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INVITED REVIEW

Novel wildlife in the Arctic: the influence of changing riparian ecosystems and shrub habitat expansion on snowshoe hares

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Abstract

Warming during the 20th century has changed the arctic landscape, including aspects of the hydrology, vegetation, permafrost, and glaciers, but effects on wildlife have been difficult to detect. The primary aim of this study is to examine the physical and biological processes contributing to the expanded riparian habitat and range of snowshoe hares (*Lepus americanus*) in northern Alaska. We explore linkages between components of the riparian ecosystem in Arctic Alaska since the 1960s, including seasonality of stream flow, air temperature, floodplain shrub habitat, and snowshoe hare distributions. Our analyses show that the peak discharge during spring snowmelt has occurred on average 3.4 days per decade earlier over the last 30 years and has contributed to a longer growing season in floodplain ecosystems. We use empirical correlations between cumulative summer warmth and riparian shrub height to reconstruct annual changes in shrub height from the 1960s to the present. The effects of longer and warmer growing seasons are estimated to have stimulated a 78% increase in the height of riparian shrubs. Earlier spring discharge and the estimated increase in riparian shrub height are consistent with observed riparian shrub expansion in the region. Our browsing measurements show that snowshoe hares require a mean riparian shrub height of at least 1.24–1.36 m, a threshold which our hindcasting indicates was met between 1964 and 1989. This generally coincides with observational evidence we present suggesting that snowshoe hares became established in 1977 or 1978. Warming and expanded shrub habitat is the most plausible reason for recent snowshoe hare establishment in Arctic Alaska. The establishment of snowshoe hares and other shrub herbivores in the Arctic in response to increasing shrub habitat is a contrasting terrestrial counterpart to the decline in marine mammals reliant on decreasing sea ice.

Keywords: herbivores, *Lepus americanus*, moose, riparian, shrub expansion, streamflow, tundra, warming

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Introduction

Warmer temperatures have caused spring to arrive earlier to the arctic landscape in recent decades (Brown *et al*., 2010). This trend is most evident in satellite records starting in the 1960s, which indicate earlier snow-free dates (Stone *et al*., 2002; Brown *et al*., 2010), ground thaw dates (Zhang *et al*., 2011), and onset of plant photosynthesis (Xu *et al*., 2013) in arctic and ecotonal regions. Earlier onset of spring is also evident in streamflow records. Freshet timing in Siberia has shifted from June to May (Yang *et al*., 2003), and hydrograph rise due to snowmelt in the Mackenzie River basin in northern Canada occurs earlier now than in the 1970s (Woo & Thorne, 2003; Burn, 2008). In contrast, changes in the timing of snow arrival dates in autumn have been negligible in most locations (Brown *et al*., 2010), including northern Alaska, consistent with the muted temperature trends observed during fall (Shulski & Wendler, 2007). Longer and warmer summers have altered energy exchange (Chapin *et al*., 2005), vegetation (Sturm *et al*., 2001; Myers-Smith *et al*., 2011), and river hydrology in the Arctic (Tan *et al*., 2011), although effects on wildlife have been difficult to detect (Post *et al*., 2009).

The earlier disappearance of snow and corresponding longer growing seasons has contributed to the establishment and expansion of shrubs into arctic tundra ecosystems (Myers-Smith *et al*., 2011), which has been pronounced in the floodplains of northern Alaska (Tape *et al*., 2006; Naito & Cairns, 2011). Arctic riparian shrubs show strong correlations between growing season length and shrub height (Walker, 1987; Pajunen, 2009), suggesting that earlier snowmelt and associated

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earlier peak streamflow (Yang *et al*., 2003) has directly or indirectly contributed to the observed shrub establishment and expansion in Arctic Alaskan floodplains (Tape *et al*., 2011).

Over the past century, shrub expansion has improved habitat for shrub-dependent wildlife (Ehrich *et al*., 2012; Joly *et al*., 2012; Henden *et al*., 2013), such as willow ptarmigan (*Lagopus lagopus, L. muta*, hereafter ptarmigan), snowshoe hares (*Lepus americanus)*, and moose (*Alces alces*). These species require shrubs above the snow in winter for forage and for cover from predators (LeResche *et al*., 1974; Boer, 2007; Christie *et al*., 2014). Moose and snowshoe hare distributions in the Arctic reach the coast in only a few locations (Telfer, 1984; MacDonald & Cook, 2009), probably due to longer winters and correspondingly shorter shrubs coastward (Walker, 1987; Bhatt *et al*., 2010). These climatic constraints on habitat and distribution appear to have loosened, though; for example, the northward establishment of moose c. 1940 along riparian corridors in the Alaskan Arctic (LeResche *et al*., 1974; Coady, 1980) may be the result of longer growing seasons and the resulting taller and more extensive floodplain shrubs after 1880 (onset of warming; Kaufman *et al*., 2009; Schreiner & Lowry, 2013). Snowshoe hares, whose North American distribution is very similar to that of moose (Boer, 2007), were also previously undocumented on the North Slope and rare in the Brooks Range (Rausch, 1951; MacDonald & Cook, 2009). In 1993, snowshoe hares became abundant along the Colville River as far north as the delta (e.g., University of Alaska Museum Mammal Collection specimen 44503) and have been present ever since (Carroll, 2011), although the timing and cause of this possibly novel establishment is unknown.

The primary aim of this study is to examine the physical and biological processes contributing to the expanded habitat and range of snowshoe hares in northern Alaska. We hypothesize that the prior absence of snowshoe hares on the North Slope was the result of insufficient forage and cover, and that floodplain shrub expansion associated with earlier peak streamflows and prolonged growing seasons created suitable habitat and stimulated the northward distribution of snowshoe hares. We explore the connections between snowmelt discharge timing, growing season temperature and length, riparian shrub dynamics, and snowshoe hare establishment in Arctic Alaska over the last four decades. Specifically, we (i) examine trends in peak discharge dates during spring snowmelt on Arctic Alaskan rivers as a metric of changing seasonality in floodplain ecosystems, (ii) estimate changes in shrub habitat using empirical relationships between thawing degree-days (TDD) and floodplain shrub height (Walker, 1987), (iii) quantify shrub patch height and canopy volume requirements for snowshoe hares, and (iv) use these empirical relationships to hindcast historic shrub habitat dynamics. Through these analyses, we describe a mechanism to account for snowshoe hare establishment in arctic ecosystems.

Materials and methods

Study area

Northern Alaska has varied topography extending from the mountains of the Brooks Range to the broad uplands and coastal wetlands of the North Slope. Ecotonal and boreal forest vegetation and discontinuous permafrost exist in the southern Brooks Range (Fig. 1), before grading into low-arctic tundra vegetation and continuous permafrost to the north (Jorgenson & Heiner, 2003; Jorgenson *et al*., 2008). Low-stature tundra vegetation is generally non-tussock and tussock sedge, dwarf-shrub, moss tundra, which is dissected by riparian corridors of dense tall shrubs ranging in size from narrow streams and gullies to river floodplains (CAVM Team, 2003). Tall riparian shrubs include numerous willow species (*Salix spp*.) and Siberian alder (*Alnus viridis*, ssp. *fruticosa*) up to and occasionally exceeding 4 m in height, which have been expanding along riparian corridors in the Brooks Range and North Slope foothills since 1950 (Fig. 2; Naito & Cairns, 2011; Tape *et al*., 2006). The few weather stations in northern Alaska with records dating to the 1970s indicate increased average temperatures from January through June (Shulski & Wendler, 2007). Accumulating snow renders forage inaccessible to snowshoe hares, and late-winter snow depth varies by a factor of two over a 100-m scale (Sturm & Benson, 2004), but lengthy records are limited to a few widely scattered point locations. Mean (±standard deviation) snow depth throughout open settings of the Kuparuk River basin (Fig. 1) was 51 ± 19 cm in 1996 and 57 ± 14 cm in 1997 (Sturm & Benson, 2004), while mean snow depth at riparian shrub sites is generally twice as deep (Pomeroy *et al*., 2006).

Changing seasonality of river flow during spring snowmelt

To quantify recent changes in the seasonality of streamflow, we analyzed long-term discharge records for Arctic Alaska. We determined the timing of peak river discharge during spring snowmelt (between May 1 and June 30) for the only four rivers in northern Alaska that had daily streamflow records longer than 25 years (Kuparuk, Sagavanirktok, Wulik, and Kobuk rivers), using data from the US Geological Survey National Water Information System Web site (NWIS, *waterdata.usgs.gov/nwis*). For our purposes, the timing of peak discharge during spring serves as a metric for assessing changes in the seasonality of floodplain ecosystems. The date of peak discharge is a particularly salient metric in riparian ecosystems because it consistently reflects combined air temperature and snow conditions in the watershed, while also indicating

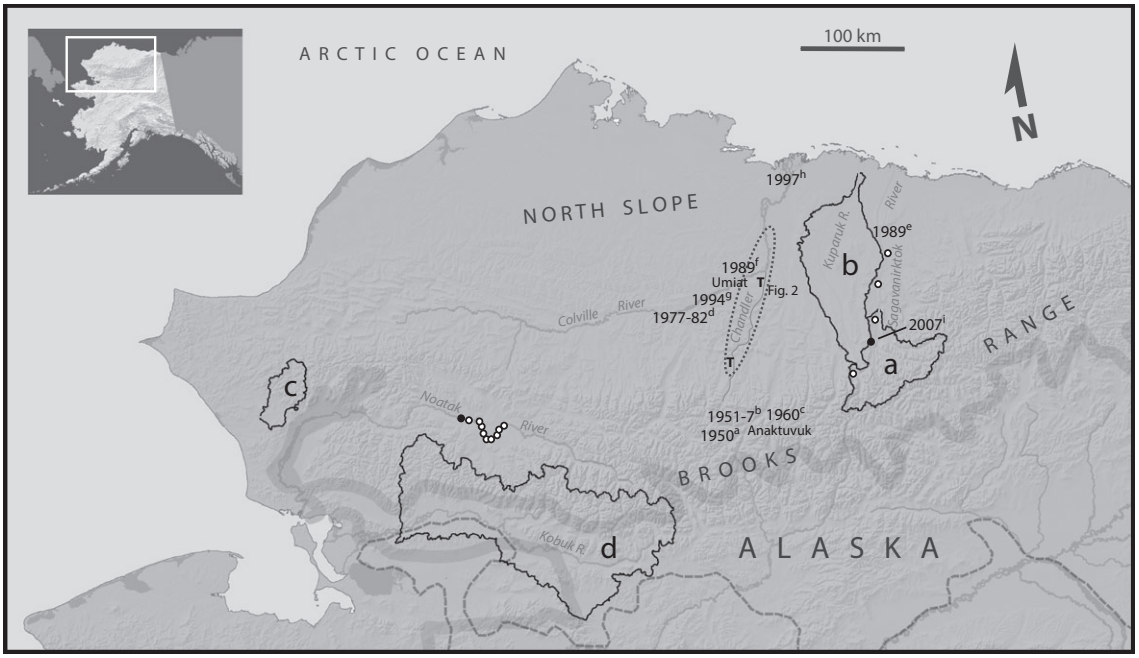


Fig. 1 Northern Alaska and the locations of watersheds (black outlines), shrub sites assessed for browsing (circles), the region sampled for shrub heights (dashed ellipse), temperature records (T) analyzed in this study, and snowshoe hare observations (dates: Table 1). Sagavanirktok River (a), Kuparuk River (b), Wulik River (c), and Kobuk River (d). Also indicated are the locations of shrub sites with hare browsing (filled circles), treeline (shaded line), and the boundary between the discontinuous permafrost zone and the continuous permafrost zone (dashed line).

when floodwaters recede and growing commences in the floodplain. The watersheds range in size from 1826 km^2 (Wulik River gauge) to 24 657 km^2 (Kobuk River gauge) and are distributed across the Alaskan Arctic (Fig. 1). The Sagavanirktok River has small glaciers in its headwaters, while the others do not, and all watersheds are largely undeveloped. The Kuparuk River has the longest record, dating from 1971 to 2012, and the Wulik River has the shortest record, dating from 1984 to 2012. We used peak streamflow dates, as opposed to a temporally integrated measure of discharge (e.g., onset of spring pulse, center of mass flow date, as reported in Stewart *et al.*, 2005), because at high latitudes, streamflow prior to ice-out is extremely difficult to measure on rivers that freeze to the channel bottom (Prowse & Beltaos, 2002; including all rivers in this study except the Kobuk), a problem that is exacerbated by having a single automated gauge.

Relationships between riparian shrubs and herbivores

In June 2012, we characterized riparian shrub cover and herbivore presence at 10 floodplain sites along the Noatak River and Dalton Highway (Fig. 1). The Dalton Highway sites were located near Galbraith Lake, at Oksrukuyik Creek, and along the Sagavanirktok River. Twenty sites along the Noatak (10 sites) and Sagavanirktok rivers (10 sites) were initially selected for sampling based on the presence of *Salix alaxensis* (Fig. 3), a common tall riparian shrub that is important in the diets of numerous arctic herbivores (Weeden, 1969; Bryant *et al.*, 1985;

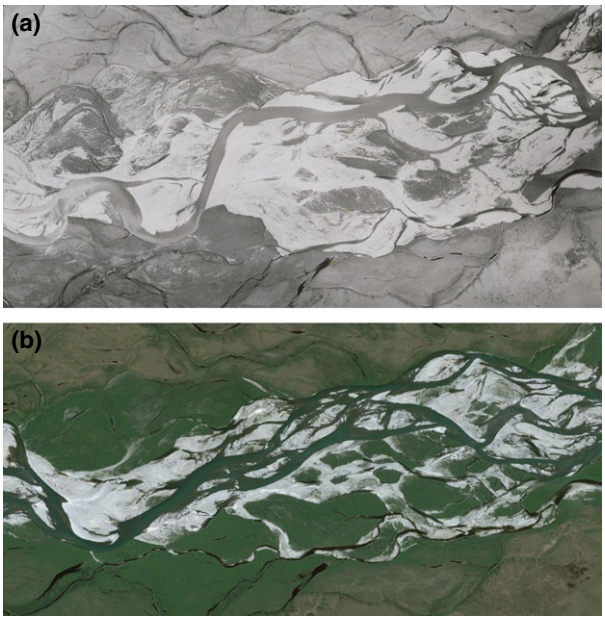


Fig. 2 Imagery from 1948 (a: US Navy) and 2006 (b: Google Earth) showing increasing shrub vegetation and bar stabilization in the floodplain of the lower Anaktuvuk River (see Fig. 1). Our results (Fig. 1, Table 1) suggest that snowshoe hares colonized this region during the interval between the old and new imagery.

Table 1 Snowshoe hare observations north of treeline in Alaska since 1950 ('Key' refers to locations on Fig. 1; O = observation, S = specimen, * herein)

Key	Year	Location	Source	
a	1950	Kalutak Creek	Manville & Young (1965)	O
b	1951–1977	Anaktuvuk Pass	PSM Mammal Collection	S
c	~1960	Anaktuvuk Pass vicinity	Manville & Young (1965)	O
d	1977–1982	Umiat and vicinity	Ray Smith*	O
e	1989	Dalton Hwy MP 33,40	UKBI Mammal Collection	S
f	1989	Colville River	AK Dept Fish & Game*	O
g	1994	Umiat	UAMN Mammal Collection	S
h	1997	Colville R. delta	UAMN Mammal Collection	S
i	2007	Oksrukuyik Creek	Huryn & Hobbie, 2012	O

Risenhoover, 1989). Of these, five sites from each study area were selected for this study using systematic sampling, with an initial random selection to determine whether the first or second of the 10 sites should be sampled, followed by alternating site sampling thereafter. Shrub patches varied in size from approximately 3–100 ha and included multiple willow species (*Salix alaxensis, S. pulchra, S. glauca/niphoclada, S. lanata*), alder (*Alnus viridis*), and birch (*Betula nana*).

At each site, shrubs were randomly sampled along three 25-m transects that ran perpendicular to the river or stream's edge. At distances of 5, 15, and 25 m along each transect, the closest shrub to the point was measured for height, canopy diameter, distance to the point, and evidence of browsing. A total of 9 points were sampled per site. The point-center quarter method (Cottam & Curtis, 1956) using both the diameter of the shrub and the distance to the transect was used to estimate total shrub cover (m^2 ha^{-1}). Shrub canopy volume (m^3 ha^{-1}) at each site was calculated using the volume formula for a cone, where we multiplied the mean shrub canopy area (πr^2) by the mean shrub height and divided by three (Bryant & Kothmann, 1979). Reported values for shrub parameters are means ± standard error of measurement. Presence of snowshoe hares was determined based on unique marks left on the plant from browsing; hares typically make sharp diagonal cuts on woody stems, whereas ptarmigan leave scars after removing buds, and moose leave ragged marks at the tips of stems (Christie *et al*., 2014). We identified minimum threshold habitat requirements for snowshoe hares using our measurements of shrub height at sites with and without hares. The bounds of the shrub height threshold were calculated as the range of shrub height values that differentiated sites with hares from sites without hares. Specifically, we estimated hare habitat as the range between the upper 95% confidence interval of shrub parameters associated with hare absence and the lowest values of those parameters (minus standard error) associated with hare presence. These thresholds are depicted graphically as gray bands in the figures.

In addition to the sites sampled for browsing, we sampled riparian shrub heights along the Chandler and Colville rivers, where the most extensive shrub patches on the North Slope occur (Beck *et al*., 2011), and where snowshoe hares were first observed in the 1970s. Between 70 and 158 shrub heights were recorded from each of eight 250 m by 250 m riparian shrub plots, selected for their abundance of tall shrubs, and the tallest 50 shrubs were subset from each plot (n = 8 plots, total riparian shrubs = 817, total 50 tallest riparian shrubs = 400).

Hindcasting of riparian shrub height and snowshoe hare colonization

We focused on the snowshoe hare, an obligate browser with a tundra distribution constrained to riparian shrub habitat (Boer, 2007; MacDonald & Cook, 2009). Snowshoe hares rely on shrub cover for protection from predators, and they are known to browse on multiple willow species and alder (Christie, unpublished data). We used the generalizable observations of snowshoe hare habitat requirements along the Noatak River and Dalton Highway in concert with the shrub height reconstructions below to estimate the timing of snowshoe hare colonization in the Chandler and Colville River valleys, where hares were first observed. We estimated past shrub height at annual time steps between 1960 and 2010 using the following equation:

$$\text{shrub height (cm)} = 0.000341(\text{TDD})^2 - 0.195(\text{TDD}) + 27.7 \quad (1)$$

Equation (1) was developed by Walker (1987) along a TDD (thawing degree-day) gradient by sampling the 50 tallest willow shrubs (*Salix lanata*) at each of eight sites starting at the Arctic Coast and extending 100 km inland along the Sagavanirktok River (Walker, 1985). We calculated annual TDD values using monthly air temperature means (SNAP, 2013), as in Eqn (1), from two locations within the Chandler/Colville River region, where we measured shrub height (Fig. 1). We used linear regression to represent any trend in TDD between 1960 and 2010.

To address uncertainty associated with the timing of snowshoe hare colonization in relation to shrub height, we calculated three different shrub height scenarios for the years 1960–2010. First, we calculated a generic shrub height trajectory for the region based only on the long-term TDD trend. For this scenario, we solved the TDD regression equation for each year between 1960 and 2010 and then calculated shrub height at annual time steps using Eqn (1). Using the TDD regression line dampens the interannual variability in TDD, and as a result, produces more realistic shrub height estimates. To hindcast shrub heights for the subsequent scenarios, we applied the annual fractional change (1.34% to 1.01%, as determined from the first scenario for generic shrub plots) to

observed shrub heights in 2010 and worked backward to 1960. In the second scenario, we hindcasted shrub heights starting with the observed 2010 height of 2.08 m, determined from the mean of the 50 tallest shrubs (as in Eqn (1)) at the Chandler/Colville sites. In the third scenario, we hindcasted shrub heights using the observed 2010 height of 1.69 m, determined from the mean of all riparian shrub heights at the same Chandler/Colville sites.

We used the latter two shrub growth scenarios to place upper and lower bounds on the timing of first snowshoe hare establishment on the North Slope. Uncertainty in hindcasted shrub heights and the corresponding timing of hare colonization was bracketed using the mean heights of the tallest 50 shrubs along the Chandler/Colville rivers as the earliest possible hare colonization date, and the mean shrub heights of all shrubs from the same sites as the latest possible colonization date. This approach assumes that calculations based on the tallest cohort of shrubs represent early colonization, because the height threshold for hare habitat was calculated using mean riparian shrub heights, rather than the tallest cohort. We also assume that predictions derived from the mean riparian shrub heights reflect late colonization, because mean shrub heights would likely not change as rapidly as that of the tallest cohort of shrubs (Walker, 1987), from which Eqn (1) was derived.

An additional assumption in applying Eqn (1) to these shrub measurements was that other dominant floodplain willow species that we measured, such as *Salix alaxensis* and *S. pulchra* have responded similarly to increases in cumulative warmth, given their comparable or taller heights and co-occurrence on floodplains with *S. lanata* (Schickhoff *et al.*, 2002). The observed mean shrub height of the 50 tallest shrubs from multiple sites along the Chandler/Colville rivers was compared to shrub height estimates derived from Eqn (1) using temperature records from that region. Air temperature data at the two locations were generated by the Scenarios Network for Alaska & the Arctic (SNAP, 2013); they were nearly identical and thus averaged. Interpolated temperature data were used, as opposed to station data, because no inland North Slope locations have station data spanning the last five decades. Mean monthly air temperatures greater than 0 °C were used to calculate TDD. Mean and standard error of the mean are reported.

Change in presence of snowshoe hares?

To explore the implications of changes in floodplain shrub height and cover, we reviewed museum collections and published and anecdotal wildlife records spanning the 20th century from the North Slope and Brooks Range to determine changes in presence or absence. Due to recent observations of Canada lynx (*Lynx canadensis*) in Arctic Alaska, and their predation on hares, we also reviewed its prior occurrences in the region. Current northern boundaries of these species' distributions were compared to their respective mid-century distributions to determine changes in species presence concurrent with streamflow records and floodplain shrub habitat expansion.

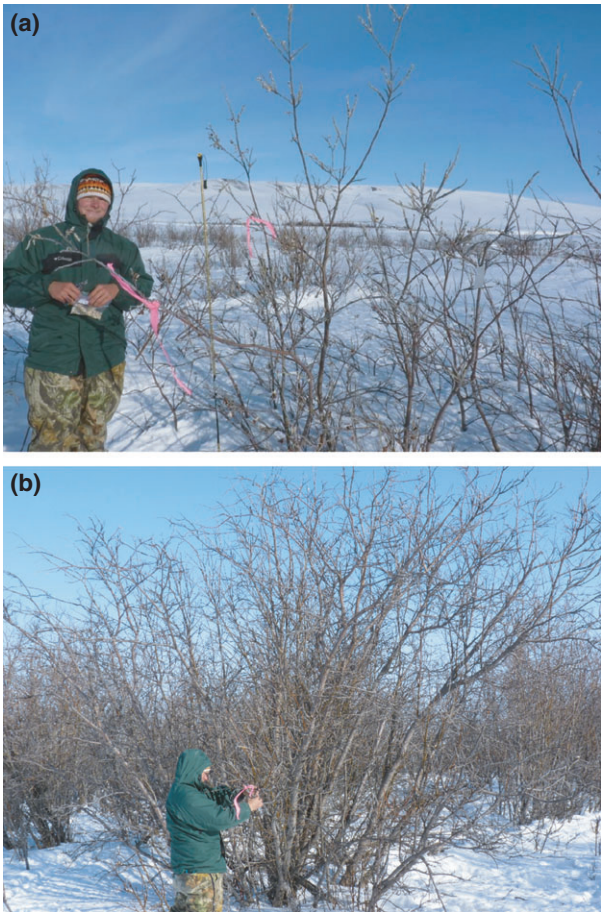


Fig. 3 Shrub willow (*Salix alaxensis*) sample sites without (a) and with (b) hare browsing, in early May 2012. The site with hare browsing (b) also had snowshoe hare observations in 2007 (Fig. 1, Table 1).

Results

Changing seasonality of streamflow and climate

Peak discharge dates during spring snowmelt occurred earlier on all four rivers in recent decades (Fig. 4), including the Kuparuk River (1.8 days per decade; $R^2 = 0.15$, $P = 0.01$), Kobuk River (3.5 days per decade; $R^2 = 0.14$, $P = 0.04$), Wulik River (4.1 days per decade; $R^2 = 0.14$, $P = 0.047$), and the Sagavanirktok River (4.2 days per decade; $R^2 = 0.15$, $P = 0.03$). This change in the timing of peak discharge is due to the earlier loss of catchment snowpack during spring snowmelt. These results, combined with the consistent snow arrival dates in the fall (Brown *et al.*, 2010), indicate that earlier peak discharge dates have contributed to a longer snow-free season following the recession of peak flows in the floodplain.

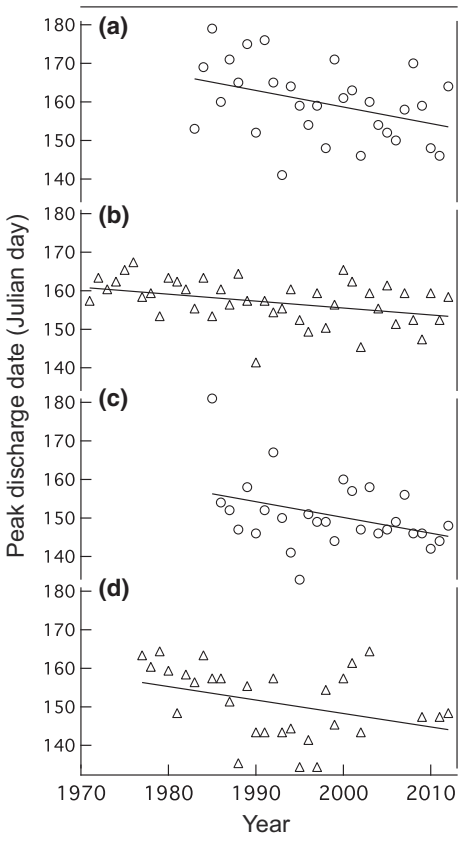


Fig. 4 Trends since the 1970s in the date of peak discharge (symbols) for four rivers in northern Alaska. Peak discharge dates during spring trended earlier on the Sagavanirktok (a: $R^2 = 0.15$, $P = 0.03$), Kuparuk (b: $R^2 = 0.15$, $P = 0.01$), Wulik (c: $R^2 = 0.14$, $P = 0.047$), and Kobuk Rivers (d: $R^2 = 0.14$, $P = 0.04$).

Shrub habitat characteristics and use by snowshoe hares

In Arctic Alaska, snowshoe hare browsing was observed at 2 of 10 sites assessed for browsing: one located near the Noatak River, and the other located near the Dalton Highway (Figs 1 and 3). The two sites with hare browsing had shrub canopy volume exceeding 9612 ± 960 m^3 ha^{-1}, constituting the two highest shrub canopy volumes measured (Fig. 5b). The two sites with hare browsing had a mean shrub height of 1.70 ± 0.13 m (1.47 m = N5; 1.93 m = D2) and were among the three tallest shrub patches sampled (Fig. 5a). Sites without snowshoe hare browsing had a mean shrub height of 0.93 ± 0.13 m. The two sites with hare browsing had mean shrub cover of 78 and 85% and were among the three patches with greatest shrub cover (Fig. 5a). Snowshoe hares in Arctic Alaska appear to require shrub patches with mean shrub height between 1.24 and 1.36 m (Fig. 5a), and a minimum canopy volume between 3497 and 8652 m^3 ha^{-1} (Fig. 5b). Moose and ptarmigan browsing were observed at all sites.

Temperature records from the Chandler and Colville rivers showed that TDD increased from 886 to 1085 TDD between 1960 and 2010 (Fig. 6a; TDD = 3.99*year – 6936; $R^2 = 0.33$, $P < 0.0001$). Using this TDD trendline in conjunction with Eqn (1), we determined that the 23% increase in TDD translated to a 78% increase in riparian shrub height, from 1.22 m in 1960 to 2.17 m in 2010 (Fig. 6b). Using the annual fractional changes from the generic shrub height curve (1.34–1.01%), we hindcasted shrub heights for the observed tallest cohort of shrubs along the Chandler/Colville rivers (2010 data: 2.08 ± 0.06 m, range = 1.86–2.37 m) to estimate a shrub height of 1.17 m in 1960 (Fig. 6b). Applying the same annual fractional changes to the observed mean shrub height along the Chandler/Colville rivers (2010 data: 1.69 ± 0.06 m, range = 1.52–1.98 m) yielded a mean shrub height of 0.95 m in 1960 (Fig. 6b). Observed mean shrub height of the 50 tallest shrubs (2.08 ± 0.06 m) was closely aligned with that predicted by Eqn (1) for 2010 (2.17 m). The tallest cohort of shrubs along the these rivers, where the most extensive shrub habitat exists and snowshoe hares were first observed north of the Brooks Range (Table 1), met our measured snowshoe hare shrub height requirement as early as 1964, while the mean shrub height along the Chandler/Colville rivers met the requirement as late as 1989 (Fig. 6b).

Review of snowshoe hare range expansion

Records show that snowshoe hares have occupied North Slope riparian corridors since as recently as the 1990s (Carroll, 2011) (University of Alaska Museum Mammal Collection specimen 44503), indicating more than a 150 km northward shift in their distribution. Mammal records for the North Slope during the mid-20th century indicate an absence of snowshoe hares (Rausch, 1951; Bee & Hall, 1956; Manville & Young, 1965). Additional evidence of the snowshoe hare's prior absence comes from an intensive study of moose browsing during 1975–76, during which thousands of stems among the most extensive shrub patches on the North Slope of Alaska (Colville River) were surveyed for moose and ptarmigan browse, without mention of hares or their distinctive browsing (Mould, 1977a,b), which would remain evident at least several years after the browsing occurred. The earliest observation of snowshoe hares on the North Slope comes from a pilot who lived at Umiat (along the Colville River) from 1975 to 1995 and regularly watched for animals and their sign (Fig. 1, Table 1). He recounted in an email: 'In 1975 there were no hares. About 1977–78 I started seeing hare trails but didn't believe it at first and attributed it to other small animals. In about the space of 5 years

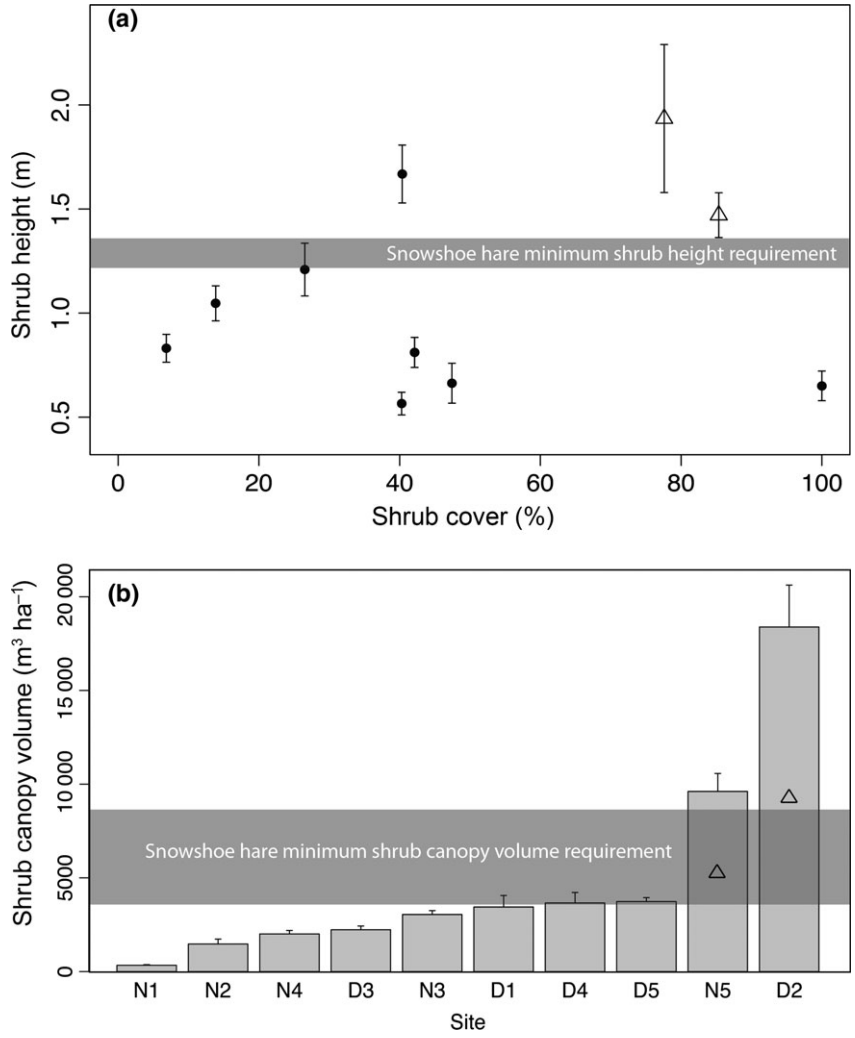


Fig. 5 Mean shrub height (a) and shrub canopy volume (b) requirements for snowshoe hares at sites along the Noatak River and the Dalton Highway, in northern Alaska (Fig. 1). Sites with evidence of hare browsing are denoted by triangles; all sites had evidence of moose and ptarmigan browsing. The lower bounds of the gray bands were determined using the upper 95% confidence interval for sites with hare absence, while the upper bounds of the gray bands were determined using the lowest value (minus SE) with hare presence.

the trails were so hard packed I could almost walk on them'. (Ray Smith, pers. comm., 2/5/2014). During annual Alaska Department of Fish and Game (ADFG) moose surveys covering riparian habitat of the Colville River system, the first recorded snowshoe hare observations were made during April of 1989 (Table 1). Specimens were collected at a similar latitude along the Dalton Highway the same year (UKBI Mammal Collection, Table 1), adjacent to the same transect used to identify the correlation between shrub height and summer warmth (Walker, 1987). These records collectively suggest that snowshoe hares became established in the Colville River drainage during the late 1970s (Fig. 1, Table 1). The observed establishment in the late 1970s coincides with the estimated establishment between 1964 and 1989 (Fig. 6b).

Likewise, Canada lynx, which specialize on snowshoe hares, were rare or absent on the North Slope according to most early and mid-20th century accounts (Hall, 1929; Bee & Hall, 1956); the northernmost report was from Eskimo observations along the western Noatak River (Rausch, 1951) at treeline. Several lynx observations and specimens from the North Slope collected thereafter (Manville & Young, 1965) indicate that lynx were present, though likely in small numbers. During annual ADFG moose aerial surveys of the riparian habitat of the Colville River system, the first lynx since mid-century were observed in 1998, and its tracks have

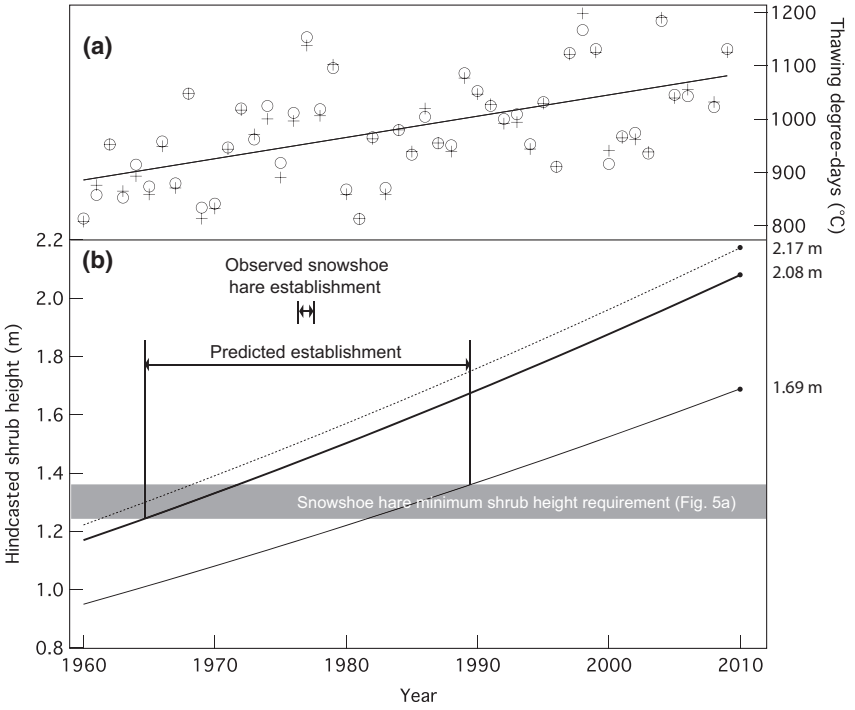


Fig. 6 Relationships between increasing thawing degree-days (TDD), hindcasted shrub height, and observed and predicted snowshoe hare colonization. TDD from 1960 to 2010 (a) has increased (TDD = 3.99*year - 6936; $R^2 = 0.33$, $P < 0.0001$) at both sites (symbols) along the Chandler/Colville Rivers (Fig. 1). Three hindcasted shrub height scenarios (b) establish upper and lower bounds on the predicted timing of first snowshoe hare colonization in the region, generated using the regression trend-line from (a) in conjunction with Eqn (1). The dotted line represents generic shrub height based only on the TDD trend-line in (a). The bold line represents hindcasted shrub heights based on the observed height of 2.08 m in 2010 (calculated using the mean height of tallest 50 shrubs at Chandler/Colville sites). The normal line represents hindcasted shrub heights based on the observed height of 1.69 in 2010 (calculated using the mean height of all shrubs at Chandler/Colville sites). To reconstruct historic shrub heights at annual time steps, we applied the annual fractional change from the generic curve to the tallest cohort and mean shrub heights in 2010 and worked backwards to 1960.

since been seen during annual aerial surveys. The first lynx harvest on the Colville River was reported in 2002 when seven were harvested by trappers, suggesting that lynx were becoming more abundant (Carroll, 2010).

Discussion

This study combines several datasets to describe a pathway by which warmer temperatures since the 1960s have caused the northward establishment of snowshoe hares in Arctic Alaska (Fig. 7). Earlier spring discharge and recession of peak flows since the 1970s indicate an earlier disappearance of snow, ice, and water from floodplains in the Alaskan Arctic. The combination of warming and the resulting earlier snowmelt and recession of peak flows (Lesack *et al.*, 2014) have extended the growing season in the floodplain and are the likely drivers of the observed shrub expansion in Arctic Alaskan floodplains (Tape *et al.*, 2006, 2011, 2012; Naito & Cairns, 2011; Myers-Smith *et al.*, 2015). During this period of shrub expansion, the hindcasted increase in shrub height surpassed the minimum snowshoe hare shrub habitat requirement identified here, making increased shrub habitat the most plausible cause of snowshoe hare's northward colonization of the region.

Multiple proxies for the onset of spring indicate that it is occurring earlier across the Arctic (Post *et al.*, 2009). Based on our analysis of rivers in the Alaskan Arctic, the timing of peak streamflow during spring snowmelt has occurred, on average, approximately 3.4 ± 0.6 days per decade earlier since 1984, which is consistent with the 4 days per decade earlier snow-free dates derived from satellite imagery for this region (Brown *et al.*, 2010). Our results from Alaska document a shift in the timing of peak discharge that is comparable to other arctic regions (Woo & Thorne, 2003; Yang *et al.*, 2003). On the Mackenzie River Delta in northwestern Canada, peak discharge dates were strongly correlated with April and May air temperatures (Lesack *et al.*, 2014), and similar relationships have been established between spring warming trends and earlier snowmelt in northern Alaska (Stone *et al.*, 2002). The length of the

snow season and opposing growing season is an important control on green-up, vegetation productivity, and carbon feedbacks to the climate system (Euskirchen *et al.*, 2006, 2009).

Warming and associated hydrologic changes in northern Alaska have created a longer growing season in and around the floodplain, conducive to shrub growth (Walker, 1987; Tape *et al.*, 2012). Based on our observations, it is likely that soils in the active floodplain have experienced earlier inundation by melt waters and earlier recession of peak flows. At the watershed scale, the earlier timing of peak discharge is associated with earlier snow-free dates (Yang *et al.*, 2003), including distal or inactive parts of the floodplain, where the ground is covered by snow, rather than ice or water.

The metric in this study that most clearly delineates the minimum habitat requirements of snowshoe hares in tundra is shrub canopy volume (Fig. 5b). Shrub canopy volume is an apt proxy for the combined forage and cover that a shrub patch affords a snowshoe hare, because it integrates both shrub height and extent. However, shrub height alone is also a relatively good predictor of snowshoe hare presence at sites in Arctic Alaska (Fig. 5a). For snowshoe hares to inhabit an area, shrubs need to protrude above the snow during winter to provide forage and cover. In riparian corridors, the valley topography and shrubs themselves reduce the erosive wind events that scour snow from the surrounding tundra, leading to snow depths more than twice as great in the shrubs (Pomeroy *et al.*, 2006). The mean late-winter snow depths of 0.51 and 0.57 m reported for successive years in the Kuparuk River basin excluded the deeper snow found in tall shrubs (Sturm & Benson, 2004); by doubling the snow depth measured in open tundra (Pomeroy *et al.*, 2006), we estimate snow depth among tall shrubs in protected settings to be 1.1 m, just under the 1.24–1.36 m minimum shrub height requirement for snowshoe hares. It is logical that shrub height at least needs to exceed snow depth during late winter to constitute habitat for snowshoe hares. Thus, spatial patterns and temporal trends in snow depth are equally important to snowshoe hares and other shrub-dependent mammal herbivores as are trends in shrub height. The complexity of snow drifting around shrubs and our crude historical record of snow depth and redistribution by wind unfortunately preclude reconstructions of past snow cover conditions in these shrub patches. To simplify the complex, three-dimensional dynamics of snow accumulation and redistribution in these ecosystems, our hindcasting only considered shrub height and not shrub volume.

Repeat photography spanning 1950–2000 showed that valley bottom shrub cover of numerous rivers in the Alaskan Arctic increased from 5% to 13%, whereas valley slopes increased from 14% to 20% (Tape *et al.*, 2006). The greater shrub expansion in the floodplain than on surrounding slopes (Naito & Cairns, 2011) is consistent with other studies showing that riparian willow and alder radial growth is much greater and more responsive to warming than open tundra willow and alder radial growth (Walker, 1987; Tape *et al.*, 2012) and that active disturbance regimes (e.g., flooding,

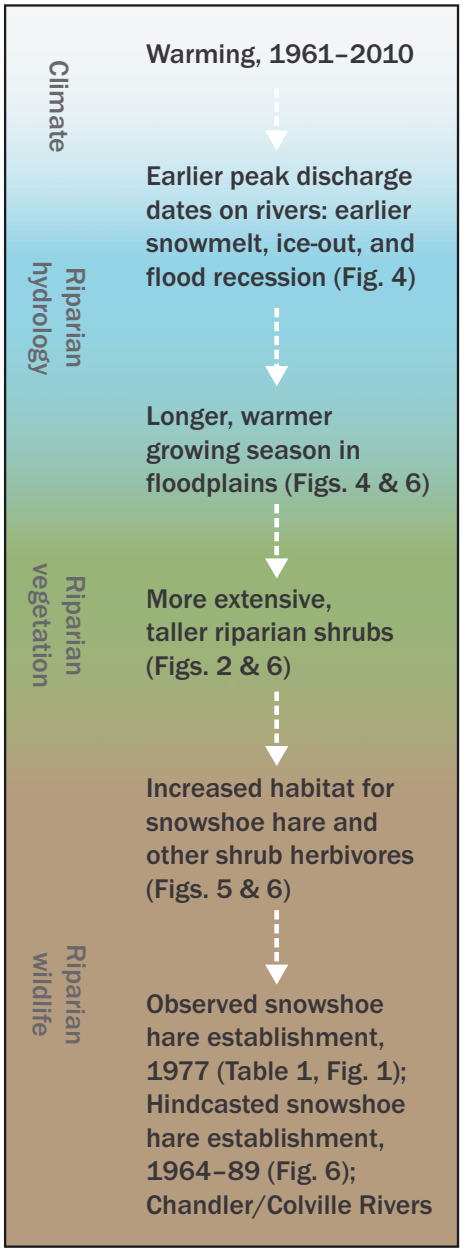


Fig. 7 One pathway, described in this study, by which warmer temperatures have altered riparian ecosystems, eventually triggering the northward establishment of snowshoe hares, and possibly other shrub herbivores, in the Arctic.

bank, and thermal erosion) magnify the response of shrubs to warming (Lantz *et al*., 2009; Myers-Smith *et al*., 2011). Similarly, riparian willows increase in height much more rapidly in response to warmer temperatures than do open tundra willows (Walker, 1987). Riparian shrubs are assumed to be growing under near-optimal moisture and nutrient conditions, with minimal competition from other plants; the main constraint on their growth is thought to be temperature (Walker, 1987; Pajunen, 2009; Tape *et al*., 2012).

Uncertainty associated with our shrub height hindcasting calculations arises from a number of factors, including local environmental conditions and variation in temperature sensitivity across shrub species (Myers-Smith *et al*., 2015). Despite this, there is general agreement between the predicted (2.17 m) and observed height (mean = 2.08 ± 0.06 m, range = 1.86–2.37 m) of tall shrubs along the Chandler and Colville rivers, lending support to the hindcasting presented here. In anomalous cases, shrub height exceeds 4 m in this region (including 9 of 400 shrubs measured along the Chandler/Colville rivers and Fig 4b), even during the early 20th century (Smith, 1925), but the extent of such shrubs is very limited, as shown by the mean values of the 50 tallest shrubs presented here and by Walker (1987). Furthermore, all shrub species decline in height with the declining length of summer approaching the coast, underscoring the overarching influence of greater summer heating on shrub height. The spatial distribution of sites and interspecific differences in shrub growth could shift the hindcasted timing of snowshoe hare establishment somewhat, but the estimated 78% increase in riparian shrub height since 1960 nonetheless places the hindcasted establishment during the period of shrub expansion, which coincides with the observed colonization (Fig. 6b).

The northern ranges of ptarmigan, moose, and snowshoe hare in the Arctic are nested, with willow ptarmigan being the furthest north (Hannon *et al*., 1998), followed by moose, and then snowshoe hare (MacDonald & Cook, 2009). This implies a lower shrub habitat requirement for ptarmigan, followed by moose, and eventually by snowshoe hare (Fig. 5a). Other studies have also noted the higher biomass and cover requirements for hare than for moose (Litvaitis *et al*., 1985; Potvin *et al*., 2005; Sullivan *et al*., 2010). The nested distributions and graduated shrub requirements of these browsers are consistent with their response to shrub expansion and their order of arrival in northern Alaska, with ptarmigan present throughout the 20th century, moose colonizing in the 1940s (Hall, 1973; Coady, 1980), and snowshoe hares arriving in the late 1970s. Given favorable hydrologic and geomorphic conditions, riparian shrubs respond more rapidly to warming than surrounding tundra shrubs (Walker, 1987; Tape *et al*., 2006, 2012). Likewise, wildlife that inhabits riparian shrub corridors may respond to warming before wildlife that inhabits the surrounding tundra.

Although there is good evidence that snowshoe hares were absent prior to the late 1970s, detailed historic records covering the entirety of the North Slope do not exist to confirm this. In the case of moose, it is implausible that this distinctive large game species could have been repeatedly missed by early explorers and Native Alaskans traveling riparian corridors now occupied by moose. The same argument might not apply to snowshoe hares or lynx, however, due to their small size, camouflaged appearance, and minor importance as a food source (Rausch, 1951), although both were trapped for their fur. Population cycles are well known for snowshoe hares, which could explain their sudden appearance in the 1970s, but the lingering evidence of browsing and lack of reports earlier in the 20th century suggest that they were absent. So although we can confirm the prior absence of resident moose on the North Slope, the evidence for prior absence of snowshoe hares is convincing, but less certain. The agreement between the timing of predicted and observed snowshoe hare colonization simply adds to the evidence that the species is a recent arrival to the region. Canada lynx rely heavily on hares as prey and similarly shifted northward, or at least increased in abundance, further supporting a recent establishment of snowshoe hares.

We have related data sources from hydrology, climate, vegetation, and wildlife to describe the pathway by which warming and extended growing seasons have facilitated the expansion of shrubby vegetation and formerly boreal wildlife along riparian corridors of the Arctic. Multiple lines of evidence, when combined, show that substantial changes have occurred in tundra riparian ecosystems. The outset of the 20th century would have witnessed riparian ecosystems with much later snowmelt and peak discharge dates, shorter summers, and correspondingly shorter, less extensive riparian shrubs (Schreiner & Lowry, 2013). Those smaller shrub patches would not have hosted snowshoe hares, moose, and possibly other species whose former absence (or presence) may have been overlooked. Shrub expansion is a circumarctic phenomenon (Sturm *et al*., 2001; Myers-Smith *et al*., 2011; Frost & Epstein, 2014), so we anticipate the northward range extension of other species reliant on tall shrub habitat, such as migratory songbirds and their associated predators (Boelman *et al*., 2015). The increase in shrub habitat and associated herbivores advancing toward the Arctic Coast as a result of 20th century warming is the

contrasting terrestrial counterpart to the decline in sea ice and associated marine mammals.

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References

Beck PS, Horning N, Goetz SJ, Loranty MM, Tape KD (2011) Shrub cover on the North Slope of Alaska: a circa 2000 baseline map. *Arctic, Antarctic, and Alpine Research*, **43**, 355–363.

Bee JW, Hall ER (1956) *Mammals of Northern Alaska on the Arctic Slope*. Museum of Natural History, University of Kansas, Lawrence, Kansas.

Bhatt US, Walker DA, Raynolds MK *et al*. (2010) Circumpolar arctic tundra vegetation change is linked to sea ice decline. *Earth Interactions*, **14**, 1–20.

Boelman NT, Gough L, Wingfield J *et al*. (2015) Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Global Change Biology*, **21**, 1508–1520.

Boer AH (2007) Interspecific relationships. In: *Ecology and Management of North American Moose* (eds Franzmann AW, Schwartz CC), pp. 337–350. Wildlife Management Institute, Washington, DC.

Brown R, Derksen C, Wang L (2010) A multi-data set analysis of variability and change in Arctic spring snow cover extent, 1967–2008. *Journal of Geophysical Research: Atmospheres 1984–2012*, **115**, 1–16.

Bryant F, Kothmann M (1979) Variability in predicting edible browse from crown volume. *Journal of Range Management Archives*, **32**, 144–146.

Bryant JP, Wieland GD, Clausen T, Kuropat P (1985) Interactions of snowshoe hare and feltleaf willow in Alaska. *Ecology*, **66**, 1564–1573.

Burn DH (2008) Climatic influences on streamflow timing in the headwaters of the Mackenzie River Basin. *Journal of Hydrology*, **352**, 225–238.

Carroll G (2010) Unit 26A Furbearer. *Furbearer Management Report of Survey and Inventory Activities 1 July 2006-30 June 2009*. Alaska Department of Fish and Game, Juneau, AK, USA.

Carroll G (2011) *Unit 26A Moose Management Report of Survey and Inventory Activities 1 July 2007-30 June 2009*. Alaska Department of Fish and Game, Juneau, AK.

Chapin FS, Sturm M, Serreze MC *et al*. (2005) Role of land-surface changes in Arctic summer warming. *Science*, **310**, 657–660.

Christie K, Lindberg M, Ruess R, Schmutz J (2014) Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic. *Polar Biology*, **37**, 1111–1120.

Coady J (1980) History of moose in northern Alaska and adjacent regions. *Canadian Field Naturalist*, **94**, 61–68.

Cottam G, Curtis JT (1956) The use of distance measures in phytosociological sampling. *Ecology*, **37**, 451–460.

Ehrich D, Henden J-A, Ims RA *et al*. (2012) The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? *Oecologia*, **168**, 141–151.

Euskirchen ES, Mcguire AD, Kicklighter DW *et al*. (2006) Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Global Change Biology*, **12**, 731–750.

Euskirchen E, Mcguire A, Chapin FS III, Yi S, Thompson C (2009) Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: implications for climate feedbacks. *Ecological Applications*, **19**, 1022–1043.

Frost GV, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology*, **20**, 1264–1277.

Hall ER (1929) *Mammals Collected by Charles D. Brower at Point Barrow*. University of California Press, AK, Berkeley, CA.

Hall ES (1973) Archaeological and recent evidence for expansion of moose range in Northern Alaska. *Journal of Mammalogy*, **54**, 294–295.

Hannon S, Eason P, Martin K (1998) *Birds of North America: Willow Ptarmigan (Lagopus lagopus)*.

Henden J-A, Yoccoz NG, Ims RA, Langeland K (2013) How spatial variation in areal extent and configuration of labile vegetation states affect the riparian bird community in Arctic tundra. *PLoS ONE*, **8**, e63312.

Huryn A, Hobbie J (2012) *Land of Extremes: A Natural History of the Arctic North Slope of Alaska*. University of Alaska Press, Fairbanks, Alaska.

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*, **3**, 1–18.

Jorgenson MT, Heiner M (2003) *Ecosystems of Northern Alaska*. The Nature Conservancy, Anchorage, AK.

Jorgenson MT, Yoshikawa K, Kanevskiy M *et al*. (2008) *Permafrost characteristics of Alaska*. Institute of Northern Engineering, University of Alaska Fairbanks, Fairbanks, Alaska.

Kaufman DS, Schneider DP, McKay NP, Ammann CM, Bradley RS, Briffa KR, Vinther BM (2009) Recent warming reverses long-term Arctic cooling. *Science*, **325**, 1236–1239.

Lantz TC, Kokelj SV, Gergel SE, Henry GHR (2009) Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. *Global Change Biology*, **15**, 1664–1675.

LeResche RE, Bishop RH, Coady JW (1974) Distribution and habitats of moose in Alaska. *Naturaliste Canadien*, **101**, 143–178.

Lesack LFW, Marsh P, Hicks FE, Forbes DL (2014) Local spring warming drives earlier river-ice breakup in a large Arctic delta. *Geophysical Research Letters*, **41**, 1560–1567.

Litvaitis JA, Sherburne JA, Bissonette JA (1985) Influence of understory characteristics on snowshoe hare habitat use and density. *The Journal of Wildlife Management*, **49**, 866–873.

MacDonald SO, Cook JA (2009) *Recent Mammals of Alaska*. University of Alaska Press, Fairbanks, AK.

Manville RH, Young SP (1965) *Distribution of Alaskan Mammals*. Bureau of Sport Fisheries and Wildlife, U.S. Goverment printing office, Washington DC.

Mould E (1977a) Habitat Relationships of Moose in Northern Alaska. *Proceedings of the North American Moose Conference and Workshop*, 13, 144–156.

Mould E (1977b) Movement patterns of moose in the Colville River area, Alaska. Unpublished M.Sc. University of Alaska, Fairbanks, Alaska, 84 pp.

Myers-Smith IH, Forbes BC, Wilmking M *et al*. (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, **6**, 045509.

Myers-Smith IH, Elmendorf SC, Beck PS *et al*. (2015) Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, doi:10.1038/nclimate2697.

Naito AT, Cairns D (2011) Relationships between arctic shrub dynamics and topographically-derived hydrologic characteristics. *Environmental Research Letters*, **6**, 1–8.

Pajunen AM (2009) Environmental and biotic determinants of growth and height of arctic willow shrubs along a latitudinal gradient. *Arctic, Antarctic, and Alpine Research*, **41**, 478–485.

Pomeroy J, Bewley D, Essery R *et al*. (2006) Shrub tundra snowmelt. *Hydrological Processes*, **20**, 923–941.

Post E, Forchhammer MC, Bret-Harte MS *et al*. (2009) Ecological dynamics across the arctic associated with recent climate change. *Science*, **325**, 1355–1358.

Potvin F, Breton L, Courtois R (2005) Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. *Canadian Journal of Forest Research*, **35**, 151–160.

Prowse TD, Beltaos S (2002) Climatic control of river-ice hydrology: a review. *Hydrological Processes*, **16**, 805–822.

Puget Sound Museum mammal collection, Available at: http://portal.vertnet.org/search (accessed 21 October 2014).

Rausch R (1951) Notes on the Nunamiut Eskimo and mammals of the Anaktuvuk Pass region, Brooks Range, Alaska. *Arctic*, **4**, 146–195.

Risenhoover KL (1989) Composition and quality of moose winter diets in interior Alaska. *The Journal of Wildlife Management*, **53**, 568–577.

Schickhoff U, Walker MD, Walker D (2002) Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: a classification and ordination analysis. *Phytocoenologia*, **32**, 145–204.

Schreiner KM, Lowry TS (2013) *Reconstruction of a High-Resolution Late Holocene Arctic Paleoclimate Record from Colville River Delta Sediments*. Sandia National Laboratories, Albuquerque, NM.

Shulski M, Wendler G (2007) *The Climate of Alaska*. University of Alaska Press, Fairbanks.

Smith PS (1925) Explorations in Northwestern Alaska. *Geographical Review*, **15**, 237–254.

SNAP (2013) Scenarios Network for Alaska and Arctic Planning: Historical Monthly Temperature and Precipitation and Historical Derived Temperature Products. University of Alaska. Available at: http://www.snap.uaf.edu/data.php (accessed 3 November 2013).

Stewart IT, Cayan DR, Dettinger MD (2005) Changes toward earlier streamflow timing across western North America. *Journal of Climate*, **18**, 1136–1155.

Stone RS, Dutton EG, Harris JM, Longenecker D (2002) Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research: Atmospheres (1984–2012)*, **107**, ACL 10-11–ACL 10-13.

Sturm M, Benson C (2004) Scales of spatial heterogeneity for perennial and seasonal snow layers. *Annals of Glaciology*, **38**, 253–260.

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

Sullivan TP, Sullivan DS, Lindgren PM, Ransome DB (2010) Long-term responses of mammalian herbivores to stand thinning and fertilization in young lodgepole pine (*Pinus contorta* var. latifolia) forest. *Canadian Journal of Forest Research*, **40**, 2302–2312.

Tan A, Adam JC, Lettenmaier DP (2011) Change in spring snowmelt timing in Eurasian Arctic rivers. *Journal of Geophysical Research: Atmospheres 1984–2012*, **116**, 1–12.

Tape KD, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686–702.

Tape KD, Verbyla D, Welker JM (2011) Twentieth century erosion in Arctic Alaska foothills: the influence of shrubs, runoff, and permafrost. *Journal of Geophysical Research*, **116**, G04024.

Tape KD, Hallinger M, Welker JA, Ruess RW (2012) Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems*, **15**, 711–724.

Team C (2003) *Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna Map No. 1*. U.S. Fish and Wildlife Service, Anchorage, AK.

Telfer ES (1984) Circumpolar distribution and habitat requirements of moose (*Alces alces*). In: *Northern Ecology and Resource Management* (eds Olson R, Hastings R, Geddes F), pp. 145–182. University of Alberta Press, Edmonton, AB, Canada.

University of Alaska Museum of the North Mammal Collection, Available at: http://www.uaf.edu/museum/collections/mammal/ (accessed 22 october 2014).

University of Kansas Biodiversity Institute & Natural History Museum, Available at: http://naturalhistory.ku.edu/collections (accessed 24 october 2014).

Walker DA (1985) Vegetation and environmental gradients of the Prudhoe Bay region, Alaska. *CRREL Report*. Cold Regions Research and Engineering Lab, Hanover, NH.

Walker DA (1987) Height and growth rings of Salix lanata ssp richardsonii along the coastal temperature gradient of northern Alaska. *Canadian Journal of Botany*, **65**, 988–993.

Weeden RB (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. *The Auk*, **86**, 271–281.

Woo M-K, Thorne R (2003) Streamflow in the Mackenzie basin, Canada. *Arctic*, **56**, 328–340.

Xu L, Myneni R, Chapin FS III *et al.* (2013) Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change*, **3**, 581–586.

Yang D, Robinson D, Zhao Y, Estilow T, Ye B (2003) Streamflow response to seasonal snow cover extent changes in large Siberian watersheds. *Journal of Geophysical Research: Atmospheres 1984–2012*, **108**, 1–14.

Zhang K, Kimball JS, Kim Y, Mcdonald KC (2011) Changing freeze-thaw seasons in northern high latitudes and associated influences on evapotranspiration. *Hydrological Processes*, **25**, 4142–4151.