels, which could be independent from biomass differences, may also have been important. To predict how these responses will evolve over time, we need to understand the mechanisms responsible, including how they interact with different environmental contexts.

7.3.4 Methodological novelty

In addition to the ecological insights that I present in my research chapters, my work also contributes methodological advances that can be incorporated into future studies. Attribution of changes to biotic driving forces, especially over large spatial scales, is challenging due to the complexity and unpredictability in how biological systems interact with numerous external factors (Parmesan et al., 2013). As a result, attribution in conservation and ecological research is not well suited to the process-based models that have been developed, for

example, for attribution of extreme weather events to anthropogenic climate change. Instead, in **Chapter 4**, I demonstrated how multiple lines of evidence can be evaluated to test hypotheses related to biotic drivers by piecing together the results from separate comparisons at a regional scale. This approach was along the lines of "associative pattern attribution," which has been employed by the Intergovernmental Panel on Climate Change (IPCC) and synthesises multiple lines of evidence to reach a conclusion based on spatial and temporal measures of association (Hegerl et al., 2009). In my analysis, I used this approach to identify a consistent link between reindeer herbivory pressure and the dynamics of tall woody vegetation and to rule out the possibility of a bottom-up, rather than top-down mechanism. This methodology could be adapted for any study testing whether biological processes explain multiple patterns in space or time.

I also applied a novel approach in my use of UAV imagery to perform robust change detection in **Chapter 5**. Although the UAV data collection was relatively straightforward and used a consumer-grade camera, I employed a new workflow for using structure-from-motion (SfM) to detect canopy height change based on the work of James et al. (2017) and Graham et al. (2021). This methodology offers a solution for differentiating between significant changes and noise in the change product by calculating what magnitude of change would be necessary to qualify as significant as a variable across the study area. Previous work incorporating UAV imagery into studies of Arctic herbivory is very limited, but Siewert & Olofsson (2021) used a novel approach to detect the impacts of small rodents with NDVI. My work showed that SfM reconstructions can be used as an alternative or in addition to spectral reflectance measurements to map the impacts of herbivory and explain their spatial heterogeneity at the landscape scale.

7.4 Implications and future directions

This thesis has demonstrated that herbivory in the Arctic has a top-down influence at the regional scale, varying impacts over fine spatial scales, and important consequences for ecosystem structure and functioning. One research avenue with great potential for further advancing our understanding of Arctic herbivory includes new applications of UAVs. In addition to detecting impacts, the ability to measure plant traits and classify species and functional types with UAVs (**Chapter 2**) can be leveraged to observe the effects of herbivory on nutrients and plant diversity continuously across a landscape. The fine-grain imagery can be used to analyse the interactions between the abiotic and biotic forces and determine the

mechanisms behind spatially heterogeneous response variables. GPS collars, camera traps, or even UAV flights capturing video during the herbivory event can simultaneously quantify and map the herbivory pressure. As I mentioned in **Chapter 5**, combining measurements of biomass removed with the number of animals, their body sizes, and their movements provides the opportunity to link consumption with energy expenditure within a comprehensive analysis of animal energetics. Thus, UAVs, which have been employed extensively to study other topics within Arctic research (Yang et al., 2022), open many new possibilities for understanding the role of herbivores within tundra ecosystems, including by bridging between field measurements and increasingly fine-grained space-borne imagery.

Future work should also focus on the Earth system responses to Arctic herbivory. Many studies, including the research chapters I have presented, highlight that herbivores, particularly reindeer, affect the albedo, carbon balance, and soil thermal dynamics (e.g., Cohen et al., 2013; Loranty et al., 2018; Olofsson & Post, 2018). However, few ecosystem models incorporate animals, and those that do, such as ArcVeg (Yu et al., 2009, 2017), typically parametrise the effect of herbivores as simply biomass removal. To inform ecosystem models, more herbivory studies need to explicitly measure responses beyond the impacts on vegetation. Remote sensing, flux towers (e.g., Lafleur & Humphreys, 2018; Virkkala et al., 2021), and modelling can be used to test hypotheses at larger scales and scale up local measurements. Ultimately, we should strive to include Arctic herbivory within Earth system models to improve future predictions of the trajectories of tundra ecosystems and global biogeochemical cycles. This goal is important given the pace of climate change in the Arctic and the potentially important mediating effects of herbivores.

Finally, within this era of rapid environmental change, there is increasing recognition that environmental managers can take action to promote biodiversity and enhance the provision of ecosystem services (Pettorelli et al., 2018). These actions can take multiple forms in the Arctic and can include legislation affecting reindeer herding, such as the widely criticised policy proposals to reduce reindeer numbers and restrict movements with fences in Yamal (Volkovitskiy & Terekhina, 2020), and rewilding with megafauna (Macias-Fauria et al., 2020). We are more often viewing manipulation of top-down forces as a solution to environmental challenges, yet, within our eagerness to act, it is crucial to ensure that we understand the complex systems in which we are intervening. Furthermore, given the unknowns, we must have tools to detect and monitor the consequences of our actions. In this

thesis, I have presented insights into the impacts of herbivores on tundra ecosystems using multiple techniques to observe a variety of responses at a range of spatial scales. This work can inform management decisions and the design of future Arctic herbivory research to support progress in this area, one of many that deserve attention within our larger efforts to tackle the climate change and biodiversity crises.

7.5 References

Bråthen, K. A., Ravolainen, V. T., Stien, A., Tveraa, T., & Ims, R. A. (2017). Rangifer management controls a climate-sensitive tundra state transition. *Ecological Applications*, *27*(8), 2416–2427. https://doi.org/10.1002/eap.1618

Cohen, J., Pulliainen, J., Ménard, C. B., Johansen, B., Oksanen, L., Luojus, K., & Ikonen, J. (2013). Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. *Remote Sensing of Environment*, *135*, 107–117. https://doi.org/10.1016/j.rse.2013.03.029

Filazzola, A., & Cahill, J. F. (2021). Replication in field ecology: Identifying challenges and proposing solutions. *Methods in Ecology and Evolution*, *12*(10), 1780–1792. https://doi.org/10.1111/2041-210X.13657

Graham, H., Benaud, P., Cunliffe, A., Puttock, A., Anderson, K., Chant, J., Elliott, M., & Brazier, R. (2021). *exeter-creww/SFM_Precision: SfM Precision and Workflow v0.2 (v0.2)*. Zenodo. https://doi.org/10.5281/zenodo.5760603

Hegerl, G. C., Hoegh-Guldberg, O., Casassa, G., Hoerling, M., Kovats, S., Parmesan, C., Pierce, D., & Stott, P. (2009). IPCC Expert Meeting on Detection and Attribution Related to Anthropogenic Climate Change The World Meteorological Organization Good Practice Guidance Paper on Detection and Attribution Related to Anthropogenic Climate Change Good Practice Guidance Paper o. In T. Stocker, C. Field, Q. Dahe, V. Barros, G.-K. Plattner, M. Tignor, P. Midgley, & K. Ebi (Eds.), *IPCC Expert Meeting on Detection and Attribution Related to Anthropogenic Climate Change*.

James, M. R., Robson, S., & Smith, M. W. (2017). 3-D uncertainty-based topographic change detection with structure-from-motion photogrammetry: precision maps for ground control and directly georeferenced surveys. *Earth Surface Processes and Landforms*, *42*(12), 1769–1788. https://doi.org/10.1002/esp.4125

Lafleur, P. M., & Humphreys, E. R. (2018). Tundra shrub effects on growing season energy and carbon dioxide exchange. *Environmental Research Letters*, *13*(5). https://doi.org/10.1088/1748-9326/aab863

Loranty, M. M., Abbott, B. W., Blok, D., Douglas, T. A., Epstein, H. E., Forbes, B. C., Jones, B. M., Kholodov, A. L., Kropp, H., Malhotra, A., Mamet, S. D., Myers-Smith, I. H., Natali, S. M., O'Donnell, J. A., Phoenix, G. K., Rocha, A. V., Sonnentag, O., Tape, K. D., & Walker, D. A. (2018). Reviews and syntheses: Changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions. *Biogeosciences*, *15*(17), 5287–5313. https://doi.org/10.5194/bg-15-5287-2018

Macias-Fauria, M., Jepson, P., Zimov, N., & Malhi, Y. (2020). Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190122. https://doi.org/10.1098/rstb.2019.0122

Metcalfe, D. B., & Olofsson, J. (2015). Distinct impacts of different mammalian herbivore assemblages on arctic tundra CO2 exchange during the peak of the growing season. *Oikos*, *124*(12), 1632–1638. https://doi.org/10.1111/oik.02085

Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761). https://doi.org/10.1098/rstb.2017.0437

Orndahl, K. M., Macander, M. J., Berner, L. T., & Goetz, S. J. (2022). Plant functional type aboveground biomass change within Alaska and northwest Canada mapped using a 35-year satellite time series from 1985 to 2020. *Environmental Research Letters*, *17*(11), 115010. https://doi.org/10.1088/1748-9326/ac9d50

Parmesan, C., Burrows, M. T., Duarte, C. M., Poloczanska, E. S., Richardson, A. J., Schoeman, D. S., & Singer, M. C. (2013). Beyond climate change attribution in conservation and ecological research. *Ecology Letters*, *16*, 58–71. https://doi.org/10.1111/ele.12098

Petit Bon, M., Inga, K. G., Jónsdóttir, I. S., Utsi, T. A., Soininen, E. M., & Bråthen, K. A. (2020). Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities. *Oikos*, *April*, 1–14. https://doi.org/10.1111/oik.07074

Pettorelli, N., Barlow, J., Stephens, P. A., Durant, S. M., Connor, B., Schulte to Bühne, H., Sandom, C. J., Wentworth, J., & du Toit, J. T. (2018). Making rewilding fit for policy. *Journal of Applied Ecology*, *55*(3), 1114–1125. https://doi.org/10.1111/1365-2664.13082

Siewert, M. B., & Olofsson, J. (2020). Scale-dependency of Arctic ecosystem properties revealed by UAV. *Environmental Research Letters*, *15*(9), 094030. https://doi.org/10.1088/1748-9326/aba20b

Siewert, M. B., & Olofsson, J. (2021). UAV reveals substantial but heterogeneous effects of herbivores on Arctic vegetation. *Scientific Reports*, *11*(1), 19468. https://doi.org/10.1038/s41598-021-98497-5

Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: Do browsing and grazing herbivores matter? *Biological Reviews*, *87*(1), 72–94. https://doi.org/10.1111/j.1469-185X.2011.00185.x

Thomson, E. R., Spiegel, M. P., Althuizen, I. H. J., Bass, P., Chen, S., Chmurzynski, A., Halbritter, A. H., Henn, J. J., Jónsdóttir, I. S., Klanderud, K., Li, Y., Maitner, B. S., Michaletz, S. T., Niittynen, P., Roos, R. E., Telford, R. J., Enquist, B. J., Vandvik, V., Macias-Fauria, M., & Malhi, Y. (2021). Multiscale mapping of plant functional groups and plant traits in the High Arctic using field spectroscopy, UAV imagery and Sentinel-2A data. *Environmental Research Letters*, *16*(5). https://doi.org/10.1088/1748-9326/abf464

Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., & Stark, S. (2014). Consequences of warming on tundra carbon balance determined by reindeer grazing history. *Nature Climate Change*, *4*(5), 384–388. https://doi.org/10.1038/nclimate2147

Virkkala, A., Aalto, J., Rogers, B. M., Tagesson, T., Treat, C. C., Natali, S. M., Watts, J. D., Potter, S., Lehtonen, A., Mauritz, M., Schuur, E. A. G., Kochendorfer, J., Zona, D., Oechel, W., Kobayashi, H., Humphreys, E., Goeckede, M., Iwata, H., Lafleur, P. M., … Luoto, M. (2021). Statistical upscaling of ecosystem CO 2 fluxes across the terrestrial tundra and boreal domain: Regional patterns and uncertainties. *Global Change Biology*, *27*(17), 4040–4059. https://doi.org/10.1111/gcb.15659

Volkovitskiy, A., & Terekhina, A. (2020). The contemporary issues of Yamal reindeer herding: discussions and perspectives (in Russian). *Etnografia*, *2*(8), 152–169.

Yang, D., Morrison, B. D., Davidson, K. J., Lamour, J., Li, Q., Nelson, P. R., Hantson, W., Hayes, D. J., Swetnam, T. L., McMahon, A., Anderson, J., Ely, K. S., Rogers, A., & Serbin, S. P. (2022). Remote sensing from unoccupied aerial systems: Opportunities to

enhance Arctic plant ecology in a changing climate. *Journal of Ecology*, *110*(12), 2812–2835. https://doi.org/10.1111/1365-2745.13976

Yu, Q., Epstein, H., Engstrom, R., & Walker, D. (2017). Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory. *Global Change Biology*, *23*(9), 3895–3907. https://doi.org/10.1111/gcb.13632

Yu, Q., Epstein, H., & Walker, D. (2009). Simulating the effects of soil organic nitrogen and grazing on arctic tundra vegetation dynamics on the Yamal Peninsula, Russia. *Environmental Research Letters*, *4*(4). https://doi.org/10.1088/1748-9326/4/4/045027

Zimov, S. A., Chuprynin, V. I., Oreshko, A. P., Chapin, F. S., Reynolds, J. F., & Chapin, M. C. (1995). Steppe-Tundra Transition: A Herbivore-Driven Biome Shift at the End of the Pleistocene. *The American Naturalist*, *146*(5), 765–794. https://doi.org/10.1086/285824

Appendix 1:
Additional co-authored articles



Description

In this Appendix, I include the first page of four additional articles to which I made substantial contributions during my DPhil. In Thomson et al. (2021), a study involving UAV mapping in Svalbard, I assisted with the study design, data collection, and data analysis. I was a co-first author of Duporge et al. (2021), which characterised UAV noise disturbance to animals, including reindeer. I performed all the data analysis, produced the figures, and created the web interface for this paper. In Kühn et al. (2022), I calculated the vegetation sensitivity index (VSI) and contributed throughout the data analysis to analyse links between root depth and vegetation sensitivity to climate. Lastly, the final paper I include is led by Joshua Ettinger and discusses the lessons learned from a student project that we initiated to collect conversations about climate change from around the world. We were awarded a runner-up prize in the University of Oxford Vice Chancellor's Environmental Sustainability Awards in 2022 for our project. The manuscript is currently in review in *Climatic Change*, and I am the last author.

Duporge, I., Spiegel, M. P., Thomson, E. R., Chapman, T., Lamberth, C., Pond, C., Macdonald, D. W., Wang, T., & Klinck, H. (2021). Determination of optimal flight altitude to minimise acoustic drone disturbance to wildlife using species audiograms. *Methods in Ecology and Evolution*, *12*(11), 2196–2207. https://doi.org/10.1111/2041-210X.13691

Kühn, N., Spiegel, M. P., Tovar, C., Willis, K. J., & Macias-Fauria, M. (2022). Seeing roots from space: aboveground fingerprints of root depth in vegetation sensitivity to climate in dry biomes. *Environmental Research Letters*, *17*(11), 114062. https://doi.org/10.1088/1748-9326/ac9d4f

Thomson, E. R., Spiegel, M. P., Althuizen, I. H. J., Bass, P., Chen, S., Chmurzynski, A., Halbritter, A. H., Henn, J. J., Jónsdóttir, I. S., Klanderud, K., Li, Y., Maitner, B. S., Michaletz, S. T., Niittynen, P., Roos, R. E., Telford, R. J., Enquist, B. J., Vandvik, V., Macias-Fauria, M., & Malhi, Y. (2021). Multiscale mapping of plant functional groups and plant traits in the High Arctic using field spectroscopy, UAV imagery and Sentinel-2A data. *Environmental Research Letters*, *16*(5). https://doi.org/10.1088/1748-9326/abf464

IOP Publishing Environ. Res. Lett. 16 (2021) 055006 https://doi.org/10.1088/1748-9326/abf464

ENVIRONMENTAL RESEARCH
LETTERS

LETTER

Multiscale mapping of plant functional groups and plant traits in the High Arctic using field spectroscopy, UAV imagery and Sentinel-2A data

Eleanor R Thomson[1,*], Marcus P Spiegel[1], Inge H J Althuizen[2], Polly Bass[3], Shuli Chen[4], Adam Chmurzynski[4], Aud H Halbritter[2], Jonathan J Henn[5], Ingibjörg S Jónsdóttir[6,11], Kari Klanderud[7], Yaoqi Li[4,8], Brian S Maitner[4], Sean T Michaletz[9], Pekka Niittynen[10], Ruben E Roos[7], Richard J Telford[2], Brian J Enquist[4], Vigdis Vandvik[2], Marc Macias-Fauria[1] and Yadvinder Malhi[1]

[1] School of Geography and the Environment, University of Oxford, Oxford, United Kingdom
[2] Department of Biological Sciences and Bjerknes Centre for Climate Research, University of Bergen, Bergen, Norway
[3] Matanuska-Susitna College, University of Alaska, Anchorage, AK, United States of America
[4] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, United States of America
[5] Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI, United States of America
[6] Faculty of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland
[7] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Aas Norway
[8] Institute of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing, People's Republic of China
[9] Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, Canada
[10] Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland
[11] Arctic Biology, The University Centre in Svalbard, Longyearbyen, Norway
[*] Author to whom any correspondence should be addressed.

E-mail: eleanor.thomson@oriel.ox.ac.uk

OPEN ACCESS

RECEIVED
28 October 2020

REVISED
25 March 2021

ACCEPTED FOR PUBLICATION
1 April 2021

PUBLISHED
21 April 2021

Original content from this work may be used under the terms of the Creative Commons Attribution 4.0 licence.

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.

Keywords: Svalbard, functional trait, tundra, moss, shrubs, remote sensing, bird cliff

Supplementary material for this article is available online

Abstract

The Arctic is warming twice as fast as the rest of the planet, leading to rapid changes in species composition and plant functional trait variation. Landscape-level maps of vegetation composition and trait distributions are required to expand spatially-limited plot studies, overcome sampling biases associated with the most accessible research areas, and create baselines from which to monitor environmental change. Unmanned aerial vehicles (UAVs) have emerged as a low-cost method to generate high-resolution imagery and bridge the gap between fine-scale field studies and lower resolution satellite analyses. Here we used field spectroscopy data (400–2500 nm) and UAV multispectral imagery to test spectral methods of species identification and plant water and chemistry retrieval near Longyearbyen, Svalbard. Using the field spectroscopy data and Random Forest analysis, we were able to distinguish eight common High Arctic plant tundra species with 74% accuracy. Using partial least squares regression (PLSR), we were able to predict corresponding water, nitrogen, phosphorus and C:N values ($r^2 = 0.61$–0.88, RMSEmean = 12%–64%). We developed analogous models using UAV imagery (five bands: Blue, Green, Red, Red Edge and Near-Infrared) and scaled up the results across a 450 m long nutrient gradient located underneath a seabird colony. At the UAV level, we were able to map three plant functional groups (mosses, graminoids and dwarf shrubs) at 72% accuracy and generate maps of plant chemistry. Our maps show a clear marine-derived fertility gradient, mediated by geomorphology. We used the UAV results to explore two methods of upscaling plant water content to the wider landscape using Sentinel-2A imagery. Our results are pertinent for high resolution, low-cost mapping of the Arctic.

© 2021 The Author(s). Published by IOP Publishing Ltd

Received: 22 February 2021 | Accepted: 9 July 2021

DOI: 10.1111/2041-210X.13691

RESEARCH ARTICLE

Methods in Ecology and Evolution

Determination of optimal flight altitude to minimise acoustic drone disturbance to wildlife using species audiograms

Isla Duporge[1] | Marcus P. Spiegel[2] | Eleanor R. Thomson[2] | Tatiana Chapman[1] | Curt Lamberth[3] | Caroline Pond[3] | David W. Macdonald[1] | Tiejun Wang[4] | Holger Klinck[5]

[1]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Abingdon, UK

[2]School of Geography and the Environment, University of Oxford, Oxford, UK

[3]Department of Zoology, University of Oxford, Oxford, UK

[4]Faculty of Geo-Information Science and Earth Observation, University of Twente, Enschede, The Netherlands

[5]Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA

Correspondence
Isla Duporge, Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney, Abingdon, UK.
Email: isla.duporge@zoo.ox.ac.uk

Funding information
Natural Environment Research Council

Handling Editor: Lian Pin Koh

Abstract

1. Unmanned aerial vehicles (UAVs) are increasingly important in wildlife data collection but concern over wildlife disturbance has led several countries to ban their use in National Parks. Disturbance is an animal welfare concern and impedes scientific data collection through provoking aberrant behaviour. Dealing with the issue of disturbance will enable wildlife researchers to use UAV technology more effectively and ethically.
2. Here we present a novel method to determine optimal flight altitude for minimising drone disturbance for wildlife using species audiograms. We recorded sound profiles of seven common UAV systems in the horizontal and vertical planes at 5-m increments up to 120 m. To understand how mammals perceive UAV sound, we used audiograms of 20 species to calculate the loudness of each UAV for each species across the measured distances. These calculations filter the UAV noise based on the sensitivity of species' hearing over the relevant frequency spectrum.
3. We have devised a method to optimise the trade-off between image spatial resolution and flight altitude. We calculated the lowest point at which either the UAV sound level decreases below an acceptable threshold, here chosen as 40 dB, weighted according to species' hearing sensitivity, or disturbance cannot be significantly further minimised by flying higher. The latter is quantified as the point above which each additional 5 m of flight altitude causes on average less than 0.05 dB decrease in sound pressure level.
4. Reliable data on appropriate flight altitudes can guide policy regulations on flying UAVs over wildlife, thus enabling increased use of this technology for scientific data collection and for wildlife conservation purposes. The methodology is readily applicable to other species and UAV systems for which sound recordings and audiograms are available.

Isla Duporge and Marcus P. Spiegel contributed equally to this work.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2021 The Authors. *Methods in Ecology and Evolution* published by John Wiley & Sons Ltd on behalf of British Ecological Society

IOP Publishing Environ. Res. Lett. 17 (2022) 114062 https://doi.org/10.1088/1748-9326/ac9d4f

ENVIRONMENTAL RESEARCH
LETTERS



OPEN ACCESS

RECEIVED
9 February 2022

REVISED
10 October 2022

ACCEPTED FOR PUBLICATION
25 October 2022

PUBLISHED
17 November 2022

Original content from this work may be used under the terms of the Creative Commons Attribution 4.0 licence.

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



LETTER

Seeing roots from space: aboveground fingerprints of root depth in vegetation sensitivity to climate in dry biomes

Nicola Kühn[1,2,*], Marcus P Spiegel[1], Carolina Tovar[2], Katherine J Willis[3] and Marc Macias-Fauria[1]

[1] School of Geography and the Environment, University of Oxford, Oxford, United Kingdom
[2] Royal Botanic Gardens, Kew, Jodrell Laboratory, Richmond, United Kingdom
[3] Department of Biology, University of Oxford, Oxford, United Kingdom
[*] Author to whom any correspondence should be addressed.

E-mail: n.kuhn@kew.org

Keywords: vegetation sensitivity, ecological resilience, climate change, climate variability, root depth, remote sensing, drylands

Supplementary material for this article is available online

Abstract

With predicted climate change, drylands are set to get warmer and drier, increasing water stress for the vegetation in these regions. Plant sensitivity to drier periods and drought events will largely depend on trait strategies to access and store water, often linked to the root system. However, understanding the role of below-ground traits in enhancing ecological resilience to these climate changes remains poorly understood. We present the results of a study in southern Africa where we analysed the relationship between root depth and the vegetation sensitivity index (VSI) (after Seddon and Macias-Fauria *et al* 2016 *Nature* **531** 229–32). VSI demonstrates remotely-sensed aboveground vegetation responses to climate variability; thus our study compares aboveground vegetation responses to belowground root traits. Results showed a significant negative relationship between root depth and vegetation sensitivity. Deeper roots provided greater resistance to climate variability as shown by lower sensitivity and higher temporal autocorrelation in vegetation greenness (as measured by the enhanced vegetation index). Additionally, we demonstrated a link between deeper roots and depth to groundwater, further suggesting that it is the ability of deeper roots to enable access to groundwater that provides ecological resistance to climate variability. Our results therefore provide important empirical evidence that the ability to access deeper water resources during times of lower water availability through deeper roots, is a key trait for dryland vegetation in the face of future climate change. We also show that belowground traits in drylands leave a fingerprint on aboveground, remotely-sensed plant–climate interactions, an important finding to aid in scaling up data-scarce belowground research.

1. Introduction

Plant traits play a fundamental role in mediating vegetation responses to climate change. Recent work has demonstrated that belowground traits (e.g. rooting depth, resprouting ability, belowground storage) might be at least as important as aboveground traits in promoting plant fitness and performance in the face of climate change (Kühn *et al* 2022), enabling plants in dryland biomes to cope with climate and associated environmental changes. The relationship between belowground plant traits and climatic/environmental factors is thus potentially important for determining plant resilience to future change. However, in comparison to other traits, roots are rarely studied due to difficulties in field extraction (Laliberté 2017). Preliminary hypotheses backed up by root research based on a limited global dataset ($n = 475$) predict that deeper roots will be more prevalent in arid and semi-arid systems than in humid ones, and more prevalent in certain growth forms (trees from savanna/thorn scrub, or seasonally dry forests) (Schenk and Jackson 2002, Schenk 2005).

Recent collation of existing data in online trait databases (GRooT, FRED, TRY, BIEN) (Enquist *et al* 2009, Kattge *et al* 2011, 2020, Iversen *et al* 2017, Guerrero-Ramírez *et al* 2021) and the advancement of remote root measuring techniques (i.e. isotope

© 2022 The Author(s). Published by IOP Publishing Ltd

Fighting the climate spiral of silence: Lessons from a COP26 climate conversations campaign

Abstract

Conversations about climate change are crucially important for mobilizing climate action, as well as for processing emotions and finding meaning in times of crisis. However, limited guidance exists on how to successfully facilitate these discussions, especially among individuals with a wide range of beliefs, knowledge levels, and opinions about climate change. Here, we describe the Talk Climate Change project – an [hidden for peer review] University student-led climate conversation campaign associated with the 2021 United Nations COP26 meeting. Over 1,000 individuals across 40 countries held climate-related discussions. They then described their discussions in submissions to an interactive conversation map (www.talkclimatechange.org), along with messages to COP26. We reflect on the campaign's outcomes and offer advice on overcoming barriers to effective climate dialogue; how to handle emotional responses; and other considerations for catalyzing meaningful and productive climate discussions. We call for a stronger focus on training conversational skills, providing context-specific discussion resources, and empowering diverse people to have conversations about climate change among their families, friends, coworkers, and communities.

Introduction

"How many of our friends and family members understand why COP26 is important or what it even is?

This is the question that we, a group of graduate students at [hidden for peer review] asked ourselves in January 2021. There was already much speculation about the potential outcomes of the 26th United Nations Climate Change Conference (COP26), to be held in November 2021 in Glasgow, Scotland. COP is the annual meeting of parties to the United Nations Framework Convention on Climate Change during which delegates assess and negotiate paths for mitigating and adapting to climate change (Evans et al., 2021). The outcomes of these negotiations affect all life on Earth. At the time, we were struck by the limited awareness of it beyond individuals directly involved in environmental work. When we mentioned COP26 to close contacts not engaged in the environmental movement in professional or personal contexts, the term was unfamiliar to most of them. Even among our fellow students, in the same country as the upcoming conference, awareness was surprisingly low. Public polling confirmed this perception. In September and October 2021, only 35% of people in Great Britain reported knowing of COP26 and understanding what it was about; this figure was even lower in the United States, where only 14% of Americans reported an awareness and understanding of it (Hudson et al., 2021).

Fortunately, awareness of COP26 increased during the conference, such as in the United Kingdom, where 60% of the public reported hearing a fair or significant amount about COP26 in November 2021 (Conner, 2021). This was most likely associated with substantial media coverage of the conference (Boykoff et al., 2021). Nevertheless, that such a pivotal meeting could remain a matter relatively confined to the environmental community is not only troubling – it is also risky. Public engagement is crucial for climate action, especially as many decarbonization and adaptation