

Simulating the effects of climate change on fire regimes in Arctic biomes: implications for caribou and moose habitat

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Abstract. Wildfire is the primary ecological driver of succession in the boreal forest and may become increasingly important within tundra ecosystems as the Arctic warms. Migratory barren-ground caribou (*Rangifer tarandus granti*) rely heavily on terricolous lichens to sustain them through the winter months. Lichens preferred by caribou can take 50 or more years to recover after being consumed by wildfires. We simulated effects of climate change on the fire regime within the winter range of one of the largest caribou herds in the world, the Western Arctic Herd, to assess how their forage may be impacted. We forecast that the total area burned (AB) in the near term (2008–2053) will be 0–30% greater than during our historic reference period (1950–2007) depending on the climate model (CGCM3.1 or ECHAM5) considered. Further into the future (i.e., 2054–2099), we forecast AB to increase 25–53% more than during our reference period. In contrast to the entire study area, which contains both tundra and boreal forest habitats, we forecast that the amount of AB in tundra alone will increase (0–61%) in the near term. Simulated high-quality caribou winter range, as indexed by tundra and spruce habitat that had not burned in ≥ 50 years, decreased modestly (<6%) in the near term over the entire study area. Simulated changes were more dramatic within the herd's core winter range, with declines in high-quality caribou winter range approaching 30%. Conversely, moose habitat was projected to increase by 19–64% within the core winter range in the near term. The simulated declines in the quantity of core winter range in the future due to larger and more frequent fires could impact caribou abundance through decreased nutritional performance and/or apparent competition with moose. These impacts would likely be detrimental to the subsistence users that rely on this resource. Additionally, changes in the fire regime and decreases in caribou abundance could amplify feedback mechanisms, such as decreasing albedo, by facilitating shrub growth that may hasten climate-driven changes to the composition and structure of vegetation communities in the low Arctic.

Key words: *Alces*; ALFRESCO; climate change; fire management; lichens; *Rangifer*; vegetation succession model; Western Arctic Herd; wildfire.

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INTRODUCTION

Climate change impacts on the habitats of arctic land mammals are predicted to be severe (Lawler et al. 2009) and have already been implicated in the decline of caribou (*Rangifer tarandus*) populations across the Arctic (Vors and Boyce 2009). Mechanisms by which climate change may negatively impact caribou include deeper snows, increased incidence of icing (rain-on-snow) events, increased human disturbance, increased insect harassment, changes to habitat quality and quantity, and increased frequency of wildfire on winter ranges (Jefferies et al. 1992, Walsh et al. 1992, Griffith et al. 2002, Putkonen and Roe 2003, Johnson et al. 2005, Rupp et al. 2006, Tews et al. 2007, Joly et al. 2011). However, the effects of climate change on caribou populations are likely not uniform due to inherent complexities of the climate system (e.g., Zalatan 2008, Joly et al. 2011). For example, increased summer temperatures and longer growing seasons may prove to be nutritionally beneficial to caribou during the summer months (Jefferies et al. 1992, Griffith et al. 2002, Tews et al. 2007).

Tundra covers over 5,000,000 km² of the Arctic (Walker et al. 2005). Additionally, vast areas of tundra are interspersed with boreal forest in the tundra-boreal forest interface that stretches around the globe north of the continuous boreal forest biome (Callaghan et al. 2002). The effects of climate change are already apparent (IPCC 2007), especially in the Arctic (Callaghan et al. 2004). Mean annual temperatures have increased by 2–3°C in the region in recent decades, with larger increases apparent during the winter months (Stafford et al. 2000, Hinzman et al. 2005). Positive feedback mechanisms, including melting snow and sea ice, increasing shrubs, and greater prevalence of wildfires will likely amplify these changes via decreased albedo (Overpeck et al. 1997, Chapin et al. 2000, Qu and Hall 2006, Balshi et al. 2009, Euskirchen et al. 2009).

Climate warming in the Arctic could have several important consequences for the fire regime and caribou winter range. Increased area burned, in both boreal forest (Duffy et al. 2005, Balshi et al. 2009) and tundra (Joly et al. 2009b, Hu et al. 2010a), is associated with warmer and drier summers. Thus, it is predicted that fire will increase in both of these biomes under climate

warming scenarios (Callaghan et al. 2004, Flannigan et al. 2000, Higuera et al. 2008, Balshi et al. 2009). Wildfire is the dominant driver of change to ecosystem structure and function in the boreal forest (Payette 1992, Chapin et al. 2006) but wildfires are less frequent and smaller in the tundra biome where lichens represent a large portion of the biomass and species diversity (Wein 1976, Holt et al. 2006). However, the Seward Peninsula and Noatak River valley regions of Alaska (Fig. 1) exhibit greater fire frequency than other areas within the tundra biome (Racine et al. 1985, Racine et al. 2004, Joly et al. 2009b, Hu et al. 2010a). While lichens are highly flammable, greater fire frequency in these regions is likely due to climate conditions rather than lichen abundance because the Noatak region has lower lichen abundance than the Seward Peninsula, and graminoids provide fine fuels that increase the potential for reburning in tundra much sooner than feather mosses of the boreal forests (Cronan and Jandt 2008, Jandt et al. 2008, Joly et al. 2009b).

Wildfires destroy terricolous fruticose lichens, a staple of the winter diet of migratory caribou (Klein 1982, Bernhardt et al. 2011). Lichens are slow to recover after being burned, with primary caribou forage species (e.g., *Cladonia rangiferina*, *C. stellaris*) often taking several decades or more to return to pre-fire levels (Holt et al. 2008, Jandt et al. 2008, Klein and Shulski 2009, Joly et al. 2010, Collins et al. 2011). Caribou avoid burned areas in the boreal forest and tundra during the winter on a time scale coincident with lichen recovery rates (Joly et al. 2003, 2007a, 2010, Collins et al. 2011). Increases in fire frequency may limit the total available habitat for wintering caribou that is old enough to support high levels of preferred lichen species and tempers the argument that fire is not important to caribou because they can simply utilize alternative ranges (see review in Rupp et al. 2006). Further, Rupp et al.'s (2006) conclusions were likely conservative because they did not address the direct detrimental impacts climate change would have on lichens through warming and drying nor the indirect impacts on lichens by enhancing growing conditions for vascular plants such as shrubs and trees (see review by Joly et al. 2009a).

Warmer and longer growing seasons induced by climate change will likely degrade permafrost,

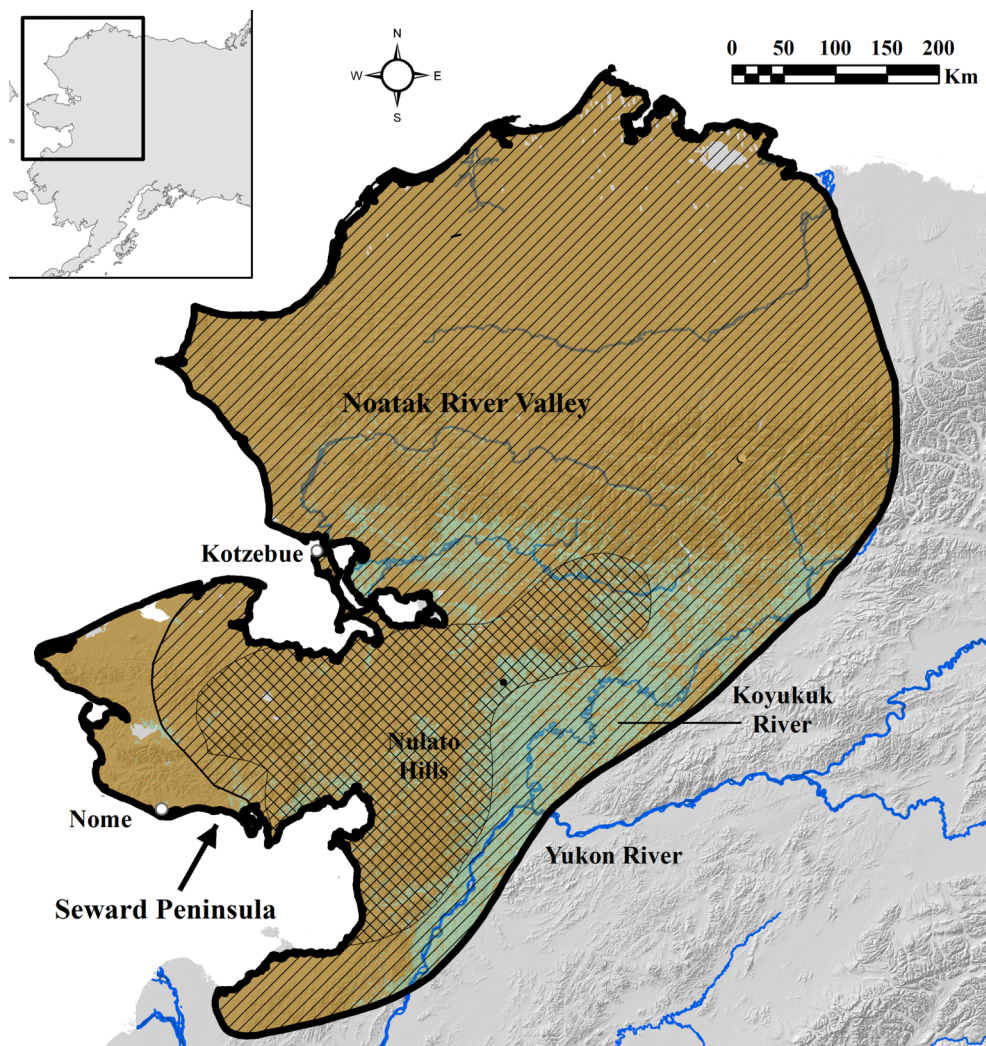


Fig. 1. Study area (outlined by thick black line) in northwest Alaska. Tundra-dominated areas are shaded brown and forest-dominated areas are in green. The range of the Western Arctic Caribou Herd is contained within the domain and is depicted with hatching, while the herd's core winter range is cross-hatched (courtesy of the Alaska Department of Fish and Game).

deepen the active layer (i.e., the top layer of soil that thaws during summer) and provide vascular plants a competitive advantage over lichens (Chapin et al. 1995, Walker et al. 2006). Increases in shrub abundance have already been detected in the sub-Arctic and Arctic (Sturm et al. 2001, Joly et al. 2007c, Forbes et al. 2010). Shrubs may further inhibit re-generation of lichens by trapping snow, increasing leaf litter, competing for resources, and closing the canopy (Joly et al., 2009a, Čabrájić et al. 2010).

Burn severity is an important factor that

determines the successional trajectory after a fire (Racine et al. 2004, Johnstone et al. 2010, Bernhardt et al. 2011). In more severe burns, stand self-replacement (e.g., birch [*Betula* spp.] forest returning to birch forest), which is common in Arctic ecosystems, is not automatic. An increase in shrubs, including fire-adapted dwarf birch (*Betula* spp.), relative to pre-fire conditions can follow fire, especially in moderate severity burns (de Groot and Wein 1999, Bret-Harte et al. 2001, Racine et al. 2004, Joly et al. 2010). This process could lead to an amplifying feedback

where more shrubs lead to increasingly severe fires (Higuera et al. 2009, Hu et al. 2010a, Xue et al. 2010). Similarly, greater burn severity in the boreal forest could alter the black spruce (*Picea mariana*) self-replacement trajectory by consuming semi-serotinous seeds and reducing organic layers which results in an early successional deciduous phase (Johnstone et al. 2010). This would also be disadvantageous for overwintering caribou as they avoid these habitat types (Joly et al. 2010, Collins et al. 2011, Joly 2011). Likewise, additional shrub cover, such as *Salix* spp., could attract herbivores associated with boreal forests, such as moose (*Alces alces*; Bryant and Reichardt 1992, Joly et al. 2010).

Unlike caribou in winter, moose select for areas with abundant early seral stage habitats (Weixelman et al. 1998, Maier et al. 2005). Thus, increased fire due to climate change may benefit this species. It has been hypothesized that more abundant moose may allow for increased wolf (*Canis lupus*) densities (i.e., a numeric response; James et al. 2004). Wolves are the main predator of caribou during winter months; thus, increases in moose densities associated with climate change-induced higher fire frequency may indirectly lead to increased caribou predation by wolves (Latham et al. 2011, Robinson et al. 2012). This would not impact neonatal survival of our study caribou herd, the Western Arctic Herd (WAH), as their calving ground is north of the Brooks Range and far (circa 150 km) from the existing tree line.

Our goals were to identify the impacts of climate change on the fire regime in tundra-dominated landscapes of northwest Alaska. Using our simulations, we projected the amount and quality of caribou winter range available under climate warming scenarios. Additionally, we quantified how the amount of preferred moose habitat changed because this may have additional indirect impacts on caribou. We hypothesized that the fire regime in northwest Alaska in the next 50–100 years would be more spatially extensive (i.e., greater area burned [AB]) as compared to the current (1950–2007) regime. We hypothesized that the potential increase in AB in northwest Alaska would lead to decreased quality and quantity of caribou winter range as determined by the amount of available habitat over 50 years old (Joly et al. 2010, Collins et al.

2011), and to an increase of high-quality moose habitat as indexed by the amount of 10 to 30-year old deciduous vegetation (Weixelman et al. 1998, Maier et al. 2005).

METHODS

Study area and wildlife

The study area is the range of the WAH and the entire Seward Peninsula of northwest Alaska (Fig. 1). The approximately 377,000 caribou in the WAH can be found distributed over some 360,000 km² (1.05 caribou/km²; Dau 2007). Overwintering caribou can be found throughout this range, though the areas of recent concentrated use have been in the Nulato Hills and Seward Peninsula (Joly et al. 2007a). While the region is dominated by arctic tundra, especially these areas of concentrated use, there are large expanses of tundra-boreal forest interface, boreal forest, alpine tundra, mountainous terrain and wetlands (Joly et al. 2010). Moose densities range from very low ($\sim 0.04/\text{km}^2$) in the northwest portion of the study area to very high ($\sim 3/\text{km}^2$) in southeast, but are low ($\sim 0.12/\text{km}^2$) over much of the study area (Alaska Department of Fish and Game [ADFG] 2008). The higher densities of moose correspond with expansive riparian complexes formed by the confluence of the large Yukon and Koyukuk Rivers.

Alaska Frame-Based Ecosystem Code (ALFRESCO)

The planet's climate system is inherently complex, including how the climate impacts fire and vegetation at a local-scale. We used Alaska Frame-Based Ecosystem Code (ALFRESCO) to explore the interactions and feedbacks among fire, climate, vegetation, and caribou and moose habitat in northwest Alaska. ALFRESCO is a spatially-explicit cellular automata model that simulates fire and vegetation successional dynamics in Alaska at a 1-km spatial resolution on a 1-year time step (Rupp et al. 2002). For the first time, we modified the model to incorporate the tundra habitats of northwest Alaska (see Vegetation section below). ALFRESCO models the relationship between climate (i.e., monthly average temperature and total precipitation) and total annual area burned (i.e., the areal extent of fire on the landscape) rather than explicitly modeling fire behavior. We used a generalized

boosting model (GBM) similar to that used by Hu et al. (2010b) to determine the effect of climate on the likelihood of cell ignition.

Annual fire occurrence, driven by climate, vegetation type and time since last fire, was simulated stochastically (Rupp et al. 2000b). The ignition of any given cell (pixel) is determined by comparing a randomly generated number against the flammability value of that cell. Fire may spread from an ignited cell to any of its eight surrounding first-order neighbor cells. The burn algorithm in ALFRESCO employs a recursive cellular automaton approach, so fire spread depends on the flammability of cells in the first-order neighborhood and any effects of natural firebreaks including non-vegetated mountain slopes and large water bodies, which do not burn. The flammability coefficient is tied to vegetation type, so ALFRESCO allows for changes in flammability that occur through succession (Chapin et al. 2003). There are different fire regimes for different ecoregions (Joly et al. 2009b), therefore we subdivided our study area into 4 subregions (Interior, Seward Peninsula, North Slope and Yukon Lowlands) and assigned each a different relative flammability and probability of ignition. These values were determined by comparing model output to observed data during the calibration phase. Additional information regarding ALFRESCO can be found in Rupp et al. 2000a, 2000b, 2002, 2006.

Vegetation

Our version of ALFRESCO reclassified the 2001 National Land Cover Database (NLCD; www.mrlc.gov; accessed 15 December 2011) vegetation classification into three vegetation types: tundra, spruce, and deciduous vegetation. We categorized non-vegetated, non-flammable NLCD cover types (e.g., open water, perennial ice) as non-vegetated. Our tundra class contained dwarf scrub, grassland, sedge, lichen and moss NLCD cover types. We categorized NLCD evergreen forests and woody wetlands (spruce bogs) as our spruce class. Our deciduous class contained NLCD deciduous and mixed forests categories. The shrub/scrub NLCD class was classified as either tundra or deciduous based on elevation, aspect and growing season temperature. White and black spruce have been differentiated using this technique in previous work

(Rupp et al. 2002), but they were combined for our simulations. Succession, occurring as either a transition from deciduous or spruce forest to early successional deciduous vegetation or the self-replacement of tundra (see Discussion), is initiated exclusively by fire (Rupp et al. 2000b). Conceptually, the deciduous vegetation type is an early successional stage of spruce forest. An exception to this successional trajectory can occur when repeated burning and/or climatic conditions preclude the transition from deciduous to spruce (Rupp et al. 2000a). We based transitional ages for deciduous to spruce succession from existing literature (Fig. 2; Viereck et al. 1986, van Cleve et al. 1991, Rupp et al. 2006, Kurkowski et al. 2008) and observational data from the Joint Fire Science Program (JFSP; Duffy 2006). Following fire in the boreal forest, flammability is low and stays low for several decades (Racine et al. 1985, 2004, Jandt et al. 2008, Joly et al. 2010). Vascular tundra vegetation quickly re-sprouts after a fire and can be difficult to differentiate from nearby unburned tundra, with the exception of the absence of caribou forage lichens, after just a couple of years (Racine et al. 1985, 2004, Jandt et al. 2008, Joly et al. 2010). Thus, in a departure from previous modelling efforts, we developed a novel, separate function for the flammability of tundra over time which reflects the speed with which fine fuels accumulate within the tundra (Fig. 2). Successional transitions were determined stochastically in ALFRESCO (Rupp et al. 2002).

Climate data

We employed the spatially explicit, global, gridded (0.5 degree by 0.5 degree) data provided by the Climatic Research Unit (CRU; Mitchell and Jones 2005; http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_1256223773328276, accessed 15 December 2011). We extracted our study area (Fig. 1) from this comprehensive dataset for the period 1901–2000. The dataset is comprised of the monthly averages for temperature and precipitation. We down-scaled by computing the differences between monthly CRU data and corresponding calculated monthly CRU climate normals (“deltas”) for 1961–1990 (Hay et al. 2000) using natural neighbor to 2 km² resolution and then added PRISM (Parameter-elevation Regression on Independent Slopes

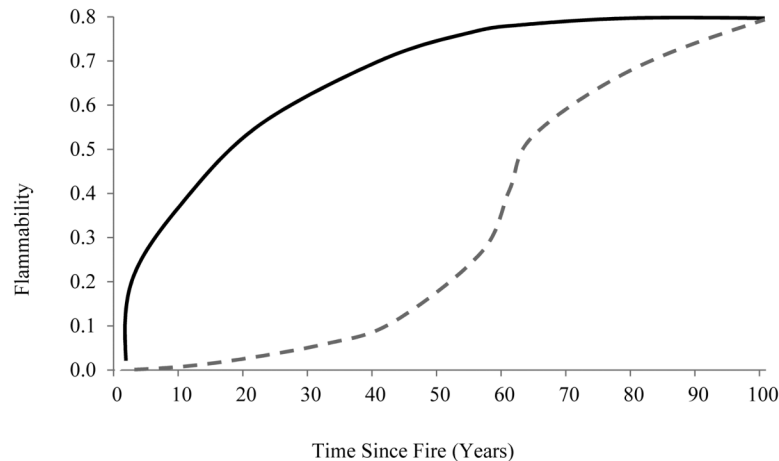


Fig. 2. Modeled flammability of pixels as a function of time since fire in northwest Alaska (boreal forest depicted with a dotted gray line and tundra with a solid black line).

Model; <http://www.prism.oregonstate.edu/>, accessed 15 December 2011) climate normals. PRISM pixels were further interpolated to 1 km² using ArcGIS (Environmental Systems Research Institute, Redlands, California, USA) nearest neighbor re-sampling.

Fire and fire sizes

The amount of AB annually in Alaska is strongly correlated with monthly weather (average temperature and total precipitation; Duffy et al. 2005, Joly et al. 2009b). We developed a GBM to quantify the impact of monthly temperature and precipitation variables on annual area burned for our study region. The GBM is a non-spatial statistical model with annual AB as the response and the corresponding year's monthly temperature and precipitation values as the explanatory variables. The utility of the GBM in this context is to provide a quantitative framework to inform the generation of spatially-explicit maps of flammability that account for the variation of temperature and precipitation across the simulation domain. The spatially-explicit maps of temperature and precipitation come from the PRISM downscaling of both CRU and Global Circulation Model (GCM)-based future climate scenarios. Quantifying the linkage between annual AB and monthly climate variables using this non-spatial approach is appropriate for large spatial domains where the climate signals conducive to fire are almost always sufficiently

accompanied by lightning ignitions (Duffy 2006). The climate-fire relationship quantified by this point model was then used as a proxy for quantifying the relative flammability of pixels in spatially-explicit maps of annual landscape flammability. The climate-fire relationship is different for tundra and forest vegetation types; hence we used a different GBM-based functional linkage between climate and flammability for tundra and forest vegetation.

In order to calibrate our model we iteratively compared existing empirical data (1950–2007) to our simulated output for the same time period. For our empirical fire perimeter data, we employed a spatially-explicit historical database maintained by the Alaska Fire Service (<http://fire.ak.blm.gov/>; accessed 15 December 2011). Estimates of AB based on these perimeters are presumed to be over-estimates due to the existence of unburned inclusions within fire perimeters (Duffy 2006). Previous research has shown that the proportional size of inclusions increases with total fire size and fires >2000 ha have approximately 5% inclusions (Eberhart and Woodard 1987). Comparable data do not exist for tundra ecosystems so we applied this factor to our analyses for northwest Alaska. The relative proportion of AB by fires of a given size is an important characteristic of fire distribution (Duffy 2006). Our analysis of the historical database for our study area revealed that most fires are small (<1000 ha) but the majority (>56%) of the

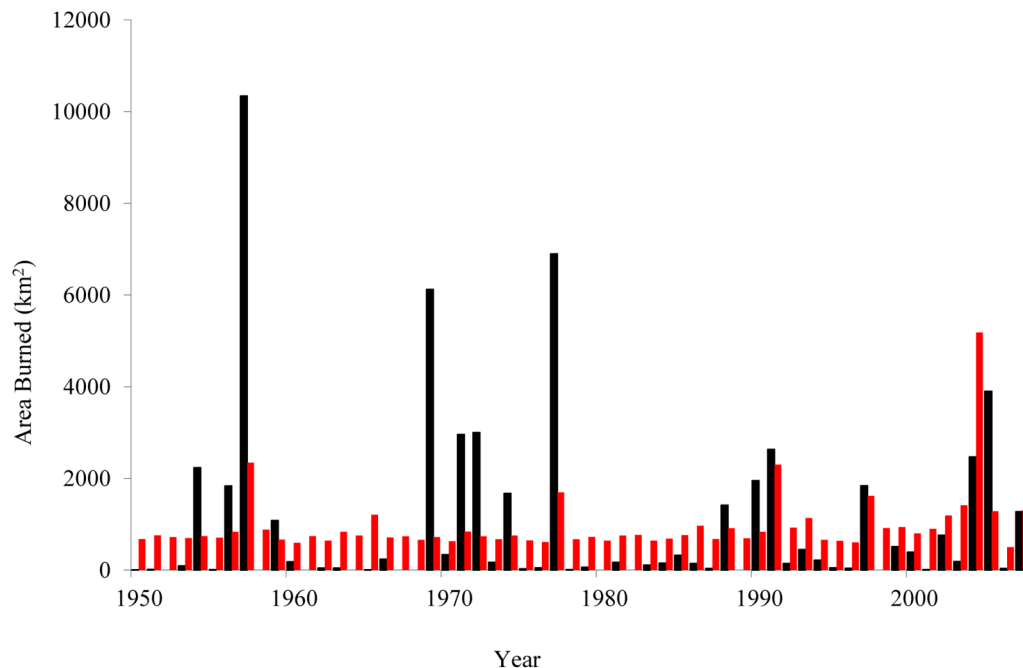


Fig. 3. A comparison of annual area burned (km^2) between observed (black bars) and the mean of 50 simulated ALFRESCO runs (red bars) for the entire study area, northwest Alaska, 1950–2007.

area burned comes from a small percentage (<5%) of fires that are much larger (>40,000 ha) than the rest. Our findings for northwest Alaska are similar to analyses conducted within the Interior region of Alaska (Kasischke et al. 2006). Therefore we focused our comparisons between historical and simulated fire size on the upper tail of the size distribution because the majority of the area burned occurs due to relatively few but large fires.

Model spin-up and validation

We developed 50 randomly-generated initial stand age/vegetation maps by running ALFRESCO for 400 years retrospectively to approximate ecologically-realistic initial conditions (2007) with respect to the current distribution and composition of vegetation (Duffy 2006). This time period is approximately twice the duration of the longest reported fire return interval in interior Alaska (Yarie 1981, van Cleve et al. 1991, Chapin et al. 2003). We assembled historical climate data for the model spin-ups consistent with Barber et al. (2004). We conducted 50 different simulations from 1860–1949 using these initial age/vegetation maps and then subjected

them to burning from 1950–2007, for comparison to historic, observed fire perimeter data, using the GBM-based flammability maps derived from the historical fire-climate relationship. This process resulted in the generation of a final spin-up consisting of 50 different stand-age maps across northwest Alaska (Duffy 2006). The spin-up phase therefore provided initial conditions with realistic patch size and age-class distributions generated over multiple fire cycles that are used as input for simulations run into the future. We compared the simulated and empirical annual AB from 1950–2007 for each of the 50 simulations generated by ALFRESCO (Fig. 3). We used simple linear regression to assess the relationship between the average annual AB from the 50 simulations to the historical data from 1950–2007. We selected the 5 most representative runs to seed the spin-ups for the 50 future simulations based on vegetation type and ratios between modeled and observed data for AB for the years 2004 and 2005; years with climatic conditions that facilitated unrealistically large modeled fires which could propagate landscape-level impacts throughout the simulation period. In other words, we chose runs that were most likely not

to exhibit unrealistically large AB in warm, dry years. The most representative runs were also selected because they most closely represent realistic depictions of the current landscape based on observed fire activity. Among the stochasticity that is driven by random ignitions, burning, and patterns of vegetation succession, these maps best represented the landscape at the starting point (2007) for the future runs.

Projections with future climate scenarios We simulated AB 92 years into the future (i.e., 2008–2099). This allowed us to compare the 58-year historic period (1950–2007), for which we have empirical data, to the next two similar length (46-year) periods of 2008–2053 and 2054–2099. From the best performing GCMs for Alaska, as determined by an analysis of 15 GCMs (Walsh et al. 2008), we selected the ECHAM5 (high-end warming) and CGCM3.1 (low-end warming) GCMs and imposed the intermediate A1B emissions scenario (Nakicenovic et al. 2000, IPCC 2007) to provide a range that captures potentially high and conservative forecasts, respectively, for future climatically-driven fire activity (Walsh et al. 2008, Balshi et al. 2009).

Analyses We calculated annual AB for the entire study area, as well as for both the tundra and boreal forest ecoregions separately, for the 3 time periods (1950–2007, 2008–2053, and 2054–2099) using R programming language scripts (R Foundation for Statistical Computing, Vienna, Austria, www.R-project.org). Similarly, we calculated the areal extent of habitat in (1) deciduous stands 10–30 years old and (2) tundra and spruce forest ≥ 50 years old. WAH caribou utilize both tundra and boreal forest habitats during winter (Joly et al. 2007a, Joly 2011). We also calculated these extents for just the herd's core winter range (Fig. 1).

RESULTS

Mean AB from our 50 ALFRESCO simulations was significantly correlated with historical, empirical data from 1950–2007 ($F = 13.19$, $P < 0.001$, $DF = 56$, $r^2 = 0.191$). While the empirical and simulated AB means were very similar (977 versus 953 km² per year, respectively), annual variability was much greater for the historical than the modeled data ($SE = 251$ versus 89, respectively). The historical data had an AB

range of 0–10345 km², whereas the modeled output was 501–5183 km². Our attempts to restrain mean AB to historic levels came at the expense of conservative maximum AB and lower variability in the simulated data. We found that allowing the variability of simulated data to approach the actual data allowed for unrealistic maximum AB in warm years (e.g., 2005). Our model presents a compromise between realistic, yet conservative, maximum AB and variability. While the one-to-one relationship between actual and modeled mean AB was not strong, several other metrics (e.g., cumulative area burned over time, maximum fire size, and mean AB of tundra) indicated that the mean tendency of our model output performed relatively well (Figs. 4–6). The strength of the correlation between each of the 50 runs to the empirical, observed data was variable (mean $r^2 = 0.092$, range = 0.001–0.372).

The average annual AB within the study area from 1950–2007 was 953 ± 89 km² (mean, SE). Our projections reveal that within the near term (2008–2053) annual AB would increase (to 1235 ± 154 km²) under the ECHAM5 GCM, but not for the CGCM3.1 (924 ± 110 km²). Total annual AB was projected to continue to increase for both CGCM3.1 (1188 ± 110 km²) and ECHAM5 (1460 ± 154 km²) in the 2054–2099 time period. These increases in AB incorporate the fire- and succession-induced changes in flammability through time.

Tundra comprised 73% of the study area; this proportion did not change throughout the study period because our model assumed burned tundra was self-replacing and did not incorporate treeline or successional changes. We did, however, allow the probability of tundra burning to vary as a function of time since last fire due to vegetation-induced changes in flammability (Fig. 2). We projected increases in the amount of tundra AB using CGCM3.1 in the latter half of the century (2054–2099; 52%), but not the near term (Fig. 7). In using ECHAM5, the amount of tundra AB increased by 61% during the near term and more than doubled in the 2054–2099 time period (Fig. 7).

The projected annual AB of spruce showed only modest increases over the coming century for either climate scenario (Table 1). However, the total amount of spruce on the landscape was

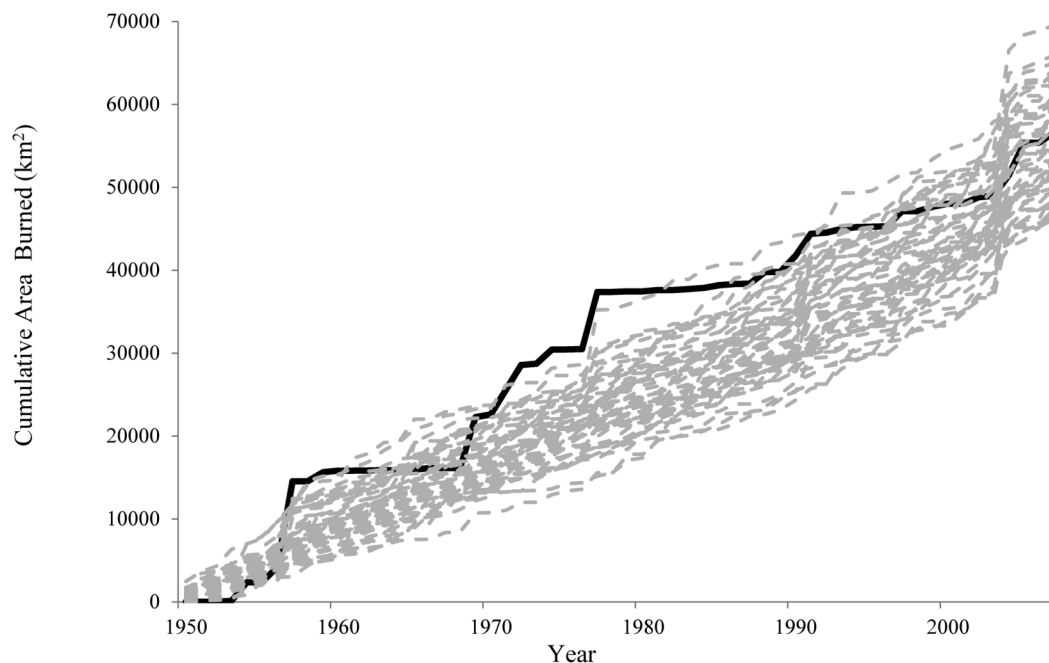


Fig. 4. Cumulative area burned (sum) as a performance metric comparing simulated (gray; $n = 50$) and historic-empirical (black line) wildfire data for the entire study area, northwest Alaska, 1950–2007.

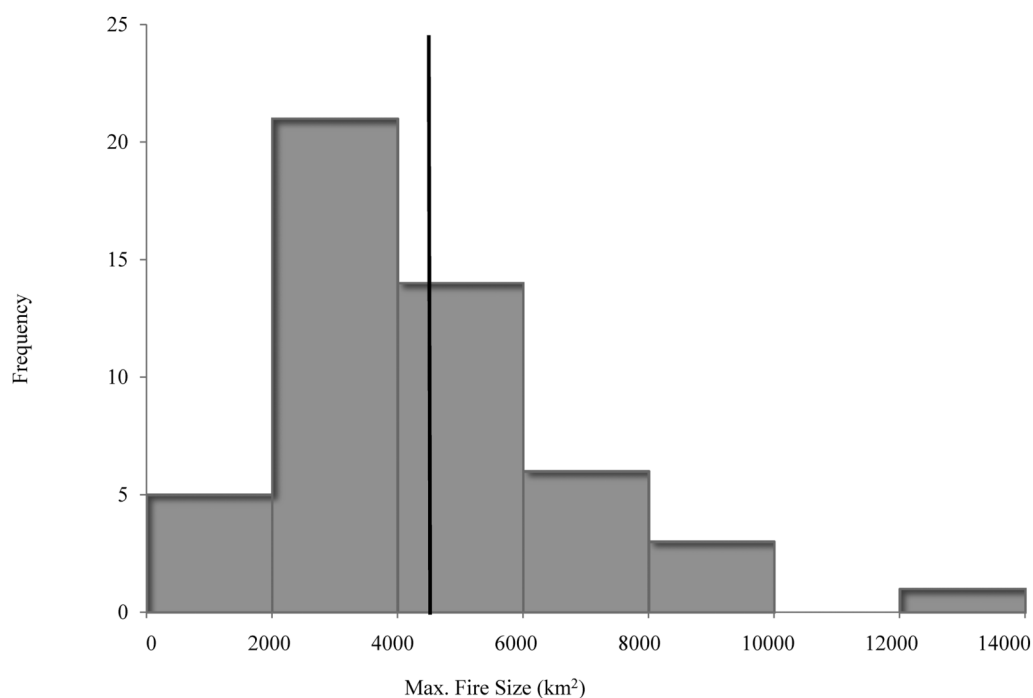


Fig. 5. Maximum fire size (areal extent) as a performance metric comparing simulated (gray; $n = 50$) and historic-empirical (black line) wildfire data for the entire study area, northwest Alaska, 1950–2007.

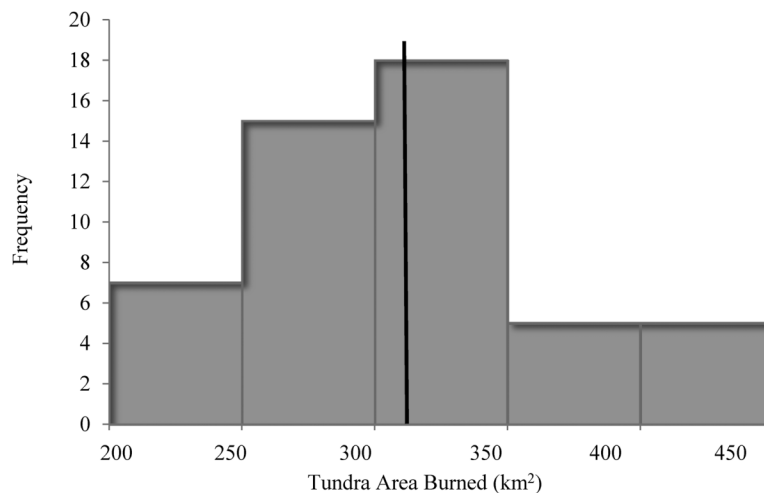


Fig. 6. Mean area burned of tundra as a performance metric comparing simulated (gray; $n = 50$) and historic-empirical (black line) wildfire data for the entire study area, northwest Alaska, 1950–2007.

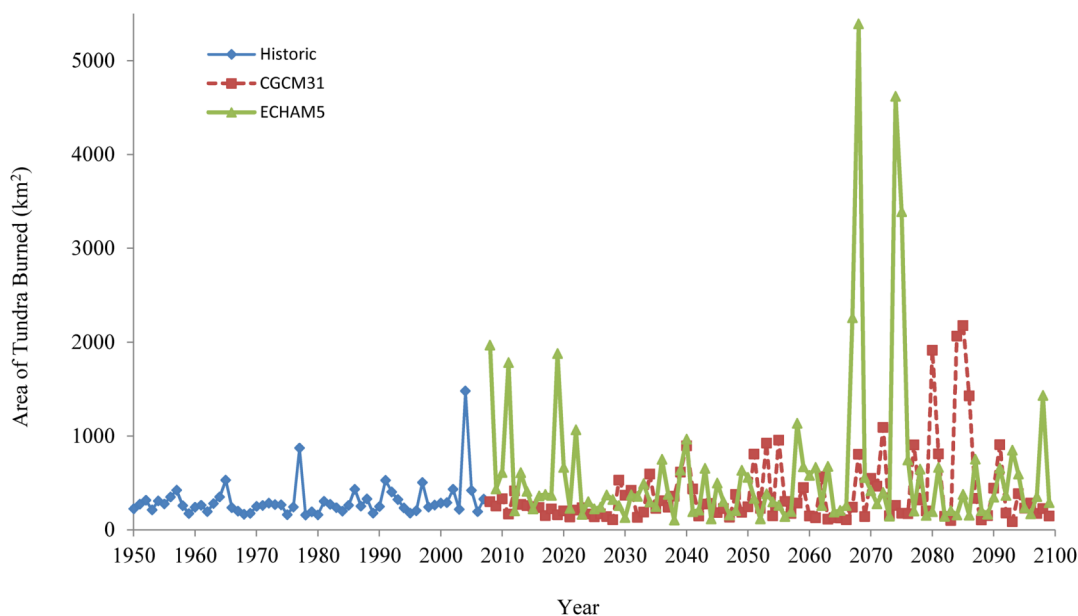


Fig. 7. Amount of tundra burned (km^2) in the entire study area, northwest Alaska, for the simulated historic reference period (1950–2007; thin solid blue line with diamond markers) and future projections using ECHAM5 (thick solid green line with triangle markers) and CGCM3.1 (dotted red line with square markers) general circulation models (GCMs) under the A1B emissions scenario.

predicted to decline substantially throughout the remainder of the century (Table 1). This result is due to conversion of spruce to deciduous forest (see *Discussion*).

AB in deciduous stands during the historic period was only $54 \pm 9 \text{ km}^2$. Using CGCM3.1,

substantial increases were detected for 2054–2099 ($98 \pm 10 \text{ km}^2$) but not the near term ($64 \pm 10 \text{ km}^2$). ECHAM5 projections revealed substantial increases in deciduous AB from 2008–2053 ($85 \pm 9 \text{ km}^2$) and 2054–2099 ($110 \pm 9 \text{ km}^2$). The total amount of deciduous forest was projected to

Table 1. Total area (km²) and area burned (mean $\pm$ SE) of various vegetation types (spruce forest, deciduous forest, tundra) in the study area, northwest Alaska, for the simulated historic record and using two climate scenarios to project into the future. Tundra was self-replacing in our model, thus its total remained unchanged.

Metric	Historic 1950–2007	CGCM3.1 2008–2053	CGCM3.1 2054–2099	ECHAM5 2008–2053	ECHAM5 2054–2099
A) Spruce					
Total area	54167 $\pm$ 156	47366 $\pm$ 175	42064 $\pm$ 175	42880 $\pm$ 227	37674 $\pm$ 227
Area burned	593 $\pm$ 54	559 $\pm$ 61	624 $\pm$ 61	656 $\pm$ 59	621 $\pm$ 59
B) Deciduous					
Total area	48643 $\pm$ 156	55444 $\pm$ 175	60746 $\pm$ 175	59930 $\pm$ 227	65136 $\pm$ 227
Area burned	54 $\pm$ 9	64 $\pm$ 10	98 $\pm$ 10	85 $\pm$ 9	110 $\pm$ 9
C) Tundra					
Total area	278544	278544	278544	278544	278544
Area burned	306 $\pm$ 44	301 $\pm$ 49	465 $\pm$ 49	493 $\pm$ 109	728 $\pm$ 109

increase substantially from the historic period (48643 $\pm$ 156 km²) for both future time periods (55444 $\pm$ 175 km² and 60746 $\pm$ 175 km², respectively) under CGCM3.1. ECHAM5 projected increases were also substantial for both time periods (59930 $\pm$ 227 km² and 65136 $\pm$ 227 km², respectively).

Potential high quality (≥ 50 years post-fire) tundra and spruce caribou winter range comprised 84% of the study area in 2007. This area was projected to decline to 82% during the near term and again to 79% during the 2054–2099 period using CGCM3.1. Larger declines were projected using ECHAM5 (79% for 2008–2053 and 75% for 2054–2099).

Quality moose habitat, expressed as deciduous cover types 10–30 years old in the simulations, during the historic period averaged 11045 $\pm$ 268 km². Using CGCM3.1, moose habitat was projected to increase in the near term (13606 $\pm$ 301 km²) and the 2054–2099 time period (14475 $\pm$ 301 km²) compared to the historic period. ECHAM5 projected an even larger (47%) increase (16247 $\pm$ 248 km²) in the near term. While lower than the near-term time period, the amount of quality moose habitat was projected to be substantially greater from 2054–2099 (14619 $\pm$ 248 km²) than during the historic period.

Amount of AB, caribou winter range, and moose habitat within the WAH's core winter range (Fig. 1) showed trends that were similar to those in the entire winter range (i.e., study area). AB within the core winter range was projected to substantially increase under the ECHAM5 in the near term (490 $\pm$ 82 km²) and for both CGCM3.1 and ECHAM5 scenarios (476 $\pm$ 52 km², 531 $\pm$ 82

km², respectively) towards the end of the century (2054–2099) as compared to the reference period (281 $\pm$ 46 km²), but not for CGCM3.1 in the near term (301 $\pm$ 52 km²). The substantial declines (15–29%) in simulated high-quality caribou winter range ≥ 50 years old were more dramatic within the herd's core winter range (Fig. 8). Simulated quality moose habitat increased substantially in the near term within the core winter range under both CGCM3.1 (2415 $\pm$ 39 km²) and ECHAM5 (3346 $\pm$ 69 km²) scenarios as compared to the reference period (2038 $\pm$ 35 km²).

DISCUSSION

Overwintering caribou that incur the energetic expenses of migration and predation, such as the WAH, utilize lichens as their major food source (Klein 1982, Russell et al. 1993, Joly et al. 2007b). They are a critical source of carbohydrates that help these caribou survive winter until emergent forage appears in the spring (Person et al. 1980, Parker et al. 2005). Unfavorable nutritional status can reduce growth, compromise in utero development of fetuses, and have multiplier effects (i.e., large impacts, ranging out to the population level, from relatively small changes in forage quality; White 1983, Parker et al. 2005). In tundra and boreal forest, caribou forage lichens can take 50–80 years or more to return to previous abundance following wildfire (Holt et al. 2006, Joly et al. 2010, Collins et al. 2011). Thus, declines in winter forage, induced by climate change and increased wildfire, could lead to lowered nutritional status of individual animals that can translate into population-level impacts.

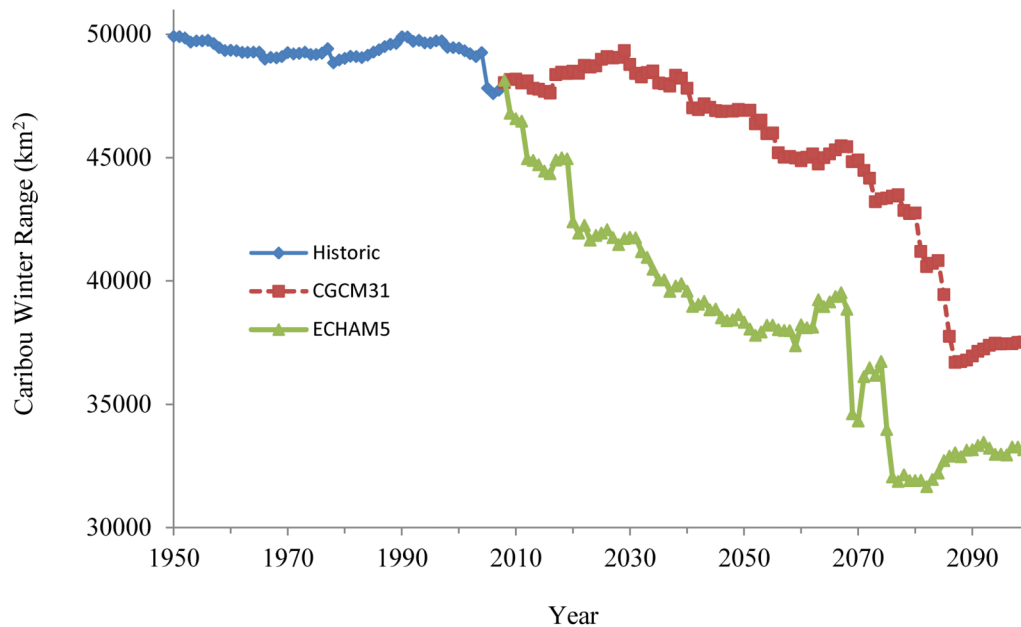


Fig. 8. Projected changes in areal extent of quality caribou winter range (>50 years of age) solely within the core winter range of the Western Arctic Herd, northwest Alaska. The simulated historic reference period (1950–2007) is depicted with a thin solid blue line with diamond markers and future projections using ECHAM5 with a thick solid green line with triangle markers (lower line) and CGCM3.1 with a dotted red line with square markers (upper line). These general circulation models (GCMs) employed the A1B emissions scenario.

We project that the combination of more burning in tundra and less overall spruce habitat should lead to modest (2–6%) reductions in the areal extent of quality caribou winter range, as indexed by tundra and spruce habitat >50 years old, in the near term. The declines were only slightly greater for the latter half of the century (2054–2099; 5–10%). The declines were more dramatic within the herd's core winter range (e.g., 15–30% of >50 year old habitat by the latter half of the century, Fig. 8). At the current population size, reductions in the quantity of high-quality winter range of this magnitude within and adjacent to the herd's core winter range could limit the ability of WAH caribou to find alternative lichen-rich winter ranges. This would make mute the argument that fire is not a key factor for caribou population dynamics because caribou can just seek out and discover new, alternative, high-quality winter ranges. The projected levels of burning will also limit the amount of habitat to reach an age where mosses have the potential to out-compete lichens, as some have argued (see Coxson and Marsh 2001).

Smaller herd and group sizes, changes in range use, increased dispersal, and diminished reproductive output are all potential consequences of decreased habitat quality and quantity.

Our simulations project that the amount of AB in northwest Alaska could increase by up to 30% in the near term (2008–2053), as compared to our reference period (1950–2007), using an intermediate-level emissions scenario (A1B). This region is dominated by tundra, which we project will see proportionately greater (0–61%) increases in AB in the near term. We forecast that these relatively modest increases in AB will continue towards the end of the century (2054–2099). While the quicker rebuilding of fuels in tundra plays a role in our projections for greater proportions of tundra burning in the future, our simulations project that the amount of AB in spruce habitats in northwest Alaska will only modestly increase during the upcoming century. This projection seemingly runs contrary to predictions for Interior Alaska (e.g., Balshi et al. 2009). However, our simulations also project that the amount of spruce on the landscape will

decline substantially, thus the proportion of spruce on the landscape that will burn is actually forecasted to increase in our simulations. The declines in spruce abundance we forecast are in line with other recent projections that predict major biome shifts within Alaska during the coming century (e.g., Gonzalez et al. 2010, Beck et al. 2011). However, spruce should be able to expand into tundra habitats as permafrost thaws and active layers deepen (Lloyd et al. 2003). Disturbance by caribou may also facilitate the expansion of spruce by exposing mineral soils (Tremblay and Boudreau 2011). Our model is not currently calibrated to allow for this transition and thus less spruce is predicted on the landscape. Further, less forecasted burning in the latter half of the century is likely a consequence of increased burns in the earlier half of the century leaving early seral stage spruce habitats that are less vulnerable to subsequent burning across the landscape. In other words, fuel loads are removed during fire events and, within spruce forests, these fuels can take decades to return to pre-fire levels.

Our simulations project that the total amount and AB of deciduous habitat will increase substantially, at the expense of spruce habitat, throughout the remainder of the century. Consistent with these forecasts, we projected large increases (19–64%) in high-quality moose habitat in the near term within the WAH's core winter range, which should facilitate increases in moose abundance there (Weixelman et al. 1998, Maier et al. 2005). In an example of apparent competition (Holt 1984), resident moose populations on or adjacent to caribou winter range may facilitate increased wolf abundance and therefore the potential for increased wolf predation on caribou (James et al. 2004). Fires may reduce spatial separation between caribou and wolves, which could also lead to higher predation rates (Robinson et al. 2012). Caribou are easier for wolves to take than moose due to their much smaller size. Latham et al. (2011) documented increases in wolf abundance and caribou predation in Alberta where deer (*Odocoileus* spp.) densities greatly expanded due to more development-induced early seral habitats. If increased fire did promote moose abundance and hence wolf predation on caribou, it would be a novel example of an indirect, detrimental impact of climate change on

caribou population dynamics. The impact of this potential relationship would be greater if the WAH experiences large population declines. Further, numerous interior Alaska herds that are already small (<2000 caribou) may be most at risk if wolf populations increase, because low-density caribou populations are thought to be more vulnerable to predation (e.g., Dale et al. 1994).

Wildfire is difficult to accurately model within the tundra and tundra-forest interface (Balshi et al. 2009, this study). We found that compromises had to be made among maximum, mean, and variability of AB to achieve realistic simulations. One important virtue of modelling efforts is that they are highly effective at identifying knowledge gaps. In order to reduce model uncertainty in the future, we suggest that subsequent efforts develop parameters for multiple tundra types (e.g., lowland wet sedge tundra, upland dwarf shrub tundra), incorporate impacts from treeline advance and herbivory, and develop more detailed successional pathways that incorporate the potential for increasing shrub abundance. Moreover, developing models that differentiate years with little to no wildfire and those with substantial wildfire should alleviate some of the difficulties we had with balancing inter-annual variability with mean AB. On a practical side, the paucity of climate stations in the Arctic, especially inland, is a serious concern and should be addressed by incorporating new stations into the existing system. In addition, given the vast expanses of tundra in Russia and Canada, we suggest future modelling efforts analyze the impacts of climate change on tundra fire regimes in these regions.

CONCLUSION

Climate change is predicted to impact caribou in many ways. Decreased forage accessibility during winter, either from icing or increased snow depths, may have a stronger impact than increased summer forage biomass (Tews et al. 2007). Although wildfires occur during the summer, they negatively impact caribou winter range, which will only exacerbate forage accessibility issues. Tundra has potential to re-burn much more quickly than boreal forests, so warmer summer conditions could lead to addi-

tional fires (Joly et al. 2009b). Increased warming and burning will also likely facilitate increases in the abundance of shrubs and trees in the tundra (Rupp et al. 2000a, Sturm et al. 2001, Joly et al. 2009a, Forbes et al. 2010, Beck et al. 2011) and thus increase the extent and severity of fires (Higuera et al. 2009, Hu et al. 2010a). Since our models did not account for potentially substantial amounts of tundra being converted or the direct, negative impacts of warmer and drier conditions on lichen growth, and that forage lichens can take longer than 50 years to recover post-fire in some areas, we believe that our results are likely an underestimate of potential changes. Due to edaphic conditions, barriers, time lags and other factors, we do not expect vast expanses of tundra being converted to forests during our study period (i.e., the next 100 years), though larger changes should be expected in the tundra-shrub transition zone (Rupp et al. 2000a, Rupp et al. 2001, Chapin et al. 2005, Lloyd 2005).

The amount of increased wildfire on caribou winter ranges we simulated may intensify discussions of the need for fire suppression/management plans for conservation. These plans should incorporate traditional ecological knowledge, co-management input, and logistical realities (Beverly and Qamanirjuaq Caribou Management Board 1994, Urquhart 1996, Klein et al. 1999), as well as scientific information, including our results, and the needs of other species of interest. These plans will likely have to be tailored to individual herds and updated regularly to take into account rapidly changing conditions. For the WAH, our forecasts for modest increases in AB over the herd's entire range suggest that any fire suppression efforts be focused on its core winter range. Expansion of moose range in Alaska and other northern regions may prove to be a conservation boon as this species faces drastic climate change-related declines in more southerly latitudes (e.g., Rempel 2011).

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LITERATURE CITED

- Alaska Department of Fish and Game. 2008. Moose management report of survey-inventory activities 1 July 2005–30 June 2007. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- Balshi, M. S., A. D. McGuire, P. D. Duffy, M. Flannigan, J. Walsh, and J. Melillo. 2009. Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. *Global Change Biology* 15:578–600.
- Barber, V. A., G. P. Juday, B. P. Finney, and M. Wilmking. 2004. Reconstruction of summer temperatures in interior Alaska from tree-ring proxies: evidence for changing synoptic climate regimes. *Climatic Change* 63:91–120.
- Beck, P. S. A., G. P. Juday, C. Alix, V. A. Barber, S. E. Winslow, E. E. Sousa, P. Heiser, J. D. Herriges, and S. J. Goetz. 2011. Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters* 14:373–379.
- Bernhardt, E. L., T. N. Hollingsworth, and F. S. Chapin III. 2011. Fire severity mediates climate-driven shifts in understory community composition of black spruce stands of interior Alaska. *Journal of Vegetation Science* 22:32–44.
- Beverly and Qamanirjuaq Caribou Management Board. 1994. A review of the fire management on forested range of the Beverly and Qamanirjuaq Herd of caribou. Technical Report 1:1–64.
- Bret-Harte, M. S., G. R. Shaver, J. P. Zoerner, J. F. Johnstone, J. L. Wagner, A. S. Chavez, R. F. Gunkelman, S. C. Lippert, and J. A. Laundre. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32.
- Bryant, J. P. and P. B. Reichardt. 1992. Controls over secondary metabolite production by arctic woody plants. Pages 377–390 in F. S. Chapin III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. *Arctic ecosystems in a changing climate: an ecophysiological perspective*. Academic

- Press, San Diego, California.
- Čabraljić, A. V. J., J. Moen, and K. Palmqvist. 2010. Predicting growth of mat-forming lichens on a landscape scale: comparing models with different complexities. *Ecography* 33:949–960.
- Callaghan, T. V., B. R. Werkman, and M. M. Crawford. 2002. The tundra-taiga interface and its dynamics: concepts and applications. *Ambio* 12:6–14.
- Callaghan, T. V., et al. 2004. Key findings and extended summaries. *Ambio* 33:386–392.
- Chapin, F. S., III, W. Eugster, J. P. McFadden, A. H. Lynch, and D. A. Walker. 2000. Summer differences among Arctic ecosystems in regional climate forcing. *Journal of Climate* 13:2002–2010.
- Chapin, F. S., III, T. S. Rupp, A. M. Starfield, L. DeWilde, E. S. Zavaleta, N. Fresco, J. Henkelman, and A. D. McGuire. 2003. Planning for resilience: modeling change in human fire interactions in the Alaskan boreal forest. *Frontiers in Ecology and the Environment* 1:255–261.
- Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711.
- Chapin, F. S., III, et al. 2005. Role of land-surface changes in arctic summer warming. *Science* 310:657–660.
- Chapin, F. S., III, L. A. Viereck, P. C. Adams, K. van Cleve, C. L. Fastie, R. A. Ott, D. Mann, and J. F. Johnstone. 2006. Successional processes in the Alaskan boreal forest. Pages 100–120 in F. S. Chapin III, M. W. Oswood, K. van Cleve, L. A. Viereck, and D. L. Verbyla, editors. *Alaska's changing boreal forest (the Long-Term Ecological Research network series)*. Oxford University Press, Oxford, UK.
- Collins, W. B., B. W. Dale, L. G. Adams, D. E. McElwain, and K. Joly. 2011. Fire, grazing history, lichen abundance, and winter distribution of caribou in Alaska's taiga. *Journal of Wildlife Management* 75:369–377.
- Coxson, D. S. and J. Marsh. 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. *Canadian Journal of Botany* 79:1449–1464.
- Cronan, J. and R. Jandt. 2008. How succession affects fire behavior in boreal black spruce forest of Interior Alaska. Technical Report 59. Bureau of Land Management, Fairbanks, Alaska, USA.
- Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology* 63:644–652.
- Dau, J. 2007. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24 and 26A caribou management report. Pages 174–231 in P. Harper, editor. *Caribou management report of survey and inventory activities 1 July 2004–30 June 2006*. Project 3.0. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- de Groot, W. J. and R. W. Wein. 1999. *Betula glandulosa* Michx. response to burning and postfire growth temperature and implications of climate change. *International Journal of Wildland Fire* 9:51–64.
- Duffy, P. A. 2006. Interactions among climate, fire and vegetation in the Alaskan boreal forest. Dissertation. University of Alaska Fairbanks, Fairbanks, Alaska, USA.
- Duffy, P. A., J. E. Walsh, J. M. Graham, D. H. Mann, and T. S. Rupp. 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. *Ecological Applications* 15:1317–1330.
- Eberhart, K. E. and P. M. Woodard. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal of Forest Research* 17:1207–1212.
- Euskirchen, E. S., A. D. McGuire, T. S. Rupp, F. S. Chapin III, and J. E. Walsh. 2009. Projected changes in atmospheric heating due to changes in fire disturbance and the snow season in the western Arctic, 2003–2100. *Journal of Geophysical Research* 114 G04022.
- Flannigan, M. D., B. J. Stocks, and B. M. Wotton. 2000. Climate change and forest fires. *The Science of the Total Environment* 262:221–229.
- Forbes, B. C., M. M. Fauria, and P. Zetterberg. 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology* 16:1542–1554.
- Gonzalez, P., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts to climate change. *Global Ecology and Biogeography* 19:755–768.
- Griffith, B., D. C. Douglas, N. E. Walsh, D. D. Young, T. R. McCabe, D. E. Russell, R. G. White, R. D. Cameron, and K. R. Whitten. 2002. The Porcupine caribou herd. Pages 8–37 in D. C. Douglas, P. E. Reynolds, and E. B. Rhode, editors. *Arctic Refuge coastal plain terrestrial wildlife research summaries*. U. S. Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD BSR-2002-0001.
- Hay, L. E., R. L. Wilby, and G. H. Leavesley. 2000. A comparison of delta change and downscaled GCM scenarios for three mountainous (sic) basins in the United States. *Journal of the American Water Resources Association* 36:387–397.
- Higuera, P. E., L. B. Brubaker, P. M. Anderson, T. A. Brown, A. T. Kennedy, and F. S. Hu. 2008. Frequent fires in ancient shrub tundra: implications of paleorecords for Arctic environmental change. *PLoS ONE* 3(3):e0001744.

- Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. S. Hu, and T. A. Brown. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* 79:201–219.
- Hinzman, L. D., et al. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climate Change* 72:251–298.
- Holt, E. A., B. McCune, and P. Neitlich. 2006. Defining a successional metric for lichen communities in the arctic tundra. *Arctic, Antarctic and Alpine Research* 38:373–377.
- Holt, E. A., B. McCune, and P. Neitlich. 2008. Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, U.S.A. *The Bryologist* 111:68–83.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124:377–406.
- Hu, F. S., J. Barnes, S. Rupp, P. Higuera, M. Chipman, M. Urban, and P. A. Duffy. 2010a. Reconstructing fire regimes in tundra ecosystems to inform a management-oriented ecosystem model. Final report 06-3-1-23. Joint Fire Science Program, Boise, Idaho, USA.
- Hu, F. S., P. E. Higuera, J. E. Walsh, W. L. Chapman, P. A. Duffy, L. B. Brubaker, and M. L. Chipman. 2010b. Tundra burning in Alaska: Linkages to climatic change and sea ice retreat. *Journal of Geophysical Research* 115:G04002.
- IPCC. 2007. Fourth Assessment Report (AR4): climate change 2007 synthesis report. Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- James, A. R. C., S. Boutin, D. M. Herbert, and A. B. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68:799–809.
- Jandt, R. R., K. Joly, C. R. Meyers, and C. Racine. 2008. Slow recovery of lichen on burned caribou winter range in Alaska tundra: potential influences of climate warming and other disturbances. *Arctic, Antarctic and Alpine Research* 40:89–95.
- Jefferies, R. L., J. Svoboda, G. Henry, M. Raillard, and R. Ruess. 1992. Tundra grazing systems and climatic change. Pages 391–412 in F. S. Chapin III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. *Arctic ecosystems in a changing climate: an ecophysiological perspective*. Academic Press, San Diego, California, USA.
- Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. *Wildlife Monographs* 160:1–36.
- Johnstone, J. F., and T. N. Hollingsworth. F. S. Chapin, III, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16:1281–1295.
- Joly, K. 2011. Modeling influences on winter distribution of caribou in northwestern Alaska through use of satellite telemetry. *Rangifer Special Issue* 19:75–85.
- Joly, K., P. Bente, and J. Dau. 2007a. Response of overwintering caribou to burned habitat in northwest Alaska. *Arctic* 60:401–410.
- Joly, K., F. S. Chapin III, and D. R. Klein. 2010. Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing and landscape characteristics in northwest Alaska. *Écoscience* 17:321–333.
- Joly, K., M. J. Cole, and R. R. Jandt. 2007b. Diets of overwintering caribou, *Rangifer tarandus*, track decadal changes in arctic tundra vegetation. *Canadian Field-Naturalist* 121:379–383.
- Joly, K., B. W. Dale, W. B. Collins, and L. G. Adams. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. *Canadian Journal of Zoology* 81:1192–1201.
- Joly, K., R. R. Jandt, and D. R. Klein. 2009a. Decrease of lichens in arctic ecosystems: role of wildfire, caribou and reindeer, competition, and climate change. *Polar Research* 28:433–442.
- Joly, K., R. R. Jandt, C. R. Meyers, and M. J. Cole. 2007c. Changes in vegetative cover on Western Arctic Herd winter range from 1981–2005: potential effects of grazing and climate change. *Rangifer Special Issue* 17:199–207.
- Joly, K., D. R. Klein, D. L. Verbyla, T. S. Rupp, and F. S. Chapin III. 2011. Linkages between large-scale climate patterns and the dynamics of Alaska caribou populations. *Ecography* 34:345–352.
- Joly, K., T. S. Rupp, R. R. Jandt, and F. S. Chapin III. 2009b. Fire in the range of the Western Arctic Caribou Herd. *Alaska Park Science* 8:68–73.
- Kasischke, E. S., T. S. Rupp, and D. L. Verbyla. 2006. Fire trends in the Alaskan boreal forest. Pages 285–301 in F. S. Chapin III, M. W. Oswood, K. van Cleve, L. A. Viereck, and D. L. Verbyla, editors. *Alaska's changing boreal forest*. Oxford University Press, Oxford, UK.
- Klein, D. R. 1982. Fire, lichens, and caribou. *Journal of Range Management* 35:390–395.
- Klein, D. R., L. Moorehead, J. Kruse, and S. R. Braund. 1999. Contrasts in use and perceptions of biological data for caribou management. *Wildlife Society Bulletin* 27:488–498.
- Klein, D. R. and M. Shulski. 2009. Lichen recovery following heavy grazing by reindeer delayed by climate warming. *Ambio* 38:11–16.
- Kurkowski, T. A., T. S. Rupp, D. H. Mann, and D. L. Verbyla. 2008. Relative importance of different secondary successional pathways in an Alaskan boreal forest. *Canadian Journal of Forest Research* 38:1911–1923.

- Latham, A. D. M., M. C. Latham, N. A. McCuthchen, and S. Boutin. 2011. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *Journal of Wildlife Management* 75:204–212.
- Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the western hemisphere. *Ecology* 90:588–597.
- Lloyd, A. H. 2005. Ecological histories from Alaska trees lines provide insight into future change. *Ecology* 86:1687–1695.
- Lloyd, A. H., K. Yoshikawa, C. L. Fastie, L. Hinzman, and M. Fraver. 2003. Effects of permafrost degradation on woody vegetation at arctic treeline on the Seward Peninsula, Alaska. *Permafrost and Periglacial Processes* 14:93–101.
- Maier, J. A. K., J. M. ver Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. *Canadian Journal of Forest Research* 35:2233–2243.
- Mitchell, T. D. and P. D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology* 25:693–712.
- Nakicenovic, N., et al. 2000. Special report on emissions scenarios: a special report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Overpeck, J., et al. 1997. Arctic environmental change of the last four centuries. *Science* 278:1251–1256.
- Parker, K. L., P. S. Barboza, and T. R. Stephenson. 2005. Protein conservation in female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. *Journal of Mammalogy* 86:610–622.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. Pages 144–169 in H. H. Shugart, R. Leemans, and G. Bonan, editors. *A system analysis of the global boreal forest*. Cambridge University Press, Cambridge, UK.
- Person, S. J., R. E. Pegau, R. G. White, and J. R. Luick. 1980. In vitro and nylon-bag digestibilities of reindeer and caribou forages. *Journal of Wildlife Management* 4:613–622.
- Putkonen, J. and G. Roe. 2003. Rain-on-snow events impact soil temperatures and affect ungulate survival. *Geophysical Research Letters* 30(4):1188.
- Qu, X. and A. Hall. 2006. Assessing snow albedo feedback in simulated climate change. *Journal of Climate* 19:2617–2630.
- Racine, C. H., R. Jandt, C. Meyers, and J. Dennis. 2004. Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research* 36:1–10.
- Racine, C. H., W. A. Patterson III, and J. G. Dennis. 1985. Tundra fire regimes in the Noatak River watershed, Alaska: 1956–1983. *Arctic* 38:194–200.
- Rempel, R. S. 2011. Effects of climate change on moose populations: exploring the response horizon through biometric and systems models. *Ecological Modelling* 222:3355–3365.
- Robinson, H. S., M. Hebblewhite, N. J. DeCesare, J. Whittington, L. Neufield, M. Bradley, and M. Musiani. 2012. The effect of fire on spatial separation between wolves and caribou. *Rangifer Special Issue* 20:277–294.
- Rupp, T. S., M. Olson, L. G. Adams, B. W. Dale, K. Joly, J. Henkelman, W. B. Collins, and A. M. Starfield. 2006. Simulating the influences of various fire regimes on caribou winter habitat. *Ecological Applications* 16:1730–1743.
- Rupp, T. S., F. S. Chapin III, and A. M. Starfield. 2000a. Response of subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska. *Global Climate Change* 6:541–555.
- Rupp, T. S., F. S. Chapin III, and A. M. Starfield. 2001. Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. *Climatic Change* 48:399–416.
- Rupp, T. S., A. M. Starfield, and F. S. Chapin III. 2000b. A frame-based spatially explicit model of subarctic vegetation response to climatic change: comparison with a point model. *Landscape Ecology* 15:283–400.
- Rupp, T. S., A. M. Starfield, and F. S. Chapin III. 2002. Modeling the impact of black spruce on the fire regime of Alaskan boreal forest. *Climatic Change* 55:213–233.
- Russell, D. E., A. M. Martell, and W. A. C. Nixon. 1993. Range ecology of the porcupine caribou herd in Canada. *Rangifer Special Issue* 8:1–168.
- Stafford, J. M., G. Wendler, and J. Curtis. 2000. Temperature and precipitation of Alaska: 50 year trend analysis. *Theoretical and Applied Climatology* 67:33–44.
- Sturm, M., C. Racine, and K. Tape. 2001. Increasing shrub abundance in the Arctic. *Nature* 411:546–547.
- Tews, J., M. A. D. Ferguson, and L. Fahrig. 2007. Potential net effects of climate change on High Arctic Peary caribou: lessons from a spatially explicit simulation model. *Ecological Modelling* 207:85–98.
- Tremblay, G. D. and S. Boudreau. 2011. Black spruce regeneration at the treeline ecotone: synergistic impacts of climate change and caribou activity. *Canadian Journal of Forest Research* 41:460–468.
- Urquhart, D. 1996. Caribou co-management needs from research: simple questions – tricky answers. *Rangifer Special Issue* 9:263–272.
- van Cleve, K., F. S. Chapin III, and C. T. Dyrness, and

- L. A. Viereck. 1991. Element cycling in taiga forests: state-factor control. *BioScience* 41:78–88.
- Viereck, L. A., K. van Cleve, and C. T. Dryness. 1986. Forest ecosystem distribution in the Taiga environment. Pages 22–43 *in* K. van Cleve, F. S. Chapin III, and P. W. Flanagan, editors. *Forest ecosystems in the Alaskan taiga: a synthesis of structure and function*. Springer-Verlag, New York, New York, USA.
- Vors, L. S. and M. S. Boyce. 2009. Global declines of caribou and reindeer. *Global Change Biology* 15:2626–2633.
- Walker, D. A., et al. 2005. The circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16:267–282.
- Walker, M. D., et al. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences* 103:1342–1346.
- Walsh, J. E., W. L. Chapman, V. Romanovsky, J. H. Christensen, and M. Stendel. 2008. Global climate model performance over Alaska and Greenland. *Journal of Climate* 21:6156–6174.
- Walsh, N. E., S. G. Fancy, T. R. McCabe, and L. F. Pank. 1992. Habitat use by the porcupine caribou herd during predicted insect harassment. *Journal of Wildlife Management* 56:465–473.
- Wein, R. W. 1976. Frequency and characteristics of arctic tundra fires. *Arctic* 29:213–222.
- Weixelman, D. A., R. T. Bowyer, and V. van Ballenberghe. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. *Alces* 34:213–238.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40:377–384.
- Xue, Y., F. de Sales, R. Vasic, C. R. Mechoso, A. Arakawa, and S. Prince. 2010. Global and seasonal assessment of interactions between climate and vegetation biophysical processes: a GCM study with different land-vegetation representations. *Journal of Climate* 23:1411–1433.
- Yarie, J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. *Canadian Journal of Forest Research* 11:554–562.
- Zalatan, R. 2008. *Climate change and caribou: the relation between climate and abundance cycles in barren-ground caribou herds of the Northwest Territories, Canada*. VDM Verlag, Saarbrücken, Germany.