Emerging priorities in terrestrial herbivory research in the Arctic

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Abstract

Herbivores are an integral part of Arctic terrestrial ecosystems, driving ecosystem functioning and sustaining local livelihoods. In the context of accelerated climate warming and land use changes, understanding how herbivores contribute to the resilience of Arctic socio-ecological systems is essential to guide sound decision-making and mitigation strategies. While research on Arctic herbivory has a long tradition, recent literature syntheses highlight important geographical, taxonomic and environmental knowledge gaps on the impacts of herbivores across the region. At the same time, climate change and limited resources impose an urgent need to prioritize research and management efforts. We conducted a horizon scan within the Arctic herbivory research community to identify emerging scientific and management priorities for the next decade. From 288 responses received from 85 participants in two online surveys and an in-person workshop, we identified 8 scientific and 8 management priorities centred on: a) understanding and integrating fundamental ecological processes across multiple scales from individual herbivore-plant interactions up to regional and decadal scale vegetation and animal population effects; b) evaluating climate change feedbacks; and c) developing new research methods. Our analysis provides a strategic framework for broad, inclusive, interdisciplinary collaborations to optimise terrestrial herbivory research and sustainable management practices in a rapidly changing Arctic.

Keywords: Arctic herbivores, climate change mitigation, horizon scan, management, tundra

Introduction

Tundra herbivores are important components of Arctic socio-ecological systems (Forbes et al. 2009). For example, vertebrate herbivores represent a key resource for many northern communities through hunting or herding (Huntington et al. 2013), and invertebrate herbivores can influence local livelihoods through their impacts on vegetation (Vuojala-Magga and Turunen 2015). Herbivores are a fundamental driver of energy flows and biogeochemical cycles of Arctic tundra ecosystems (McKendrick et al. 1980; Barrio and Hik 2020). Through selective grazing, trampling and waste deposition, herbivores influence the composition of plant and animal communities, with consequences to climate feedbacks (Zimov et al. 1995; Koltz et al. 2022). The importance of herbivores in the functioning of tundra ecosystems is amplified by their interactions with other drivers of change, as herbivores can buffer warming-induced plant responses and diversity loss (Post and Pedersen 2008; Cahoon et al. 2012; Kaarlejärvi et al. 2017; Jessen et al. 2020; Post et al. 2023), reduce deciduous shrub encroachment (Verma et al. 2020; Vuorinen et al. 2022; Spiegel et al. 2023) or increase the resilience of Arctic ecosystems to warming (Post 2013; Kaarlejärvi et al. 2015).

Recent syntheses have shown a wealth of scientific studies on the role of herbivores in Arctic environments while also highlighting important knowledge gaps, including biases in the geographical, taxonomic and environmental coverage of existing literature (Metcalfe et al. 2018; Soininen et al. 2021). Coordinated research efforts such as the activities of the Herbivory Network (Barrio et al. 2016b) or the International Tundra Experiment (Henry et al. 2022), and long-term monitoring programmes, like the Climate-Ecological Observatory for Arctic Tundra (COAT; Ims and Yoccoz 2017) or the Greenland Ecosystem Monitoring (GEM; Schmidt et al. 2021), have been instrumental in generating new knowledge about the role of herbivores in Arctic ecosystems. In addition, the development of new, more affordable technologies like high-resolution satellites and unmanned aerial vehicles (Siewert and

Olofsson 2021), high-throughput DNA sequencing (Soininen et al. 2009) or artificial intelligence (AI; Christin et al. 2019), will continue to help advance our knowledge of Arctic herbivory. Together with the accelerating impacts of climate change on herbivores and their habitats, these developments open new possibilities for both research and management of Arctic herbivores.

Building on these advances and the need to prioritize research efforts to address those knowledge gaps, we used a horizon scan to identify future needs in Arctic herbivory research as perceived by the scientific community. Horizon scanning is a tool to create lists of research priorities (Dey et al. 2020) that is often conducted as a democratic process by consolidating expert advice (Sutherland and Woodroof 2009). The goal of horizon scans is to guide future research and inform subsequent knowledge-based decision-making (Wintle et al. 2020). Considering the unprecedented rate of climate change at higher latitudes and the diversity and interconnectedness of ecological, conservation and socio-economic issues regarding Arctic herbivory, a horizon scan offers an effective way to identify viewpoints and establish a consensus on strategic research needs related to Arctic herbivory for the next decade. By prioritizing the most urgent research needs, we aim to guide scientific efforts more effectively, so that the most critical questions to understanding and managing Arctic ecosystems in the face of accelerating environmental change are addressed, as well as to provide a basis for discussions with the broader community of rights holders and stakeholders.

Methods

The idea for this project emerged from an Herbivory Network workshop organized in June 2023 in Cambridge Bay, Nunavut (Canada) as a contribution of the Arctic herbivory research community to the Fourth International Conference on Arctic Research Planning (ICARP IV) process. To identify emerging priorities in terrestrial herbivory research in the Arctic, we followed a Delphi-approach commonly used in horizon scanning and research prioritization exercises (Sutherland et al. 2011; Mukherjee et al. 2015; Dey et al. 2020). The process encompassed three key steps: 1) an elicitation of expert knowledge through an online survey (hereafter 'elicitation survey'), 2) a follow-up online survey requesting participants to score a list of responses (hereafter 'scoring survey') and 3) an in-person workshop to summarize the information (hereafter 'workshop'; **Figure 1**).

We solicited researchers with expertise in Arctic terrestrial ecology to participate in the project. An initial call for collaboration was published on the Herbivory Network website on June 28, 2023, and on the UArctic website on July 26, 2023, and announced through the Herbivory Network email list (ca. 200 subscribers). An announcement was also placed on social media and forwarded to researchers with relevant background. In January 2024, the elicitation survey was sent to Herbivory Network members as a personalized email (**Supplementary Materials S1a**) and advertised through the website of the Nordic Society Oikos Conference 2024. Additional reminders were sent through the Herbivory Network email list. The initial two-week period for submitting responses to the elicitation survey was extended from January 15 to January 28, 2024.

In the elicitation survey, participants were asked to provide their perspectives on Arctic herbivory research for the coming decade by formulating up to five research priorities and needs (**Supplementary Materials S1b**). Here we define the Arctic following Virtanen et al. (2016), including the oroarctic tundra, the high elevation regions at higher latitudes (~ north of 59°), as these areas are climatically and ecologically more similar to the Arctic tundra than to truly alpine ecosystems farther south. Information about the participants' career stage, gender, and geographic scope of their research was collected for the purpose of analyzing demographics of participants. Optionally, participants provided a contact email address to stay informed about the project and contribute towards the next stages. Email addresses were saved separately from the survey data, rendering the survey data anonymous. All survey participants agreed that their answers would be used for summary purposes in the horizon scan, as part of the Herbivory Network's input to ICARP IV research prioritization.

The elicitation survey compiled 288 responses from 85 participants (**Figure 1**; the full list of responses can be found in **Supplementary Materials S2**). A core group of authors collated and edited the responses to improve clarity and remove duplication into 146 responses. In the elicitation survey, participants were invited to formulate their priorities and needs as questions, but some responses were not formulated as questions; for these, no attempt was made to write them in question form. The collated list of responses was randomly split into two equally sized subsets (73 responses each) that were used in the scoring survey (**Figure 1; Supplementary Materials S1c**). The scoring survey was sent to the 83 participants that had indicated their willingness to be involved in the next steps of the research as a link in a personalized email (**Supplementary Materials S1d**) on February 12, 2024. Participants were given two weeks to respond (until February 25, 2024) and were asked to score the responses according to two criteria: scientific relevance (i.e., resolving the issue will address an important knowledge gap) and management relevance (i.e., resolving the issue will have important management implications). The scores included four possible values: “not relevant at all”, “little relevant”, “relevant” and “very relevant”.

A total of 63 participants responded to the scoring survey. Participants were randomly split into two groups and each group scored one of the subsets of responses, so that each response was scored by 31-32 participants. Scores for each response were transformed to integer values between 0 (not relevant at all) and 3 (very relevant) and averaged per response (the average scores for each response can be found in **Supplementary Materials S2**).

The workshop was attended by 26 participants, who discussed the top 25% of scored responses for each criterion (42 responses for scientific relevance, 38 for management relevance; **Figure 2**). During the workshop, discussions took place initially in four small groups of 5-8 participants. All groups were tasked with synthesizing the top-ranked responses in each criterion (ca. 60 min per criterion). After the four groups had synthesized the responses independently, all workshop participants met again to establish a final consensus list of broad priorities that were formulated as questions. A total of 16 broad priorities were identified (eight priorities for each criterion; **Figure 1**). It is important to emphasize that the horizon scan's objective was to prioritise the scientific questions with important implications for management rather than listing management needs per se. Therefore, management relevance here reflects the views and experiences of the scientists participating in this study.

After the workshop, the conclusions were summarized and prepared as a manuscript draft. The full list of participants that had contributed to the different parts of the process (ca. 170 researchers) were contacted again and invited to contribute to the resulting manuscript (79 researchers co-authored the manuscript).

Results and discussion

Over half of the participants in the elicitation survey were senior researchers (five or more years since obtaining a research position; 56.5%), followed by recently established researchers (15.3%), postdoctoral fellows (15.3%), PhD (11.8%) and BSc (1.2%) students (**Supplementary Materials S1e**). Of the 85 participants, 43 self-identified as males, 40 as females, and 2 as non-binary. Regarding the geographical scope of the participants' research, multiple responses were possible per participant. Fennoscandia was mentioned by 40 participants, pan-Arctic scope was indicated by 25, followed by Greenland (16), Canada (15), Iceland (13), Russia (10), Alaska (9) and Svalbard (5), while 5 reported their scope to be (also) outside the Arctic (**Supplementary Materials S1e**). Although we did not collect information about the participants' country of professional affiliation, the author list represents a broad geographic coverage with residents in 18 countries, including all Arctic states.

The horizon scan identified 16 distinct priorities (eight for each criterion) based on the top-ranked responses resulting from the scoring survey (42 responses for scientific relevance, 38 for management relevance). Only three of these responses were identified as relevant (top 25%) for both criteria (**Figure 2**), and all these three responses were included within the respective broad priority related to "climate change" (**S4** and **M1**; **Figure 3**). This is not surprising, given that climate change has high societal relevance and serves as a cross-cutting theme that impacts both human and non-human lives in the Arctic. About half of the responses identified as a priority under one criterion had below-average scores for the other criterion (scientific relevance: 21 out of 42; management relevance: 19 out of 38). These differences are possibly linked to variable research fields and experience with applied research in management among the participants contributing to the scoring survey. Management priorities differ across the Arctic and are context dependent (e.g., type of ecosystems and threats, management strategies, legislations, etc.), and participants likely had varying experience in translating science into practical management advice or different perceptions of management strategy feasibility. Future studies should consider these different perspectives. For instance, submitting the same questionnaire to relevant decision-makers, rights holders and stakeholders, such as local herders and hunters, and comparing the resulting ranking of priorities, would provide further important context of the priorities presented here.

The workshop developed a consensus definition of 8 broader priorities (questions) for each criterion (**Figures 3 and 4**; for an overview of priorities and descriptions see **Tables S3.1 and S3.2**). Although face-to-face workshops bear the risk of cognitive biases, such as the 'bandwagon effect' where participants indiscriminately follow the majority opinion (Winkler and Moser 2016), they have been considered a suitable way to reach consensus and tend to be more inclusive and productive than other group-based techniques (Sutherland et al. 2023). Furthermore, the division of the workshop participants into four groups to independently evaluate the priorities prior to evaluating them by the entire group was intended to minimize biases. The following sections present each of the broad priorities identified for the scientific and management criteria, ordered by their highest scoring response (**Figure 4; Supplementary material S2**).

Scientific relevance

S1. How do herbivory and climate change interact to impact Arctic ecosystems?

Climate change can modify the impact of herbivores on different levels of biological organization, from individual organisms to ecosystems. Nine responses identified the interactive effects between herbivory and climate change on Arctic ecosystems as a priority (**Figure 4**), which received the highest average score (2.47) for scientific relevance.

Herbivores can interact with climate change to affect Arctic tundra plant phenology, physiology and performance. For instance, plant phenology can be advanced by warming but be delayed by herbivory (Radville et al. 2016). In turn, changes in plant phenology can drive habitat selection by herbivores and lead to changes in the distribution of grazing pressure across the landscape (Anderson et al. 2012; Iversen et al. 2014; see **S4** and **S8**). Earlier onset of spring in the Arctic allows migratory herbivores like geese to arrive and start foraging sooner at Arctic breeding sites (Lameris et al. 2018; Hupp et al. 2018), with potentially large effects on forage quality (Beard et al. 2019a) and other plant traits (Choi et al. 2019). Climate change and herbivory can also affect the physiology of forage plants synergistically. For example, both insect and mammalian herbivory can amplify the emission of plant volatile organic compounds, simultaneously increased by warming (Li et al. 2019; Brachmann et al. 2023).

The effects of herbivores and climate change on plant phenology, physiology or performance may scale up to impact Arctic plant distributions and vegetation composition. For instance, herbivores may modulate vegetation responses to climate change (Post and Pedersen 2008; Barrio et al. 2016a) through inhibiting warming-driven expansion of woody species and buffering shrub- and treeline advance (Christie et al. 2015; Virtanen et al. 2021). Vertebrate herbivores may also constrain the expansion of warm-adapted forbs (Kaarlejärvi et al. 2013; Eskelinen et al. 2017), but the paucity of studies focusing on non-woody plant species prevents generalisations (but see e.g., Saccone et al. 2014; Post et al. 2022). By selectively feeding on common species (see **S2**) vertebrate herbivory can counteract the negative effects of warming on species diversity (Kaarlejärvi et al. 2017; Post et al. 2023). While vertebrate herbivores may slow down tundra greening at regional scales (Sundqvist et al. 2019; Spiegel et al. 2023), their influences on overall pan-Arctic greening trends remains unaddressed (Myers-Smith et al. 2020).

Herbivory can also modulate the effects of climate change on Arctic ecosystem functioning (Koltz et al. 2022). By removing vegetation through grazing, herbivores suppress the responses of gross ecosystem productivity to warming (Cahoon et al. 2012; Spiegel et al. 2023). Herbivores can indirectly alter tundra carbon cycling and modify soil nutrient availability through trampling and by selective feeding, which shifts vegetation trajectories (Ylänne et al. 2015; Vowles and Björk 2019; Pichon et al. 2023), but these effects can differ under warming (Ylänne et al. 2015, 2020). We still lack a detailed understanding of the conditions under which the indirect effects of herbivores on Arctic carbon and nutrient cycling might interact with climate change.

Finally, it is important to recognize that climate change entails factors other than warming, such as changing precipitation patterns, altered frequency of freeze-thaw cycles during spring melt and higher frequency and intensity of extreme weather events (IPCC 2021). Yet, how herbivory might modulate the role of these key environmental change drivers on ecosystem functioning is virtually unknown, and we urge future studies to test their potentially interactive effects.

S2. How does herbivory influence ecosystem processes in the Arctic?

Beyond their interactions with climate change (see **S1**), herbivory influences ecosystem processes directly and indirectly. Through the consumption of biomass, the deposition of waste products, and habitat-modifying behaviours, herbivores exert a strong influence on Arctic ecosystems (Koltz et al. 2022). Despite the rich literature on herbivore effects on Arctic tundra (Soininen et al. 2021; Barbero-Palacios et al. 2024), we are only beginning to understand these direct and indirect influences and how they may interact. This priority included the largest number of responses (11; **Figure 4**), many of them with high scores for scientific relevance, indicating that we still lack basic understanding of herbivore effects on tundra ecosystem processes. Responses covered a variety of taxa and topics, including the effects of vertebrate and invertebrate herbivores on the biodiversity, resilience and resistance of tundra ecosystems and on key ecosystem processes like nutrient cycling.

Herbivores can affect competitive relationships between plants and thus influence the biodiversity of Arctic ecosystems (Ramirez et al. 2024). Both large and small herbivores can reduce the decline in plant species richness in tundra by selectively removing shrubs and allowing rare species to persist (see **S1**; Kaarlejärvi et al. 2017; Gibson et al. 2021). Alternatively, consistent feeding on palatable species can result in dominance of less palatable species that outcompete herbaceous plants (Bråthen et al. 2007). In addition, disturbance from large herbivores can alter resource and habitat availability for other vertebrate (den Herder et al. 2008, 2016) and invertebrate herbivores (den Herder et al. 2004), further influencing tundra biodiversity. The impact of large herbivores, however, depends on the intensity of grazing (Bråthen et al. 2017) and on the diversity of herbivores (Olofsson and Post 2018). Large herbivores can preserve the integrity of tundra ecosystems by preventing shrub encroachment and tree establishment (Moen et al. 2008; Bråthen et al. 2017; Olofsson and Post 2018). In turn, high grazing pressures can shift shrub-dominated tundra towards graminoid dominance (Van der Wal 2006). To better understand the effects of herbivores on biodiversity and the resilience and resistance of tundra ecosystems, we need a better grasp of the role of different intensities of grazing pressure (Bråthen et al. 2017).

Herbivores directly contribute to nutrient cycling through the deposition of waste products, including faeces and urine (Barthelemy et al. 2018; Beard et al. 2023), carcasses (Danell et al. 2002), and natal fluids (Ferraro et al. 2024). In nutrient-limited Arctic systems, nutrient supply commonly occurs in pulses linked to animal inputs (Danell et al. 2002; Barthelemy et al. 2015). These inputs can accelerate the pace of cycling (Barthelemy et al. 2018), increase forage quality (Petit Bon et al. 2022; Ferraro et al. 2024), change plant community composition (Danell et al. 2002), influence plant biomass (Barthelemy et al. 2015), topsoil microclimate (Deschamps et al. 2023) and ultimately shape landscape heterogeneity (Ferraro et al. 2022). As such, animal inputs seem to be an important mechanism of accelerated nutrient cycles in Arctic ecosystems, but their impacts are modified by the underlying biophysical conditions, including soil conditions and plant-mycorrhizal associations (Ferraro et al. 2022).

Finally, our understanding of the impact of invertebrate herbivores in Arctic ecosystems remains sparse. Background levels of invertebrate herbivory in the Arctic are low (Barrio et al. 2017; Rheubottom et al. 2019) and have limited overall impacts on ecosystem-level processes such as carbon and nutrient cycling (Koltz et al. 2017; Kristensen et al. 2020; but see Silfver et al. 2020). However, population outbreaks of herbivorous insects can severely impact tundra productivity (Lund et al. 2017) and are predicted to become more common with warming temperatures in some regions (Finger-Higgens et al. 2021; Jepsen et al. 2023). As well, insect outbreaks can interact with reindeer grazing, modulating the trajectories of vegetation recovery after massive defoliation events (Vindstad et al. 2019). Further work investigating the role of invertebrate herbivores in shaping Arctic ecosystem-level processes is needed.

S3. How can we improve measurements of herbivory?

The need for standardized protocols and coordinated efforts to measure herbivory across the tundra has been long recognized (Barrio et al. 2016b, 2021; see also **M7**), but challenges remain in scaling up from individual organisms and plot-level to landscape- and ecosystem-level impacts. Although only two responses were included within this priority (**Figure 4**), participants ranked the need to improve measurements of herbivory with high scientific relevance.

Several field-based methodologies for measuring herbivory and herbivore use have been used, ranging from observational assessments of herbivore habitat use by pellet counts and other signs of herbivore activity, to the use of exclosures to experimentally manipulate the presence of vertebrate herbivores (Barbero-Palacios et al. 2024). Standardizing existing field methodology is an obvious and necessary first-step towards accurate measurements of herbivory that allow meaningful comparisons of data collected across studies. Traditional field-based approaches provide a basic understanding of the impacts of herbivores, but additional insights can be gained by leveraging GPS technologies to understand how herbivores use space and resources. GPS collars on animals are a key tool to track movement patterns and identify key habitats for foraging. New devices like tri-axial accelerometers that track specific behaviours (Rautiainen et al. 2022) and camera collars that capture visual data on feeding behaviours and plant species consumed (Ehlers et al. 2024) may expand our ability to track and analyze the impact of herbivory on Arctic ecosystems.

Recent advances in Unmanned Aerial Vehicles (UAVs) and satellite remote sensing have also opened new possibilities for monitoring herbivore impacts on vegetation. The emergence of pre-processed high- (~1-5 m, e.g., PlanetScope, Worldview) and medium-resolution (~5-30m, e.g., Sentinel-2, Landsat) satellite remote sensing products facilitates incorporating spatially explicit information, including phenology metrics, into predictive models. Additionally, UAVs offer the opportunity to monitor herbivory across the spatially heterogeneous Arctic tundra at fine-scale resolutions currently unavailable with satellite imagery (Alonzo et al. 2020; Assmann et al. 2020; Eischeid et al. 2021; Siewert and Olofsson 2021; Villoslada et al. 2023). UAVs can also be used in combination with satellite data through upscaling approaches (Villoslada et al. 2024), resolving sub-pixel heterogeneity while expanding the spatial reach of models (but see Eischeid et al. 2021).

Despite these promising technological advances for monitoring herbivore populations and herbivory in the Arctic, significant challenges remain regarding validation and characterization of environmental controls (Beamish et al. 2020). Using several technological approaches will be our best bet for improving measurements of herbivory in the Arctic. For example, Spiegel et al. (2023) used spaceborne remote sensing and participatory mapping to identify regional migrations of domesticated reindeer herds and vegetation changes, showing the potential to capture herbivore impact on Arctic vegetation over large spatial scales. Field-based measurements of herbivory are still crucial for ground-truthing and developing reliable remote sensing models and provide the necessary link between herbivory and remotely sensed information. Importantly, scale mismatches between plot-level data and satellite imagery can introduce uncertainties in modelling outputs (Beamish et al. 2020; Siewert and Olofsson 2021). In turn, the rapid recovery of vegetation after herbivory also poses challenges in detecting the impacts of herbivory in a timely manner (Ravolainen et al. 2011). The use of remote sensing technologies can allow collecting a great volume of data, but requires cooperation between scientific disciplines and participation of stakeholders (e.g.,Spiegel et al. 2023), to efficiently interpret and process large amounts of data. Advances in deep machine learning and automated image recognition may offer tools for increased processing speed and data interpretation (Christin et al. 2019; Tuia et al. 2022; Wang et al. 2024).

S4. How will climate change affect herbivores and their ecological role in Arctic ecosystems?

Ultimately, the effects of climate change on herbivore populations will lead to altered herbivore densities and distributions (see **S5**), with consequences for both vegetation and tundra ecosystem functions (see **S1** and **S2**). Nine responses described climate change effects on herbivores as a priority, and three of these responses also scored as relevant (top 25%) for management (orange points in **Figure 2**). These three responses highlighted the need for a better understanding of the impact of extreme weather events on herbivore populations, how herbivores will respond to climate-driven changes in vegetation and the direct and indirect effects of climate change on herbivore populations (**Table S3.1**).

The observed increases in the frequency and intensity of extreme weather events, like rain-on-snow or warmer winter spells, can dramatically impact herbivore populations (Hansen et al. 2011; see **M1**). Refreezing of water on the ground after rain-on-snow events can form basal ice layers that prevent access to food by herbivores (Hansen et al. 2013). Examples of the devastating effects of winter warming on herbivore populations include extensive mortality of reindeer in Yamal, Russia (Forbes et al. 2016) and the decline of the entire herbivore community following 'rain-on-snow' events on Svalbard (Hansen et al. 2013). Autumn rains also have strong effects on lemming demography, as they create a hard ground ice layer that prevents lemming access to food (Domine et al. 2018). While some information is available on how winter warming and rain-on-snow events affect herbivores (Hansen et al. 2013; Loe et al. 2016), knowledge about the effect of other extreme weather events associated with a changing climate, like extreme summer heat and droughts, is virtually missing.

Climate change can also affect herbivores through its effects on forage quantity, quality and availability and by altering the overall vegetation structure. For example, shrubification associated with climate warming alters forage quality, quantity and availability to many herbivores (Joly et al. 2009; Thompson and Barboza 2014; Doiron et al. 2014). Changes in plant phenology associated with climate change (Prevéy et al. 2017) can lead to trophic mismatches if the availability of highly nutritious forage plants decouples from the timing of high herbivore nutritional demands (Doiron et al. 2015). Trophic mismatch can lead to reduced herbivore reproductive success (Post and Forchhammer 2008) and limited offspring growth and survival (Kerby and Post 2013b; Doiron et al. 2015; Lameris et al. 2018; see **M1**). By altering vegetation structure, warming-induced shrubification enhances habitat quality for biting and parasitic insects and affects herbivores by increasing insect harassment (Johnson et al. 2021). Shrubification can also alter habitat connectivity, potentially benefiting browsers such as moose (*Alces alces*; Zhou et al. 2020), but negatively impacting grazers such as barren-ground caribou (Fullman et al. 2017) or other herbivores like Arctic ground squirrels (*Urocitellus parryii*; Wheeler et al. 2015) that rely on the openness of the tundra to spot predators.

The combined direct and indirect effects of climate change on herbivores are species- and context-specific, and therefore complex to predict. For instance, warmer springs may lead to shallower snowpacks and can influence lemming populations directly by providing less thermal insulation and increasing their thermoregulatory costs (Poirier et al. 2023) and indirectly by exposing them to greater predation (Domine et al. 2018). In turn, earlier springs also lead to enhanced food availability for muskoxen, indirectly increasing their fecundity and reducing their mortality (Duncan et al. 2021). Further, the effects of climate change need to be considered across seasons. For example, warmer summers and autumns increase forage availability for wild reindeer, while warm spells during winter can encase vegetation in basal ice and hence reduce access to forage (Albon et al. 2017; Loe et al. 2021). The strength of these climate-induced effects can also vary spatially, resulting in different population trends (Hansen et al. 2019b). Our understanding of the complex interplay between climate change and herbivore population dynamics remains superficial and requires long term ecosystem-based monitoring programs to disentangle the direct and indirect effects of climate change, and their combined effects on herbivore populations.

S5. How do compositional changes in herbivore communities affect ecosystem functioning of Arctic ecosystems?

Arctic herbivore community dynamics are driven by the complex interplay of many factors. Climate change, through its direct and indirect impacts on herbivores (see **S4**) is a particularly strong driving force, currently altering the composition of herbivore communities in the Arctic (Speed et al. 2021). Understanding how these changes will influence the functioning of Arctic ecosystems is a key scientific priority. Three responses in the horizon scan described this priority (**Figure 4**), with a focus on understanding the combined effects of guild-specific herbivore impacts on ecosystem functioning, and the effects of changing herbivore diversity and community composition on tundra ecosystems.

Tundra ecosystems host a range of functionally different herbivores (henceforth referred to as “guilds”), from invertebrates to migratory geese and large herbivores (Speed et al. 2019b). Differences in body size, habitat preferences and population dynamics across guilds imply different impacts on ecosystem functioning (Barbero-Palacios et al. 2024). For instance, heavy grazing by reindeer can increase albedo at a regional scale by reducing shrub height and abundance (Cohen et al. 2013; Te Beest et al. 2016), while lemmings and long-term grazing by geese can locally and regionally decrease albedo through the consumption of vegetation and subsequent exposure of darker soils (Lara et al. 2017; Conkin and Alisauskas 2017). Even herbivore species within the same guild can have contrasting effects on ecosystem processes. For example, hay piles constructed by lemmings increase soil phosphorus content, but this effect is not observed under vole hay piles (Roy et al. 2022). Further, the combined effect of herbivore guilds on tundra ecosystems is less well understood and most evidence comes from effects on plants (Barbero-Palacios et al. 2024). The effects of one guild may complement or buffer the effects of another. For example, the combined effects of grazing by reindeer and small rodents can suppress the growth of tall shrubs (Ravolainen et al. 2014), while these groups of herbivores dampen each other's effects on plant nutrient content (Petit Bon et al. 2020). As such, changes in the composition of herbivore communities will determine the overall effects of herbivores and their spatiotemporal variation across the landscape.

Around the Arctic, ongoing environmental and management changes modulate the abundance and distribution of herbivore populations (e.g., Mallory and Boyce 2018; Ehrich et al. 2019; Cuyler et al. 2020), which further shapes the composition of herbivore communities (Speed et al. 2019a; Defourneaux et al. 2024; Sokolova et al. 2024) and their impact on tundra ecosystems. For example, some boreal herbivores like moose (*Alces alces*; Tape et al. 2016) and beaver (*Castor canadensis*; Tape et al. 2018) are expanding their distribution into the Arctic tundra, while the ranges of other Arctic species are shrinking (van Beest et al. 2023), leading to the borealization of Arctic herbivore assemblages (Speed et al. 2021). Due to the important role of herbivores in Arctic ecosystems (see **S2**), it is necessary to understand the differences between species, their interactions and how they may change to predict how Arctic systems will function under future herbivore community assemblages.

S6. How are Arctic food webs structured and how do they vary over time and space?

Herbivores are embedded in complex food webs where they interact directly and indirectly with multiple species at different trophic levels. Understanding how Arctic food webs are structured and how they vary over time and space was identified as a key scientific priority in three responses (**Figure 4**).

Arctic herbivores have been instrumental for developing food web ecology as a discipline. Early studies investigated the fluctuating population dynamics of small herbivores using the long-term population records collected by Canadian fur trading companies, such as the emblematic Hudson Bay's lynx-hare and fox-lemming datasets (Elton 1924). More recent studies have focused on understanding the mechanisms behind Arctic herbivore population cycles (Gilg et al. 2003; Ims and Fuglei 2005; Gruyer et al. 2008). Consumer-resource interactions under the constraints of the harsh Arctic environment provide plausible mechanisms accounting for these cycles (Ims and Fuglei 2005), but questions remain about the relative importance of herbivore-plant or predator-herbivore interactions as drivers of these cycles (Gilg et al. 2003; Gruyer et al. 2008; Ruffino et al. 2016).

Compared to temperate ecosystems, Arctic terrestrial food webs are relatively simple (Elton 1927). Our understanding of the major trophic linkages and compartments in Arctic food webs has been greatly enhanced by comprehensive ecosystem-based monitoring programmes (Pedersen et al. 2019; Schmidt et al. 2021; Gauthier et al. 2024). However, the functional links between species can be complex and dynamic and require the explicit integration of spatial and temporal variations in trophic interactions. High-resolution data on replicated food webs can improve ecological assumptions and predictive capacity (Soininen et al. 2018) but require data-heavy approaches (Kissling et al. 2014). Sampling trophic interactions remains a challenge, but the relatively-well integrated research community could also be harnessed to adopt a truly circumpolar food web approach, as exemplified in Mellard et al. (2022b). This will require developing cost-efficient standard protocols to enable a coordinated and spatially replicated sampling of trophic interactions (see e.g., Kankaanpää et al. 2020). Deploying high-throughput methods for diet analysis such as stable isotopes and DNA metabarcoding (e.g., Pansu et al. 2022; Hiltunen et al. 2022) should be part of the toolkit, enabling the broad-scale but detailed characterization of multi-trophic interactions. DNA metabarcoding already offers great scope for unlocking the hidden dimensions of animal diets and trophic niche partitioning (Soininen et al. 2009; Neby et al. 2024), and revealing winter diet in voles (Soininen et al. 2015). The genomic approach can be generalized to fill the current knowledge gaps in seasonal foraging of other herbivore species (see **S8**). However, work should also be carried out in parallel to address current methodological limitations: i.e., assessing the quantitative performance of DNA metabarcoding (Kamenova et al. 2024) and developing plant DNA reference databases for Arctic regions outside Fennoscandia where these databases are relatively complete (Voldstad et al. 2020). The structure of food webs is an important determinant of ecosystem functioning and stability (Tylianakis and Morris 2017) that can influence their resilience and transformation in response to biological invasions (Frost et al. 2019). This is highly relevant to Arctic food webs, given the projected changes in herbivore population dynamics and resource use stemming from climate warming-driven processes such as tundra borealization or Arctic greening (see **S1** and **S2**; Wirta et al. 2015; Schmidt et al. 2017; Gauthier et al. 2024).

S7. What is the role of herbivores in the long-term stability of Arctic ecosystems?

Understanding the role of herbivores in the long-term stability of Arctic ecosystems is an urgent priority, considering the rapid pace of environmental changes in the region. Two responses in the horizon scan identified this priority (**Figure 4**).

Reconstructions of past megaherbivore assemblages offer important insights into how the distribution, density and diversity of herbivores have shaped community and ecosystem dynamics from 300 million years ago up to the large mass extinctions (Owen-Smith 1987). This work has contributed to the “keystone herbivore” hypothesis (Owen-Smith 1987), which posits that the productivity of the steppe-tundra during the Pleistocene was maintained by megaherbivores. The “keystone herbivore” hypothesis is further supported by archived time series of dietary samples. Dietary reconstructions for species such as the woolly mammoth, including analyses of the composition of gut tissue (Cucina et al. 2021), gut and lower intestine content (Ukraintseva 1981), or coprolites (Polling et al. 2021) provide strong support for a diet dominated by herbaceous plants and shrubs, with occasional consumption of lichens, mosses and green algae. In this context, dietary samples can provide a key tool to assess long-term changes in plant-herbivore interactions (see also **S6**).

The mass extinction of megaherbivores towards the end of the Pleistocene coincided with a decline in the steppe-tundra and the expansion of the shrub tundra in the Arctic (Willerslev et al. 2014; Wang et al. 2021). Whether this change in vegetation was driven by climate or by the extinction of megahebivores, and whether the mass extinction of megaherbivores was caused by changes in climate or by human hunting, has been debated (Zimov et al. 1995; Monteath et al. 2021; but see also Svenning et al. 2024). There has been much recent interest in re-establishing extinct past herbivore assemblages (i.e., rewilding; Olofsson and Post 2018) and on the capacity of current tundra vegetation to sustain these herbivore assemblages (Poquérusse et al. 2024). The potential to reintroduce large herbivores in the Arctic could mitigate some of the effects of warming (Olofsson and Post 2018; Macias-Fauria et al. 2020) but requires biological, social and ethical considerations (Burak et al. 2024; see **M3** and **M8**).

Following the mass extinctions of megaherbivores, large mammalian grazers have continued to be important regulators of vegetation patterns worldwide, including in the Arctic (see **S1** and **S2**). For instance, research on historical reindeer milking grounds and enclosures in Fennoscandia reveal long-term legacy effects of high local densities of semi-domesticated reindeer (Egelkraut et al. 2018; Huusko et al. 2024). These studies show that locally, high reindeer densities can lead to shifts from shrub-dominated tundra to alternative stable vegetation states dominated by herbaceous plants which can persist for hundreds of years (Normand et al. 2017). Small mammalian herbivores, such as voles and lemmings, may further contribute to limiting shrub growth in these historical milking grounds (Egelkraut et al. 2018).

Through their effects on vegetation, nutrient cycling and climate feedbacks (see **S2**), herbivores are important regulators of long-term ecosystem processes and ecosystem stability in tundra ecosystems, although effects vary across spatial scales (see **S8**) and among herbivore assemblages (see **S5**). Improved understanding of the mechanisms that determine large-scale and long-term effects of plant-herbivore interactions is an important avenue of research.

S8. How do the effects of herbivores on Arctic ecosystems vary in space and time?

It has long been recognized that the effects of herbivores vary greatly depending on where and when herbivory takes place. Two responses in the horizon scan identified the spatiotemporal variability of herbivore impacts as a scientific priority (**Figure 4**).

Herbivores' use of landscapes is heterogeneous, and their foraging choices span multiple spatial scales, from individual plants to the landscape level (Senft et al. 1987). Foraging decisions, in turn, may lead to an uneven distribution of herbivore impacts across the landscape (see **S1**). One notorious example is the profound spatial variation in the intensity of the interactions between small rodents and plants, where strong impacts have been documented in some parts of the Arctic (Olofsson et al. 2012; Roy et al. 2022) but not in others (Bilodeau et al. 2014). Even within the same region, the effects of small rodents on vegetation can differ between river catchments 20 km apart (Ravolainen et al. 2011). Differences in primary productivity and in food web structure could account for these pronounced spatial differences between different tundra ecosystems (Gauthier et al. 2011; Oksanen et al. 2020).

Another source of variation in plant-herbivore interactions is timing, which is particularly important in highly seasonal environments like the Arctic tundra (Post et al. 2008). Some migratory herbivores are only present in the Arctic during summer, while other herbivores are resident year-round (Speed et al. 2019b). In addition, herbivore populations generally fluctuate among years, leading to temporal variations in grazing impacts on vegetation. For example, the population cycles of voles and lemmings cause synchronous fluctuations in plant biomass (Olofsson et al. 2012; Siewert and Olofsson 2021), and periodic outbreaks of geometrid moths can lead to vegetation shifts in the tundra-forest ecotone (Vindstad et al.

2019). Changes in the timing of herbivory can have important ecosystem consequences. For example, grazing by early arriving migratory geese can shift tundra ecosystems from a C sink to a source, while delayed goose arrival can lead to opposite outcomes (Beard et al. 2019b). Further, food preferences of herbivores change throughout the growing season in response to phenological changes in food quality and availability (Iversen et al. 2014; Barboza et al. 2018; see **S4**). Parallel to these changes in food quality, the chemical composition of waste deposition also varies seasonally (Beard et al. 2023), potentially leading to varying seasonal impacts of herbivores on tundra biogeochemistry. Understanding the drivers of the spatiotemporal variability of herbivore effects is crucial for predicting how tundra ecosystems will respond to ongoing environmental changes. This will require targeted efforts that include underrepresented Arctic environments (Soininen et al. 2021) and special attention to the timing and multiple spatial scales at which these effects manifest.

Although we have a relatively good understanding of changes in herbivory during the growing season, there is a clear gap in our knowledge on herbivore impacts during winter and shoulder seasons (autumn and spring). Snow properties, including the distribution of snow and timing of snowmelt, can influence the spatiotemporal variability of herbivore impacts across the landscape (Rixen et al. 2022). A recent synthesis suggested that the effects of small rodents on vegetation may be most pronounced during winter (Soininen and Neby 2024), with winter browsing strongly suppressing heavily defended dwarf shrubs (Dahlgren et al. 2009). Similarly, winter browsing by ptarmigan and moose has strong effects on the growth, reproduction and architecture of willows (Christie et al. 2014). In turn, food availability during winter has large repercussions for population dynamics of resident Arctic herbivores and ultimately determines the carrying capacity (Albon et al. 2017; see **M4**). A better understanding of plant-herbivore interactions during winter and their consequences to both plants and herbivores is therefore needed.

Management relevance

M1. What are the management implications of the effects of climate change on Arctic herbivores?

Climate change will affect Arctic herbivores in direct and indirect ways (see **S4**). From a management perspective, changes in disease dynamics of plants and herbivores, herbivore habitat or behaviour, herbivory rates, food availability (e.g., access to food in winter) or in the adaptive capacity of herbivores (e.g., physiological tolerance to climate extremes), are highly relevant. This priority included the largest number of responses (12) but received the lowest average score for management relevance among the identified management priorities (average score: 2.3; **Figure 4**), including the highest and the lowest ranked responses (scores 2.61 and 2.16 respectively).

Rapid changes in abiotic and biotic conditions in the Arctic will influence herbivore populations (see **S4**) and create new challenges for natural resource managers and local livelihoods. Effective herbivore management in a changing climate requires high-quality data on herbivore abundances and vital rates, and on drivers like abiotic factors, including weather variability and extreme weather events. Effective management will also require anticipating and mitigating the various ecological and evolutionary disruptions caused by rapid climate change. At broader spatial scales, these ecological disruptions include shifting distributions of plants, other herbivores, predators and pathogens (van Beest et al. 2021; Yarzábal et al. 2021) and the subsequent changes in biotic interactions (Mellard et al. 2022a; see **S6**). For example, the northward expansion of deer and moose has indirectly resulted in increased predation pressure on caribou by grey wolf (Festa-Bianchet et al. 2011). In addition, the spread of novel diseases represents formidable challenges for management of herbivore populations. Range expansion of southern deer species increases the risk of new zoonotic pathogens and parasites not formerly present in the Arctic, which become lethal when infecting new hosts (Pickles et al. 2013). For instance, the outbreak of chronic wasting disease (CWD) in Norway in 2016 required the extirpation of the third-largest wild reindeer population to prevent the spread of the disease (Mysterud and Rolandsen 2018; Mysterud et al. 2024). These examples demonstrate the need for assessing and monitoring the spread of diseases and their vectors (Di Francesco et al. 2021; Johnson et al. 2023).

An important management concern, as reflected explicitly by three responses, is how climate change will influence food availability and its consequences to herbivore diet composition and quality. As mentioned in **S4**, rain-on-snow events that prevent herbivore access to food in winter are predicted to become more frequent under climate change, and these events can lead to extensive mortality, particularly when reindeer densities are high (Hansen et al. 2019a, 2019b). Warming-related changes in plant community composition, including decreases in lichen availability can reduce pasture quality (Joly et al. 2009) and negatively impact herbivore population growth, as described for caribou herds across North America (Fauchald et al. 2017). Further, trophic mismatches associated with climate change (see **S4**) can reduce herbivore reproductive success, as documented for caribou in West Greenland (Post and Forchhammer 2008). Some herbivores might be susceptible to phenological mismatches (Gustine et al. 2017), while others might be able to adjust their behaviour to buffer some of the negative effects of climate change (Kerby and Post 2013a; Loe et al. 2016). However, understanding and predicting the adaptive capacity of Arctic herbivores to rapid abiotic and biotic changes is a critical step for effective management of herbivore populations in the Arctic.

M2. How will increasing human pressure in combination with environmental changes affect Arctic herbivores?

As human impact in the Arctic accelerates and becomes more ubiquitous, herbivore populations are increasingly exposed to direct and indirect impacts affecting population abundances and vital rates (Klein 2000). Understanding how increasing human pressure and other environmental changes will affect Arctic herbivores was identified as a key priority for management, with the third highest average score (**Figure 4**). Human pressures include a wide range of impacts, such as habitat loss to infrastructure, land use changes and fragmentation, natural resource exploration and exploitation, recreational activities, farming and the spread of diseases (see **M1**). Responses included in this priority highlighted studying the ability of herbivores and the livelihoods that depend on them to adapt to both the individual and the cumulative impacts from multiple stressors.

The impacts of anthropogenic activities on Arctic herbivores have been well documented, particularly for muskoxen (*Ovibos moschatus*; Cuyler et al. 2020) and wild and semi-domesticated *Rangifer* spp. (Festa-Bianchet et al. 2011; Skarin and Åhman 2014). Human infrastructure and resource extraction directly cause habitat loss, fragment landscapes and can disrupt migration routes for herbivores between seasonal habitats (Severson et al. 2023; Boulanger et al. 2024). Noise pollution, visual disturbance, dust deposition and pollutant contamination (Plante et al. 2018; Skarin et al. 2018; Watkinson et al. 2021) effectively increase the zone of influence and lead to avoidance behaviour. Avoidance may vary with season, level of human activity, type of industry and herbivore species. For example, large herbivores usually have the largest avoidance during calving and higher tolerance towards disturbances during the insect harassment period (Skarin et al. 2018; Prichard et al. 2020; Johnson et al. 2020). One major challenge is identifying the spatial and temporal extent and variation of the zone of influence within which herbivores respond to disturbances and their cumulative impacts (Niebuhr et al. 2023). Tolerance to disturbance varies with species, domestication, handling and taming of the animals. Tolerance can also increase if resources are scarce, hiding possible adverse effects of disturbances. While some studies conclude that habituation towards disturbances is possible (Colman et al. 2013), others find it weak or absent (Johnson et al. 2014, Johnson et al. 2020). Thus, predicting the effect of increased anthropogenic impacts remains difficult and highly context dependent. Long-term studies across habitats and seasons are needed to understand the implications of increasing human activities on the habitats of Arctic herbivores and how these impacts translate to population level consequences. Furthermore, we need to understand better how habitats can be restored to maintain the carrying capacity for viable large herbivore populations to sustain the hunting and herding livelihoods that depend on them. This includes, for instance, restoring mining sites once mineral resources have been depleted, as well as alternative forest management and increased landscape connectivity for seasonal migrations.

M3. Can herbivores be used as a climate change mitigation strategy?

Using large wild and domestic herbivores as a management tool to mitigate some of the effects of climate change is receiving increasing attention (see **S7**). Three responses (**Figure 4**) referred to the potential use of herbivores to restore lost ecosystem functions, counteract climate change effects on tundra ecosystems, or prevent further warming through their effects on climate feedbacks.

Herbivores in the Arctic and the sub-Arctic can help mitigate climate change (Cromsigt et al. 2018; Beer et al. 2020; Macias-Fauria et al. 2020; Windirsch et al. 2022). Browsing on shrubs and trees by large herbivores prevents the expansion of woody plants (Olofsson et al. 2009; Olofsson and Post 2018) and can promote graminoids, forbs and other low-lying biotic ground cover such as lichens (Stark et al. 2002; Olofsson et al. 2004; see **S1** and **S2**). These vegetation shifts can have a cooling effect, as graminoids, forbs and in particular lichens reflect more sunlight than darker, taller shrubs and trees and increase albedo (Zimov et al. 2012; Cohen et al. 2013; Te Beest et al. 2016). However, the most important albedo effect of low-lying vegetation is in the continuous snow layer that it promotes, which results in large quantities of solar energy reflected in the shoulder seasons, especially spring, as compared to landscapes where tall vegetation protrudes from the show layer and enhances snow melt and energy absorption. In addition, low lying vegetation can also help mitigate permafrost thaw, as it promotes wind-packing of snow, reducing the insulation capacity of the snowpack and maintaining colder soil temperatures (Sturm et al. 2001b, 2001a). In addition, large herbivores trample snow in winter, increasing soil exposure to cold air, aiding permafrost maintenance and expansion (Beer et al. 2020; Macias-Fauria et al. 2020). Yet, observations of accelerated permafrost degradation in mires grazed in summer by semi-domestic reindeer in Fennoscandia (Holmgren et al. 2023) suggest that the effects of large herbivores on permafrost strongly depend on environmental context and grazing regimes. To be able to increase albedo and permafrost preservation through herbivore management, we need further studies on the role of herbivore density, plant community composition and environmental context.

Large herbivores in Arctic systems could also mitigate the impacts of climate change by increasing soil carbon storage. Grazing-induced graminoid-dominated systems can store more carbon than shrub-dominated systems due to faster biomass turnover and relatively deep and dense root structures, increasing soil carbon storage within the first meter of soils (Olofsson et al. 2009; Windirsch et al. 2022). Herbivores also accelerate nutrient cycles (Van der Wal and Brooker 2004), facilitating ecosystem carbon uptake (Falk et al. 2014). Modelling studies suggest that they can also enhance net primary production (Zhu et al. 2018). However, this effect is not universal and grazing intensity, grazing regime and environmental context are important mediators of net effects (Burak et al. 2024). For instance, intense grazing in upland systems can reduce vegetation biomass, muting any increase in ecosystem carbon storage (Jefferies et al. 2006; Väisänen et al. 2014). In contrast, grazing in wetter landscapes can decrease the ratio of emitted methane-to-CO_2, reducing the global warming potential without changing the net C-balance (Fischer et al. 2022). A more comprehensive understanding of the biotic and abiotic factors influencing herbivore-carbon interactions, the spatiotemporal variability in herbivore impacts, and how herbivores influence other elemental cycles (Koltz et al. 2022) will lead to better predictive models of where and when large herbivores may affect carbon storage and energy balance and thus effectively be used to mitigate climate change effects.

Although large herbivore management has the potential to be used as a climate mitigation tool, the feasibility of applying such strategies remains questionable. To have a significant effect on global climate, drastic increases in the diversity and density of herbivore assemblages would be needed (Macias-Fauria et al. 2020; Ylänne and Stark 2025). Such increases might only be feasible at very local scales as induced by human management, but also pose other problems associated with environmental degradation following overgrazing (Windirsch-Woiwode 2024).

M4. Can we manage herbivores to enhance biodiversity and ecosystem functioning in Arctic ecosystems?

In addition to the potential application as a climate change mitigation and adaptation strategy (see **M3**), management of large wild and domestic herbivores can enhance biodiversity and ecosystem functioning in the tundra (Bråthen et al. 2017; see **S2**). In our horizon scan, this priority was described in four responses (**Figure 4**).

Current management of large herbivores varies across the Arctic due to differences in legislations, and these differences may lead to different impacts on tundra biodiversity and ecosystem functioning (Forbes and Kumpula 2009). For example, in Northern Fennoscandia, reindeer herding practices differ among countries, from seasonal migration to sedentary regimes, driving contrasting vegetation patterns and ecosystem impacts (Holand et al. 2022). Reindeer herds fluctuate due to both environmental and management changes. For instance, the collapse of the Soviet Union caused large declines in some domesticated reindeer herds but increases in others (Uboni et al. 2016). In addition, pressures from competing land uses (see **M2**) prevent the use of some pastures, concentrating grazing pressure in the remaining pastures (e.g., Horstkotte et al. 2022). The additive effects of co-occurring herbivore species also need to be considered (see **S5**). Although herbivore diversity has been shown to slow the decline in biodiversity driven by warming (Post et al. 2023) and enhance ecosystem functioning (e.g., Ravolainen et al. 2014), managing multiple species with different population densities and dynamics within the same area brings additional challenges.

Taking domesticated reindeer in Eurasia as an example, the possibility of managing herbivores to enhance biodiversity and ecosystem functioning lies primarily in the right to use the pastures and self-determination of the Indigenous reindeer herding groups (Larsson Blind 2022). Biodiversity and ecosystem functioning could be enhanced, especially in summer pastures, by re-establishing long-term grazing practices that have been lost or re-distributing grazing pressure to allow heavily grazed pastures to recover. However, such measures include a number of challenges as they would require maintaining or even increasing herd sizes (Uboni et al. 2020). This is difficult because herd sizes are largely constrained by forage availability during winter (Moen et al. 2006)., which is in turn reduced by climate change and increased pressures from competing land uses (Uboni et al. 2020). Supplementary feeding could increase reindeer survival and production but is costly and difficult to maintain (Åhman et al. 2022), and results in fundamental behavioural changes that affect the overall ecosystem effects of herbivory as well as increasing the risk of disease (Tryland et al. 2019). Further, the maximum number of reindeer allowed in a herding district is based on winter grazing ground carrying capacity and is set by government authorities, thus affecting self-governing by the herders (Sarkki et al. 2022). In addition, a main constraint to actively steering herds to appropriate summer pastures to avoid excessive grazing of some areas is the availability of labour, as the number of herders has declined in parts of Fennoscandia (Uboni et al. 2020). In the extensive reindeer husbandry systems that prevail, herds roam freely in summer, apart from certain activities such as calf markings, and their habitat selection is largely dependent on forage availability and other biotic and abiotic factors, including human disturbance (see **M2**). The possibility to explicitly manage domesticated herbivores for maintaining biodiversity and the provision of ecosystem services will thus be a complex process that includes considering the annual pasture cycle, competing land uses and the political systems of governance.

M5. How can we effectively interweave different types of knowledge to identify relevant questions and solve management issues regarding Arctic herbivores?

The value of experiential knowledge, derived from a close cultural connection to the land and passed down through generations, and Indigenous knowledge, rooted in specific ethnic contexts and shaped by the cultures, traditions, practices and beliefs of descendants of people who inhabited a region prior to colonization, is increasingly recognized within the scientific community for its contribution to understanding ecological and environmental processes and wildlife management (Berkes et al. 2000; Hill et al. 2020; Jessen et al. 2022). Three responses mentioned the importance of interweaving experiential, Indigenous and scientific knowledge in managing herbivores and their ecosystem effects. Participants ranked this priority the highest (average score: 2.49; **Figure 4**).

Experiential and Indigenous knowledge are often described as integrated into a way of life and associated with practices such as hunting, trapping or herding. In this sense, knowledge is cumulative and is culturally transmitted through language, skills and practices, and is continuously tested against recent observations and is thus adaptive to environmental change (Savo et al. 2016; Ford et al. 2020). This knowledge is embedded in specific norms, values and holistic worldviews (Berkes et al. 2000; Brondízio et al. 2021). Taken out of its context, there is a risk that the meaning and significance of these forms of knowledge will be lost (Albuquerque et al. 2021). Successfully interweaving different ontologies for knowledge co-production, and particularly Indigenous knowledge, therefore requires establishing mutual trust, respectful engagement of cultural approaches, and equal power relations between partners to overcome the historical burden of colonialism and marginalization of Indigenous peoples (Wheeler et al. 2020). The participation of knowledge holders in all stages of the research process, from identifying relevant questions, agreeing on methods, data collection and analysis as well as knowledge dissemination is vital to prevent extractive processes, but may vary in agreement with involved research partners (David-Chavez and Gavin 2018).

Contributions of interweaving various forms of knowledge for Arctic herbivore management have led to deeper insights of species and population trends, spatial and temporal changes in migration patterns, responses to disturbance, spread of diseases and the effects of climate change and integrity of the Arctic social-ecological system (e.g., Parlee et al. 2005; Peacock et al. 2020; Gagnon et al. 2023). For instance, Gagnon et al. (2023) developed predictive models of caribou distribution and hunters' access to the herds in response to environmental factors, based on hunters' Indigenous knowledge, GPS collared caribou and climate models, as a tool to assess the effects of climate change on the local communities' food security and cultural relation to caribou. As this example demonstrates, considering the impacts of human activities and climate change, co-developing adaptive management and conservation strategies to protect both herbivore populations and their habitats is critical. Implementing these strategies also requires bridging the interface between experiential and Indigenous knowledge, scientific knowledge and government policies (Yua et al. 2022). For instance, policies that restrict hunting quotas or implement limits for semi-domesticated reindeer herd size, while at the same time promoting the exploitation of natural resources can erode trust and increase the potential for frictions between government and communities, thus preventing meaningful knowledge co-production and adaptive management (Parlee et al. 2018; Larsson Blind 2022; Sarkki et al. 2022). However, the co-development of new management strategies offering solutions to address current caveats is also on the rise (Simba et al. 2024). For instance, the use of quality checked protocols for stakeholder involvement, such as the strategic foresight protocol (Hamel et al. 2022) and Community-Benefits Agreements (CBA; Gunton and Markey 2021) can help define assets, incentives, risks, and roles and can create a roadmap of shared purpose among participants involved in herbivore management across rights holders and stakeholders who bring diverse ways of knowing.

M6. What is the role of herbivores in Arctic socio-ecological systems?

The roles of herbivores within Arctic socio-ecological systems span biological, economic and cultural dimensions. Six responses emphasized the need to understand these roles and their relevance to maintaining viable rural communities in the Arctic and sub-Arctic (**Figure 4, Table S3.2**).

Reindeer/caribou, moose, muskoxen, ptarmigan, waterfowl and hares are hunted across the Arctic, providing food for subsistence use, while other herbivores like reindeer are herded in parts of the range. Aside from food, materials like furs, antlers and bones can be reworked by local artisans to make items for personal use or for sale, including clothing, jewelry and tools (Aslaksen et al. 2009). Carrying out these practices provides Arctic people with material resources, as well as opportunities to facilitate the transmission of cultural knowledge and skills (e.g., Pearce et al. 2015; Laptander 2023). The language, behaviour and stories shared during these practices can maintain community bonds and allow more intangible spiritual understandings about purpose, identity and how to relate to other beings to be communicated and enacted (Justice 2018; Ravna 2020; Salusky et al. 2022). In the wider ecological system, the grazing and fertilizing action of herbivores maintains multiple ecological processes, creating habitats that support other plants and animals that Arctic people rely on and can influence climate feedback processes (Olofsson et al. 2004; Te Beest et al. 2016; Ylänne et al. 2021), thus affecting humans globally. Despite the importance of herbivores to the livelihood and subsistence of local communities, these activities often do not represent a main economic source for the country (e.g., in comparison to fisheries; Bjørndal and Munro 2012), resulting in lack of priority national funding for long term monitoring Nevertheless, there are some positive counterexamples such as the subnational support for preserving Indigenous country food practices in Nunavut (Warltier et al. 2021).

Several aspects of the role of herbivores in these socio-ecological systems require more research. The full extent of the impact of herbivores on global climate processes is not yet well understood (Koltz et al. 2022; Stark et al. 2023), and larger spatial coverage of research on reindeer and other herbivores across the Arctic would be valuable (Soininen et al. 2021). Similarly, how herbivores are adapting to changes in climate and anthropogenic land use requires more study so that the consequences to food security can be predicted (Cuyler et al. 2020; Stoessel et al. 2022; van Beest et al. 2023). Given the tight interplay between ecological and socio-political factors in the Arctic (e.g., Naylor et al. 2021), interdisciplinary approaches encompassing natural, social and Indigenous sciences will be needed to address these gaps in understanding, and to reliably inform policy and management strategies going forward (Riseth et al. 2011; Baztan et al. 2017; Pedersen et al. 2020; Moirano et al. 2020; Tsuji et al. 2020; Kater 2022).

M7. How can we gather information on Arctic herbivores that is relevant to management?

Focus on improving and further developing methods to monitor herbivore abundance and population dynamics, and the use of new technologies to collect data at spatial and temporal scales that are relevant to management is a key priority. Two responses were included under this priority (**Figure 4**).

Gathering information that is relevant to management should be grounded in robust conceptual models that can integrate the diversity of spatial and temporal data existing for a system and guide new data collection. These conceptual models can help define key system-specific parameters to monitor and identify data gaps and guide adaptive management approaches. An excellent example of a framework where conceptual models guide monitoring and data collection is the Climate Ecological Observatory for Arctic Tundra (COAT; Ims and Yoccoz 2017). In COAT’s conceptual models, climate and management are the main drivers of change and data collection is tailored to management needs. These needs are defined based on long-term involvement of rights holders including Indigenous people (herders), stakeholders and managers, and are guided by national and international management plans. For example, the need for reliable data on abundance and distribution of herbivores is set by management goals targeting population sizes. Based on these data, management decisions will guide different actions depending on whether the goal is to increase, reduce or maintain stable populations.

Collecting data at spatial and temporal scales relevant to the herbivore and the management setting in question remains challenging. However, recent technological developments in remote sensing, GPS tracking, and bio-logging (see **S3**) to gather detailed information on herbivore movements, feeding patterns, and real-time responses to environmental changes represent a significant advance. In addition, high-resolution and non-invasive methods such as genomic sequencing of pathogens (Seru et al. 2024) and faecal material (Soininen et al. 2009; Neby et al. 2024), microhistology (Filella et al. 2023) or near-infrared spectroscopy (NIRS; Tuomi et al. 2023) can provide spatially and temporally explicit information on herbivore disease and diet, that can inform harvesting, herding or other management decisions.

The rapid changes faced by herbivores in many ecosystems demand that managers anticipate future changes to implement short- and long-term strategies to reduce negative, unwanted impacts. Near-term ecological forecasts provide a framework for such predictions (see Marolla et al. 2021 for a specific example on rock ptarmigan). Management contexts and goals differ, and management actions must be based as much as possible on scientific evidence and knowledge co-production (see **M5**). Focusing on well-described, transparent and scientifically robust processes that set up the communication and workflows between scientists, managers and local communities involved is therefore key to jointly defining research questions and study designs using an adaptive approach (Lindenmayer et al. 2011). For example, Henden et al. 2020) offer a case study for stakeholder involvement in management of willow ptarmigan in northern Norway, where collective learning allowed defining questions and guided data collection. Successfully interweaving knowledge systems (see **M5**) and developing strong partnerships requires investment of time and funding to facilitate cooperation between stakeholders, and building initiatives on key lessons learned from successful initiatives (e.g., Hamel et al. 2022).

M8. Which societal obstacles prevent the use of Arctic herbivores in ecosystem management and how can these obstacles be overcome?

Knowledge is of little practical value if societal obstacles prevent its use in management. Two responses mentioned the attitudes of Arctic stakeholders and the societal obstacles that prevent the use of Arctic herbivores in ecosystem management (**Figure 4**).

Obstacles that prevent the translation of knowledge into practice and policies can relate to economic, cultural, legislative, ethical, and behavioural factors. These factors can be identified for example by mapping the attitudes of participants (Bauer et al. 2009) or promoting the use of deliberative democracy methods in which public consultation with citizens is central to democratic processes (Lépy et al. 2018). Other approaches, like tackling legislative barriers across country borders (Trouwborst et al. 2016; see also Heininen et al. 2020), collaborating with environmental ethicists (Ferraro et al. 2021), and developing micro- and macroeconomic solutions to enable financing of more sustainable herbivore management (Karolyi and Tobin-de la Puente 2023) could also help overcome these obstacles. These approaches, however, remain little used in the Arctic.

Interestingly, the two responses included in this priority were ranked among the lowest in scientific importance (average scores for scientific relevance 1.90 and 1.31), which might reflect the predominant natural science background of survey participants and their varying experience in translating science into applied research and management advice. Future prioritization exercises could engage more social scientists, reinforcing inter- and transdisciplinary research (see Ivanov et al. 2024) to identify the social dimensions of management decisions. Thus, in addition to strengthening our knowledge on herbivores and their interaction with climate change from a natural sciences perspective, there is a need for economic, socio-political, cultural, juridical, ethical, and human behavioural studies around herbivores and their use (see Artner and Siebert 2006; Burak et al. 2024).

Conclusions

This horizon scan has identified sixteen emerging priorities in the field of Arctic terrestrial herbivory research that should be addressed over the next decade. The horizon scan concluded that understanding the impacts and effects of herbivory and herbivores on tundra ecosystems in rapidly changing environments remains a high priority. However, one general observation from this horizon scan is that there is still a need for closer integration of research and management priorities. We chose to balance the number of research and management questions (**Figure 3**), but also recognize that there is often a persistent gap between ecological science and environmental management priorities (Underwood 1998; Gosselin et al. 2018).

Our categories of *science* and *management* are complementary only to the extent that their knowledge perspectives have an obvious interface. Researchers should be able to improve the applicability of their research through interacting better with resource managers and Indigenous organizations who are directly responsible for management decisions and interventions. Further, we encourage partnerships to co-design applied management research based on relevant questions and knowledge needs. Future research that addresses the priorities that we have identified will benefit from a more deliberate effort to conduct studies that incorporate management perspectives, including testing of management interventions and investigating alternatives when current practices fail (Underwood 1998).

Our consensus was that the most important research questions for the next decade pertain to fundamental ecological processes at different scales, climate change, technology and innovation, sustainability and the co-production of knowledge and solutions. Climate change was featured in several scientific (**S1**, **S4**) and management (**M1**, **M3**) priorities. The impacts of climate change are seen and felt across Arctic environments and are particularly impactful at the local and community level, for example for herbivores that are harvested for subsistence. The impacts of climate change will influence how research is conducted and may affect the implementation of natural resource use, management and conservation practices.

The upcoming Fifth International Polar Year in 2032-33 will provide considerable motivation for planning and developing new research initiatives on Arctic herbivores. These initiatives should include coordinated ecosystem-based and circumpolar efforts that incorporate diverse knowledge systems into future research programs. It will be important to match the current state-of-knowledge and emerging technology with the quickly changing dynamics of many Arctic herbivores and the environmental changes occurring in tundra ecosystems. Addressing these priorities will require developing new methods and inclusive, interdisciplinary collaborations.

Including diverse research communities and management bodies are both prerequisites for effective cross-domain knowledge sharing and adoption. This new knowledge can be incorporated into formal institutional policies and processes. In terms of facilitating and enhancing the interface between science and management, we are hopeful that our horizon scan research prioritization will help to create and sustain informal “communities of practice”, for example through the Herbivory Network (Barrio et al. 2016b; http://herbivory.lbhi.is) or independently. These efforts will also enable periodic updates of this horizon scan, complemented with the additional insights from diverse stakeholders.

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Competing interests

The authors declare there are no competing interests.

Author contribution statement

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Data availability statement

Data and scripts used to generate the figures presented in the manuscript are available on GitHub: https://github.com/icbarrio/ArcticHerbivoryHorizonScan

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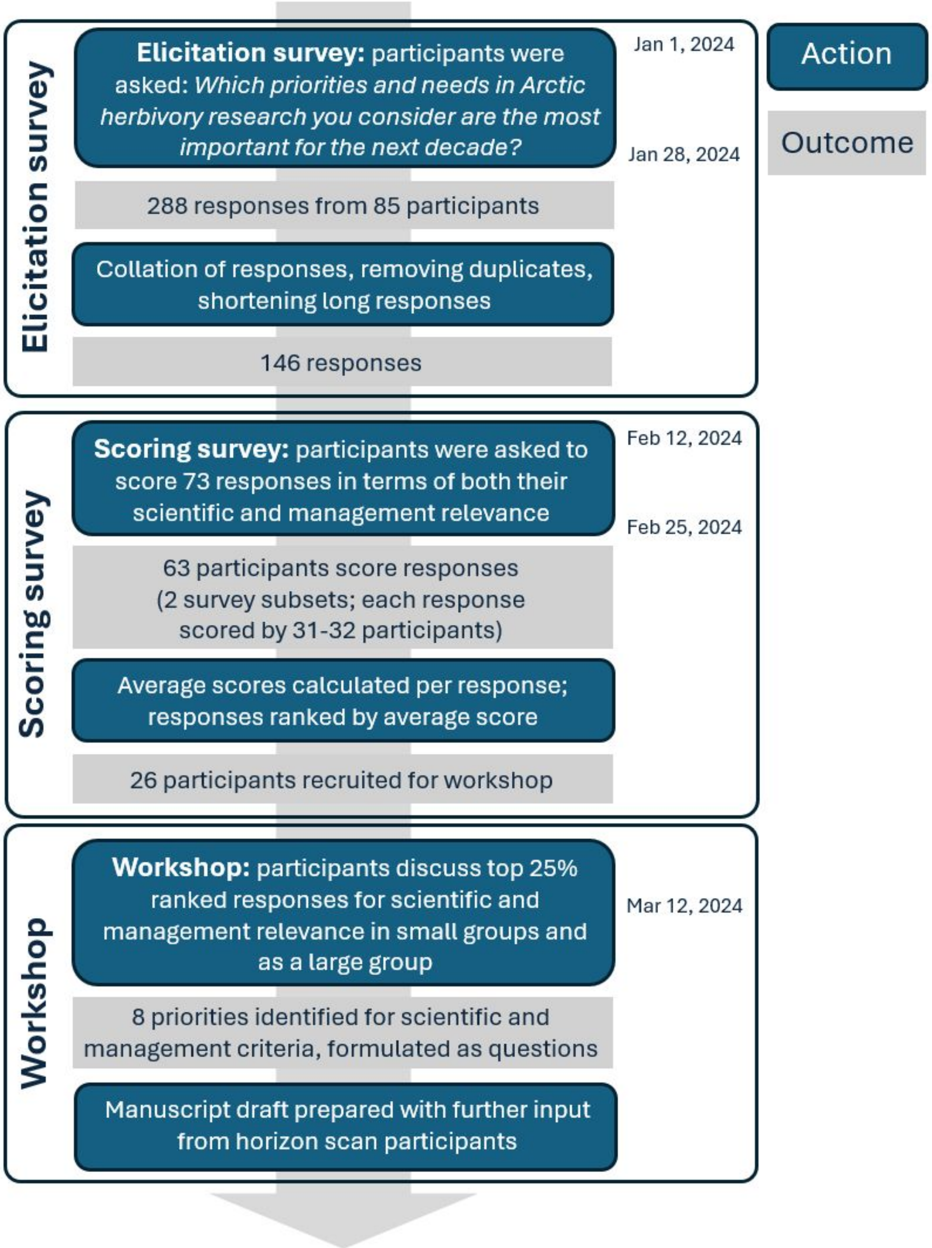

Figure 1. Schematic diagram of the Arctic herbivory horizon scan process. The process was structured in three key steps: 1) an elicitation of expert knowledge through an online survey (Elicitation survey), 2) an online survey requesting participants to score a list of responses (Scoring survey), and 3) an in-person workshop to summarize the information (Workshop).

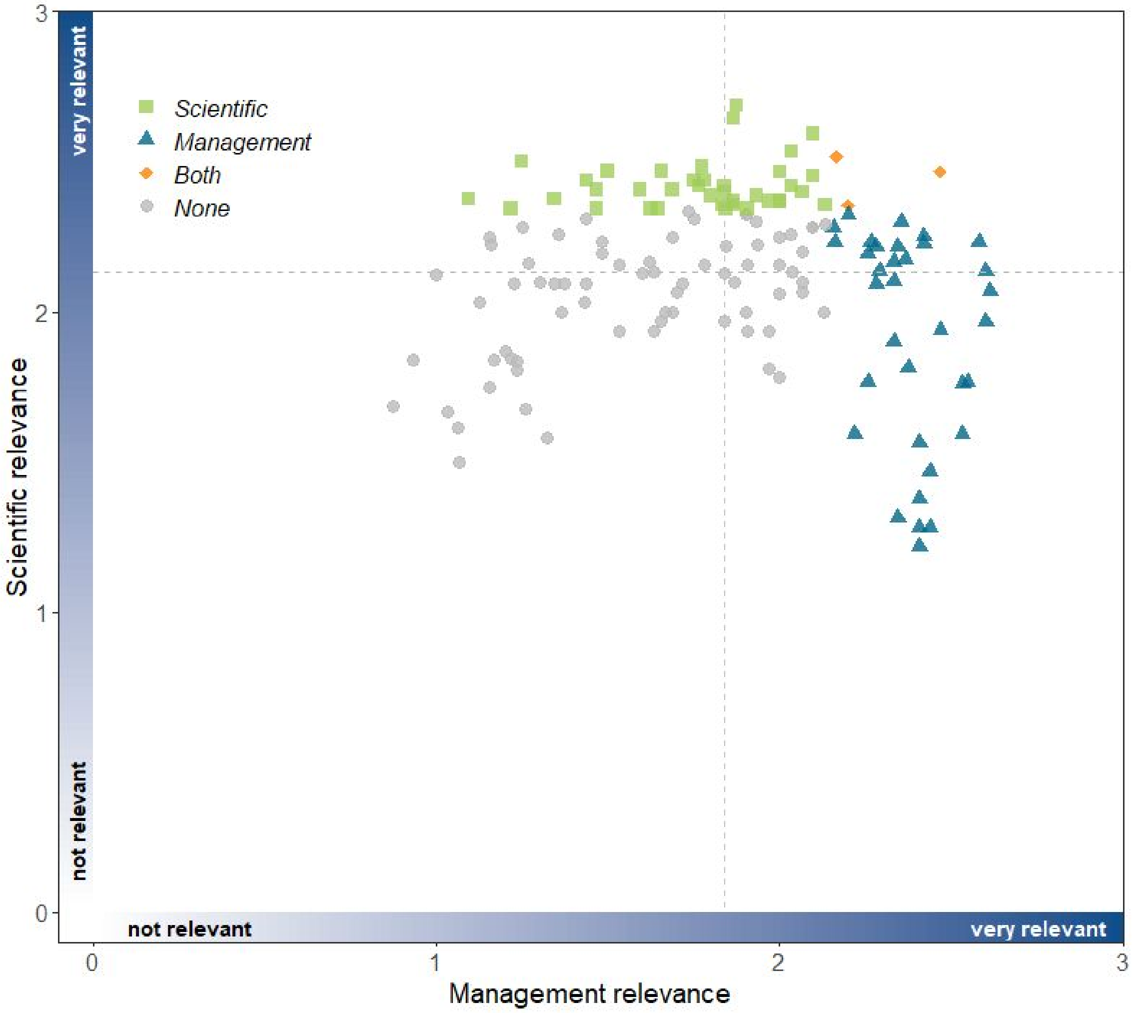

Figure 2. Relationship between the scientific and management relevance scores assigned to 146 responses by the 63 Arctic herbivory experts participating in the scoring survey. Scores for individual responses included in each priority ranged between 0 (not relevant) to 3 (very relevant). Each point represents the average score for one response, with colours and shapes indicating whether the response was scored in the top 25% responses according to its scientific relevance (green squares), management relevance (blue triangles) or both (orange diamonds), or if the scores were not among the top 25% of either criterion (grey circles). Dashed grey lines indicate average scores across responses for scientific (2.84 points) and management relevance (1.84 points).

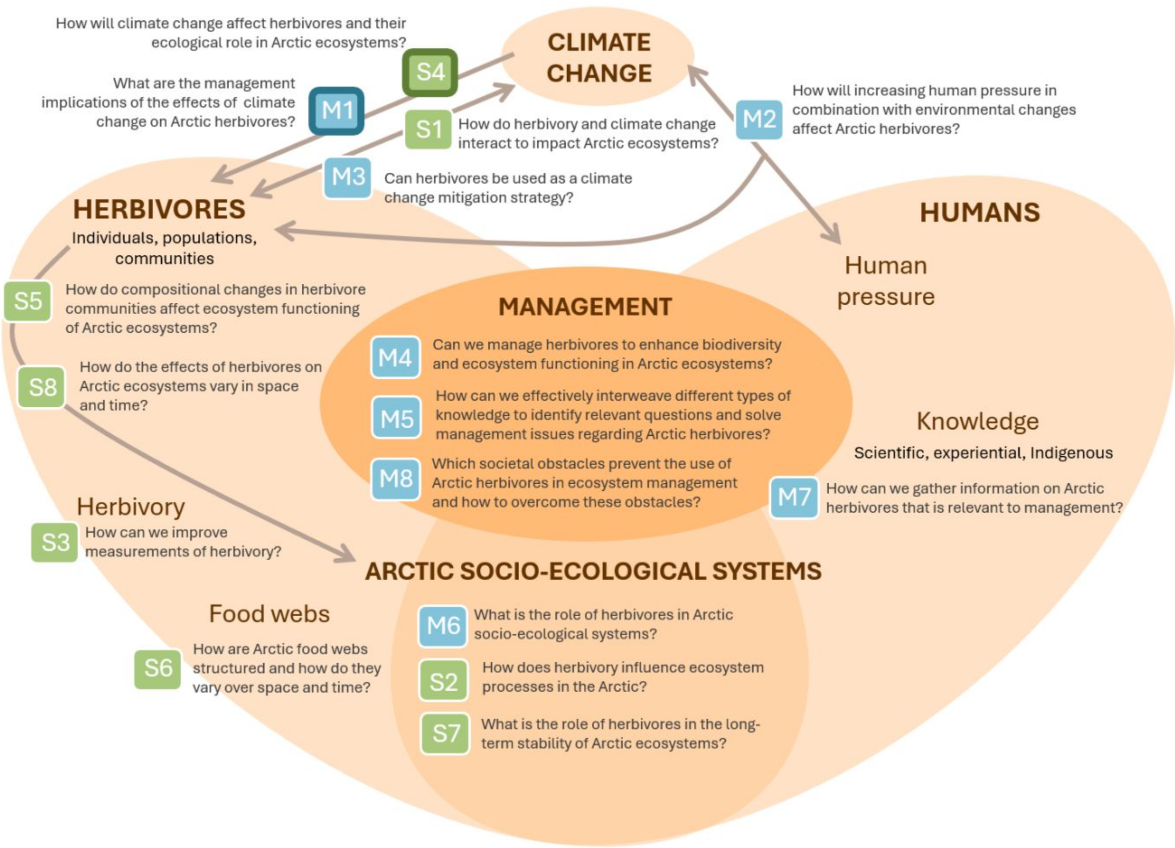

Figure 3. Overview of the relationships between the eight scientific (green) and eight management (blue) priorities identified by 26 Arctic herbivory experts in the in-person workshop of the horizon scan. Priorities with wide outline (**S4**, **M1**) indicate priorities that included responses identified with both scientific and management relevance. S = scientific priority, M = management priority

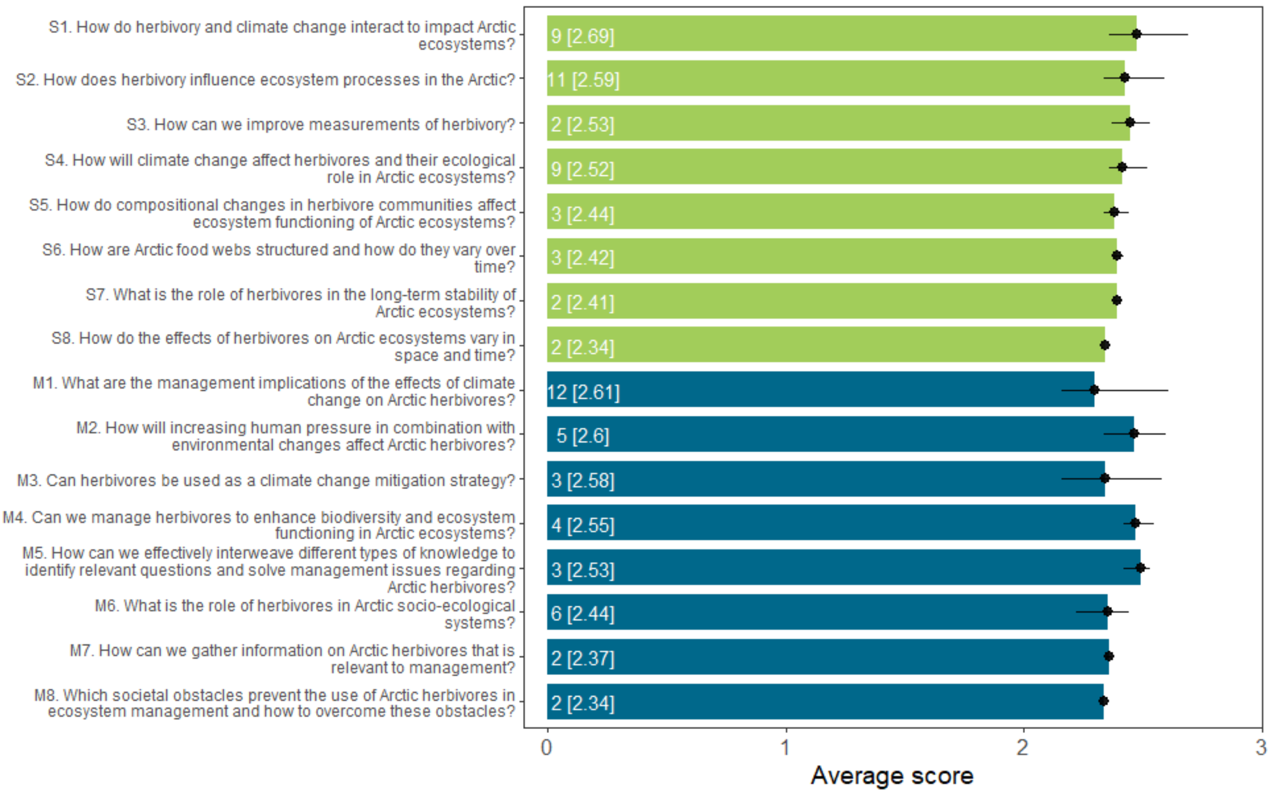

Figure 4. Average scores for each of the eight scientific (green) and management (blue) priorities identified during the horizon scanning exercise, as assessed by 63 Arctic herbivory researchers who participated in the scoring survey. Each priority included between two and twelve responses (number of responses included in each priority are indicated at the base of each bar). Scores for individual responses included in each priority ranged between 0 (not relevant) to 3 (very relevant). The ordering of scientific (**S1-S8**) and management (**M1-M8**) priorities is based on their highest-scoring individual response (indicated by the numbers in square brackets to the right of the bars). Average scores are indicated by black dots, and the horizontal lines represent the range of scores of individual responses (min, max).