**Shrubification in the Western Arctic   
and its Effects on the Porcupine Caribou Herd Habitat**

Table of Contents

[Introduction 1](#_Toc93737044)

[**Objectives and Rationale** 7](#_Toc93737045)

[**Research Questions and Hypotheses** 7](#_Toc93737046)

[Methods 9](#_Toc93737047)

[Study Site 9](#_Toc93737048)

[Study Species 9](#_Toc93737049)

[Data Collection 9](#_Toc93737050)

[Data Analysis 9](#_Toc93737051)

[Bibliography 10](#_Toc93737052)

# 

# **Introduction**

**Arctic Amplification**

The **Arctic is warming more than twice as fast** as the global average (Post et al., 2019). Since the late 19th century, the Earth has warmed by approximately 0.8°C, while the Arctic has warmed by 2-3°C (Post et al., 2019; IPCC, 2013). This phenomenon is known as the **Arctic amplification (AA)** (Serreze & Barry, 2011) and is driven by complex and intertwined anthropogenic and natural processes (Cohen et al., 2020). Notably, rising greenhouse gas (GHG) concentrations in the atmosphere increase radiative forcing in the Arctic region (Stroeve et al., 2012; Gillett et al., 2008). This leads to a positive feedback, as decreased surface albedo due to sea ice loss replacing highly-reflective ice sheets with dark, poorly-reflective sea water, exacerbating warming (Winton, 2006). The **surface albedo feedback** is considered one of the major contributors of AA (Serreze & Barry, 2011). Other drivers of AA include increased cloud cover exacerbating the greenhouse effect (Graversen & Wang, 2009), the reduced longwave emissions per unit warming from the Arctic compared to the tropics (Pithan & Mauritsen, 2014), and deposits of black carbon on surfaces (Shindell & Faluvegi, 2009). Arctic temperatures are also sensitive to atmospheric currents driving warm and moist air from the tropics northward (Graversen et al., 2008).

**The Arctic is expected to reach 4°C mean annual warming under the +2°C global warming scenario** (Post et al., 2019). By the end of the century, the Arctic is predicted to warm by 3-5°C in spring and 7-13°C in autumn, according to climatic models (Overland et al., 2014). This rapid warmingwould exacerbate and accelerate the ongoing loss of land and sea ice, with the potential development of an ice-free Arctic ocean in the summer (Wang & Overland, 2009), increasing global sea level rise (Post et al., 2019). The amplification of warming in the Arctic has been linked to extreme weather events such as floods, droughts and heat waves in mid-latitudes (Post et al., 2019). However, divergence between observational and model studies obfuscate our clarity of understanding of the influence of AA on midlatitudes weather (Cohen et al., 2020). Arctic warming is also likely to increase net methane emissions from wetlands and permafrost thawing, leading to a positive feedback in the global climate system (Arctic Monitoring and Assessment Programme (AMAP), 2017).

Warming temperatures are influencing growing season length, soil hydrology and nutrient levels – which are affecting vegetation in complex way**s**, including changes in vegetation composition, productivity, structure and phenology (Stow et al., 2004). Some of the most devastating consequences of pronounced Arctic warming would be suffered by the wildlife feeding on tundra vegetation and the human livelihoods depending on these for nutritional, economic and cultural reasons (Post et al., 2019).

**Warming-induced *Shrubification***

Concurrent with Arctic warming, **aboveground biomass of tundra vegetation has been increasing** since the 20th century (Epstein et al., 2012; Ju & Masek, 2016). This has been shown by field (Elmendorf et al., 2012c) and remote-sensing (Jia, Epstein & Walker, 2003) studies, as well as repeat photography (Fraser et al., 2014; Sturm, Racine & Tape, 2001) in high-latitude and Arctic ecosystems. Indeed, remote sensing detected an increase by 16.4% in peak NDVI - indicating green vegetation - between 1981-2001 in northern Alaska (Jia, Epstein & Walker, 2003), with greening (increasing vegetation productivity). Plot-based warming studies such as the **International Tundra Experiment (ITEX)** have consistently shown increases in vegetation height (Walker et al., 2006). In particular, **deciduous shrubs including willow, alder and birch, have expanded in relative abundance and cover** with variability across the Arctic region (Fraser et al., 2014; Elmendorf et al., 2012a; García Criado et al., 2020; Elmendorf et al., 2012b; Myers-Smith et al., 2011).

“Shrubs are woody plants with diverse growth forms including tall multi-stemmed shrubs (0.4–4.0 m), erect dwarf shrubs (0.1–0.4 m) and prostrate dwarf shrubs ( < 0.1m) that grow laterally along the ground surface.” (Myers-Smith et al., 2011).

**The phenomenon of shrub expansion as a response to climate change is known as Arctic *shrubification****,* and itoccurs in the form of infilling of existing patches through lateral growth, increased canopy height, and advancing of shrublines (Myers-Smith et al., 2011). Indeed, some species of shrubsuch as *Betula nana* are favoured by the increasing air temperatures (Myers-Smith et al., 2011). Nevertheless, the local responses of shrub cover to increased temperatures have been highly heterogeneous across the region(Myers-Smith et al., 2015).***Shrubification* on the North slope of Alaska has been found to occur mainly in valley bottoms and hillsides (Tape, Sturm & Racine, 2006), wet and warm sites, favouring microbial activities in the soil** (Myers-Smith et al., 2011). In Alaska and the Yukon Territory, willow and alder species are advancing upslope(Dial et al., 2007). Woody species such as *Betula*, *Alnus*, *Salix spp.* arestarting to dominate the Arctic landscape (Mekonnen et al., 2021). Shrub expansion may result in the out shading of understory shade-intolerant vegetation species, reducing overall species richness (Pajunen, Oksanen & Virtanen, 2011) and impacting food webs (Myers-Smith et al., 2011). Notably, lichen – an important forage species for many herbivores - has been found to decrease as shrub cover increases (Dawes et al., 2011; Joly, Jandt & Klein, 2009; Cornelissen et al., 2001). Moreover, shrubs may outcompete moss species, impacting their soil insulation function(Myers-Smith et al., 2011; Blok et al., 2011). Shrub expansion thus modifies ecosystem processes such as snowpack depth, nutrient exchange, and surface albedo. Continued *shrubification* is expected to alter carbon sequestration, fire dynamics and productivity in the Arctic regions (Myers-Smith et al., 2011). Overall, *shrubification* of tundra vegetation has the potential to mitigate and aggravate warming (Wookey et al., 2009).

Although coarse-scale satellite imagery indicates widespread arctic greening (Raynolds et al., 2012), site-level studies indicate that primary productivity in the tundra is highly heterogeneous (Kremers, Hollister & Oberbauer, 2015). Indeed**, the spatial resolution of coarse satellite imagery is 250 m–8 km, whereas the spatial distribution of shrubs in the tundra is heterogenous** (1-100m)(Myers-Smith et al., 2011). Validation via *in-situ* studies is therefore crucial to confirm low-resolution satellite information(Myers-Smith et al., 2011). However, bias from site-based research in the Arctic being highly clustered must be taken into account when making generalisations about vegetation trends (Metcalfe et al., 2018).

**Warming-induced Phenological Shifts and the Potential for Mismatch**

**Rapid warming is influencing phenology** – the timing of lifecycle events related to climate (Collins et al., 2021). Increasing temperatures have in fact altered snow regimes, accelerated decomposition rates, shortened flowering seasons (Prevéy et al., 2019) and extended growing seasons (Ernakovich et al., 2014). Experimental warming through open-top chambers (OTCs) is a widely used methodology to study the influence of warming on phenology (MARION et al., 1997; Walker et al., 2006; HENRY & MOLAU, 1997). The **International Tundra Warming Experiment,** uses such method across Arctic sites, and found through that periodic seasonal phenomena – different *phenophases* - have been altered by experimental warming in different ways (Collins et al., 2021). Leaf green up and **reproductive phases** such flowering and seed maturation and dispersal advanced in time (Bjorkman et al., 2015). Whereas **vegetative phases** such as leaves senescence were delayed by warming (Bjorkman et al., 2019). Specifically, a synthesis of the ITEX experiments across the Arctic, sub-arctic and alpine ecosystems found that, as response to an average 1.4°C experimental warming, leaf greenup and reproductive phenophases advanced by 0.7-2.9 days and leaf senescence was delayed by 0.8 days (Collins et al., 2021). This means the overall growing season has increased by ~3% (Collins et al., 2021).

\*\*diagram of phenology\*\* : greenup 🡪 flowering 🡪 end of flowering 🡪 fruiting 🡪 seed dispersal 🡪 leaf senescence (see Collins)

Phenological responses of plants to warming may affect trophic webs. For instance, specialist herbivores consuming preferably specific plant phenophases may be disadvantaged by phenological shifts (Barboza et al., 2018). Phenological shifts have the **potential of resulting in mismatches in the synchrony of interacting species**, in particular consumer and resource species (Post et al., 2019; Beard et al., 2019). A mismatch can occur if plant green-up advances as a result to warming temperatures, while timing of herbivore calving remains unaltered or advances at a slower rate (Mallory & Boyce, 2018). This phenological asynchrony is known as trophic mismatch, and occurs by decoupling the availability of highly nutritious forage plants in the calving grounds and the timing of high nutrition demands during lactation (Doiron, Gauthier & Lévesque, 2015). This may results in a reduction in reproductive success, as documented in caribou in West Greenland (Post & Forchhammer, 2008). **Trophic mismatches** may be contributing to the global declines in caribou (Vors & Boyce, 2009). Nevertheless, **trophic mismatches are less likely in Arctic caribou**, since it is characteristic for these to calve before the spring greenup and since they rely heavily on fat stores from the previous summer (Gustine et al., 2017). Earlier onset of spring could also benefit caribou by providing early access to high-nutritional forage and increase the growing season (Cebrian, Kielland & Finstad, 2008). The migratory patterns of caribou are flexible in response to environmental change(Corre, Dussault & Côté, 2017). However, adaptation and plasticity to changing environmental conditions may hit a threshold, hampering food web stability (Iler et al., 2013).

**Arctic Warming affects Large Herbivores**

Changes in vegetation community composition and plant phenology influence the abundance and distribution of Arctic herbivores (Mallory & Boyce, 2018). **Large herbivores are crucial determinants of ecosystem dynamics in the Arctic**, and have resource and socioeconomic value for indigenous communities livelihoods (Post et al., 2019). The **complex feedbacks between herbivores and ecosystem function** in the Arctic are still being investigated, with recent findings linking herbivores to climate mitigation by affecting carbon uptake (Cahoon et al., 2012), land surface albedo (te Beest et al., 2016), and plant diversity (Post, 2013). Notably, **herbivores play a vital role in preserving Arctic biodiversity** by hindering plant growth and favouring low-growing plants, avoiding their competitive exclusion (Kaarlejärvi, Eskelinen & Olofsson, 2017).

\*\*Flow chart of herbivore and ecosystems feedbacks\*\*

**Caribou (*Rangifer tarandus*)** are among the most abundant long-range migratory herbivores in the Northern Hemisphere (Mallory & Boyce, 2018). Following a negative global trend (Vors & Boyce, 2009), Arctic caribou have suffered a 40% decline over three generations – thus are classified as **vulnerable** by the IUCN red list (Gunn, 2015). Migratory tundra caribou population abundance undergoes seasonal cycles and quasi-cyclic fluctuations over 40-90 year timescales (Ferguson, Williamson & Messier, 1998; Zalatan, Gunn & Henry, 2006), meaning their influence on shrub populations is likely to change across time and space (Post et al., 2009). Fluctuations are thought to be related to climate oscillations (Joly et al., 2011), interactions with forage plants (Messier et al., 1988; Manseau, Huot & Crete, 1996) and predators (Bergerud, 1996). However, rapid climate-driven vegetation changes in the Arctic may alter this typical seasonality (Gunn, 2015). Indeed, **the nutritional value of vegetation is declining and insect harassment is increasing**, counteracting the positive effects of increased vegetation biomass on caribou abundance (Gunn, 2015). Overall, climate change is expected to impact caribou populations both positively and negatively (Mallory & Boyce, 2018), via changes in forage quantity and quality, increased wildfire in winter ranges (Joly, Duffy & Rupp, 2012), increased summer insect harassment (Witter et al., 2012), increased icing events (Loe et al., 2016), changing spring phenology (Corre, Dussault & Côté, 2017) and changes to distribution and migration (Sharma, Couturier & Côté, 2009).

The **causes of global caribou decline remain uncertain**, but likely the main causes include habitat change and *shrubification* (Fauchald et al., 2017). Caribou **population size responds negatively to vegetation change since caribou require late successional habitats** (Apps et al., 2001) and tend to browse in areas containing abundant lichen cover (Joly et al., 2003). Caribou are **generalist grazers** (with diets including sedges, forbs, lichens, and shrubs) and **seasonally selective**: preferring to forage on slow-growing lichens in the winter (Russell, Martell & Nixon, 1993). Warming-induced shrubification may result in a reduction in overall species richness (Pajunen, Oksanen & Virtanen, 2011). Woody plants have higher chemical and structural defences against herbivory and lower protein than grasses, forbs and sedges – and could have negative consequences on Arctic caribou diets and potentially drive altered habitat selection (Thompson & Barboza, 2014). Studies also suggest increased summer temperatures may lead to a decrease in nitrogen concentration (Hansen et al., 2006) via dilution effects and increased net carbon production within plants (Turunen et al., 2009), which may also alter caribou forage quality (Mallory & Boyce, 2018).

**The Porcupine Caribou Herd (PCH)**

Distributing across the U.S-Canadian border, the **Porcupine Caribou Herd (PCH)** is one of the largest herds in North America (Severson et al., 2021). The PCH plays a key role in the ecosystem by supporting predator populations such as bears and wolves (Musiani et al., 2007) and by grazing on vegetation (Wal, 2006). The PCH also has irreplaceable economic and cultural value, being crucial for the livelihoods of Indigenous peoples such as the Inuit and Tlicho (Kerber, 2015). **Arctic shrubification could deteriorate the herd’s pasture quality**, **with shrubs outcompeting lichen and mosses - caribou’s preferred diet** in winter and spring - resulting in potential declines in PCH populations (Fauchald et al., 2017).

While human-driven threats to caribou such as land-use change and energy production are well documented (Gunn, 2015), the impacts of climate change on caribou population dynamics are still unclear. Understanding how the PCH distribution may respond to shrubification is therefore crucial to inform habitat conservation commitments across the Alaska-Yukon border. The effectiveness of protected areas in landscape management is contentious since such conservation actions havenot slowed down caribou decline (Johnson, Ehlers & Seip, 2015). Given the migratory nature of caribou, conservation efforts should aim to provide a network of protection for annual ranges, across international borders.  Warming temperatures and improved access to resources in the northern Arctic are likely to increase industrial activity and development (Severson et al., 2021), increasing disturbance within the PCH habitat. Anthropogenic disturbance may further hamper caribou’s ability to adjust to environmental change (Vistnes & Nellemann, 2008). Some known mechanisms causing disruption include anthropogenic barriers, unregulated hunting, and habitat fragmentation disrupting migration routes (Vistnes & Nellemann, 2008).

Map

Description automatically generated

Fig. . Predicted probabilities of PCH calving habitat use during years of early **phenology (2015) and late phenology (2018)** (Severson et al., 2021).

It is therefore crucial to **understand how suitable habitat may be distributed in the future in order to protect the PCH habitat and to support its role in the ecosystem and ensure the subsistence of Indigenous communities** (Severson et al., 2021).

## **Objectives and Rationale**

The overarching aim of this research is to investigate vegetation change in the PCH Alaskan summer range habitat between 2007-2016, including vegetation cover, community composition, and landscape-scale trends. The research will study the relationships between shrubification in the PCH summer range and climate variables including summer temperature and precipitation as well as phenology. The research will conclude with a comparison of landscape-scale and plot-scale vegetation trend estimates. The research will allow to determine where and how shrubification has affected the summer range of the PCH over the 10-years study period.

## **Research Questions and Hypotheses**

I will answer the following research questions (RQ), focusing on the PCH Alaskan summer range:

**RQ0: How much of the PCH summer range is shrub covered?**

**RQ1: Are shrubs more likely present in warmer and wetter areas of the range?**

H1:Shrubs are more likely present in wetter and warmer areas of the range.

H10:Shrubs are not more likely present in wetter and warmer areas of the range.

H1a:Shrubs are more likely present in drier and colder areas of the range.

Prediction1: Shrub presence is more likely correlated with higher summer temperature and precipitation due to enhanced soil microbial activity facilitating shrub growth (Myers-Smith et al., 2011).

**RQ2: Is there greater shrub cover in early or late phenology years?**

H2:There isgreater shrub cover in early phenology years.

H20: Early phenology years do not have greater shrub cover.

H2a: There isgreater shrub cover in late phenology years.

Prediction2: Greater shrub cover is found in early phenology years due to increased growing season length (Collins et al., 2021).

**RQ3: How has vegetation community cover changed over time?**

H3: Shrub cover has increased over time.

H30: Shrub cover has not increased over time.

H3a: Shrub cover has decreased over time.

Prediction3: Shrub cover has increased over time outcompeting other plant functional types (Myers-Smith et al., 2011).

**RQ4: Do plot-based and landscape estimates of vegetation trends match?**

H4: NDVI vegetation trends correlate with plot-based vegetation cover estimates.

H40: NDVI vegetation trends do not correlate with plot-based vegetation cover estimates.

H4a: NDVI vegetation trends undermine with plot-based vegetation cover estimates.

Prediction4: NDVI will show vegetation greening in the region, confirming the increased shrub cover (Myers-Smith et al., 2019).

# Methods

## Study Site

\*\*Map\*\*

## Study Species

**The Porcupine Caribou Herd**

This study is based on the PCH summer range. Like most caribou populations, the **PCH undertakes annual long-distance migration between summer and winter ranges**, to **track emergent vegetation** and to **decrease predation risk** and parasitism from insects during the calving season (Mallory & Boyce, 2018). The PCH migrates in spring from the Yukon and Northwest Territories to its calving grounds in Alaska (Kerber, 2015). High-quality summer forage is critical for female (cow) body condition during lactation, with females having a window of 2 months over the summer to restore their fat reserves and gain enough fat to reproduce the following year (Barboza et al., 2018). The PCH enters its winter range with relatively low fat reserves, but manages to survive thanks to low snow and high lichen cover (Gunn et al., 2009). North of the tree line, in spring, the main dietary elements become evergreen shrubs and mosses, until the green-up of vegetation after snowmelt (Gunn et al., 2009). The timing of the green-up is crucial in determining the fate of new-born calves after the first month, with evidence of warmer springs favouring calf survival (Gunn et al., 2009). Indeed, nitrogen-rich emerging forage is crucial for milk production (Gunn et al., 2009).

\*\*\*map of migratory route of PCH\*\*\*

It is important to note that the PCH has had the lowest capacity for growth among Alaska barren-ground herds, indicating it has the lowest tolerance to anthropogenic and climate-change driven stressors (Douglas et al., 2002). Changes in plant phenology have been found to affect PCH spatial distribution, with caribou tracking protein-rich vegetation in early growth stages and **predominantly using Alaskan habitat in years of accelerated phenology** (Severson et al., 2021); Fig.1). Phenological shifts could alter the present PCH migrationroute. Since herds are a prey base for large carnivores, the consequences of changes in PCH migratory behaviour could have cascading effects across food webs (Musiani et al., 2007).

**Plant species**

## Data Collection

I gathered data from different open-access sources. I used the following datasets:

**Climate data** **from CHELSA**

CHELSA (Climatologies at high resolution for the earth's land surface areas) dataset(CHELSA, 2022). CHELSA has a very high resolution (30 arc sec, ~1km). It is hosted by the Swiss Federal Institute for Forest, Snow and Landscape Research WSL. CHELSA is based on statistical downscaling of global reanalysis data or global circulation model output. Data is freely available.

I gathered:

* Mean annual precipitation timeseries: one mean value per year (1979-2013).
* Warmest quarter annual timeseries: one mean value per year (1979-2013).

**Shrub cover data** **from Berner et al. 2018**

The data includes 30-m gridded estimates of total plant aboveground biomass (AGB), the shrub AGB, and the shrub dominance (shrub/plant AGB) for non-water portions of the Beaufort Coastal Plain and Brooks Foothills ecoregions of the North Slope of Alaska (Berner et al., 2018). Berner et al. calculated estimates by linking biomass harvests from 28 published field datasets with NDVI from a regional Landsat mosaic derived from Landsat 5 and 7 satellite imagery (Berner et al., 2018).

I gathered:

* Shrub ABG between 2007-2016.

**PCH core range data from 2016**

I used the Alaskan summer range.

**ITEX vegetation cover data**

The International Tundra Experiment (ITEX) is a collaborative network of researchers examining the impacts of warming on tundra ecosystems across the Arctic(Anon). In particular, it examines the effects of increased summer temperatures on cold-adapted plant species. Each study conducted under the ITEX programme must follow the ITEX manual (Molau, Mølgaard, & ITEX, 1996), so that standardised protocols allow the comparison of results across sites.

I gathered:

* Mosses, lichens, forbs, shrubs, and graminoids percentage cover in the Arctic national wildlife refuge (ANWR) between 1981-2020.

**Phenology data:**

I gathered:

* Day of year of the greening phenophase of shrub spp. (*Salix*) in Toolik lake and Qikiqtaruk (close enough to PCH summer range) and Atqasuk, Utqiaġvik that are on the North slope of Alaska between 1992-2019.

**NDVI data**

\*\*diagram on data wrangling\*\*

## Data Analysis

* 1. **RQ0: Shrub percentage cover in the PCH summer range**
* Overlay a shrub cover map of the Alaskan North Slope from 2007-2016 (Russell, Martell & Nixon, 1993) with a caribou summer range map from 2016.
* Crop the shrub map to the summer range map and I estimate shrub percentage cover.
  1. **RQ1: Shrub presence-absence in climatic regions**
* Point-extracted climate data (summer temperature and precipitation) and shrub presence-absence from polygons within the map.
* ANOVA to compare shrub dominance VS climate data.
  1. **RQ2. Shrub cover in early VS late phenology years**
* Plot shrub cover over time using hierarchical linear models.
* Plot a shrub phenology variable (Prevéy et al., 2021) over time, and determine late/early phenology years using an arbitrary threshold.
* ANOVA to compare late or early phenology year VS shrub cover.
  1. **RQ3. Vegetation trends over time**
* Plot percentage cover of various plant functional types (shrubs, mosses, lichens, forbs) over time using hierarchical linear models.
  1. **RQ4. Vegetation trends across scales**
* Find NDVI trends (browning, greening, no change) in the region.
* Correlate plot-based estimated of vegetation cover with NDVI estimates of vegetation cover trends.

# Bibliography

Anon. International Tundra Experiment (ITEX) - Grand Valley State University [web site]. (https://www.gvsu.edu/itex/, accessed 26 January 2022).

Apps CD et al. (2001). Scale-Dependent Habitat Selection by Mountain Caribou, Columbia Mountains, British Columbia. *The Journal of wildlife management*, 65(1):65–77.

Arctic Monitoring and Assessment Programme (AMAP) (2017). Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017 | AMAP [web site]. (https://www.amap.no/documents/doc/snow-water-ice-and-permafrost-in-the-arctic-swipa-2017/1610, accessed 16 January 2022).

Barboza PS et al. (2018). The nitrogen window for arctic herbivores: plant phenology and protein gain of migratory caribou (Rangifer tarandus). *Ecosphere*, 9(1):e02073.

Beard KH et al. (2019). The Missing Angle: Ecosystem Consequences of Phenological Mismatch. *Trends in ecology & evolution (Amsterdam)*, 34(10):885–888.

te Beest M et al. (2016). Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. *Environmental research letters*, 11(12):125013-.

Bergerud AT (1996). Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer*, 16(4):95-.

Berner LT et al. (2018). Tundra plant above-ground biomass and shrub dominance mapped across the North Slope of Alaska. *Environmental research letters*, 13(3):35002-.

Bjorkman AD et al. (2015). Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global change biology*, 21(12):4651–4661.

Bjorkman AD et al. (2019). Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring.

Blok D et al. (2011). The Cooling Capacity of Mosses: Controls on Water and Energy Fluxes in a Siberian Tundra Site. *Ecosystems (New York)*, 14(7):1055–1065.

Cahoon SMP et al. (2012). Large herbivores limit CO2 uptake and suppress carbon cycle responses to warming in West Greenland. *Global change biology*, 18(2):469–479.

Cebrian MR, Kielland K, Finstad G (2008). Forage Quality and Reindeer Productivity: Multiplier Effects Amplified by Climate Change. *Arctic, antarctic, and alpine research*, 40(1):48–54.

CHELSA, 2022. Chelsa Climate – Climatologies at high resolution for the earth’s land surface areas [web site]. (https://chelsa-climate.org/, accessed 26 January 2022).

Cohen J et al. (2020). Divergent consensuses on Arctic amplification influence on midlatitude severe winter weather. *Nature Climate Change*, 10(1):20–29.

Collins CG et al. (2021). Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nature Communications*, 12(1):3442.

Cornelissen JHC et al. (2001). Global Change and Arctic Ecosystems: Is Lichen Decline a Function of Increases in Vascular Plant Biomass? *The Journal of ecology*, 89(6):984–994.

Corre ML, Dussault C, Côté SD (2017). Weather conditions and variation in timing of spring and fall migrations of migratory caribou. *Journal of mammalogy*, 98(1):260–271.

Dawes MA et al. (2011). Growth and community responses of alpine dwarf shrubs to in situ CO₂ enrichment and soil warming. *The New phytologist*, 191(3):806–818.

Dial RJ et al. (2007). Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: Evidence from orthophotos and field plots. *Journal of Geophysical Research: Biogeosciences*, 112(G4):G04015-n/a.

Doiron M, Gauthier G, Lévesque E (2015). Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology*, 21(12):4364–4376.

Douglas DC et al. (2002). Arctic Refuge coastal plain terrestrial wildlife research summaries. :90.

Elmendorf SC et al. (2012a). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature climate change*, 2(6):453–457.

Elmendorf SC et al. (2012b). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology letters*, 15(2):164–175.

Elmendorf SC et al. (2012c). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, 2(6):453–457.

Epstein HE et al. (2012). Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental research letters*, 7(1):15506-.

Ernakovich JG et al. (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global change biology*, 20(10):3256–3269.

Fauchald P et al. (2017). Arctic greening from warming promotes declines in caribou populations. *Science advances*, 3(4):e1601365–e1601365.

Ferguson MA, Williamson RG, Messier F (1998). Inuit Knowledge of Long-Term Changes in a Population of Arctic Tundra Caribou. *Arctic*, 51(3):201–219.

Fraser RH et al. (2014). Warming-Induced Shrub Expansion and Lichen Decline in the Western Canadian Arctic. *Ecosystems (New York)*, 17(7):1151–1168.

García Criado M et al. (2020). Woody plant encroachment intensifies under climate change across tundra and savanna biomes.

Gillett NP et al. (2008). Attribution of polar warming to human influence. *Nature geoscience*, 1(11):750–754.

Graversen RG et al. (2008). Vertical structure of recent Arctic warming. *Nature*, 451(7174):53–58.

Graversen RG, Wang M (2009). Polar amplification in a coupled climate model with locked albedo. *Climate Dynamics*, 33(5):629–643.

Gunn A et al. (2009). Facing a Future of Change: Wild Migratory Caribou and Reindeer. *Arctic*, 62(3):iii–vi.

Gunn A (2015). IUCN Red List of Threatened Species: Rangifer tarandus. *IUCN Red List of Threatened Species*. (https://www.iucnredlist.org/en, accessed 25 September 2021).

Gustine D et al. (2017). Advancing the match-mismatch framework for large herbivores in the Arctic: Evaluating the evidence for a trophic mismatch in caribou. *PLOS ONE*, 12(2):e0171807.

Hansen AH et al. (2006). Long-Term Experimental Warming, Shading and Nutrient Addition Affect the Concentration of Phenolic Compounds in Arctic-Alpine Deciduous and Evergreen Dwarf Shrubs. *Oecologia*, 147(1):1–11.

Henry G, Molau U (1997). Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global change biology*, 3(S1):1–9.

Iler AM et al. (2013). Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Philosophical transactions. Biological sciences*, 368(1624):20120489-.

IPCC (2013). AR5 Climate Change 2013: The Physical Science Basis — IPCC. (https://www.ipcc.ch/report/ar5/wg1/, accessed 25 September 2021).

Jia GJ, Epstein HE, Walker DA (2003). Greening of arctic Alaska, 1981–2001. *Geophysical research letters*, 30(20):2067-n/a.

Joly K et al. (2003). Winter habitat use by female caribou in relation to wildland fires in interior Alaska. *Canadian journal of zoology*, 81(7):1192–1201.

Joly K et al. (2011). Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. *Ecography (Copenhagen)*, 34(2):345–352.

Joly K, Duffy PA, Rupp TS (2012). Simulating the effects of climate change on fire regimes in Arctic biomes: implications for caribou and moose habitat. *Ecosphere (Washington, D.C)*, 3(5):art36-18.

Joly K, Jandt RR, Klein DR (2009). Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. *Polar Research*, 28(3):433–442.

Ju J, Masek JG (2016). The vegetation greenness trend in Canada and US Alaska from 1984–2012 Landsat data. *Remote sensing of environment*, 176:1–16.

Kaarlejärvi E, Eskelinen A, Olofsson J (2017). Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nature communications*, 8(1):419–8.

Kremers KS, Hollister RD, Oberbauer SF (2015). Diminished response of arctic plants to warming over time. *PloS one*, 10(3):e0116586–e0116586.

Loe LE et al. (2016). Behavioral buffering of extreme weather events in a high‐Arctic herbivore. *Ecosphere (Washington, D.C)*, 7(6):n/a.

Mallory CD, Boyce MS (2018). Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environmental reviews*, 26(1):13–25.

Manseau M, Huot J, Crete M (1996). Effects of Summer Grazing by Caribou on Composition and Productivity of Vegetation: Community and Landscape Level. *The Journal of ecology*, 84(4):503–513.

Marion G et al. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global change biology*, 3(S1):20–32.

Mekonnen ZA et al. (2021). Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance. *Environmental research letters*, 16(5).

Messier F et al. (1988). Demography of the George River Caribou Herd: Evidence of Population Regulation by Forage Exploitation and Range Expansion. *Arctic*, 41(4):279–287.

Metcalfe DB et al. (2018). Patchy field sampling biases understanding of climate change impacts across the Arctic. *Nature ecology & evolution*, 2(9):1443–1448.

Molau U, Mølgaard P, ITEX (1996). *ITEX manual*. Cph., Danish Polar Center.

Musiani M et al. (2007). Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. *Molecular ecology*, 16(19):4149–4170.

Myers-Smith IH et al. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities.

Myers-Smith IH et al. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, 5(9):887–891.

Myers-Smith IH et al. (2019). Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change. *Ecological Monographs*, 89(2):e01351.

Overland JE et al. (2014). Future Arctic climate changes: Adaptation and mitigation time scales. *Earth’s future*, 2(2):68–74.

Pajunen AM, Oksanen J, Virtanen R (2011). Impact of shrub canopies on understorey vegetation in western Eurasian tundra: Impact of shrub canopies on understorey vegetation. *Journal of vegetation science*, 22(5):837–846.

Pithan F, Mauritsen T (2014). Arctic amplification dominated by temperature feedbacks in contemporary climate models. *Nature Geoscience*, 7(3):181–184.

Post E et al. (2009). Ecological Dynamics Across the Arctic Associated with Recent Climate Change. *Science*. (https://www-science-org.ezproxy.is.ed.ac.uk/doi/abs/10.1126/science.1173113, accessed 22 January 2022).

Post E (2013). Erosion of community diversity and stability by herbivore removal under warming. *Proceedings of the Royal Society. B, Biological sciences*, 280(1757):20122722-.

Post E et al. (2019). The polar regions in a 2°C warmer world. *Science advances*, 5(12):eaaw9883–eaaw9883.

Post E, Forchhammer MC (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1501):2367–2373.

Prevéy JS et al. (2019). Warming shortens flowering seasons of tundra plant communities.

Prevéy JS et al. (2021). The tundra phenology database: more than two decades of tundra phenology responses to climate change. *Arctic Science*:1–14.

Raynolds MK et al. (2012). A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. *Remote Sensing Letters*, 3(5):403–411.

Serreze MC, Barry RG (2011). Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change*, 77(1):85–96.

Severson JP et al. (2021). Spring phenology drives range shifts in a migratory Arctic ungulate with key implications for the future. *Global change biology*, 27(19):4546–4563.

Sharma S, Couturier S, Côté SD (2009). Impacts of climate change on the seasonal distribution of migratory caribou. *Global Change Biology*, 15(10):2549–2562.

Shindell D, Faluvegi G (2009). Climate response to regional radiative forcing during the twentieth century. *Nature Geoscience*, 2(4):294–300.

Stow DA et al. (2004). Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment*, 89(3):281–308.

Stroeve JC et al. (2012). The Arctic’s rapidly shrinking sea ice cover: a research synthesis. *Climatic Change*, 110(3–4):1005–1027.

Sturm M, Racine C, Tape K (2001). Increasing shrub abundance in the Arctic. *Nature*, 411(6837):546–547.

Tape K, Sturm M, Racine C (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global change biology*, 12(4):686–702.

Thompson DP, Barboza PS (2014). Nutritional implications of increased shrub cover for caribou (Rangifer tarandus) in the arctic. *Canadian Journal of Zoology*, 92(4):339–352.

Turunen M et al. (2009). Does climate change influence the availability and quality of reindeer forage plants? *Polar biology*, 32(6):813–832.

Vistnes I, Nellemann C (2008). The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biology*, 31(4):399–407.

Vors LS, Boyce MS (2009). Global declines of caribou and reindeer. *Global Change Biology*, 15(11):2626–2633.

Wal R van der (2006). Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, 114(1):177–186.

Walker MD et al. (2006). Plant Community Responses to Experimental Warming across the Tundra Biome. *Proceedings of the National Academy of Sciences - PNAS*, 103(5):1342–1346. (From the Cover).

Wang M, Overland JE (2009). A sea ice free summer Arctic within 30 years? *Geophysical research letters*, 36(7):L07502-n/a.

Winton M (2006). Amplified Arctic climate change: What does surface albedo feedback have to do with it? *Geophysical Research Letters*, 33(3). (http://onlinelibrary.wiley.com/doi/abs/10.1029/2005GL025244, accessed 20 January 2022).

Witter LA et al. (2012). Gauging climate change effects at local scales: weather-based indices to monitor insect harassment in caribou. *Ecological applications*, 22(6):1838–1851.

Wookey PA et al. (2009). Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global change biology*, 15(5):1153–1172.

Zalatan R, Gunn A, Henry GHR (2006). Long-term Abundance Patterns of Barren-ground Caribou Using Trampling Scars on Roots of Picea Mariana in the Northwest Territories, Canada. *Arctic, antarctic, and alpine research*, 38(4):624–630.