

# Herbivores in Arctic ecosystems: Effects of climate change and implications for carbon and nutrient cycling

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## Abstract

Arctic terrestrial herbivores influence tundra carbon and nutrient dynamics through their consumption of resources, waste production, and habitat-modifying behaviors. The strength of these effects is likely to change spatially and temporally as climate change drives shifts in herbivore abundance, distribution, and activity timing. Here, we review how herbivores influence tundra carbon and nutrient dynamics through their consumptive and nonconsumptive effects. We also present evidence for herbivore responses to climate change and discuss how these responses may alter the spatial and temporal distribution of herbivore impacts. Several current knowledge gaps limit our understanding of the changing functional roles of herbivores; these include limited characterization of the spatial and temporal variability in herbivore impacts and of how herbivore activities influence the cycling of elements beyond carbon. We conclude by highlighting approaches that will promote better understanding of herbivore effects on tundra ecosystems, including their integration into existing biogeochemical models, new applications of remote sensing techniques, and the continued use of distributed experiments.

## KEYWORDS

consumptive effects, element cycling, nonconsumptive effects, species interactions, tundra

## INTRODUCTION

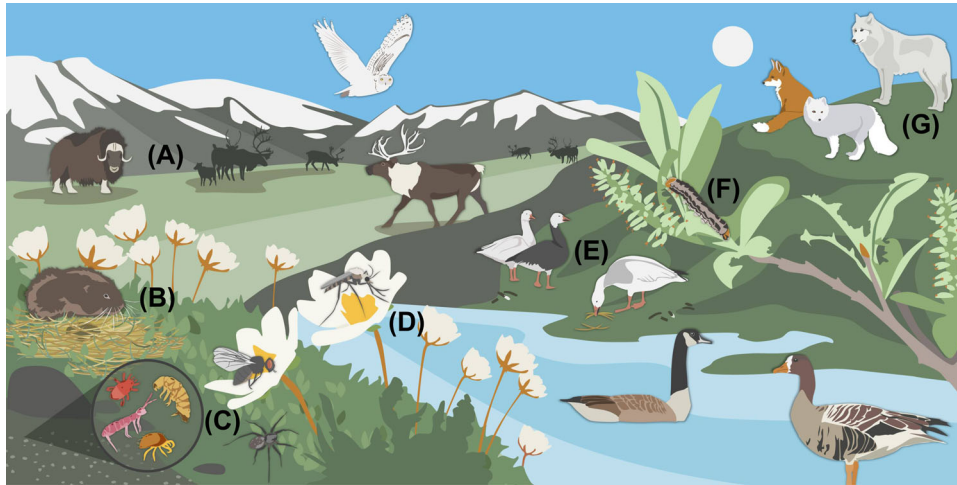
Terrestrial food webs were recognized as having a central role in carbon and nutrient cycling in arctic ecosystems nearly a century ago. In their seminal paper, Summerhayes and Elton<sup>1</sup> conceptualized the nitrogen (N) cycle for the Bear Island High-Arctic food web, including trophic transfer of N between aboveground-belowground habitats and across terrestrial-aquatic systems. Yet, over the following decades, the functional roles of animals—defined as their impacts on carbon (C) and nutrient dynamics—were largely missing from theoretical and empirical ecological work, because arctic food webs gained a reputation for being “simple” after a version of the Summerhayes and Elton<sup>1</sup> figure was reproduced in Elton’s 1927<sup>2</sup> text on Animal Ecology. A perception of terrestrial arctic food webs as being largely

inconsequential for C and nutrient cycling (hereafter referred to as “element cycling”) was furthered by a historical focus by arctic ecosystem ecologists on abiotic constraints and resource availability (i.e., bottom-up regulation)<sup>3</sup> rather than on effects of consumers (i.e., top-down regulation) despite acknowledgment that both simultaneously affect tundra ecosystems. Thus, with a few notable exceptions (e.g., plant consumption by vertebrate herbivores), there have been limited integrative efforts among organismal and ecosystem ecologists to characterize the broader functional roles played by arctic terrestrial animals (Figure 1).

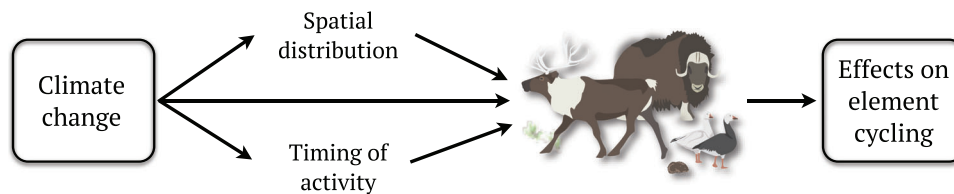
Recently, the structure and function of arctic communities are being revisited. For example, there is growing recognition that tundra food webs contain more complexity than formerly realized due to some of the largest invertebrate diversity pools having been masked by

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**FIGURE 1** Representative functional groups of animals from the arctic terrestrial food web, including (A) large mammal herbivores, (B) small mammal herbivores, (C) invertebrate detritivores and predators, (D) biting insects, (E) avian herbivores, (F) invertebrate herbivores, and (G) vertebrate predators.



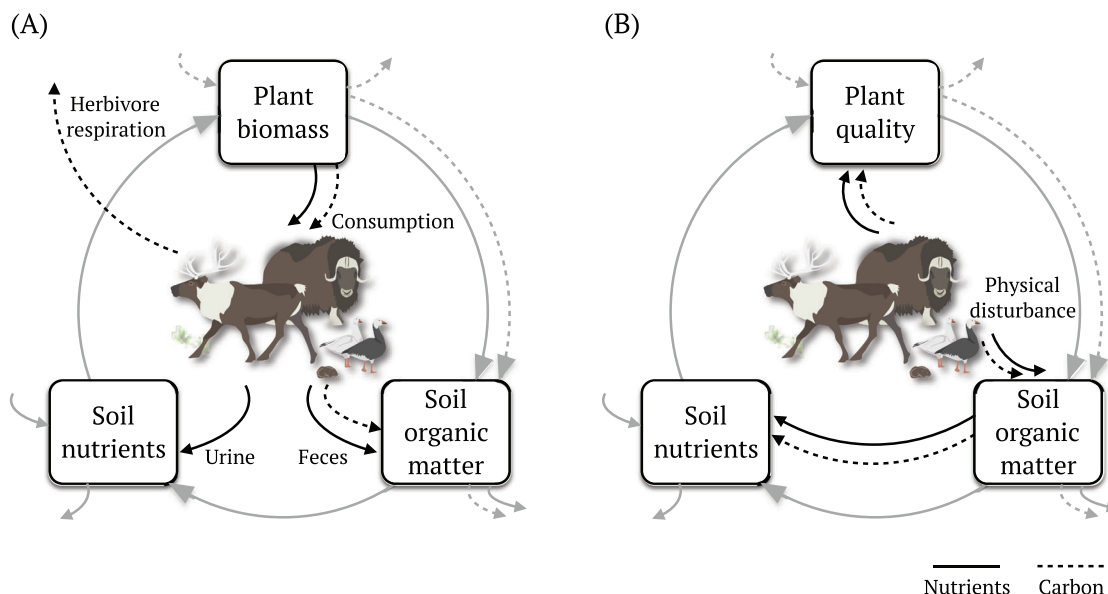
**FIGURE 2** Climate change is modifying the spatial and temporal distribution of herbivore impacts on element cycling in terrestrial tundra ecosystems. Herbivore responses to climate change reflect changes in both abiotic and biotic conditions and include shifts in their distribution, interannual population cycles, and the seasonal timing and local intensity of activity. These changes subsequently alter species-specific consumptive and nonconsumptive impacts on localized element dynamics.

unresolved nodes in previously drawn webs.<sup>4,5</sup> This has led to new work aimed at better characterizing the species interactions within these communities.<sup>4,6</sup> Increasing appreciation that terrestrial organisms can have wide-ranging impacts on C and nutrient cycling<sup>7–9</sup> is also motivating new studies on these processes with vertebrates and invertebrates across the Arctic.<sup>10–13</sup>

At the same time, arctic ecosystems and the organisms within them are responding to rapid and dramatic climate change. Although temperatures are increasing globally, the Arctic is warming notably faster than many other areas.<sup>14</sup> Some effects of this rapid warming include changing precipitation regimes, increased greenhouse gas fluxes, reductions in sea ice extent, and advancing plant phenology.<sup>15,16</sup> In addition, the Arctic is experiencing an increased frequency of major disturbances, such as wildfire and winter rain-on-snow events.<sup>17</sup> With all of these varied ecological disturbances, the fate of large stores of C contained in permafrost soils is of particular concern.<sup>18</sup> As microbial activity increases under warmer conditions, this C could be released to the atmosphere as carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>). Satellite observations also indicate that photosynthetic biomass is increasing in the Arctic<sup>19</sup> from greater plant growth and higher abundance of deciduous shrubs<sup>20,21</sup> as a consequence of numerous factors, including increased nutrient availability.<sup>22</sup> Although vegetation changes could offset some of the increased soil C emissions, herbivore activity is likely to moderate these processes (e.g., Ref. 23).

Responses by arctic animals to warming and other types of environmental change include changes in abundance and diversity, distribution, and timing and intensity of activity (Figure 2; see Ref. 16). Such responses are likely to alter the functional roles of arctic organisms,<sup>24–26</sup> changing the strength and timing of their localized impacts on elemental cycling of C, N, and P and ultimately affecting land–atmosphere feedbacks (Figure 2). A major challenge in quantifying these effects is that both animal responses to climate change and their ecosystem impacts are often context-dependent and spatially heterogeneous. Achieving a better understanding of potential feedbacks among climate change, animal responses, and element cycling is particularly important in the Arctic, because even small changes could have meaningful impacts on global biogeochemical cycles when scaled across the entire region.<sup>18</sup>

In this paper, we aim to advance our understanding of the changing functional roles of arctic terrestrial animals and identify priority areas for future research. We focus on herbivores because their ecosystem impacts and climate change responses are the best documented of any animal group in the Arctic, but we also consider how changing interactions among herbivores and other consumer groups may alter their impacts. We review and synthesize recent evidence of how (1) herbivores contribute to element cycling, (2) climate change drives spatial and temporal changes in herbivore activity, and (3) these changes might alter herbivore impacts on element cycling in the future.



**FIGURE 3** Herbivore effects on element cycling in arctic tundra ecosystems. Gray lines show nutrient flow between plants, soil organic matter, and soil nutrients in the absence of herbivores, and black lines show how herbivores affect nutrient pools in each of these compartments. Solid and dashed lines are indicative of nutrient (N, P) and carbon flow, respectively. Consumptive effects in (A) are due to direct consumption of plant matter. Nonconsumptive effects in (B) include physical disturbance that modifies soil structure through trampling (*Rangifer*, muskox, and geese), building hay piles (voles), or grubbing (geese). Changes in plant quality (shown in panel B) due to direct and indirect effects of herbivore activity include changes in plant functional traits, plant nutrient content or stoichiometry, and plant community composition (see text for detail).

Using geese as a case study, we highlight how these various factors may interact to affect tundra ecosystem functioning. We also discuss (4) how herbivores mediate existing plant and soil responses to climate change, which can result in further feedbacks to climate change. Finally, we present several remaining gaps in our knowledge on these topics and provide suggestions as to how they might be addressed to stimulate further research on the consequences of animal responses to environmental change in rapidly changing arctic ecosystems.

## EFFECTS OF HERBIVORES ON TERRESTRIAL ELEMENT CYCLING

The Arctic is a low-productivity system where bottom-up, nutrient-driven processes are typically thought to be more important than top-down effects exerted by animals. However, research findings over recent decades show that tundra element cycling is influenced by top-down consumptive and nonconsumptive effects of tundra herbivores (Figure 3). Here, we consider herbivore consumptive effects to be the direct and indirect effects associated with feeding on live plant biomass (i.e., herbivory). Waste production, which provides nutrient inputs to soils, is a direct consequence of consumption and thus also considered a consumptive effect. Although nonconsumptive effects are often not explicitly included in food webs,<sup>27</sup> behaviors that cause physical disturbance to soil or affect the breakdown of litter can also impact element cycling. Some of these behaviors include trampling, digging, and creating tunnels and hay piles. Lastly, herbivores influence element cycling by inducing changes in plant quality and composition through both the

direct and indirect effects of their consumptive and nonconsumptive activities.

Arctic terrestrial systems are characterized by only a few species or functional groups with measurable ecosystem impacts (Figure 1). Key groups of mammalian herbivores include two species of large mammal (caribou or reindeer [hereafter *Rangifer*] and muskox) and a few species of small mammals (primarily voles and lemmings). Although both mammal groups are active year-round, large mammal effects are more dispersed, because *Rangifer* and some muskox herds are migratory and may not follow the same migration routes every year. Small mammal home ranges are much smaller, so their ecosystem impacts tend to be localized. Impacts of some small mammal species also vary widely between years due to regular fluctuations in population densities across the Arctic and Subarctic regions (e.g., see Refs. 28 and 29). Overall arctic avian diversity is low; however, diversity of some groups, such as geese and shorebirds, is highest at arctic latitudes.<sup>30</sup> Most of these species are migratory and present only in the summer when densities can become quite high. Research connecting the avian community to arctic element cycling has largely been with geese on the coastal plain; for this reason, we focus on geese as well. Lastly, invertebrates have the highest local abundances and diversity of any herbivore group in the Arctic but are active only in summertime.

We review the evidence for consumptive and nonconsumptive effects of these herbivore groups in tundra ecosystems and consider how herbivore-induced shifts in plant community composition and/or quality may affect element cycling (Figure 3). Given that effects are caused by herbivore activity, we assume localized impacts on element cycling scale with density (Figure 2). We also briefly consider

how consumers from other trophic levels have the potential to modify herbivore impacts on element dynamics.

## Consumptive effects

### Biomass consumption

Herbivore impacts on tundra plant biomass, nutrient dynamics, and ecosystem C exchange vary depending on the local composition of the herbivore community, herbivore activity levels, and the timing or consistency of their consumptive effects. Overall, the collective community of mammalian herbivores tends to reduce primary production. Experimental mammal exclusions have repeatedly shown that plant biomass is higher in the absence of herbivores in numerous arctic and sub-arctic ecosystems, including heathlands,<sup>28,31</sup> coastal meadows,<sup>32</sup> and mountain snowbeds.<sup>33</sup> However, these effects can vary seasonally due to differential foraging and human management patterns<sup>34</sup> between summer and winter for some herbivores, such as *Rangifer*. Herbivore effects also vary spatially. For example, results from a recent meta-analysis indicated that *Rangifer* consistently have negative effects on lichen but effects on other plant growth forms differ by study location.<sup>35,36</sup> With the exception of their calving grounds,<sup>37</sup> grazing impacts of *Rangifer* are also variable in any given location between years due to variation in annual migration routes, with impacts being lower in low-density years.<sup>36</sup> Muskox herbivory also causes reductions in plant biomass in wetland communities, but the magnitude of this effect can depend on whether the population moves between winter and summer ranges.<sup>38</sup>

In contrast, small mammal impacts are extremely localized but occur throughout the year, because most species are present and active year-round. In the case of wet tundra, long-term experimental exclusion of small mammals caused the area to transform from being a C sink into a C source because the lack of herbivory led to litter buildup, which decreased the net ecosystem exchange of C.<sup>39</sup> The annual magnitude of small mammal effects on plant biomass and C-uptake varies with their population cycles and is likely ecosystem specific.<sup>40</sup> However, following peak rodent years, herbivory effects can be large enough to detect via satellite recorded normalized difference vegetation index.<sup>28</sup>

Geese also have large effects on vegetation structure and ecosystem function, particularly in the arctic coastal plain.<sup>41</sup> Direct consumption of plant material is one of the main effects of geese activity on tundra C dynamics. Geese can consume 80% of aboveground net primary production (NPP) in grazed marshes,<sup>42</sup> and these high rates of plant consumption have been shown to result in decreased net ecosystem C uptake.<sup>11</sup> Due to their intense impacts, recent increases in goose population sizes are associated with widespread degradation of arctic wetlands. In a study of nine sites, goose activity caused a large expanse (35,000 ha) of intertidal saltmarsh to transition to an alternative stable state of unvegetated sediment.<sup>43</sup>

Background levels of invertebrate herbivory in the tundra are very low and thus, invertebrate herbivores have limited direct effects on C cycling through C consumption.<sup>10,44,45</sup> However, recent evidence

from the Subarctic indicates that background insect herbivory can still significantly weaken CO<sub>2</sub> uptake by plants, thus reducing the potential for northern ecosystems to be C sinks under warmer conditions.<sup>46</sup> In addition, occasional larval moth outbreaks in West Greenland have had severe negative consequences for ecosystem productivity.<sup>47,48</sup> Outbreaks in subarctic and boreal forest, which are more frequent, also have large impacts on food webs and element cycling,<sup>49,50</sup> and can potentially drive ecosystem transitions.<sup>51</sup> Some evidence suggests that these particular types of outbreaks may spread to the tundra in the future.<sup>52</sup>

### Waste production

Animal waste production converts nutrients from plant material or animal prey into forms that are more available for plant and microbial uptake (i.e., inorganic and simple organic forms found in urine and feces<sup>53</sup>). Thus, herbivore waste impacts soil chemistry<sup>54</sup> and increases nutrient availability for tundra plants. For example, urine-derived nutrients are readily absorbed by cryptogams, vascular plants, and the soil microbial community<sup>55</sup> and can alter their stoichiometry.<sup>56</sup> Soil nutrient availability tends to be higher in areas with animal waste, as shown through fecal addition experiments from geese<sup>57</sup> and *Rangifer*.<sup>58</sup> Increased soil nutrient availability associated with *Rangifer* feces can have localized impacts on plant productivity, plant composition, microbial biomass, and microbial methane production.<sup>58,59</sup> Soil nutrients are elevated near lemming and ground squirrel burrows<sup>60</sup> compared to nearby, undisturbed areas as well.

Herbivore movement between areas of resource consumption and waste production also transfers nutrients between locations. For example, *Rangifer* were found to modify nutrient distribution across the landscape through their migration and daily movements.<sup>61</sup> Muskox transfer significant amounts of nitrogen between community types by consuming vegetation in wet fen areas but preferentially defecating in drier snow beds.<sup>62</sup> The spatial extent and distribution of these impacts depend on animal size, behavior, and movement distance. For instance, while feeding impacts of voles and lemmings can be spatially diffuse, many species defecate in latrines<sup>63</sup> that concentrate waste and nutrients in small areas. Carcasses also create nutrient hotspots, although the nutrients are not as immediately available as those from other waste products.<sup>60</sup> In extreme cases, aquatic subsidies of invertebrate carcasses can even fertilize tundra soils and stimulate plant growth and litter decomposition.<sup>64,65</sup>

### Nonconsumptive effects

Physical disturbances by herbivores, such as trampling, alter element cycling through effects on soil structure, plant cover, and plant composition (reviewed in Ref. 12). Studies on the effects of trampling in tundra ecosystems have largely focused on large mammals, showing that large mammal activity reduces the abundance of trampling-sensitive dwarf shrubs,<sup>66,67</sup> bryophytes,<sup>68</sup> and lichens.<sup>69</sup> Trampling also

compacts soil,<sup>70</sup> which reduces abundances of soil biota.<sup>71,70</sup> Although less well studied, geese trampling has some similar effects to that of large mammals.<sup>72</sup> Small mammals have localized trampling effects through their repeated use of trails (i.e., runways),<sup>63</sup> which reduces vegetation cover and compacts soils.

Trampling effects on vegetation cover and composition can have cascading consequences for ecosystem properties. Reduced trampling after the extinction of large herbivores may have been a driving force behind the large-scale vegetation transition of the Pleistocene Steppe to a low productivity tundra.<sup>12</sup> Recent work from muskox enclosure experiments in wet tundra showed trampling significantly reduced moss cover, raised the water table, and decreased soil temperature.<sup>68</sup> There was also greater CO<sub>2</sub> uptake, lower CH<sub>4</sub> emissions,<sup>73</sup> and lower plant C and N pools<sup>68</sup> in trampled areas compared to those inside herbivore enclosures. In some cases, trampling effects can even increase resource availability for the soil microbial community. By trampling litter into coastal arctic soils, geese activity was shown to increase N-mineralization.<sup>72</sup>

Herbivores also influence element cycling through burrowing, tunneling, and by constructing haypiles or other types of winter nests. By creating burrows, small mammals, such as lemmings<sup>63</sup> and arctic ground squirrels,<sup>60</sup> move soil between horizons. This activity increases nutrient availability locally and helps to make previously inaccessible materials available to microbes and plants.<sup>74</sup> Soil biota activity also modifies soil structure, which improves the circulation of nutrients, gases, and water.<sup>75,76</sup> In contrast, disruptions to the soil organic layer caused by goose foraging for rhizomes early in the growing season causes soil erosion and loss of organic C and N.<sup>41</sup>

## Effects on plant community composition and traits

Herbivore-driven changes in plant community composition are caused by a combination of direct and indirect consumptive and nonconsumptive effects. A direct effect of consumption on plant species composition may include selective foraging that reduces the abundance of a particular plant species, while an indirect effect of consumption would be a change in competitive outcomes within the plant community. Evidence from the Arctic generally supports ecological theory predicting that as palatable plant species are removed by herbivores and become less competitive, the composition of the plant community shifts toward less palatable species.<sup>77</sup> This process has been recognized numerous times through reductions in graminoid and forb biomass caused by various herbivores, including *Rangifer*,<sup>78</sup> geese,<sup>79</sup> and lemmings.<sup>32</sup> Herbivory outcomes can be idiosyncratic, though, and in some cases, plant communities shift toward more palatable species. For example, vole presence was associated with increased graminoid abundance in multiple tundra types.<sup>33,80</sup> Long-term, intensive *Rangifer* activity was also shown to cause a shift from heath to grass-dominated vegetation.<sup>34</sup> Changes in plant composition can also arise from nonconsumptive activities by herbivores. For example, haypiles created from graminoid tissue reduce living graminoid abundance (direct effect), while changes

in ecosystem properties from trampling could affect plant competitive outcomes (indirect effect).

Lower shrub abundances are a well-documented example of a plant compositional shift caused by herbivores in tundra ecosystems. Tall deciduous shrubs have expanded in numerous areas in response to reduced *Rangifer* abundances.<sup>78,81,82</sup> Similarly, high densities of domesticated *Rangifer* can reverse such shrub expansion.<sup>83</sup> Exclusion of small mammals also increased deciduous and evergreen shrub abundance in tundra<sup>31,80</sup> and the forest-tundra ecotone.<sup>84</sup> Herbivore-induced reductions in shrub abundance are broadly relevant to arctic element dynamics, because they could counteract some effects of climate-induced shrub expansion.<sup>21</sup> However, in some cases, interactions among shrubs and vertebrate herbivores are weak<sup>85,86</sup> or dependent on ecosystem type.<sup>80</sup> Moth outbreaks in Greenland also dramatically reduce the biomass and aboveground production of deciduous shrubs,<sup>47,48</sup> but it remains unexplored whether low levels of background invertebrate herbivory<sup>10,44</sup> affect community composition more generally.

Due to differences in N-content between tundra plant species and growth forms, herbivore-driven changes in plant composition can alter community-level N content.<sup>87,88</sup> In some cases, indirect effects of herbivory can have larger impacts on overall N-content of aboveground plant biomass than direct effects of consumption.<sup>34</sup> Nutrient contents of individual plant species are influenced by herbivory as well; this has been documented through increased graminoid N content caused by geese grazing<sup>42</sup> and decreased N content in shrub leaves infested with gall mites.<sup>89</sup> Changes in plant nutrient concentrations at the species or community level also have cascading effects on processes, such as decomposition. Increased N-content of plant tissue and consequently, of litter, is one of the primary mechanisms behind observed increases in litter decomposition and nutrient cycling in grazed areas.<sup>82,88</sup> Likewise, by promoting dominance of certain plant types, such as evergreen dwarf shrubs, herbivores can induce shifts in soil chemistry and microbial community composition that promote soil C sequestration.<sup>90</sup>

If herbivore-induced changes to the plant community result in lower biomass or photosynthetic capacity, C dynamics may be affected as well. For example, CO<sub>2</sub> uptake of an arctic wet meadow was reduced due to barnacle geese activities that decreased graminoid abundance but sustained moss cover.<sup>79</sup> Exclusion of *Rangifer* increased the biomass of the deciduous shrub *Betula nana*, resulting in increased community-level photosynthesis.<sup>91</sup> Reduced herbivory associated with the exclusion of small mammals similarly caused higher plant biomass and led to increased litter accumulation and slower decomposition.<sup>32,33</sup> Recent work also showed that the structure and function of the methanotroph community within peat soils depended on previous exposure to goose grazing, which could have implications for C-cycling.<sup>92</sup> In addition, invertebrate herbivores may have an underappreciated role in influencing C dynamics at the individual plant level. Moth outbreaks in Greenland were associated with lower production and reduced structural support of the common shrub *Salix glauca* due to changes in the lignin and carbohydrate contents

of the plant fibers.<sup>93</sup> Invertebrate herbivory was also documented as driving increased plant emissions of volatile organic compounds (VOCs).<sup>94</sup>

## Variation in herbivore effects caused by higher trophic levels

Beyond activities such as waste production or denning that directly affect tundra nutrients,<sup>95</sup> arctic predators and parasites indirectly influence element cycling through interactions with herbivores. Specifically, by altering herbivore density, activity, movement, or traits, organisms in higher trophic levels can alter the strength, timing, and location of herbivore impacts (Figures 2 and 3). The extent to which these interactions matter for element cycling at the regional scale remains unclear. However, predator activity has been associated with increased plant biomass in areas with particularly strong predator–prey interactions.<sup>96,97</sup> Tundra productivity has also been shown to be higher on islands with vertebrate predators,<sup>98</sup> suggesting the occurrence of trophic cascades in those areas. Among invertebrates, experimental increases in predatory spiders did not affect localized herbivore-induced plant damage in Greenland<sup>99</sup> but were found to lead to higher soil N-availability in Alaska.<sup>25</sup> In other cases, although nutrient cycling has not been explicitly addressed, it seems plausible that predators and parasites could have cascading ecosystem impacts. For example, fox activity was associated with landscape distribution of snow geese,<sup>100</sup> a species with extensive impacts on element cycling. Many small mammal population cycles are likely driven in part by top-down effects of predators as well.<sup>101</sup> For instance, increases in arctic fox populations from greater reliance on marine resources during low lemming years could delay the recovery of lemming populations<sup>102</sup> and their associated impacts. Even the risk of predation reduced snowshoe hare survival in boreal ecosystems,<sup>103</sup> as well as the survival<sup>104</sup> and breeding<sup>105</sup> of ungulates in alpine tundra. Likewise, parasitic infections<sup>106</sup> and harassment by biting flies<sup>107</sup> reduce *Rangifer* herbivory. Biting insects may also alter spatial and temporal effects of *Rangifer* by influencing their movement and migration timing.<sup>108,109</sup> While predator and parasite effects on ecosystems are generally understudied in tundra ecosystems, their interactions with herbivores have potential to cause changes in local biogeochemistry.

## HERBIVORE RESPONSES TO CLIMATE CHANGE

By altering when and where animals are physically present and active on the landscape, climate change is modifying the strength and timing of their impacts on arctic ecosystems (Figure 2). Herbivore responses to climate change include shifts in annual and interannual population densities, seasonal timing of activity, distribution, and key functional traits (Table 1). Temperature changes may even drive shifts in herbivore community structure, as recently shown for vertebrate herbivore groups within the boreal forest and arctic tundra.<sup>110</sup> While some herbivore responses result directly from climate change and may

be density-independent (e.g., warmer temperatures affecting animal physiology or plant resources; effects of greater frequency of wild-fire), others are density-dependent (e.g., increased exposure to novel pathogens). Regardless of the mechanism, changes in individual and population-level traits can alter the consumptive and nonconsumptive effects of herbivores with subsequent consequences for local element dynamics (Figure 2).

In this section, we review general knowledge of climate change responses for several key groups of herbivores (large and small mammalian herbivores, geese, and invertebrates). In each case, we consider the recent evidence for how climate change is affecting their population densities, spatial distribution, and timing of activity. Then, in the following section, we provide examples of how these climate change responses could alter herbivore consumptive and nonconsumptive effects on element cycling.

## Large mammals

Changes in climate, land-use, and herding management have had synergistic effects on *Rangifer* and muskox,<sup>111</sup> but generalizations across the Arctic are challenging due to variation in responses by individual populations. These two species may also respond to different climate change cues, so insights gained from one likely do not apply to the other.<sup>112</sup> For example, recent studies indicate *Rangifer* herds have been declining globally,<sup>113,114</sup> suggesting reductions in the strength of their consumptive and nonconsumptive ecosystem impacts. However, *Rangifer* utilize a wide range of habitats (both within and among years) and their abundances fluctuate across space and time, suggesting their impacts also fluctuate widely.<sup>35–37</sup> Evidence also indicates some *Rangifer* ranges are shifting or may shift in the near future to account for changing resource availability (reviewed in Ref. 114). A recent study of the Porcupine Caribou Herd in North America suggests as spring phenology advances, the herd will shift its geographic range to access necessary resources during and after calving.<sup>115</sup> In addition, many *Rangifer* populations use ice-covered landscapes to facilitate long distance movements in winter.<sup>114</sup> As ice becomes less common with warming, migratory routes might become extended to avoid open water. This would impose energetic costs on those populations and in turn, cause stronger effects on tundra areas that were historically less impacted.

For *Rangifer* and muskoxen, changing seasonality and weather patterns may force behavioral changes to ensure adequate food availability. In general, less is known about muskox phenology responses than for *Rangifer*, but earlier plant green-up associated with warmer temperatures has been correlated with greater muskox abundance and higher rates of plant consumption.<sup>16</sup> Long-term data from Greenland showed the local muskox population experienced substantial fluctuations in number and population structure over a recent 18-year period driven by spring snow patterns;<sup>116</sup> however, not all muskox populations display similar fluctuations (reviewed in Ref. 38). Some evidence suggests that reproductive timing of *Rangifer* may be flexible, which could partially buffer them from some elements of climate change. In a

**TABLE 1** Representative examples of how major groups of terrestrial arctic organisms are predicted to or are already responding to climate change in ways that could affect element cycling (see main text for additional discussion)

Organism	Abundance	Distribution	Phenology
Large mammal herbivores	<ul style="list-style-type: none"> <li>Responses by <i>Rangifer</i> (caribou/reindeer) and muskox populations highly variable<sup>38,114</sup></li> </ul>	<ul style="list-style-type: none"> <li>Some <i>Rangifer</i> populations may be driven north as predation and human activities increase in southern regions of ranges<sup>114</sup></li> <li>Some muskox populations migrating north, while others migrating south<sup>38</sup></li> <li>Northern range expansion by moose from boreal forest to tundra habitat<sup>208</sup></li> </ul>	<ul style="list-style-type: none"> <li><i>Rangifer</i> calving occurring earlier in some populations<sup>114,117</sup></li> </ul>
Small mammal herbivores	<ul style="list-style-type: none"> <li>Reduced frequency and magnitude of microtine rodent peaks associated with warming<sup>127</sup>, but see Refs. 128, 209, and 210</li> </ul>	<ul style="list-style-type: none"> <li>Predicted northern shifts of rodents and shrews in Alaska<sup>130,211</sup></li> </ul>	<ul style="list-style-type: none"> <li>Unclear for voles and lemmings</li> <li>Arctic ground squirrels breed earlier with earlier snowmelt<sup>134</sup></li> </ul>
Geese	<ul style="list-style-type: none"> <li>Multiple geese species increasing in population size<sup>162,163,212</sup></li> </ul>	<ul style="list-style-type: none"> <li>Predicted to expand northward in some areas<sup>137</sup></li> </ul>	<ul style="list-style-type: none"> <li>Earlier arrival at breeding grounds, earlier nesting and fledgling dates documented<sup>138,140,141</sup></li> </ul>
Invertebrates	<ul style="list-style-type: none"> <li>Herbivores expected to increase with warmer temperatures<sup>145,213</sup></li> <li>Declines in abundances of some pollinators<sup>146,152</sup></li> <li>Detritivores responding in various ways<sup>6,145,214–218</sup></li> <li>Declines in some spiders but no changes in others<sup>219,220</sup></li> </ul>	<ul style="list-style-type: none"> <li>Some herbivore pests expanding northward (e.g., winter moth)<sup>52,147</sup></li> <li>Recent detections of alien aphid pest in Svalbard and Greenland<sup>221,222</sup></li> <li>Some pest and parasite species expanding northward, including ticks,<sup>223,224</sup> and floodwater mosquitoes,<sup>225</sup> parasitic nematodes<sup>226,227</sup></li> <li>Increased black fly richness in recent decades on Victoria Island, Canada<sup>228</sup></li> <li>Geoengineering earthworms may move northward as conditions become milder<sup>229,230</sup></li> </ul>	<ul style="list-style-type: none"> <li>Insect life history events occurring earlier with warming<sup>231–233</sup></li> <li>Some herbivores<sup>213,234–236</sup> and canopy arthropods<sup>151</sup> track phenology of plant resources</li> <li>Additional reproductive opportunities for spiders<sup>237</sup> and some aquatic invertebrates (Kendrick and Huryn unpublished) with longer summers</li> </ul>
Vertebrate predators	<ul style="list-style-type: none"> <li>Snowy owl abundance declining as prey availability decreases<sup>238</sup></li> </ul>	<ul style="list-style-type: none"> <li>Red fox moving north, negatively affecting arctic fox and ptarmigan<sup>239–242</sup></li> <li>Other predators expanding northward, including brown bear, badger, and gulls<sup>122</sup></li> <li>Polar bears moving southward to use terrestrial resources<sup>243</sup></li> </ul>	<ul style="list-style-type: none"> <li>Gray wolf denning dates shifted earlier from 2000 to 2017<sup>244</sup></li> <li>Golden eagle arrival at summering grounds occurs earlier following “warm phase” Pacific Decadal Oscillations in winter<sup>117</sup></li> </ul>

review of potential mismatches between the timing of *Rangifer* calving and plant green-up, the authors found that earlier spring onset could benefit *Rangifer* by providing higher quality forage during the calving season.<sup>114</sup> Results from the Arctic Animal Movement Archive<sup>117</sup> revealed the timing of *Rangifer* calving in some populations shifted earlier in warmer years, suggesting they might maintain reproductive success if they can adapt to warmer summers (Table 1; see Ref. 118). If these shifts align with greater food availability, calf survival may increase as well. However, decreases in winter food abundance may counteract some of those effects. Predicting overall annual responses to climate change by large mammals remains challenging due to this

combination of shifting phenologies by both the herbivores and their resources.

Extreme events associated with climate change have impacted some large mammal populations. *Rangifer* are negatively affected by the increasing frequency of tundra fires, because lichens, their primary winter food source, are very slow to recover from wildfire.<sup>119</sup> Increasing rain on snow events<sup>120</sup> also negatively affects grazing herbivores and reduces their ecosystem impacts by limiting access to vegetation during winter and early spring.<sup>16,114,121</sup>

Large mammal responses to climate change are particularly pronounced in the southern areas of their distributions.<sup>122</sup> Direct and

indirect human influences in these areas may have compounding effects on *Rangifer* and muskox as climate change continues. For example, concentrated human activities in the southern Arctic may have detrimental effects on *Rangifer* populations that will drive them and their associated impacts northward.<sup>123</sup> Though most muskox populations do not migrate, there is evidence that some may be migrating southward in Canada, which would also shift the distribution of their ecosystem impacts (Table 1).

### Small mammal herbivores

Multiyear studies suggest that climate change may alter the natural population cycles of some lemmings and voles (i.e., microtine rodents; Table 1). In particular, changing winter weather patterns have been associated with reductions in population peaks and population sizes.<sup>124,125</sup> Near Utqiagvik, Alaska, lemming populations historically peaked every 3–5 years,<sup>29</sup> but there have been no large population peaks in the last decade.<sup>126</sup> However, understanding changes in small mammal population cycles continues to be a challenge because climate change responses are highly context dependent. Temporal patterns in population cycles vary between regions with different climatic conditions, with those in some areas more strongly linked to growing season than winter<sup>127</sup> and little evidence of change in others.<sup>128</sup>

Climate change is also driving range expansions among some small mammal species. Subsequent shifts in local community composition among these groups could have consequences for element cycling. As the Arctic warms, some research suggests that currently dominant species might be replaced by locally subdominant or novel species as their distributions expand.<sup>129</sup> Small mammal species inhabiting northern coastlines are already experiencing range contractions and changes in species interactions as southerly species move northward.<sup>130</sup> Models predict that species with more northerly distributions will be those most negatively affected by climate change; some of these northern small mammal species may lose over 25% of habitat space as they shift their ranges further northward (Table 1 and Ref. 130). Subsequent changes in community composition will result in overall changes to small mammal impacts on elemental cycling, because the various species of small mammals have different diets,<sup>131</sup> periodicity in their population cycles,<sup>132</sup> and peak population sizes (e.g., brown vs. collared lemmings<sup>133</sup>).

Changing seasonality is likely to affect small mammals differently than some of the other groups reviewed here because they remain locally present and active year-round in the tundra. An exception is arctic ground squirrels, a group that hibernates during winter but has been shown to end hibernation and breed earlier in areas with early snowmelt.<sup>134</sup> However, there is still a general lack of data about arctic small mammal phenology, because key life history events (e.g., breeding and reproduction) for many species occur under snow during wintertime.<sup>135</sup> The extent to which changing seasonality might affect the phenology of these species remains an open area of research.

### Avian herbivores: Geese

Geese are one of the most well-studied groups of birds in the Arctic due to their large numbers and ecological impact. Population of several goose species have increased over the past few decades in North America, Greenland, and Svalbard and are expected to continue increasing (Table 1; see case study below). Geese ranges and the types of habitats they utilize are also shifting with climate change and habitat degradation. Specifically, habitat degradation caused by high geese densities in breeding grounds has expanded occupancy into less degraded areas over recent decades, indirectly fueling continued population growth.<sup>136</sup> As the minimum frost-free period increases on Svalbard, pink-footed geese are also predicted to expand their breeding range to the north and east.<sup>137</sup>

Similar to other migratory groups, climate change has the potential to disrupt the timing of major life history events and species interactions for geese and other tundra-breeding birds. Despite their growing numbers, warmer temperatures and changes in plant phenology may ultimately have some negative effects on geese populations in the future. Earlier geese arrival to their arctic breeding grounds does not always match the more advanced dates of plant green-up (Table 1 and Refs. 138–141). Key snow goose phenology events (e.g., nesting and fledging timing) have also not advanced fast enough to track changes in vegetation phenology, such as the timing of high N content in plants.<sup>136,138,141</sup> For multiple species, increasing mismatches between peak gosling hatch and peak forage quality<sup>138,141</sup> has led to lower gosling survival.<sup>136</sup>

### Invertebrate herbivores

Temperature, snowmelt, soil moisture, and plant composition are among the most important drivers of invertebrate composition in the Arctic (e.g., Refs. 142 and 143). As these conditions change, invertebrates are responding in kind. Long-term data from Greenland indicate that overall invertebrate community composition is changing,<sup>6,144,145</sup> particularly in arid habitats.<sup>144,145</sup> Warming is largely expected to benefit herbivores due to increased plant biomass and alleviation of harsh abiotic conditions (Table 1). However, general assessments of invertebrate responses across the Arctic remain limited by a lack of long-term data from most regions and because abiotic conditions are rarely measured in microhabitats of relevance to the organisms themselves.<sup>142,143</sup> Characterizing the effects of climate change is also a challenge because invertebrate responses in diversity and abundance display high degrees of variation.<sup>144</sup> For example, while abundances of some pollinator species are declining,<sup>146</sup> others exhibit high spatial and interannual variability with no clear population trends (e.g., Lepidoptera in Iceland and Greenland<sup>143</sup>). Differences in responses among groups are likely due to shifting species interactions and complicated life histories for many species, including the use of multiple habitats. Recent efforts aimed at teasing apart the relative impacts



of abiotic versus biotic drivers are a promising way forward to better characterize direct and indirect effects of climate change within this group.<sup>6</sup>

Despite projections of northward range expansion by more southerly species, there are only a few examples of invertebrate range shifts or new species introductions in the Arctic (Table 1). A notable example is the winter moth (*Operophtera brumata*), a species prone to outbreaks that has expanded its distribution northward into the low-arctic zone in Fennoscandia in response to warmer temperatures.<sup>52,147</sup> Range expansions by other invertebrate pests, parasites, and disease vectors<sup>148</sup> (Table 1) may also impose novel stressors on wildlife with indirect effects on tundra nutrients. However, knowledge of species boundaries, distributions, and even basic ecology remains limited for most arctic invertebrates.<sup>143,149</sup> Without updated distribution maps and the establishment of more invertebrate monitoring programs, detection of northward range expansions and new introductions will remain a challenge.<sup>143</sup>

Most research on changes in arctic invertebrate phenology has been in the context of potential disruptions to food resources for birds and pollination. Many species of arctic invertebrates experience long periods of winter dormancy, with emergence timing and seasonal activity patterns largely driven by snowmelt and air temperature.<sup>150</sup> As snowmelt occurs earlier and temperatures rise, activity windows for some groups are shifting earlier and becoming extended (Table 1). For example, evidence suggests the biomass and activity of herbivores and other canopy-dwelling invertebrates<sup>151</sup> track those of their host plant resources. On the other hand, lower pollinator abundances<sup>146</sup> and shorter flowering seasons<sup>152</sup> have shrunk pollination time windows,<sup>153</sup> which could have long-term impacts on plant community composition.

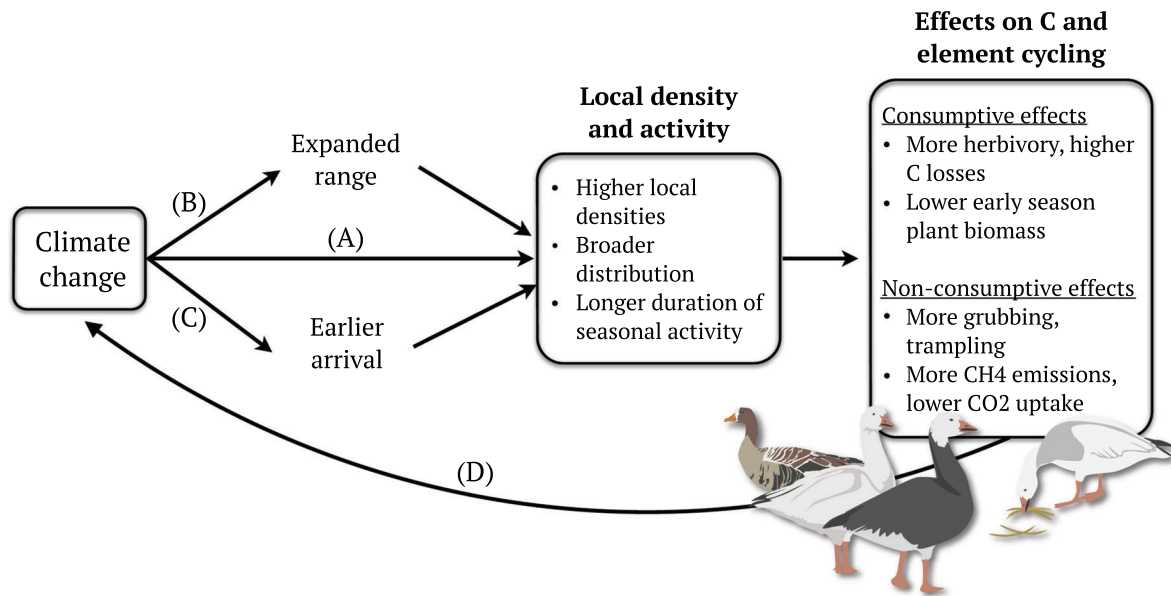
## EFFECTS OF CLIMATE CHANGE ON HERBIVORE IMPACTS

As global change alters the spatial and temporal distribution of herbivore activity (Table 1), effects of herbivores on element cycling will also change (Figure 2). In some cases, effects may be relatively straightforward, such as increases or decreases in abundance that cause stronger or weaker species-specific consumptive and nonconsumptive impacts on plant and soil nutrients. For example, declines in small mammals<sup>124</sup> or *Rangifer*<sup>114</sup> would reduce their localized impacts on element cycling. However, the consequences of many climate change responses will not be so straightforward. Just as climate change responses vary spatially and temporally, so too will herbivore impacts. For example, shifts in migration routes or species distributions will change the strength of herbivore activity in any given location. Locations of some migratory species' summer breeding and foraging grounds are also changing, as are distributions for some resident herbivore species (Table 1). Increased energetic costs associated with extended migration routes (e.g., *Rangifer*)<sup>114</sup> may have other cascading effects on plants via changes in feeding intensity and forage selection as well.

Climate change is also influencing the timing of herbivore impacts within years and the strength of population-level impacts between years. Phenological shifts by some groups, such as geese, include changes in migration timing and earlier arrival to breeding grounds (Table 1 and Figure 4). Such shifts in herbivore activity timing have the potential to disrupt the highly seasonal progression of tundra element availability.<sup>154</sup> Changes in interannual abundances also contribute to the temporal variability in herbivore impacts on ecosystem processes. This may be particularly relevant for herbivorous rodents, which undergo regular population cycles every 3–5 years, and can have 250% higher density in peak years compared to low years.<sup>29</sup> Recent evidence suggests that population cycles are being suppressed due to climate change (Table 1), which could reduce the overall impacts on landscape nutrient dynamics in the long-term. In contrast, more frequent insect herbivore outbreaks<sup>52,147</sup> could drive higher interannual variability in standing plant biomass, with consequences for primary productivity and nutrient cycling.

Changes in species interactions due to climate change may also have unexpected consequences for element dynamics. Differential responses to climate change could decouple interactions among consumers and higher trophic levels, cause trophic mismatches, and alter existing trophic cascades. For example, recent experimental work showed that warming can reverse the indirect effects of spiders on decomposition due to changes in invertebrate predator–prey dynamics.<sup>25</sup> Although similar examples for herbivores are limited, substantial indirect evidence suggests that changes in species interactions will modify the strength of herbivore impacts on nutrient cycling. For instance, temperature increases have been associated with higher predation intensity across the Arctic, suggesting that climatic warming may cause a switch from bottom-up to top-down regulation of herbivore populations in some areas.<sup>155</sup> Greater predation pressure associated with warming could thus reduce overall herbivore activity and impacts on element cycling. The density, activity, and impacts of some large mammals may also be reduced as the prevalence of various parasites, diseases, and insect harassment increases in a warming Arctic.<sup>38,114,148,156</sup>

In other cases, changes in species interactions could weaken existing trophic cascades or change them altogether. Due to a combination of changing precipitation regimes<sup>157</sup> and increased black fly attacks,<sup>158</sup> some avian predators have experienced reduced nesting success. Weakened predation pressure by these groups could lead to higher densities of small mammal prey, thereby strengthening local herbivore consumptive and nonconsumptive effects. As nonarctic large mammals, such as moose and white-tailed deer, expand northward, exposure to novel pathogens<sup>114</sup> could negatively impact arctic herbivore populations and reduce their overall ecosystem impacts. Finally, species-specific responses to climate change could alter competitive interactions that result in changes to element cycling. For example, climate-driven reductions in lemming populations indirectly reduce geese effects on local element dynamics, because when lemming abundances are low, geese experience higher predation pressure and reduced breeding success<sup>159</sup> (Figure 4).



**FIGURE 4** Geese are key arctic herbivores whose densities and activity are changing due to rapid climate change in the Arctic. Changes in the local densities of geese (A), their spatial distribution (B), and timing of activity (C) reflect responses to changing conditions. These responses, in turn, alter the consumptive and nonconsumptive effects of geese on element cycling and can result in feedbacks (D) to climate change.

### Geese case study

In the following section, we use geese to provide examples of how climate-driven changes in spatial and temporal variation in herbivore activity could have cascading effects on element dynamics. Geese make an excellent case study group, because climate-driven changes in their densities (Figure 4A), distribution (Figure 4B), and activity timing (Figure 4C) are already having measurable impacts on tundra ecosystems.

Populations of several geese species are increasing due to multiple interacting drivers in their wintering grounds and summer breeding areas (Table 1). For example, hunting bans and agricultural change have created more favorable conditions in their wintering grounds.<sup>160,161</sup> Progressively earlier spring onset and earlier goose arrival to arctic breeding grounds<sup>138,141</sup> have also contributed to population increases. In particular, the combination of advanced goose phenology and higher food availability during the early spring nesting period has led to earlier hatching dates,<sup>162</sup> higher egg production, and reports of improved hatchling success.<sup>163,164</sup> These responses have resulted in increased geese densities and more intense early season activity (Figure 4). Geese are also progressively impacting larger areas of tundra; changing climatic conditions are facilitating range expansion<sup>137</sup> and geese are expanding into new areas as habitats become degraded due to high population densities.<sup>136</sup>

More geese translates to higher consumption of plant material<sup>42</sup> and increased intensity of nonconsumptive activities, such as grubbing<sup>41</sup> and trampling.<sup>72</sup> The dramatic increases in geese populations have caused proportional increases in geese impacts on soil C and N stocks.<sup>43</sup> Notably, earlier grazing by geese on their breeding grounds can have even larger effects on ecosystem C-fluxes<sup>11,26</sup> and

soil N<sup>165</sup> than the earlier start to the growing season. For example, higher consumption of plants early in the season reduces overall plant biomass and decreases overall seasonal CO<sub>2</sub> uptake by the plant community.<sup>11,166</sup> Early season feeding by geese can also reduce vegetation height and cause higher soil respiration.<sup>26</sup> Effects of geese activity have even been found to amplify warming-associated increases in methane emissions from coastal wetlands,<sup>11</sup> which could potentially cause feedbacks to climate change (Figure 4D).

### HERBIVORE-DRIVEN CHANGES IN ECOSYSTEM RESPONSES TO CLIMATE CHANGE

Climate change has different effects on tundra biogeochemistry depending on whether herbivores are present or not. Specifically, mounting evidence suggests that herbivore activity can dampen or exacerbate existing plant and soil responses to climate change (e.g., Ref. 167) and even have unexpected feedbacks to climate change. For example, by reducing shrub growth,<sup>23,83</sup> herbivores ranging from small to large mammals have been found to counteract the effects of climate-induced shrub expansion in the Arctic.<sup>20,168,169</sup> Herbivores may also contribute to the resilience of shrub-dominated systems to warming; in one case, after long-term, experimental warming treatments were discontinued, warming-induced shrub growth was reduced in the presence of herbivores but continued in areas where they were absent.<sup>170</sup> Extreme outbreaks of insect herbivores also dramatically reduce standing plant biomass and have lasting impacts on nutrient cycling.<sup>47,52</sup> Experimental work suggests that tundra ecosystems may have reduced resilience to such outbreaks under future climate change.<sup>171</sup> Plant community responses to climate-associated

increased nutrient availability<sup>31</sup> may also be amplified by small mammal activity. For example, herbivory was found to reverse the impacts of warming on plant diversity and to modify the combined effects of fertilization and warming.<sup>172</sup>

In addition to influencing plant community responses, herbivores have been shown to mediate plant responses to climate change at the individual level. Plants exposed to both long-term warming and mimicked moth herbivory emitted far higher levels of VOCs than those exposed to either warming or herbivory in isolation,<sup>94</sup> suggesting that invertebrate herbivory will exacerbate plant VOC emissions as the Arctic warms.

Direct effects of climate change on soil C and nutrients are also mediated by herbivore activity. Depending on whether areas have been grazed or not and the associated changes in soil microclimate, increasing nutrient availability had differential impacts on soil microbial cycling of C and N.<sup>173</sup> Grazing geese were found to exacerbate warming-associated increases in methane emissions in coastal wetlands as well.<sup>26</sup> Reindeer grazing history can also alter the composition of soil microbial communities<sup>90,174</sup> and influence microbial responses to global change drivers, such as warming and nutrient availability.<sup>175</sup> Although evidence is limited, these examples suggest that changes in localized herbivore impacts could modify direct effects of climate change on element cycling.

## FUTURE RESEARCH PRIORITIES AND SUGGESTED APPROACHES

Significant gaps remain in our understanding of how climate change is affecting herbivore impacts on element dynamics in the Arctic. Research over the past several decades has primarily focused on consumptive impacts of herbivores, while impacts of nonconsumptive effects have been less studied. Existing evidence is also biased toward vertebrates and particular geographic areas and thus does not represent the full range of ecological contexts or climatic changes experienced by herbivores across the Arctic.<sup>176</sup> In addition, much of our knowledge of consumer impacts on element cycling in the tundra remains limited to C. Multiple arctic ecosystems are suggested to be N-limited or co-limited by N and P, while others are more P-limited.<sup>177–179</sup> Long-term *Rangifer* grazing has been found to shift whole plant communities from being N-limited to P-limited.<sup>180</sup> Work from the boreal forest also suggests that even in unproductive ecosystems, invertebrate herbivore-mediated N and P fluxes to the soil can be comparable to those from plant litterfall<sup>181</sup> (but see Ref. 182). Better knowledge of how herbivores contribute to the dynamics of these understudied nutrients will be increasingly important under changing climate scenarios.

As described earlier, climate change is affecting herbivore activity—and, therefore, impacts—both spatially and temporally. Herbivore responses to climate change reflect combinations of reactions to changing environmental conditions and interactions with other species, which can result in indirect effects of climate that are often challenging to quantify.<sup>6,110,144,183</sup> Further complicating matters is

that both responses to climate change and subsequent effects on nutrient cycling are likely to be context-dependent and vary with environmental conditions across the heterogeneous arctic landscape. For example, while warming is expected to lead to higher rates of invertebrate herbivory due to higher abundances (Table 1), predicted increases in precipitation may reduce these impacts in some areas.<sup>184</sup> In many cases, there is not even consistency in climate change responses among closely related species at the same location,<sup>144</sup> which limits our ability to generalize across groups. In addition, while functional diversity of arctic animals varies regionally,<sup>185</sup> most of our knowledge about species responses to climate change comes from just a few places that are not representative of the full suite of environmental conditions across the Arctic.<sup>186,187</sup> Impacts of large herbivores, such as *Rangifer* and some predators (e.g., wolves and red foxes), may also vary depending on management regimes. As effects of climate change continue to manifest differently in different parts of the Arctic, predicting species—and food web—effects on element dynamics will depend on our ability to characterize these context dependencies.

A key component of this is improving our understanding of the temporal drivers of herbivore abundance and activity. Data from outside the summer season are especially lacking given the expectation that changing fall, winter, and spring conditions<sup>188</sup> will have widespread effects on population dynamics of both year-round<sup>124</sup> and summer-active animals.<sup>144,145</sup> As snowmelt occurs earlier and growing seasons become longer, the duration of activity time for summer-active animals will increase. These changes will continue to modify seasonal food web composition<sup>189</sup> and subsequent ecosystem impacts.<sup>11,165</sup> Some groups, such as voles and muskox, feed year-round, but their winter activities are understudied. Repeated field sampling across multiple years in more locations is necessary to better understand long-term trends and the subsequent ecosystem consequences. This is especially important in efforts to differentiate indirect versus direct effects of climate change and to capture the overall temporal trends that can be inconsistent due to the many interacting factors driving consumer populations in the Arctic (e.g., Refs. 144 and 190).

In addition, intra- and interannual patterns in herbivore activity are disrupted by the increasing frequency of acute disturbances in the Arctic. These disturbances are not well understood or easily predicted, but they are likely to cause short- and long-term changes to species interactions and localized animal impacts.<sup>191</sup> For example, the frequency and intensity of tundra fires are increasing<sup>192</sup> and may have significant effects on short- or even long-term herbivore densities.<sup>193</sup> More frequent rain on snow events may also reduce herbivore impacts on element cycling by limiting grazer access to vegetation and dampening small mammal population peaks.<sup>124,125</sup> In all cases, there is potential for mismatches in the timing of species interactions, the result of which could have cascading effects on element cycling.

Lastly, while vertebrate herbivore impacts are fairly well characterized, those of other trophic levels remain largely unexplored. Estimating the overall food web-driven effects on ecosystem-level processes will require the collection of standardized biomass

estimates across functional and trophic groups, which to our knowledge has not been conducted for all vertebrate and invertebrate components of the arctic food web in any location. Although the impacts of their activities may not be as immediately apparent as those of herbivores, predators can change the heterogeneity of element distribution across the landscape even when abundances are low.<sup>95,194</sup> For example, denning activities and waste production by red foxes near the Arctic treeline caused an increase in localized soil N, soil P, and plant richness.<sup>195</sup> Brown bear predation on salmon in SW Alaska also has transient effects on soil nutrients through the transfer of marine-derived nutrients to riparian habitats.<sup>196</sup> Detritivores are important drivers of decomposition and nutrient cycling<sup>9,197</sup> that could indirectly regulate soil biogeochemistry via changes in microbial activity<sup>65,76,198</sup> as well. It is unclear whether direct and indirect effects of organisms within other trophic levels are detectable at the regional scale. However, this is an area that warrants further investigation, particularly as these groups continue to respond in variable ways to climate change (Table 1).

Many of the knowledge gaps discussed above can be approached using distributed experiments, models, remote sensing, meta-analysis, and traditional ecological knowledge. In almost all cases, interdisciplinary teams of scientists and arctic residents are needed to incorporate data from multiple scales, disciplines, and techniques. Given that field research in the Arctic is expensive and logistically difficult, these approaches can help guide targeted field campaigns to maximize the use of existing resources, data, and infrastructure. In addition, broader use and dissemination of data could engage more scientists, students, and the general public in arctic research.

Some of the issues associated with scaling from local to regional scales are being addressed using distributed experiments and meta-analysis techniques. Collaborative, coordinated networks of field scientists can enable researchers to overcome some logistical challenges and extrapolate results to more locations. Such an approach has proven particularly successful in the Arctic for groups such as the International Tundra Experiment, ShrubHub, the Herbivory Network, and the Network for Arthropods of the Tundra. The Herbivory Network recently published standardized protocols for characterizing herbivore activity at three different spatial scales in the tundra,<sup>13</sup> as well as an evaluation of where herbivore effects on plants have been measured.<sup>176</sup> These efforts will hopefully spur additional measurements that can be compared across spatial scales within and among study areas to better characterize herbivore impacts. Organizations like INTERACT also foster these collaborations. However, even with the growth of these collaborative approaches, establishing and securing additional adaptive long-term monitoring programs (e.g., COAT in Norway) and funding continues to be extremely important in the Arctic. Ensuring that field data from published studies and long-term research sites (e.g., NEON and Long-Term Ecological Research Network sites in the United States or BioBasis Programme locations in Greenland) are continually made publicly available is also an important means to foster meta-analytic approaches and provide opportunities for scientists unable to physically travel to the Arctic to contribute to this work.

Pronounced heterogeneity in animal and plant responses to climate change has also demonstrated the need to incorporate measurements at multiple spatial scales.<sup>199</sup> Increased use of integrated satellite and plot-level remote sensing data is a promising approach to help quantify and better understand this heterogeneity. For example, technological advances in remote sensing and unmanned aerial vehicles are increasingly being used in the Arctic to track animal movements to gain a better understanding of migration patterns, habitat use, and impacts.<sup>28,40,48,117,200</sup> New approaches are also being used to quantify insect abundances, interactions, and ecosystem impacts on finer spatial and temporal scales.<sup>201,202</sup> Further incorporation of the presence and movement of consumers across trophic levels with plant and soil measures made at various scales could elucidate some of the outstanding questions related to spatial and temporal variation in their impacts.

Another critical approach to better understand the role of consumers in the Arctic is to incorporate animal effects into existing biogeochemical models. There are multiple nutrient cycling models calibrated for different types of tundra (e.g., TEM,<sup>203</sup> GEM,<sup>204</sup> and MEL<sup>205</sup>) at different scales. By incorporating consumptive and non-consumptive interactions (Figure 3) into these models, they can test hypotheses about the various roles of animals in arctic ecosystems. A recent example of this illustrated how a biogeochemical model can underestimate tundra ecosystem responses to increased temperature and CO<sub>2</sub> if grazing effects by small mammals are not considered explicitly.<sup>206</sup> Model development and calibration phases can then be used to prioritize targeted field campaigns to gather additional data to improve model fit and understand how model predictions differ across tundra types and locations.

Finally, incorporation of multiple knowledge types, including local, traditional, and scientific knowledge (e.g., Ref. 207), would contribute to building a richer understanding of the historical role of herbivores and other animals within arctic ecosystems and how their impacts are changing over time. Meaningful engagement of Indigenous Peoples and the codevelopment of new arctic research has been the focus of several recent workshops in the United States and elsewhere as the scientific community increasingly recognizes the value of traditional knowledge.

## CONCLUSION

Herbivores are not typically considered in models of element cycling for the Arctic, but the findings from the work reviewed here suggest this should be revisited. Through their consumptive and nonconsumptive effects, herbivores influence local C stocks and nutrient availability and can even move elements across large geographic areas. The extent to which herbivore impacts are important at larger spatial scales or how they may influence regional element cycling is unknown but an important area of ongoing research. As the Arctic continues to change, understanding the shifting roles of terrestrial consumers in ecosystem functioning will become increasingly critical. Given that the Arctic plays a disproportionate role in global biogeochemistry, these changes could have meaningful ecological consequences. We suggest that (1) additional long-term monitoring of animal populations, including during fall,

winter, and spring; (2) incorporating herbivores and other consumers into ecosystem models; (3) using existing research infrastructure and methods in new collaborative ways; and (4) incorporating traditional ecological knowledge and local expertise will help address some of these critical knowledge gaps.

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## AUTHOR CONTRIBUTIONS

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## COMPETING INTERESTS

The authors have no competing interests to disclose.

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