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Citation
Osterrieth, M., & Bosker, T. (2024). Impacts of terrestrial mammalian herbivores on vegetation change in the arctic. *Polar Biology*, *47*, 1307-1321. doi:10.1007/s00300-024-03302-4

Version:	Publisher's Version
License:	Creative Commons CC BY 4.0 license
Downloaded from:	https://hdl.handle.net/1887/4177114

Note: To cite this publication please use the final published version (if applicable).

Polar Biology (2024) 47:1307–1321
https://doi.org/10.1007/s00300-024-03302-4

REVIEW

Impacts of terrestrial mammalian herbivores on vegetation change in the arctic

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Received: 1 June 2023 / Accepted: 18 September 2024 / Published online: 17 November 2024
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Abstract

There are increasing concerns about regional ecosystem shifts in the Arctic due to climate change. Notably, warming-induced increases in Arctic vegetation cover can have important consequences for surface energy balance, habitat changes, permafrost, and more. Mammalian herbivory is an important potential force to counteract this effect. In this systematic literature review, we examine the role of terrestrial mammalian herbivory on warming-induced increases in Arctic vegetation. We analyse the effects of terrestrial mammalian herbivory on vegetation cover, abundance, growth, survival, and ecosystem productivity. Our results show that herbivory has an overall significant negative influence on Arctic vegetation, particularly on vegetation biomass, growth, and productivity, as indicated by the Normalised Difference Vegetation Index (NDVI). Importantly, we demonstrated a significant role of herbivores in controlling carbon dioxide exchange and carbon uptake, whilst acknowledging that the relationship between herbivory and ecosystem productivity is highly complex and site-dependent. Our results confirm the important role that herbivory can play in buffering observed and predicted warming-induced Arctic vegetation increases. We also find that this is strongly affected by plant palatability, trampling occurrence, and herbivore density.

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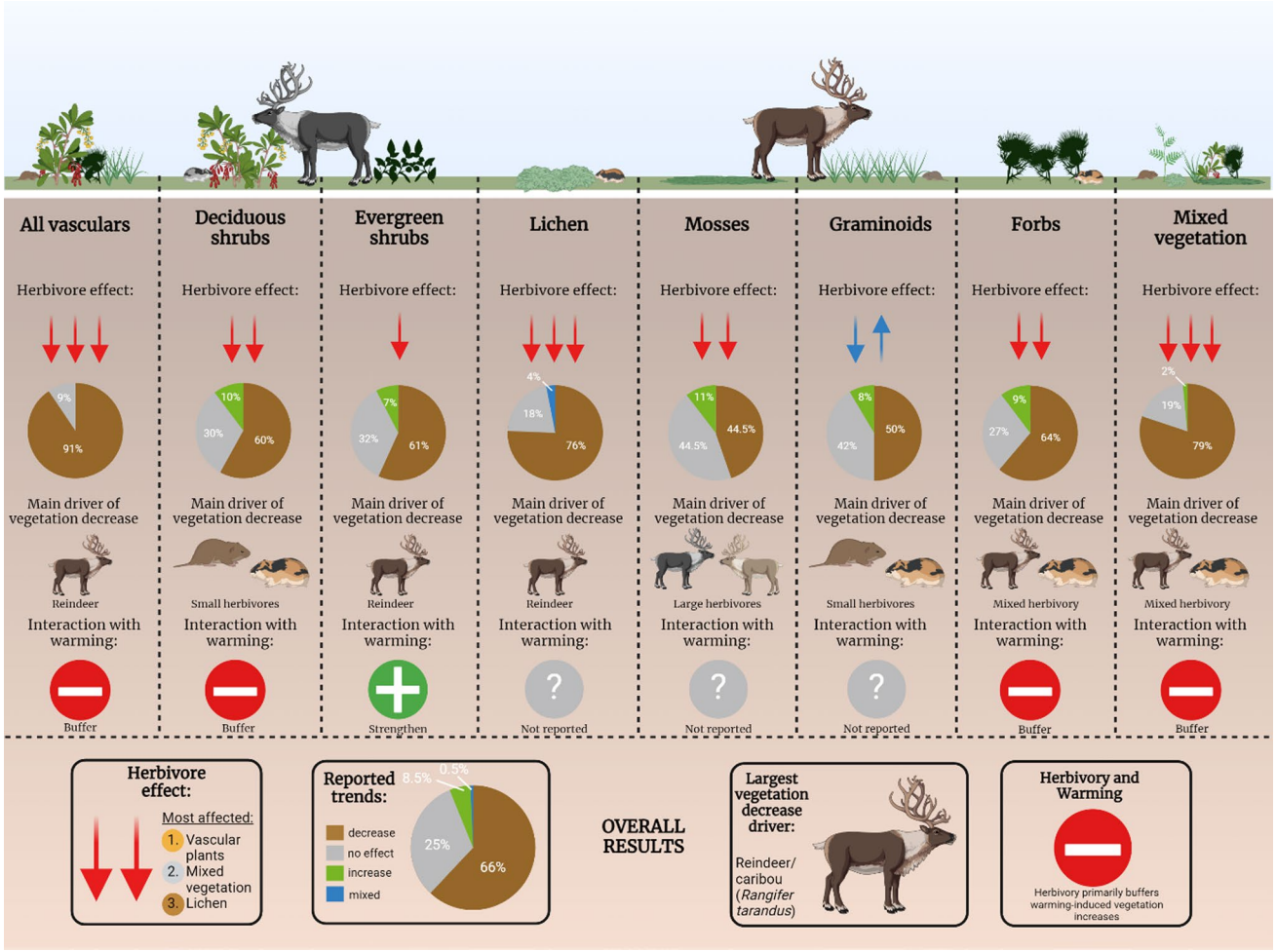
Graphical Abstract



Keywords Systematic literature review · Climate change · Mammalian herbivory · Vegetation change · Arctic

Introduction

Climate change-induced warming is particularly pronounced in Arctic regions, where it is predicted to be double that of global averages, thereby driving ecological and ecosystem changes (Wang & Friedl 2019; Taylor et al. 2020). As a result, there are significant shifts in the distribution and abundance of flora and fauna within the region, which can result in alterations of the surface energy balance (Myers-Smith et al. 2011, 2020; Villareal et al. 2012). Arctic vegetation shifts further influence important processes such as soil temperature, decomposition rates, and organic matter levels (Zhang et al. 2013; Bjorkman & Gallois 2020). Moreover, shifts in flora distribution, density, and composition have led to changes in albedo and carbon feedback loops (Zhang et al. 2013; te Beest et al. 2016; Bjorkman & Gallois 2020; Limpens et al. 2021). In turn, changes in circumpolar vegetation alter evapotranspiration rates, and influence permafrost thaw rates (te Beest et al. 2016). Modifications in primary productivity can also cause loss in Arctic habitat, and the northward shift of non-native thermophilic plants and animals (Ims et al. 2019).

These Arctic vegetation shifts can lead to visible changes in vegetation cover, which can be assessed via time-series data from satellite imagery using the Normalised Difference Vegetation Index (NDVI) (Epstein et al. 2013; Wang & Friedl 2019). Productivity and cover changes in the region can also correlated with and explained by changes in vegetation characteristics, such as abundance, plant density, leaf size, growth, and survival (Epstein et al. 2013; Arndt et al. 2019; Ims et al. 2019; Piao et al. 2020). There is a substantial heterogeneity of vegetation responses within the Arctic, with both increases and decreases in vegetation observed. The main drivers of vegetation increase include carbon dioxide

(CO_2) fertilisation, climatic changes, land-use changes, nitrogen (N) deposition, and herbivory (Zamin & Grogan 2013; Olofsson & Post 2018; Piao et al. 2020). Meanwhile, negative trends in vegetation are also driven by herbivory, as well as large winter warming events, limited precipitation, and permafrost thaw (te Beest et al. 2016; Ju & Masek 2016; Callaghan et al. 2022). Interestingly, much of the region also displays surprising stability despite warming (Myers-Smith et al. 2020; Callaghan et al. 2022). Arctic vegetation stability has been explained by micro-scale spatial heterogeneity, functional redundancy of polar vegetation, the inability of plants to respond to changing temperatures, and herbivory (Callaghan et al. 2022).

As highlighted above, herbivory presents varied impacts on Arctic vegetation change, driven by grazing, trampling, and their excrements (Sundqvist et al. 2019; Tuomi et al. 2020; Koltz et al. 2022). Under current warming scenarios, northward shifts of flora and fauna are expected to increase herbivore abundance, diversity, and, as a result, this might influence their impacts on Arctic vegetation trends (Virtanen et al. 2010; Bernes et al. 2015). Systematically reviewing the impacts of the extensive literature on herbivory can provide an improved understanding of the extent to which different herbivore species impact Arctic vegetation and which vegetation types are most sensitive (Koltz et al. 2022). Recent reviews have focused on mapping the evidence base of herbivory studies (Soininen et al. 2021; Ramsay et al. 2022), and the effects of herbivore diversity more specifically (Barrio et al. 2022). In this study, we systematically review the literature to synthesis the predominant effects of terrestrial mammal herbivory on Arctic vegetation trends. This will help reinforce and inform conservation and modelling efforts, and provide suggestions for future research. Specifically, this review aims to answer the question: how does terrestrial mammal herbivory affect changes in vegetation trends within the Arctic region?

Methodology

Scoping process

This systematic literature review (SLR) followed Siddaway et al. (2019) in combination with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) checklist to ensure the thorough analysis and inclusion of past literature on the subject (Moher et al. 2009). Such methods enabled an unbiased and complete inclusion of the knowledge, facilitating the synthesis of findings for future use and identification of research needs (Siddaway et al. 2019). We only used peer-reviewed scientific research articles, and no additional grey literature was included.

Search terms

The search terms were chosen based on keywords and topics, and fell under several categories to ensure the inclusion of all relevant sub-topics. Main topics were separated by Boolean "AND" operators, and included all relevant synonyms and their variations using "OR" operators. The final search string was as follows:

(("Arctic" OR "Circumpolar*" OR "Circumpolar*" OR "Polar" OR "North* Pole*" OR "High* Latitude*" OR "Tundra*" OR "Boreal" OR "North* Latitude*" OR "Nordic Region*")*
AND
("Arctic Greening*" OR "Arctic* Browning*" OR "Arctic-Greening*" OR "Arctic-Browning*" OR "Veget* Shift*" OR "Plant* Shift*" OR "Specie* Shift*" OR "Greening*" OR "Browning*" OR "Green* trend*" OR "Brown* Trend*" OR "NDVI" OR "Normalised Difference Vegetation Inde*" OR "Shrub*" OR "Lichen*" OR "Grass*" OR "Sedge*" OR "Graminoid*" OR "Bryophyte*" OR "Forb*" OR "Tree*")*
AND
("Climat Chang*" OR "Climate-Change*" OR "Global Warming" OR "Warm*" OR "Climat* Shift*" OR "Climat* Warming")*
AND

Table 1 Exclusion criteria utilised for article screening as part of the PRISMA methodology

Exclusion criteria	
I	Is a review article or not peer-reviewed (i.e. only peer-reviewed research articles were selected)
II	Response variables were irrelevant to vegetation changes (i.e. only articles that included measurements concerning impacts on plants were included)
III	Study sites are located primarily outside of the Arctic Circle (66°N)
IV	Is not primarily focussed on terrestrial mammalian herbivores
V	Is published before 2010

("Herbivor" OR "Graz*" OR "Mammal*" OR "Brows*"))*

In February 2023, these search terms were entered into Web of Science and PubMed, two highly reliable search engines (Falagas et al. 2008; NLM 2023; WebofScience 2023).

Screening and data extraction

In this review, the term "articles" refers to individual papers, and "study sites" are defined as locations of data collection within articles. Within the study sites, "observations" refer to specific findings attributed to a certain type of herbivory and to a specific response variable. Therefore, multiple observations can occur within one study site, depending on whether different types of herbivores and response variables were assessed.

After the search, we first removed duplicates and non-English language papers from the search results. Next, the titles and abstracts of all remaining results were screened based on pre-defined exclusion criteria (Table 1).

Articles with study sites predominantly below the Arctic Circle (66°N) were excluded to keep a consistent and well-defined border to the definition of "Arctic" vegetation and herbivores. Importantly, several study sites were outside of the Arctic circle but were part of articles in which multiple study sites were included, most of which were above the required latitude. Articles before 2010 were also excluded to narrow the search down to recent findings which reflect the most up-to-date state of the literature. After the screening of the title and abstract, the remaining articles were read in full, and screened based on the exclusion criteria. Articles included in the final list of papers (Table S1) were analysed in full. Several borderline cases were identified, and the reasons for exclusion are provided in Table S2. Finally, the bibliographies of the included articles were screened for any additional papers.

Next, information on the study site(s), methodology, assessed response variables, investigated species (herbivores/vegetation), and the main trends and findings were extracted from the articles (Database S1; Database S2), and summarized (Table S3-S7). Main observations in vegetation were compiled and presented to reflect predominant trends and differences in the effects of various species of herbivores. Additionally, main trends of expansion or reduction of different plant functional groups (e.g. deciduous/evergreen shrubs, mosses, graminoids) were created, thereby visualising which plant species were impacted by herbivory and in what direction (Table 3; Table 4; Table S8; Table S9).

Given the wide range of study approaches used within the articles, we opted for a qualitative summary of the results, over a more quantitative approach, such as a meta-analysis. The direction of vegetation changes were therefore categorised in one of six categories: "decrease", "small decrease", "increase", "small increase", "mixed results", and "no significant effect". Observed changes in vegetation were summarised within these categorisations based on the results presented in combination with the interpretations of these findings within the articles. Observed changes were categorised as "small decrease" or "small increase" when it was made explicit by authors in their description or discussion of results that the effect was deemed relatively small. Observed changes were categorised as "mixed results" if results presented both directions of change at one study site for the same herbivory/vegetation type and response variable. When aggregating these observations together to estimate the overall effect per herbivory type or response variable, a

Table 2 Response variables addressed within articles placed into relevant response variable groups covering changes caused by herbivory on Arctic vegetation

Response variable group	Response variable within the grouP
Vegetation cover	Albedo Leaf Area Index (LAI) Normalised Difference Vegetation Index (NDVI) Plant cover
Vegetation abundance and density	Plant biomass Plant abundance Plant density
Vegetation growth	Growth rate Flowering rate Plant height
Vegetation survival	Survival rate Plant damage Recruitment rate
Ecosystem productivity	Gross primary productivity (GPP) Gross ecosystem photosynthesis (GEP) Net ecosystem exchange (NEE) Ecosystem respiration (ER)

weight-based system was used. Cumulative grouped trends were calculated by assigning a fixed weight-based value for every individual observation based on their observed trend (increase = 2, light increase = 1, no change = 0, light decrease = −1, decrease = −2). The sum of these observation values was then averaged and rounded to the nearest whole number. If there was a strong variation within the observations [defined here as at least one increase (score 2) and decrease (score -2)], a mixed-result outcome was reported. The heterogeneity of study designs and foci made our selected method a pragmatic choice for our research goals. Furthermore, this approach helps to highlight research consensuses (or lack thereof) in an accessible and intuitive manner. Due to the numerous response variables assessed within relevant articles, response variables were organised in the groups shown within Table 2.

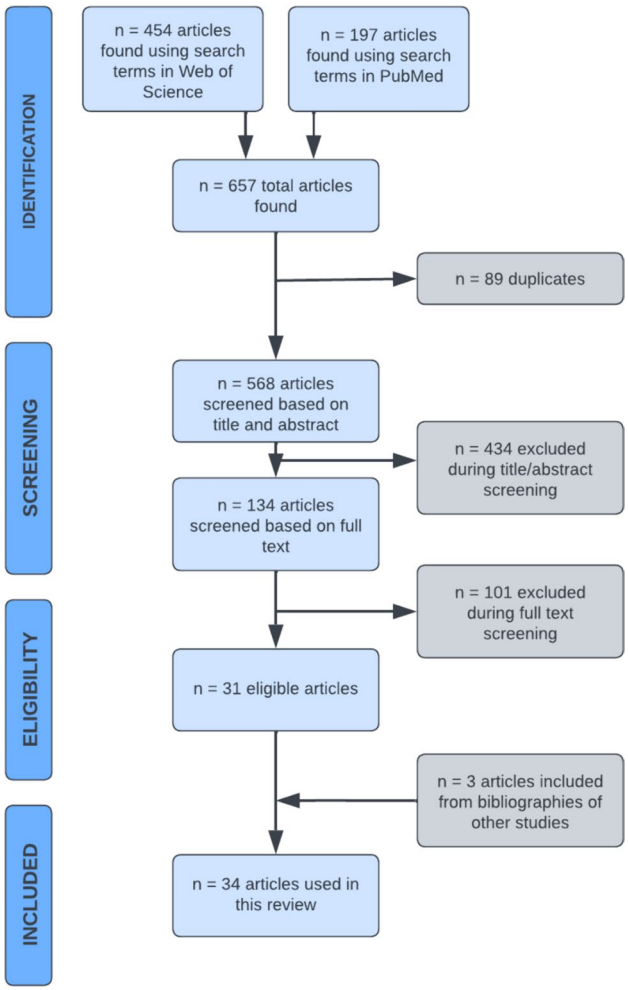


Fig. 1 Summary of the systematic review screening and eligibility process according to the PRISMA (Preferred Reporting Items for Systematic reviews and Meta-Analyses) methodology, with n referring to the number of articles in each step of the process (Moher et al. 2009)

Since some articles included different combinations of herbivores in their study sites, classifications of herbivore groups were also made. "Mixed small herbivores" was used for when mammals such as lemmings, voles, and hares were studied together. "Mixed large herbivores" included reindeer/caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*). Lastly, "mixed small and large herbivores" was used when mammals from both small and large herbivores were studied together.

Results and discussion

Search returns

A total of 657 articles were found: 454 from Web of Science, and 197 from PubMed (Fig. 1). Following the duplicate-removal stage and the initial title/abstract screening process, 134 articles were left for full-text screening (Fig. 1). During the full-text screening, an additional 101 articles were removed. Key reasons for removal at this stage were related to geographical location, the focus on non-mammalian herbivores (particularly birds and invertebrates), and a focus on irrelevant response variables (e.g., no data on vegetation cover and change, vegetation was instead used as a predictor of herbivore movement and health). As a result, 31 articles were included in the systematic review, and an additional three articles were included after screening the bibliographies of the original 31 articles (Fig. 1).

Experimental designs

Over half ($n = 18$; Fig. S1) of the articles used herbivore exclosures (i.e., removing herbivores at one certain site in tandem with controls where herbivory was still present). Several other articles ($n = 6$) implemented such exclosures with open-top chamber (OTC) warming treatments to study the effect of climate warming alongside herbivory. Three papers used pre-existing field sites of naturally exclosed or grazed sites to study differences in vegetation response. Two other articles implemented varied exclosures of different herbivory types which allowed for a gradient of grazing intensity, and two used aerial or satellite-driven data to analyse the effects of herbivory on vegetation. Lastly, three others used ArcVeg models to predict future impacts of herbivory on vegetation. Study length varied between 1 and 53 years, averaging at 14.3 years, and ranged between the years 1959 and 2019. The number of study sites per article varied, with 52 study sites differentiated across all articles.

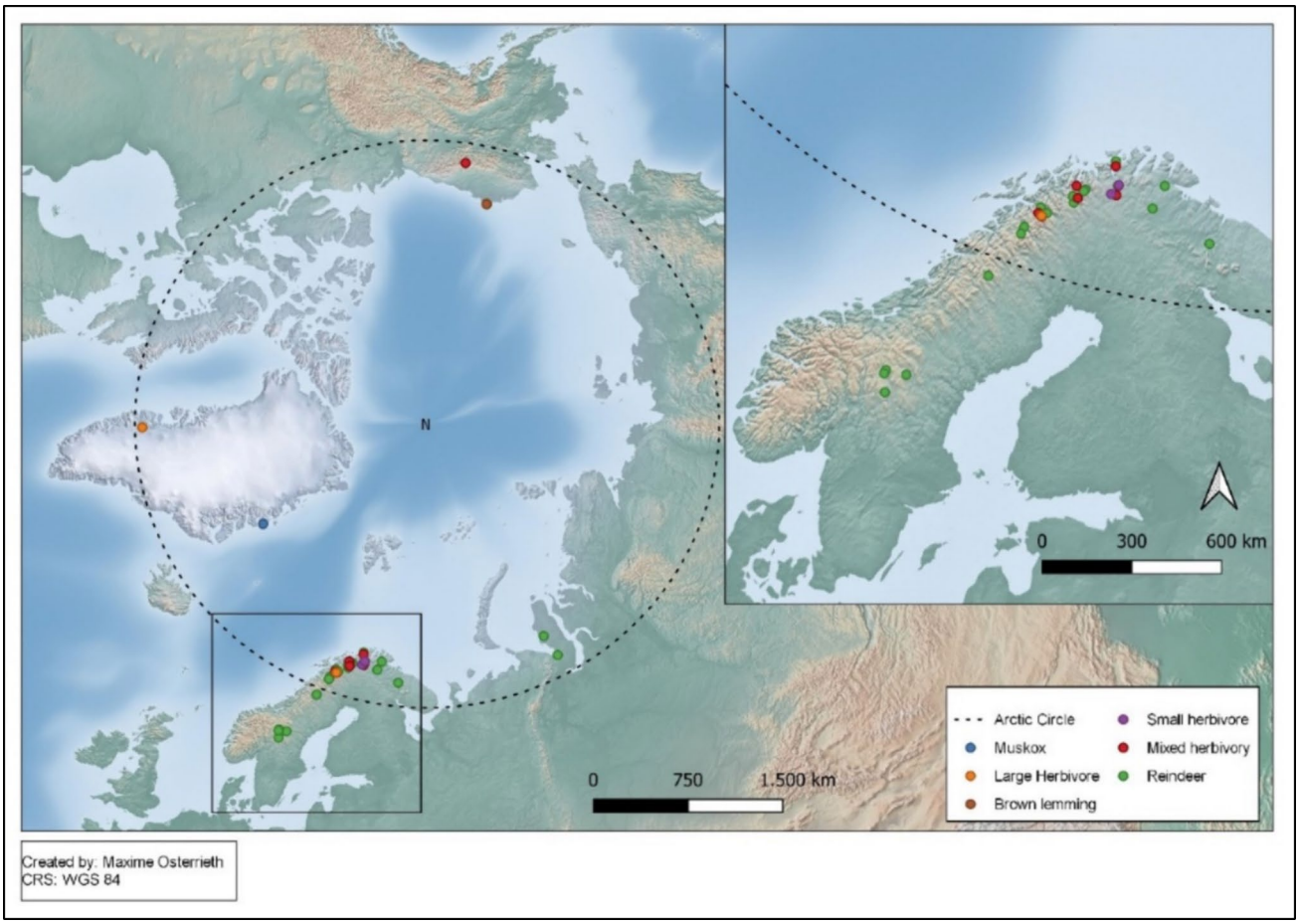


Fig. 2 Map of study sites included in the peer-reviewed articles from 2010 to present that were used in the systematic review, highlighting their location and the herbivores which were studied, with a more specific focus on Scandinavia due to higher concentration of study sites. Note: several study sites were included outside of the Arctic Circle: these are part of articles in which multiple study sites were included, most of which were above the required latitude

Most herbivores analysed within the articles were reindeer ($n = 13$; Fig. 2). Several others were conducted on muskoxen ($n = 2$) and brown lemmings (*Lemmus trimucronatus*; $n = 3$). A total of 11 articles focused on several different species at once (both large and small).

Out of all study sites ($n = 52$), 76.9% ($n = 40$) were located in Scandinavia and Finland, whilst only 5.8% ($n = 3$) were in Russia, 5.8% ($n = 3$) in Greenland, 7.7% ($n = 4$) in Alaska, and another 3.8% ($n = 2$) involved most of the Arctic biome. Importantly, several study sites ($n = 5$; Fig. 2) were outside of the Arctic Circle, but were included in the review as they were part of articles in which multiple study sites were included, most of which were above the required latitude.

A wide variety of response variables relating to Arctic vegetation shifts were studied throughout all included articles (Fig. S2). A total of 50% of articles ($n = 17$) addressed plant abundance response variables, and 41.2% ($n = 14$) looked at plant biomass as an indicator of herbivory effect. A further 12 articles looked at NDVI, 10 at LAI and plant cover, eight at NEE and plant height, and seven at ecosystem respiration. For the remaining response variables (see Table 2), a maximum of four articles reported on them.

Overview of herbivory impacts on Arctic vegetation

Vegetation cover

Most research on vegetation cover response variables found that herbivory reduced local plant cover. A total of 69% ($n = 29$) of observations on vegetation cover reported negative effects from herbivory, and only 5% ($n = 2$) reported increased vegetation cover. Apart from one article finding no significant results, grazer exclusion or low-herbivory sites were shown to significantly and consistently increase local LAI in at least one study site. Additionally, almost all Scandinavian observations highlight that grazing significantly reduced NDVI (Biuw et al. 2014; te Beest et al. 2016;

Table 3 Observed changes in vegetation response variables separated into vegetation cover changes, abundance and density changes, growth changes, and survival changes. The number of observations which evaluate such response variables (for any of the herbivory and vegetation types) is indicated in the column headings. For noted changes, red (↓) = decrease, light red (⌄) = small decrease, blue (↑↓) = mixed results, light green (↑) = small increase, green (↑) = increase, and grey (⊘) = no significant effect

	Vegetation cover (n = 42)	Vegetation abundance (n = 91)	Vegetation growth (n = 33)	Vegetation survival (n = 10)	**General trend[a]**
Mixed small and large herbivory					
Mixed vegetation	↓	↓	↓	↓	↓
Vascular plant		↓	↓	↓	↓
Deciduous shrub		⌄			⌄
Evergren shrub		⌄			⌄
Lichen	↓	↑↓	↓		↓
Moss		⊘			⊘
Graminoid		↓			↓
Forb		↓	↓		↓
Mixed large herbivores					
Mixed vegetation	↓	↓			↓
Deciduous shrub		↓	⌄		↓
Evergreen shrub			⌄		⌄
Lichen	↓	↓			↓
Moss			↓		↓
Forb			↓		↓
Reindeer/caribou (*Rangifer tarandus*)					
Mixed vegetation	⌄	⌄	↓	⌄	⌄
Vascular plant	↓		↓	↓	↓
Deciduous shrub	↓	⌄	↓	⊘	⌄
Evergreen shrub	⌄	⌄	↓	⊘	⌄
Lichen	↓	↓	↓		↓
Moss	⊘	⌄			⊘
Graminoid	↓	↑↓			⌄
Forb		↑↓			↑↓
Muskoxen (*Ovibos moschatus*)					
Mixed vegetation	↓	↓			↓
Moss		↓			↓
Graminoid		↑			↑
Mixed small herbivores					
Mixed vegetation	↓	⊘		↓	↓
Deciduous shrub		↓	↓		↓
Evergreen shrub		↓	⊘		⌄
Lichen		↓			↓
Moss		↑↓			↑↓
Graminoid		↓			↓
Brown lemmings (*Lemmus trimucronatus*)					
Mixed vegetation	↓				↓
Deciduous shrub	⊘	⊘			⊘
Lichen		↓			↓
Moss	⊘	↓			⌄
Graminoid		↑			↑
Forb	⊘	↓			⌄
CUMULATIVE					
Grouped[a]	↓	⌄	↓	↓	↓

Table 3 (continued)

[a] General and cumulative grouped trends were calculated by assigning a fixed weight-based value for every individual trend (increase = 2, light increase = 1, no change = 0, light decrease = −1, decrease = −2), and then averaged and rounded to the nearest whole number, with the overall trend following the same aforementioned value-trend pairs. If the average is closest to 0 but characterised by strong variation between decreases and increases (at least one increase and decrease reported), a mixed-result outcome was shown

Sundqvist et al. 2019; Linden et al. 2021). Alaskan observations reinforce such trends, finding that lemming herbivory reduced mean NDVI from 0.551 to 0.465 (Plein et al. 2022). Two articles reported no effect from herbivory on NDVI trends (Ylänne et al. 2015; Sundqvist et al. 2019).

Strong negative effects of herbivory on plant cover were also reported, with Pajunen et al. (2012) demonstrating that exclosure of reindeer in Finnish Lapland, resulted in a 780% increase in deciduous shrub cover. Within Scandinavian study sites, albedo was higher under heavier grazing in both dry and humid sites (Biuw et al. 2014; te Beest et al. 2016). In contrast, an Alaskan study found higher albedo values in wet sites with the exclosure of brown lemmings (Lara et al. 2017). Brown lemmings had little impact on vegetation cover variables, with a negative impact on mixed vegetation but no significant effect on deciduous shrubs, mosses, and forbs (Table 3). This could be caused by the natural periodicity of lemming densities, with some periods having very low lemming densities, and others experiencing intense peaks of activity with up to 90% of vegetation being destroyed (Villareal et al. 2012). Such irregular lemming disturbances may limit the ability to detect significant effects on vegetation change during certain periods (Sørensen et al. 2018). Importantly, irregular herbivory may also make regional vegetation shifts unpredictable, thereby hindering the capacity to model and anticipate future ecosystem changes.

Overall, this review finds a general trend that terrestrial mammalian herbivores reduce vegetation presence. Notably, several articles demonstrated that caribou can prevent long-term shrub cover expansion despite significant warming (Damgaard et al. 2016; Andruko et al. 2020), and that grazing pressures have the potential to reduce the cover of various shrubs and lichens (Forbes & Kumpula 2009; Virtanen et al. 2010; Saucier et al. 2019). Nevertheless, overall cover change is difficult to predict as it depends on the composition of vegetation within a site (Villareal et al. 2012). As we focused on general trends across regions within this study, we did not investigate site-specific variability in vegetation. Therefore, whilst our results strongly suggest that there is a general trend of herbivory leading to a decrease in plant cover (Table 3), it is important to note that smaller-scale heterogeneity in cover change occurs.

A key driver in the variation of research outcomes is likely linked to interspecific competition and plant palatability (Olofsson & Post 2018). Plants with low palatability, such as evergreen shrubs for reindeer or all shrub types for brown lemmings, are less likely to be grazed and therefore gain a competitive advantage (Johnson et al. 2011; Damgaard et al. 2016; Yu et al. 2017). Our results support this hypothesis, as herbivores have smaller cumulative negative effects on evergreen shrubs, and brown lemmings show no effects on deciduous shrubs (Table 3). Additionally, the response of graminoids to herbivory was highly variable. Negative impacts were observed from mixed small and large herbivory, and reindeer, but positive impacts occurred from muskoxen and brown lemmings. Graminoid increases may result from compensatory growth strategies, with herbivory reducing biomass in the short-term, but promoting greater biomass in the long-term (Johnson et al. 2011). The extensive clipping of graminoids, which is common during large rodent outbreaks, may facilitate and accelerate graminoid biomass production due to higher decomposition rates and nutrient cycling (Johnson et al. 2011). Such effects may potentially fuel ecosystem compositional shifts. In fact, several articles suggested that heavy selective grazing on lichen and lower grazing on moss may result in a change from lichen-dominated to moss-dominated ecosystems (Yu et al. 2017; Olofsson & Post 2018). These also suggested shifts towards graminoid-dominated systems, which may have implications for vegetation diversity in the Arctic (Yu et al. 2017; Olofsson & Post 2018). Moreover, warming conditions may cause thermophilic graminoids to outcompete other woody plants, thereby creating a positive feedback loop resulting in additional ecosystem dominance (Yu et al. 2017). Graminoids also decompose quickly, maintain oxygenated soils, and produce high-quality litter, which ensures a nutrient-rich environment. This could drive greater vegetation increases and reduce the competitive advantage of Arctic plants, which are adapted to low-productivity environments (Christie et al. 2015; Yu et al. 2017; Koltz et al. 2022).

Vegetation abundance

Compared to vegetation cover, a greater variation in results was found in vegetation abundance (Table 3). Reindeer herbivory in particular shows variable results with 46% ($n = 15$) of observations on reindeer reporting negative impacts on abundance, and a further 39% ($n = 13$) reporting no significant changes. Much of this variation resulted from the divergent responses of different plant functional groups, with both increases and decreases in cover being regularly expressed. For instance, half of observations on graminoids, all within Scandinavia, showed that reindeer herbivory positively impacted their abundance (te Beest et al. 2016; Sundqvist et al. 2019; Kolari et al. 2019). Graminoids were also positively impacted by brown lemmings within Alaska and by muskoxen in Greenland (Johnson et al. 2011; Falk et al. 2015). Increases in graminoid abundance are supported by the wider literature, which points to compensatory growth strategies as the reason for this trend (Johnson et al. 2011; Villareal et al. 2012; Olofsson & Post 2018; Sørensen et al. 2018). Malhi et al. (2022) confirm in their literature review that herbivory constrains woody vegetation to the benefit of flowering plants and graminoids. Such selective browsing may slow Arctic warming trends, as it could promote greater albedo, preserve permafrost due to reduced snowpack

insulation, and increase soil carbon storage capacity (Malhi et al. 2022).

Mixed small and large herbivores were found to have varying effects on shrubs. Research in Sweden found that herbivory decreased deciduous shrub abundance, but increased evergreen shrub abundance (Ylänne et al. 2015). Nevertheless, *Betula nana* (a deciduous shrub) was found to decrease under exclusion of mixed small herbivores within Norway (Kaarlejärvi et al. 2015). Other articles also found a positive effect of reindeer density index (RDI) on deciduous shrub abundance (Sundqvist et al. 2019). Despite such heterogenous results, the majority of articles studying mixed small herbivores (76%), brown lemmings (60%), muskoxen (80%), mixed large herbivores (100%), and mixed small and large herbivores (57%) still reported overall negative impacts on vegetation. In total, 60% ($n = 54$) of observations on vegetation abundance reported decreasing trends as a result of herbivory.

Sub-Arctic ecosystems, which are often more herbivore-dense, likely experience stronger negative effects from herbivory on vegetation abundance compared to Arctic ecosystems. Research shows that increased herbivore densities cause reduced overall aboveground biomass, although the effects on graminoids and evergreen shrubs are less clear (Manseau et al. 1996; Olofsson et al. 2009; Zamin & Grogan 2012; Zamin & Grogan 2013; Olofsson & Post 2018; Sørensen et al. 2018). These greater negative effects are also to be expected due to the higher presence of thermophilic vegetation in lower latitudes. Such vegetation is more vulnerable to herbivory due to higher N concentrations and larger leaf area which makes them highly palatable to herbivores (Olofsson & Post 2018).

Vegetation declines were particularly pronounced with lichen, which experienced consistent negative effects from multiple herbivory types (Table 3). Reindeer browsing also consistently caused decreases in lichen abundance, which is likely explained by extensive selective grazing of lichen patches during winter months (Vowles et al. 2016). Intensive reindeer grazing has been shown to reduce lichen biomass by 90% when compared to non-grazed patches (Heggenes et al. 2020). Lichen are also sensitive to trampling, particularly whilst dry and brittle, as reindeer hooves easily break structurally important components which prevents regrowth (Heggenes et al. 2020). Larger herbivores generally show a greater average impact on vegetation than smaller ones. This is likely related to hoof size and trampling, larger calorific needs, and greater inflicted damage to vegetation as they browse for larger twigs which cause greater biomass loss (Vowles et al. 2016).

There were limited effects of reindeer and mixed small and large herbivores on the abundance of deciduous shrubs despite being considered highly palatable (Olofsson and Post 2018). There were also limited differences in abundance between deciduous shrubs and evergreen shrubs, even though the latter often benefits from Arctic herbivory (Christie et al. 2015; Vowles et al. 2017b). This may be due to different densities and intensities of herbivory. At medium herbivore densities, a clear targeting of palatable deciduous shrubs may occur, thereby allowing evergreen shrubs to gain a competitive advantage (Christie et al. 2015). However, at very high herbivore densities both functional groups may be impacted by herbivory as grazing will become less selective and trampling damage will increase (Christie et al. 2015). Moreover, negative effects on deciduous shrub abundance may be limited due to compensatory growth strategies (Champagne et al. 2012).

Vegetation growth

A total of 82% (n = 27) of observations on vegetation growth showed a negative impact from herbivory (Table 3). Notably, Bråthen et al. (2017) found that shrub height was negatively correlated with reindeer density index (RDI) in Scandinavia. Shrub height decreased by 50% when local densities reached 3–6 reindeer/km^2, which remains on the lower range of observed regional RDI (Bråthen et al. 2017). An article on *Salix* spp. recruits demonstrated that larger ungulate grazing constrained vertical growth of plant recruits in Norway, whilst smaller rodent herbivory constrained horizontal cover expansion (Ravolainen et al. 2014). Reduced vertical growth from herbivory may be caused by the allocation of plant nutrients to photosynthetic tissue recovery at the expense of investment into stem radial growth needed to facilitate vertical growth (Morrissette-Boileau et al. 2017). Nevertheless, plants have some resistance to grazing as they sometimes use accumulated reserves of nutrients to continue habitual growth rates (Morrissette-Boileau et al. 2017). Negative impacts of herbivory on flowering rates were also identified, as forbs flowered almost exclusively under herbivory exclosures due to the selective grazing of their reproductive organs (Kaarlejärvi et al. 2013; Kaarlejärvi and Olofsson 2014).

Sub-Arctic research does not always align with our results, as many highlight a lack of significant changes in shrub height or apical stem growth (e.g., Virtanen et al. 2010; Zamin and Grogan 2012; Maliniemi et al. 2018). Non-significant or less severe impacts on vegetation growth in sub-Arctic regions may result from interactions with other site-specific factors, which may cause opposing trends in local vegetation growth. For instance, some vegetation had lower regenerative capacity due to the negative interactions with surrounding trees at certain sites, which are often more abundant at lower latitudes (Bognounou et al. 2018). Furthermore, growth of shrubs and other vascular plants could be limited by a site's snow cover which protects from winter

grazing, and by permafrost which limits nutrient access (Zamin & Grogan 2012; Plante et al. 2014).

Vegetation survival

Whilst the number of articles investigating vegetation survival is low, they highlight limited effects from herbivory, with 40% ($n = 4$) of articles finding no significant impact. Reindeer were not found to have any significant effects on vegetation mortality, but observations on mixed small herbivores did find some indication of plant damage and mortality (Ravolainen et al. 2014; Hoset et al. 2017). Moreover, an exclosure study demonstrated that *P. sylvestris* seedlings had lower emergence and growth rates when under herbivory than in exclosure sites (Bognounou et al. 2018). Such trends were further supported by similar Norwegian research (Biuw et al. 2014; Ravolainen et al. 2014). Research also found increased vegetation damage when herbivores were present (Ravolainen et al. 2014; Hoset et al. 2017; Bognounou et al. 2018).

Certain herbivores' continuous movement along the landscape likely induces soil mixing due to trampling, and their dung may carry seeds and improve ground fertilisation (Munier et al. 2010; Malhi et al. 2022). Herbivores may therefore promote seed propagation and emergence, thereby off-setting some negative effects caused by grazing or trampling. This may also explain greater negative impacts from mixed small herbivores, as their soil mixing capabilities would not be as pronounced as heavier and larger-hooved reindeer or muskoxen.

Plant palatability was found to affect mortality, with *S. planifolia* and *S. glauca* experiencing much higher mortality rates than the less palatable *B. glandulosa* (Morrissette-Boileau et al. 2018). Furthermore, 92% of *S. glauca* individuals experienced 50 + % shoot damage, compared to only 72% of *B. glandulosa* plants (Plante et al. 2014).

Ecosystem productivity

Mixed results were reported on the impacts of herbivory on both gross primary productivity (GPP) and gross ecosystem photosynthesis (GEP; Table 4). In both cases, this was based on a small number of articles. Net ecosystem exchange (NEE) and ecosystem respiration (ER) demonstrated high variability in their response to herbivory, with mixed cumulative effects (Table 4). In Northern Norway, lightly grazed reindeer sites were 70% stronger C sinks than heavily grazed sites (Väisänen et al. 2014). ER was not significantly influenced by mixtures of herbivores in Scandinavia and Alaska, but was positively influenced by reindeer in Northern Norway (Väisänen et al. 2014; Metcalfe & Olofsson 2015; Min et al. 2021). Modelled NEE predictions support such findings, highlighting that herbivore absence could shift dry heath tundra landscapes from source to sink during growing seasons (Table 4; Min et al. 2021).

Mixed or marginal results of mammalian herbivores on ER could be explained by the contrasting effects herbivores may have on soils and vegetation. For instance, whilst grazing and trampling damages vegetation and may therefore lower N stocks and decelerate soil C cycling, herbivores can still increase N input and mineralisation through urination and defecation (Forbes & Kumpula 2009; Sørensen et al. 2018; Sundqvist et al. 2019). Mixed results may also arise from increased photosynthetic activity of damaged or defoliated plants, which have been shown to maintain

Table 4 Observed changes in ecosystem productivity response variables and per herbivory species/class, which includes Gross Primary Productivity (GPP), Gross Ecosystem Photosynthesis (GEP), Net Ecosystem Exchange (NEE), and Ecosystem Respiration (ER). The number of observations which evaluate such response variables (for any of the herbivory and vegetation types) is indicated in the column headings. For noted changes, red (↓)=decrease, light red (↑↓)=small decrease, blue (↑)=mixed results, light green (↑)=small increase, green (↑)=increase, and grey (⊘)=no significant effect

	GPP (n = 3)	GEP (n = 4)	NEE (n = 8)	ER (n = 7)
Mixed small and large herbivory	↓	⊘	↑	⊘
Mixed large herbivores		↓	↓	⊘
Reindeer/caribou (*Rangifer tarandus*)			↑	↑
Muskoxen (*Ovibos moschatus*)	↓		↑	
Mixed small herbivores			↓	
Brown lemmings (*Lemmus trimucronatus*)			↑↓	↓
CUMULATIVE[a]	↓	↓	↑↓	↑↓

[a]Cumulative grouped trends were calculated by assigning a fixed weight-based value for every individual trend (increase = 2, light increase = 1, no change = 0, light decrease = −1, decrease = −2), and then averaged and rounded to the nearest whole number, with the overall trend following the same aforementioned value-trend pairs. If the average is closest to 0 but characterised by strong variation between decreases and increases (at least one increase and decrease reported), a mixed-result outcome was shown

Table 5 Main overall trends, observations, and expected trends reported regarding the interactive impacts between herbivory and warming on Arctic vegetation

Herbivore	Article	Vegetation	Reported impacts	Trend
Mixed small and large herbivores	Kaarlejärvi et al. 2013	Mixed	Despite warming and fertilisation effects, herbivory prevents a northward shift of lowland species	Buffer
		Epilobium	Biomass increased under warming, but only when herbivory was removed	Buffer
		Solidago	Warming increased biomass, but herbivory entirely prevented it from flowering	Buffer
		Silene	Biomass was significantly higher in exclosure warmed plots than grazed warmed plots	Buffer
	Kaarlejärvi et al. 2015	Vasculars	Warming increased vascular plant biomass (+58%), but high rodent peaks caused strong declines	Buffer
		Shrubs	Increase in biomass caused by warming, important decline when grazers were introduced compared to continued exclosures	Buffer
	Ylänne et al. 2015	Deciduous shrubs	2003–2007 warming increased deciduous shrub abundance only in exclosure plots	Buffer
		Evergreen shrubs	Post-2013 herbivory enhanced evergreen shrub growth and was highest in warmed plots	Strengthen
		Mixed	Herbivory had no additional effects on general vegetation cover or ecosystem productivity when paired with warming	No effect
	Eskelinen et al. 2017	Lowland vegetation	Positive impact of warming on species establishment was hindered by herbivory	Buffer
Mixed large herbivores	Cahoon et al. 2012	Mixed	Exclosures paired with warming led to highest LAI and GEP, and lowest NEE	Buffer
Reindeer (*Rangifer tarandus*)	Johnson et al. 2011	Shrubs	Warming-induced increases in shrubs are only taking place in areas of low-grazing	Buffer
	Väisänen et al. 2014	Mixed	Warming effects on plant abundance were weaker under heavy-grazing than herbivore exclosures	Buffer
	Bråthen et al. 2017	Shrubs	Browse trap established at five animals/km^2 prevented any shrubline advance despite climatic warming	Buffer
	Yu et al. 2017	Mixed	Reindeer constrained NPP and biomass increases caused by warming	Buffer
	Bråthen et al. 2018	*Empetrum nigrum*	Biomass was positively affected by warming and further aided by higher grazing intensities	Strengthen
	Verma et al. 2020	Shrubs	No change in shrub cover despite increased warming and increased herbivory, suggesting counteraction of warming effects by herbivory	Buffer

net photosynthesis levels despite reduced leaf area or leaf number (Zvereva et al. 2012). In some cases soil temperatures were higher under heavy-grazing conditions than light-grazing conditions (e.g., Väisänen et al. 2015), which could play an important role in dictating ecosystem productivity as higher soil temperatures are claimed to increase ecosystem productivity (Heinze et al. 2017; Hu et al. 2021).

Nevertheless, negative overall trends of GEP, GPP, and partly of NEE highlight the important role of herbivory in controlling CO_2 exchange and C uptake (Väisänen et al. 2014; Metcalfe and Olofsson 2015). Reductions in dominant shrub species are shown to hinder the uptake capacity of ecosystem C, and reductions in NEE when herbivores are absent show that herbivores can maintain ecosystems as C sources (Metcalfe & Olofsson 2015; Lara et al. 2017; Min et al. 2021).

Herbivory and climatic change

Based on this review, we highlight the potential buffering capacity of mammalian herbivores against climate warming in the Arctic (Table 5). For example, herbivory can limit the northward encroachment of thermophilic vegetation, as high palatability and subsequent selective grazing of their

reproductive organs limits recruitment success (Kaarlejärvi et al. 2013). The buffer trends of herbivores are supported by further literature. Poor shrubline advancement, marginal vegetation response to greatly increased temperatures, and a lack of increases in ecosystem productivity are all commonly reported across Scandinavian, alpine, and North American study sites (Virtanen et al. 2010; Maliniemi et al. 2018; Olofsson & Post 2018; Andruko et al. 2020). Research has demonstrated that grazers often buffer warming through "browsing traps", in which areas with low vegetation density are grazed as vegetation expands, thereby restricting vegetation density and abundance (Bråthen et al. 2017). Since browsing traps are less common with poorly palatable plants, these gain a competitive advantage which increases their potential to grow under warming conditions (Bråthen et al. 2018). As a result, herbivores may constrain much of the effects of future warming on vegetation trends, as they browse primarily on plants that benefit most from climate trends in the Arctic (Olofsson & Post 2018).

In the few cases where herbivory strengthened warming's impact on vegetation, the effect was primarily observed in less palatable plants, especially evergreen shrubs (Table 5; Bråthen et al. 2018). Given that unpalatable vegetation has been shown to respond positively to warming, herbivory is thus reinforcing the climate-driven increase in less palatable plant species (Johnson et al. 2011). For example, based on models evergreen shrubs may gain a significant competitive advantage under warming and herbivory in low-productivity areas (Christie et al. 2015). Importantly, increased vegetation growth may initiate positive feedback loops, as taller and more extensive vertical vegetation cover have both been reported to increase snow cover (Plante et al. 2014). This may further enhance vegetation increases due to insulation and subsequent soil warming causing heightened soil microbial activity and nutrient abundance (Plante et al. 2014).

Despite clear buffer trends of mammalian herbivores for most vegetation types, future influences of herbivory on projected vegetation increases remain unclear. For example, in some Scandinavian regions declines in domestic livestock grazing and reindeer herds are reported (Christie et al. 2015; Løkken et al. 2019). Reduced herbivore densities would thereby entail increased growth and facilitated northward shifts of thermophilic functional plant groups (Løkken et al. 2019). In contrast, in Alaska consistent northward herbivore expansions are reported, suggesting region-specific differences in the capacity to buffer warming-induced vegetation increases (Zhou et al. 2017).

Lastly, some articles add that winter warming instead of summer warming may actually lead to further vegetation decreases in the Arctic (Vowles et al. 2017a). Temporary higher temperatures in winter may thaw and re-freeze soils and vegetation, inducing frost damage (Vowles et al. 2017a). Such processes, paired with higher extreme weather events caused by climate change, would severely hinder northward vegetation shifts and general increases in Arctic vegetation abundance (Myers-Smith et al. 2011; Vowles et al. 2017a).

Conclusions and recommendations

Here we systematically reviewed the impact of mammalian herbivory on vegetation trends within the Arctic Circle. With nearly two-thirds of observations suggesting negative vegetation trends, we found that in general mammalian herbivory leads to negative Arctic vegetation trends, effectively buffering warming's aforementioned positive influence (Table 5). Yet, herbivory impacts remain highly variable, with clear differences in effects depending on the species of herbivores as well as the plant functional groups under investigation (Fig. 3). Whilst these findings are an important step towards modelling and predicting upcoming Arctic vegetation and ecosystem shifts, future research should analyse the impacts of herbivory in combination with other Arctic influences.

Based on our review, we suggest the following important avenues for future research:

- Firstly, this study focuses on terrestrial mammalian herbivores, whilst other species (e.g., birds and invertebrates) also play important roles (Carlson et al. 2018; Finger-Higgins et al. 2021). Expanding research on these species is needed to fully grasp the influence of herbivory under changing Arctic conditions. In addition, there was also an overall poor focus on mountain hares (*Lepus timidus*), Norwegian lemmings (*Lemmus lemmus*), and voles, which are common in several Arctic regions (Vowles et al. 2016).
- Secondly, greater geographical diversity would benefit the understanding of future Arctic vegetation trends. The focus on Fennoscandia implies that most observations came from some of the warmest Arctic regions, and that some important mechanisms occurring exclusively in colder regions may be overlooked (Martin et al. 2017). There is a clear gap in research in northern Canada, with no relevant articles identified for this region. Siberia is also poorly covered, as it remains an understudied site of important reindeer husbandry and low summer temperatures (Heijmans et al. 2022).
- Lastly, we suggest including a greater focus on soil nutrient measurements in future research, as Arctic vegetation growth is strongly limited by soil nutrient availability, and herbivory is capable of significantly impacting soil

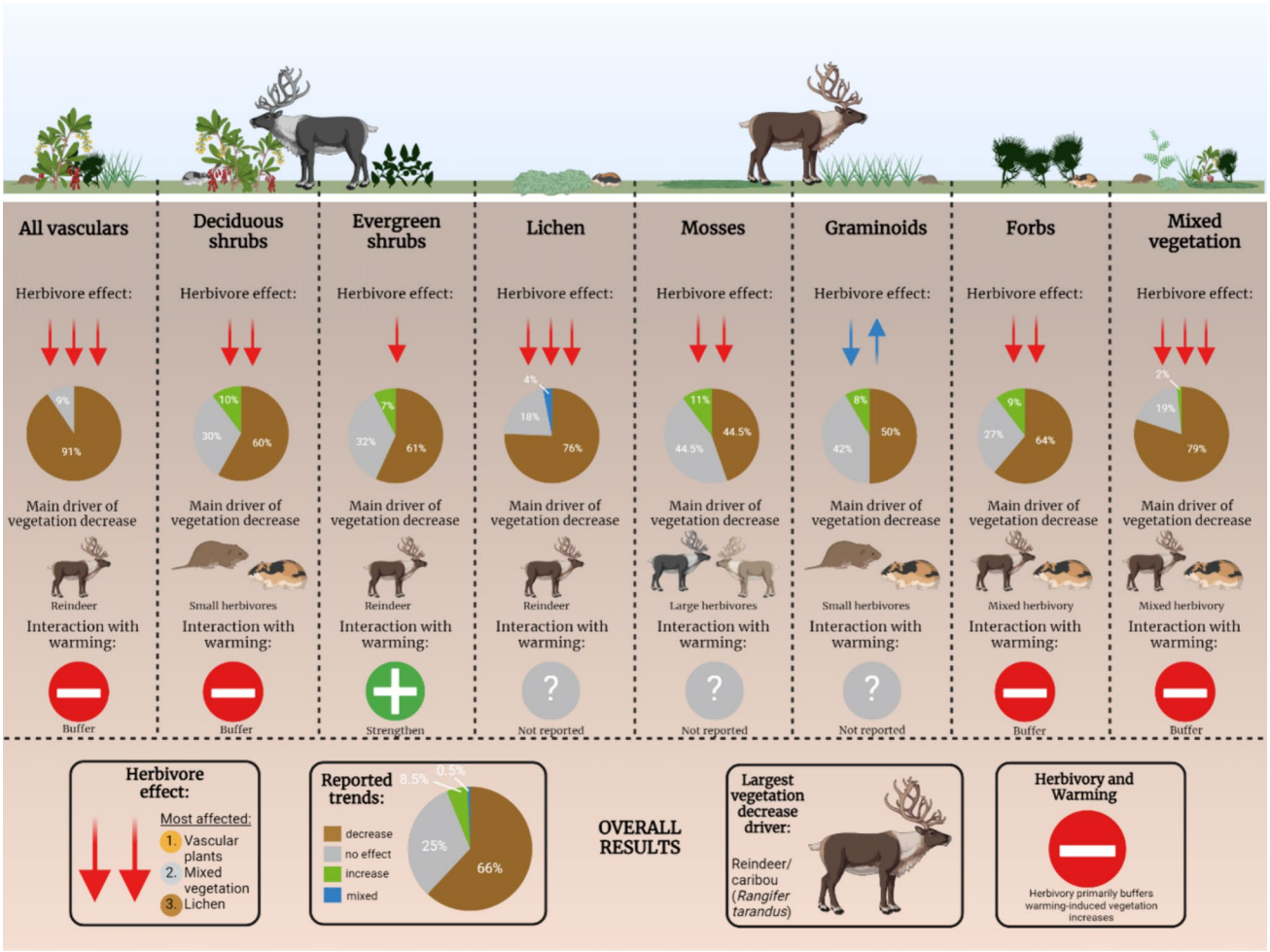


Fig. 3 Overview and summary of main trends caused by herbivory on different plant species highlighted by the included articles. Illustration made via BioRender

nutrient levels (Zamin & Grogan 2013; Turkington et al. 2014; Martin et al. 2017).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-024-03302-4.

Acknowledgements We would like to thank Max Pons, Cerys Strang, Sandra Schmidt-Tauscher for providing feedback on an earlier version of this manuscript, and an anonymous reviewer for providing detailed and valuable feedback. We are also very grateful for all the support from Meghan McMorrow, Koko Nomura, and Bernardo Oliva Vieira.

Author contributions MO came up with the idea for the review, MO and TB were responsible for designing the review, MO performed the literature search and collected the data and did a first synthesis of the data, MO wrote a first draft of the manuscript, TB supervised the work and critically revised the work, MO and TB edited the final manuscript before submission.

Declarations

Conflict of interest The authors did not receive support from any organization for the submitted work. The authors have no competing interests to declare that are relevant to the content of this article.

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