Received: 20 September 2017 | Revised: 9 April 2018 | Accepted: 22 May 2018
DOI: 10.1111/gcb.14332

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Tundra be dammed: Beaver colonization of the Arctic

Ken D. Tape[1] | Benjamin M. Jones[1,2] | Christopher D. Arp[1] | Ingmar Nitze[3,4] | Guido Grosse[3,4]

[1]Water and Environmental Research Center, University of Alaska, Fairbanks, Alaska
[2]U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska
[3]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Potsdam, Germany
[4]Institute of Earth and Environmental Science, University of Potsdam, Potsdam, Germany

Correspondence
Ken D. Tape, Water and Environmental Research Center, University of Alaska, Tanana Lp., Fairbanks AK 99775.
Email: kdtape@alaska.edu

Funding information
Alaska EPSCoR NSF, Grant/Award Number: OIA-1208927; State of Alaska; European Research Council, Grant/Award Number: 338335; Helmholtz Association Initiative and Networking Fund, Grant/Award Number: ERC0013; European Space Agency GlobPermafrost; University of Alaska Fairbanks Office of Vice Chancellor for Research

Abstract
Increasing air temperatures are changing the arctic tundra biome. Permafrost is thawing, snow duration is decreasing, shrub vegetation is proliferating, and boreal wildlife is encroaching. Here we present evidence of the recent range expansion of North American beaver (*Castor canadensis*) into the Arctic, and consider how this ecosystem engineer might reshape the landscape, biodiversity, and ecosystem processes. We developed a remote sensing approach that maps formation and disappearance of ponds associated with beaver activity. Since 1999, 56 new beaver pond complexes were identified, indicating that beavers are colonizing a predominantly tundra region (18,293 km^2) of northwest Alaska. It is unclear how improved tundra stream habitat, population rebound following overtrapping for furs, or other factors are contributing to beaver range expansion. We discuss rates and likely routes of tundra beaver colonization, as well as effects on permafrost, stream ice regimes, and freshwater and riparian habitat. Beaver ponds and associated hydrologic changes are thawing permafrost. Pond formation increases winter water temperatures in the pond and downstream, likely creating new and more varied aquatic habitat, but specific biological implications are unknown. Beavers create dynamic wetlands and are agents of disturbance that may enhance ecosystem responses to warming in the Arctic.

KEYWORDS
arctic tundra, beaver, climate change, permafrost, population recovery, salmon, shrub expansion, stream

1 | INTRODUCTION

1.1 | Transitions in the tundra

The Arctic is warming and thawing. Air temperatures in the Arctic warmed by 1.8°C since the end of the 19th century, which is 1.6 times faster than the Northern Hemisphere average (Bekryaev, Polyakov, & Alexeev, 2010; Serreze & Barry, 2011). In Alaska, warming has been most pronounced in arctic coastal regions during the fall, winter, and spring (Wendler, Moore, & Galloway, 2014). Snowmelt is also occurring earlier across the Arctic (Brown, Derksen, & Wang, 2010). Perennially frozen ground, or permafrost, has warmed rapidly since the 1980s (Romanovsky, Smith, & Christiansen, 2010), initiating thermokarst (Liljedahl et al., 2016). Rivers and lakes are breaking up earlier (Šmejkalová, Edwards, & Dash, 2016; Tan, Adam, & Lettenmaier, 2011; Tape, Christie, Carroll, & O'Donnell, 2016), and rivers are flowing more during the winter (St. Jacques & Sauchyn, 2009). Trends toward thinner lake ice over the last several decades are occurring due to warmer and snowier winters, resulting in shifting lake ice regimes (Arp, Jones, Lu, & Whitman, 2012; Surdu, Duguay, Brown, & Fernández Prieto, 2014), as well as sublake permafrost degradation (Arp et al., 2016). River systems may be responding similarly with an upstream regime shift from bedfast to floating ice, with impacts to fluvial geomorphology and aquatic habitats (McNamara &

 © 2018 John Wiley & Sons Ltd

Kane, 2009). Tundra vegetation has been 'greening' as increased spring and growing season temperatures have fostered increased photosynthesis and deciduous shrub vegetation (Sturm, Racine, & Tape, 2001; Xu et al., 2013), particularly in riparian zones or areas of permafrost thaw or disturbance (Lantz, Kokelj, Gergel, & Henry, 2009; Myers-Smith et al., 2011).

Wildlife appear to be responding to these changes in arctic tundra regions. For example, formerly boreal forest wildlife such as moose and snowshoe hares, which depend on shrub forage protruding from the snow in winter, have exploited the increase in height and extent of riparian shrubs by extending their range into Arctic Alaska, where they now compete with ptarmigan (*Lagopus* spp.) and other species for willow forage in winter (Tape, Gustine, Ruess, Adams, & Clark, 2016; Tape, Christie, et al., 2016). Pacific salmon (*Oncorhynchus* spp.) are shifting their distribution northward, though they have not successfully reproduced in most of Arctic Alaska (Dunmall, Mochnacz, Zimmerman, Lean, & Reist, 2016; Grebmeier et al., 2006; Nielsen, Ruggerone, & Zimmerman, 2013).

1.2 | Beaver colonization of the Arctic?

Terrestrial and aquatic changes may have primed the arctic tundra biome for beaver colonization. Beavers were nearly extirpated from the boreal forest of Alaska during the 19th and early 20th centuries, as they were throughout North America in previous centuries, by trapping for their valuable fur pelts (Bockstoce, 2009). Trapping regulations implemented in the early 20th century instigated their comeback in the boreal forest of Alaska. As they returned to the boreal forest in Alberta during the mid-20th century, beavers explained 80% of a ninefold increase in open water extent, which dwarfed the effects of climate (Hood & Bayley, 2008). Beavers are a keystone species whose engineering heavily influences streams, rivers, riparian corridors, and lakes throughout the boreal forest and other biomes.

The northern edge of beaver distribution has historically been limited to forested areas (Bockstoce, 2009; McCulloch & Hopkins, 1966). Prior to the 20th century, evidence of beavers in tundra regions is scant, but beaver-gnawed trees found in some river exposures date to the early Holocene (7,270 ± 350 C^{14} ya, and earlier), when climate was warmer than present (McCulloch & Hopkins, 1966). It is possible that a lack of sufficient woody vegetation or unfrozen water in winter has, until recently, made the tundra uninhabitable for beavers; both of these habitat constraints have loosened with warming (St. Jacques & Sauchyn, 2009; Sturm et al., 2001). It is also possible that beaver populations are still rebounding from heavy trapping during the 19th and early 20th centuries. Recent observations suggest beaver movement from forest into tundra of western and northwestern Alaska (Brubaker et al., 2011; Rabung, Sam and Norton Sound Bering Straight Regional Planning Team, 2015), and northwestern Canada (Jung, Frandsen, Gordon, & Mossop, 2017), but beavers are thought to be absent from the North Slope of Alaska (Huryn & Hobbie, 2012). Because beavers are well known agents of disturbance and wetland formation in their contemporary distribution, it is important to understand where and how rapidly beavers will colonize the Arctic, and how this will impact riparian and freshwater ecosystems set within permafrost landscapes. Is beaver colonization of arctic tundra regions more widespread than previously observed, and are beavers poised to disrupt arctic stream and riparian ecosystems?

Here we use satellite imagery to detect formation and disappearance of beaver ponds. We demonstrate that beavers have recently colonized arctic tundra regions of northwest Alaska (Figure 1), dramatically altering numerous tundra streams on local to regional scales. We explore the observed and predicted ramifications of

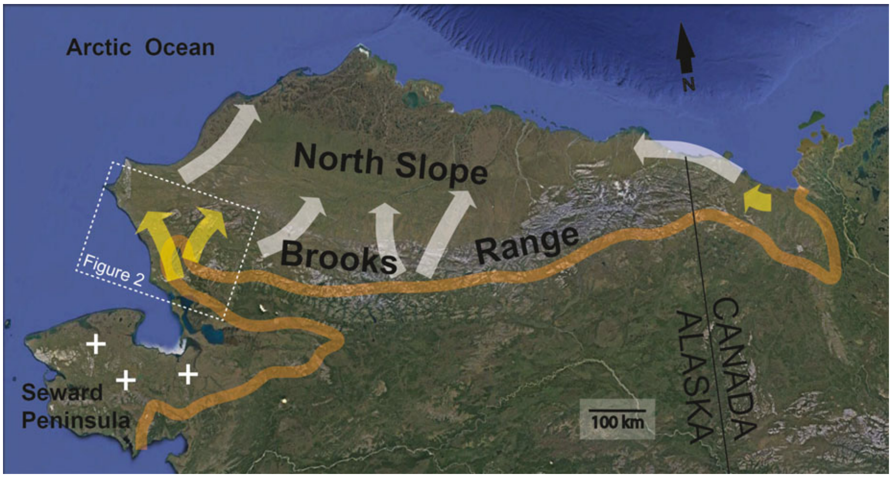

FIGURE 1 Map of recent beaver colonization in arctic tundra of Alaska and northwestern Canada. Orange line approximates treeline, which was historically considered to be the range limit of beavers (Bockstoce, 2009; McCulloch & Hopkins, 1966). Yellow arrows denote known beaver colonization routes since 1999, including an observation of a new dam on the Babbage River in Canada (Jung et al., 2017), and evidence of many new dams and ponds in the white box covering the western Brooks Range. White arrows speculate future colonization routes, and plus signs indicate observations of beaver ponds beyond treeline on the Seward Peninsula

beaver colonization in tundra ecosystems, with particular attention to physical processes and salmon habitat.

2 | MATERIALS AND METHODS

2.1 | Observing beaver activity in NW Alaska from space

We identified sites of recent beaver activity and dam building in the Lower Noatak River, Wulik, and Kivalina River watersheds (combined: 18,293 km^2) in the arctic tundra region of NW Alaska by detecting formation and disappearance of beaver ponds. This region was selected because it is representative of treeline and low-arctic tundra, and lacking steep mountain passes that could impede beaver dispersal. The Lower Noatak River watershed is predominantly tundra, with 3.5% forest cover concentrated along rivers and streams (Homer et al., 2015). The Wulik and Kivalina River watersheds are tundra. Basic permafrost, vegetation, and geographic attributes were calculated for the watersheds using available geospatial data.

To detect beaver activity, we used the entire archive of Landsat images available for the Lower Noatak, Wulik, and Kivalina River watersheds between 1999 and 2014, then filtered acquisition dates to the peak summer months of July and August, with cloud cover of <70%. Landsat TM, ETM+ and OLI images acquired during this time period were analyzed since there were very few observations prior to 1999 in this region. Imagery was acquired as the surface reflectance data product from the United States Geological Survey (USGS) via the EROS Science Processing Architecture (ESPA) ordering system. After masking clouds, shadows, and snow using the masking algorithm FMask (Zhu, Wang, & Woodcock, 2015), we calculated trends of different multispectral indices (Tasseled Cap Brightness, Greeness, and Wetness; Normalized Difference Vegetation Index NDVI; Normalized Difference Moisture Index NDMI) to map changes in surface properties (Nitze & Grosse, 2016; Nitze et al., 2017). We then categorized the temporal trends of each multispectral index (slope, intercept, confidence intervals) into four classes: stable land, stable water, transition from land to water (wetting), and transition from water to land (drying). A Random Forest supervised machine learning classification was used, which was trained using more than 500 training samples with 200 decision trees. This additional step translated the spectral-temporal signal into semantic information with probability values for the four classes based on multiple indices. Pixels with a probability >50% indicating a wetting or drying trend were extracted for further analysis. The year of pond formation or disappearance was estimated by identifying a 30% or more annual change in the wetness index.

To further refine the potential beaver activity map, we selected groups of pixels >0.5 ha in area (minimum mapping unit) that represented wetting or drying in the Landsat trend analysis. We selected the minimum mapping unit to be about three times the size of the minimum resolution of the imagery, or more than five (0.54 ha) pixels, consistent with the limitations in image resolution (Homer et al., 2015). We then created a 30 m buffer of the NHD (National Hydrological Dataset, https://nhd.usgs.gov/) streams layer and a 60 m buffer of the NHD rivers layer. The overlapping area of these two polygons was removed to ignore objects associated with river migration, but to include groups of wetting pixels that might not have directly intersected the NHD streams layer due to incongruities between sources. Landsat wetting and drying trend pixel groups of at least 0.5 ha with their centroid located in this masked area were extracted for further analysis. Extracted areas were again refined by removing areas that had burned between 1999 and 2014 or shared a boundary with a waterbody in the NHD lakes layer to avoid misclassification due to burning or false positives due to natural thermokarst lake expansion. Some coastlines or river deltas appeared to be wetting unrelated to beavers, so locations within 1 km of the ocean were also removed. An IfSAR digital terrain model from 2012 was also used to create a slope layer and all wetting and drying objects with a slope >10° were removed to avoid false positives caused by cloud or mountain shadows.

The locations of all potential beaver activity determined by extraction of wetting and drying objects from the Landsat-based trend analysis were then verified using recent (post-2005) submeter resolution commercial satellite imagery (i.e., Quickbird, IKONOS, Geoeye, Worldview) available freely in Google Earth or in the National Geospatial-Intelligence Agency image archive. Beaver activity was verified in high-resolution vertical time series imagery by the appearance or disappearance of ponds associated with dams visible in the submeter resolution imagery. Beavers that did not build dams and change water levels were not detected using this method, as were not beaver dams that were constructed prior to 1999 and maintained a stable surface water feature. In some locations historical aerial photography from the 1940s and later was used to confirm absence of beaver activity prior to Landsat imagery starting in 1999.

3 | RESULTS

The Landsat and high-resolution time series imagery analysis revealed that beavers have colonized the arctic tundra of northwestern Alaska between 1999 and 2014 (Figure 2). Eighty-three locations of potential beaver dam building activity were identified using the Landsat time series analysis: 70 locations representing wetting trends and 13 representing drying trends. After verification using high-resolution satellite imagery, 80% of the wetting locations identified using Landsat imagery were confirmed as representing beaver activity (damming and pond formation), 11% of the mapped wetting locations were unrelated to beavers (no apparent evidence of dam building activity), and 9% of the wetting locations could not readily be distinguished as being beaver related or not. For the drying locations, 31% represented beaver activity (pond drying due to dam abandonment), 62% were unrelated to beavers, and 7% were undetermined (Figure 2, Table 1). Wetting trend locations that were falsely flagged commonly occurred as a result of thermokarst. Falsely flagged drying trend locations were mostly due to lake and pond drying or drainage that appeared to be unrelated to beaver activity.

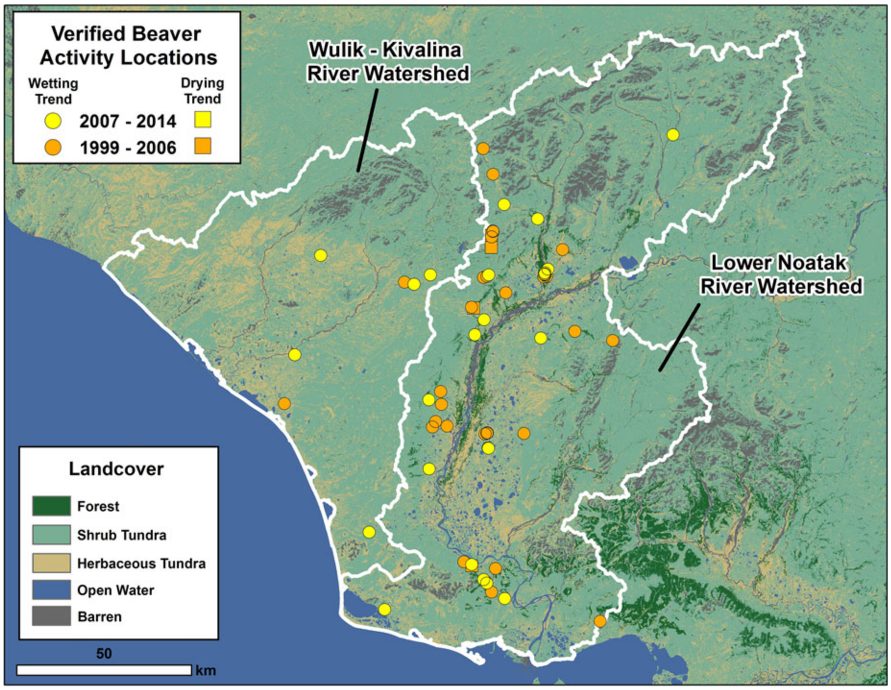

FIGURE 2 Map, inset from Figure 1, showing the influx of beavers and formation of wetlands along streams in predominately arctic tundra regions of northwestern Alaska. Locations and timing were derived from Landsat time series analysis from 1999 to 2014 that was refined to identify beaver ponds and then validated using recent, high-resolution satellite imagery

The pattern of beaver colonization suggests that beavers are rapidly expanding their range via major rivers and streams, as well as along the coast (Figure 2). We estimate that range expansion in the northwest arctic of Alaska has occurred at an average rate of 8 km/year, calculated as the linear distance along a swath of the study region (Figure 2) divided by the 16-year interval. Additional reconnaissance outside our study area using aerial overflights of the region and Google Earth revealed numerous beaver dams on the Seward Peninsula (even further from treeline than in the primary study region in Figure 2) and a dozen potential beaver dams in the tundra regions of north-central Brooks Range of Alaska. The location of these dams indicates that beavers likely are colonizing the north-central Brooks Range via interconnected lakes and streams in the broad passes constituting the headwaters of the Alatna, Nigu, and Etivluk Rivers, the latter two of which drain into the Colville River on the North Slope.

Remote sensing shows that beaver activity transforms arctic streams into dynamic pond-wetland systems. High-resolution satellite imagery consistently shows relatively stable stream and river channels prior to beaver colonization, followed by pond formation, evolution, and channel modification or diversion resulting from beaver activities (Figures 3 and 4). Thermokarst landforms have developed adjacent to new ponds and new stream channels made by beavers, as well as downstream of failed beaver dams (Figure 5). Wintertime images show unfrozen water downstream of beaver ponds (Figure 6).

TABLE 1 Results from remote sensing detection of beaver activity and geospatial analysis

	Lower Noatak River	Wulik-Kivalina River
Potential beaver disturbances[a]		
Wetting (*n*)	60	10
Drying (*n*)	10	3
Validation of beaver disturbances	Yes, no, uncertain	Yes, no, uncertain
Wetting (*n*)	49, 7, 4	7, 1, 2
Drying (*n*)	4, 5, 1	0, 3, 0
Mean beaver pond distance to treeline		
Wetting	6.1 km	33.1 km
Drying	6.3 km	–
Hydrologic unit size[b]	11,650 km^2	6,643 km^2
Soil characteristics		
Probability of permafrost in upper 1 m (%)[c]	73.7	84.9
Vegetated land cover[d]		
Herb tundra	12.8%	21.2%
Shrub tundra	70.7%	72.5%
Forest	3.5%	0.4%

Note. [a]Mapped as riparian area wetness trend derived from Landsat TM, ETM+, OLI time series analysis; [b]HUC level 8 WBD Alaska National Hydrography 2004, clipped along coast with 2012 IfSAR DTM; [c]Pastick et al. (2015); [d]Simplified from National Land Cover Database for Alaska 2011.

FIGURE 3 New beaver activity since 1999 converting an arctic tundra stream (top) into a wetland (center) on the Seward Peninsula, Alaska. For scale, the lodge at center is approximately 8 m in diameter. Oblique aerial photo: Chris Arp. N 65°51.71′, W 165°18.44′

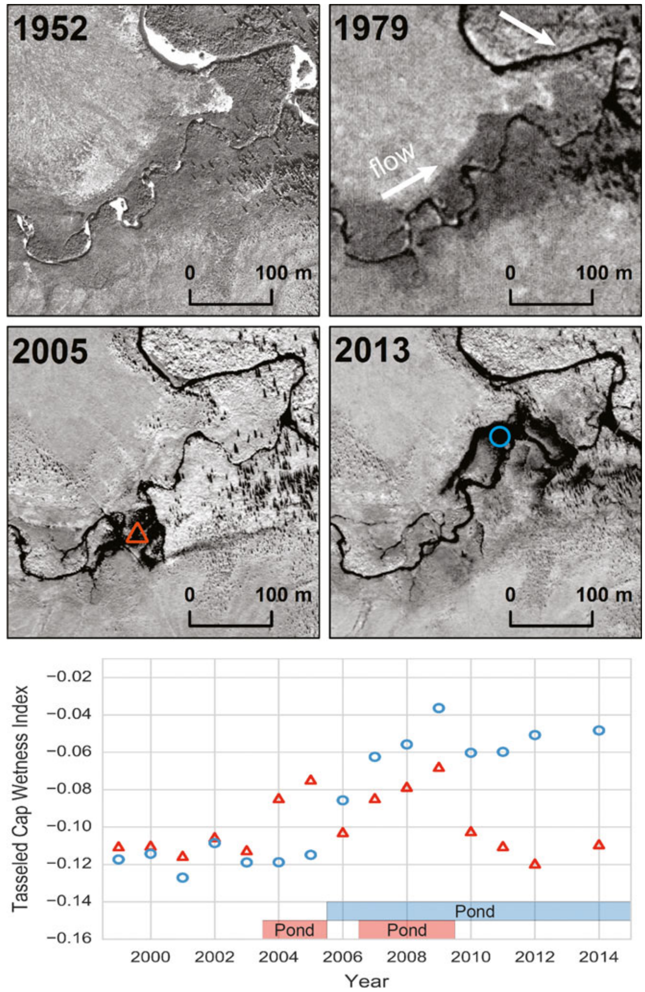

FIGURE 4 Time series of high-resolution imagery showing a relatively stable stream channel prior to beaver colonization evident in 2005 image. Dam construction, pond formation (2005 imagery), and pond relocation (2013 imagery) demonstrate the rapid change and disturbance imposed by beavers on arctic stream ecosystems. Image time series consists of aerial photography (1952 and 1979), Digital Globe Inc. Quickbird imagery (2005), and Worldview 2 imagery (2013); spruce trees dot the right part of the images. Graph shows time series of Landsat tasseled cap wetness index indicating timing of pond formation and duration for the two beaver ponds shown in imagery. N 67°40.33′, W 163°7.31′

4 | DISCUSSION

4.1 | Probable causes of beaver range expansion

In northern regions, beavers need a reliable water source underneath ice at its maximum thickness to provide overwintering habitat, mobility, protection from predators, and access to cached shrub forage (MacFarlane et al. 2015). Woody vegetation is needed for forage, and for building dams that impound streams, lake outlets, river backwaters, and hillslope springs, as well as for constructing lodges. Streams or rivers of intermediate size and low gradient are considered optimal habitats in many regions (MacFarlane et al. 2015). We suspect that similar habitat requirements also apply to the tundra (Aleksiuk, 1970), and that both lentic and lotic environments with bedfast ice or sparse riparian forage have in the past prevented beavers from colonizing tundra regions.

The constraints of unfrozen water and woody vegetation have been loosening as winter and summer temperatures have increased in arctic and boreal regions. Riparian shrubs have increased in height and extent across the Arctic (Myers-Smith et al., 2011), including northern and western Alaska, increasing forage and woody material for dam building. Unlike the resident browsers moose and snowshoe hares, beavers are not limited to forage sticking above the snow during winter, but they do harvest and cache primarily willow shrubs during July and August for consumption during winter (Aleksiuk, 1970). Some reaches of bedfast ice in streams and rivers are likely shifting to floating ice regimes (McNamara & Kane, 2009), along with increases in winter river discharge (St. Jacques & Sauchyn, 2009), creating room for beavers to maneuver under the ice.

These critical components of beaver habitat in the arctic tundra are improving, but, like for moose, the causes of beaver range expansion into tundra are complicated by the overtrapping of beavers (Bockstoce, 2009) and possible overhunting of moose in the 19th and early 20th centuries (Coady, 1980). It is possible that the expansion of beavers into the Arctic is part of a population recovery and range expansion that began a century ago, or that this rebound has combined with the improved habitat to produce the recent range expansion. One key question that would address this but remains unanswered is "Prior to the recent (last half-century) wave of colonization, have beavers occupied arctic tundra regions of Alaska during the last thousand years?" If beavers were not present in the tundra prior to the fur trade, then climate and habitat amelioration might explain their recent colonization of tundra; if beavers were present in the tundra prior to the fur trade, then the current colonization could be a recovery and reoccupation of their former range. Based on (a) the observed rates of beaver expansion into tundra, and (b) improving tundra and stream habitat, beavers could

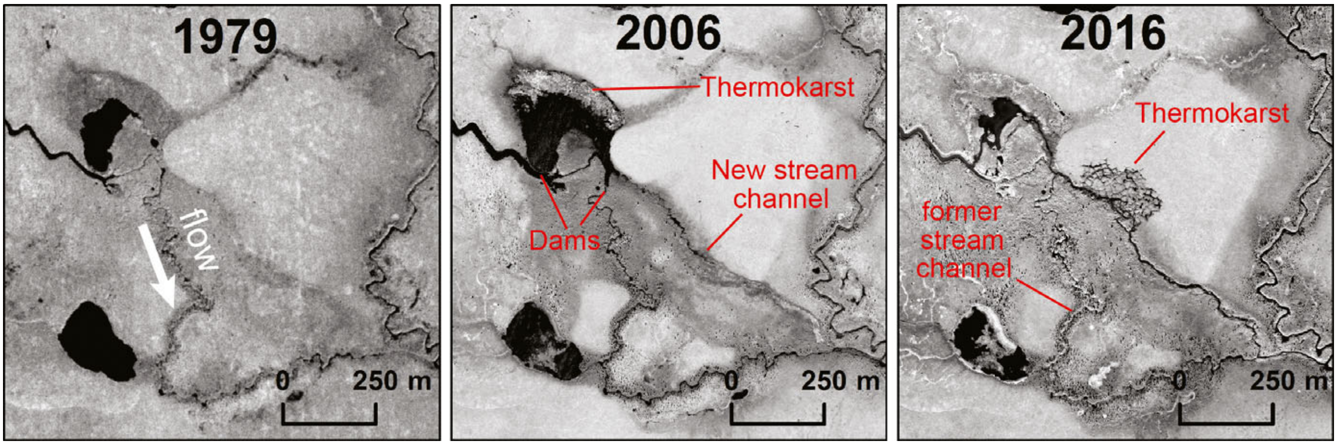

FIGURE 5 Examples of changes visible from aerial photography and satellite imagery resulting from beaver activity in tundra, including wetting (upper pond), drying (upper and lower ponds), stream diversion, and thermokarst development related to wetting. It appears that beavers began damming this area between 1999, when our Landsat time series begins, and 2006. Image time series consists of aerial photography (1979), Digital Globe Inc. Quickbird imagery (2006), and Worldview 2 imagery (2016). N 67°35.34′, W 163°3.05′

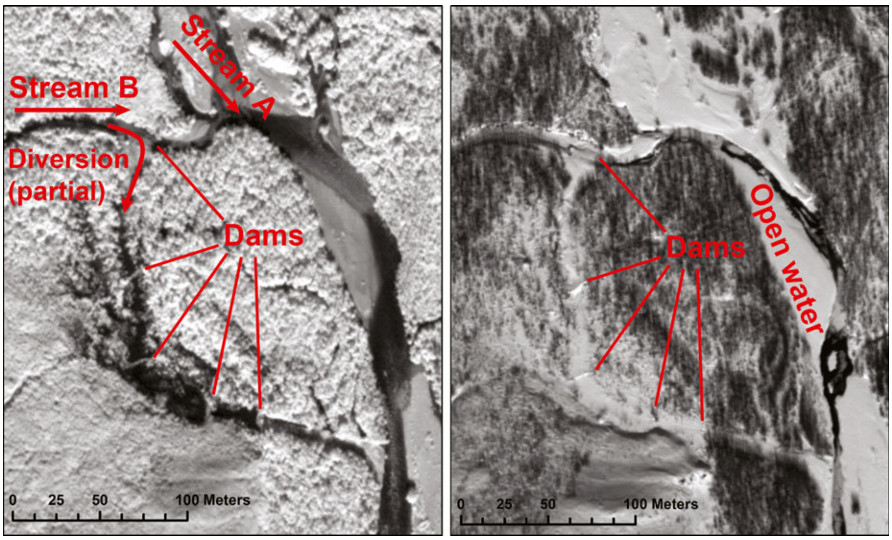

FIGURE 6 Summer and winter satellite images of a stream confluence showing beaver dams among poplar stands (left), with open water downstream during winter (right). We surmise that the dams and ponding allow water to remain warmer and unfrozen during winter, emanating downstream as hyporheic flow or leakage through the dam. It is unclear whether the open water existed prior to beaver colonization; damming could have produced that, but beavers also seek springs or upwellings as habitat. Image pair consists of Digital Globe Inc. Quickbird imagery acquired in 2008 (left) and Worldview 2 imagery acquired in 2010 (right). N 67°58.89′, W 162° 43.37′

colonize selected streams, rivers, and lakes with suitable woody vegetation and water all over Arctic Alaska during the next 20–40 years (8 km/year × 40 years = 320 km).

4.2 | Beaver impacts in the boreal forest and lower latitudes

By constructing dams, beavers severely alter the stream hydrologic regime, which alters freshwater physical habitat, biotic composition, and habitat connectivity (MacFarlane et al. 2015). Changes in hydrologic regime facilitate the invasion of new species, including riverine plants, invertebrates, and fish (Bunn & Arthington, 2002). In the boreal forest and more southerly ecosystems, consequences of beaver activity in streams include a more open canopy, increased temperature variability, increased wetland area and a shift toward anaerobic biogeochemical cycling and nitrogen accumulation, as well as greater trapping of sediment, nutrients, and detritus (Naiman, Melillo, & Hobbie, 1986). Pond formation induces a shift from lotic to lentic communities. The increase in diversity of freshwater habitats in low order streams typically increases biocomplexity (Naiman & Rogers, 1997). On low-order streams, the impact of beavers on fishes has been mostly positive (Pollock, Pess, Beechie, & Montgomery, 2004), though negative impacts include siltation of spawning beds, low oxygen conditions in ponds, and dams blocking passage (Kemp, Worthington, Langford, Tree, & Gaywood, 2012). Beaver dams do not consistently impede salmonid movements, however, as shown by

Bonneville Cutthroat Trout (*Oncorhynchus clarkii Utah*) and Brook Trout (*Salvelinus fontinalis*) movement through 21 dams in two northern Utah streams (Lokteff, Roper, & Wheaton, 2013). Beavers have been reintroduced to improve salmon habitat in low order streams of the western U.S. (Pollock et al., 2014). Significant increases in Steelhead (*Oncorhynchus mykiss)* returns were observed after constructing human-made 'beaver dam analogs' that facilitated further beaver dam construction (Bouwes et al., 2016).

4.3 | Predicted beaver impacts to the physical environment of arctic tundra streams

In the Arctic, by building dams, beavers have transformed stream reaches into wetlands (e.g., Figure 4), likely with similar effects as at lower latitudes, such as the shift from lotic to lentic environments and increased variability in aquatic habitat. The Arctic, however, may have unique responses related to the tundra vegetation, presence of thaw-susceptible permafrost soils, scarcity of water in winter, and limited biodiversity. The predictions below are not intended to be exhaustive, but rather highlight some of the profound changes that are likely to occur in response to beaver colonization. The most reliable predictions pertain to physical processes such as pond formation and resulting changes in water temperature or permafrost stability, which have been studied in the Arctic for decades. In contrast, biological changes are more complex and poorly studied, due to beaver's recent colonization of tundra regions.

In the tundra environment, lake or stream bed temperatures during winter increase with water depth relative to ice thickness and thermal stratification of the water column (Arp et al., 2016). When beavers dam streams to create ponds, this not only provides them winter access to cached forage but also elevates water and ambient sediment temperatures, in some cases shifting stream systems from previously bedfast conditions to floating ice regimes. This localized regime shift, which also extends downstream as warmer water leaks from the dam (Figure 6), could alter river physical processes similar to regional shifts from bedfast to floating ice hypothesized under continued warming (Figure 7). River ice regimes are linked to channel morphology, flood effectiveness, mode of ice breakup, and sediment transport (McNamara & Kane, 2009).

If mean annual waterbody bed temperature exceeds 0°C, then subriver and substream permafrost will thaw. Inundation of surrounding areas during beaver pond formation typically triggers permafrost degradation and thermokarst (e.g., Figure 5). The permafrost that constitutes arctic tundra soils thus makes the tundra uniquely vulnerable to beavers. Water bodies in permafrost regions cause the greatest (among all land cover classes) difference between ground temperatures and regional air temperatures, increasing sediment temperatures up to 10°C above the mean annual air temperatures and allowing permafrost under lakes to thaw, even in cold permafrost regions (Brewer, 1958; Jorgenson et al., 2010; Lachenbruch, Brewer, Greene, & Marshall, 1962; Smith, 1975). Models simulating the thermal disturbance caused by shallow (<1 m) ponds show thermokarst occurring four- to fivefold

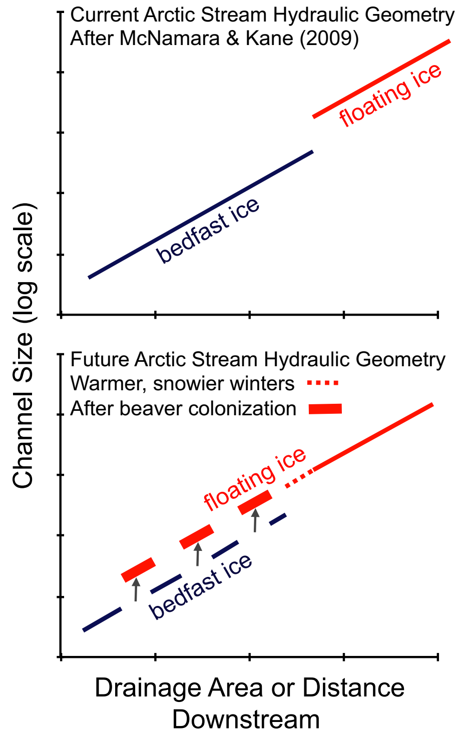

FIGURE 7 Conceptual diagram showing current arctic stream hydraulic geometry (top), and hypothesized changes due to climate change and beaver colonization (bottom). Beaver establishment leads to warmer winter water temperature and increased floating ice regimes in streams, which adds heterogeneity to aquatic habitat

faster and 30–40 years earlier than the surrounding tundra (Langer et al., 2016). Thawing permafrost and destabilizing streambanks and riparian corridors could increase stream nutrients and sediment loads (Bowden et al., 2008; Kokelj et al., 2013), but beaver dams also attenuate these fluxes.

4.4 | Predicted beaver impacts to biological processes

How beaver colonization will impact the biology of arctic stream and riparian ecosystems has not been studied. Throughout beaver's (non-arctic) range, the biological responses to beaver colonization vary according to numerous local attributes, as well as to the age of the dam (Ecke et al., 2017), and we anticipate much of that variability to also be present in the Arctic. However, the increasing water temperatures and permafrost disturbance associated with beaver dams may enhance biological processes in the Arctic more so than in other biomes. Many arctic freshwater species are limited by insufficient unfrozen water during winter, or by low water temperatures (Reist et al., 2006), suggesting that greater unfrozen water or elevated water temperatures associated with beaver activity (Figures 6 and 7) will make conditions suitable for new freshwater species. New beaver ponds are moderating the stream thermal regime, varying aquatic thermal habitat, and likely increasing biodiversity, thus functioning like springs or oases in the Arctic.

4.5 | Predicted beaver impacts to salmon habitat in the Arctic

Beaver ponds in the tundra may improve fish habitat and facilitate establishment of new species. Warmer water and substrate temperatures above and below beaver dams may promote successful salmon reproduction in arctic streams sooner than expected. Pacific salmon, notably Chum salmon (*O. keta*) and Pink salmon (*O. gorbuscha*), have been observed in many rivers across the North Slope of Alaska. However, it appears that most arctic freshwater ecosystems are too cold for successful salmon reproduction and egg incubation; juveniles are extremely rare (Craig & Haldorson, 1986; Dunmall et al., 2016). Rivers on the western North Slope have few perennial water sources, but perennial groundwater sources on the eastern North Slope into northwestern Canada raise winter stream temperatures and locally permit Dolly Varden (*Salvelinus malma*) spawning and reproduction (Craig & McCart, 1975; Daum, Rost, & Smith, 1984). Dolly Varden share general spawning habitat requirements with Pink salmon and Chum salmon, but Dolly Varden need a spawning temperature of only 3°C, whereas Pink salmon and Chum salmon require 4°C. Perennial groundwater sources (springs) in certain arctic streams and rivers provide the needed warmer water spawning and incubation conditions for Dolly Varden, and possibly in a warmer future for stray salmon (Dunmall et al., 2016).

Dam-induced hyporheic upwelling downstream of beaver ponds (Westbrook, Cooper, & Baker, 2006; Woo & Waddington, 1990) may increase interstitial gravel (substrate) temperatures during winter, permitting successful egg incubation and spawning by stray salmon or other fishes (Figures 6 and 7). Although we predict the net effect of beavers on salmon in the Arctic to be positive, we anticipate complex interactions and variable responses depending on the local attributes, including the setting of the dam on a floodplain (Malison, Kuzishchin, & Stanford, 2016), stream, hillslope spring, or lake outlet. Furthermore, though the creation of salmon habitat could have positive effects, other changes due to beavers such as dams blocking passage or siltation of spawning beds could outweigh those effects and lead to negative outcomes for salmon. Nonetheless, beaver creation of salmon habitat suggests that if beavers continue to colonize the arctic tundra of Alaska in the coming decades, they may facilitate established salmon runs in arctic streams and rivers.

Beaver encroachment and impacts to salmon and other fishes are a major concern for people in tundra communities (Moerlein & Carothers, 2012). Salmon is a critical commercial and subsistence resource wherever it occurs in Arctic Alaska (Fall et al., 2009). The harvest and importance of salmon decreases as their prevalence decreases, with northern arctic communities in Alaska (Kivalina, Point Hope, Point Lay, Wainwright, Barrow, Nuiqsut, Kaktovik, Anaktuvuk Pass) catching occasional (stray) salmon, but lacking successfully reproducing (established) salmon (Fall et al., 2009). In arctic communities without established salmon the few stray salmon harvested may be the seeds of an important resource awaiting warmer water temperatures, and beaver colonization could accelerate or negate distributional shifts in salmon.

4.6 | Predicted beaver impacts to arctic riparian ecosystems

After beaver establishment in a tundra riparian corridor, we anticipate an immediate decline in shrub height and extent due to inundation or to beavers cutting them down for forage caches and to build dams. We predict that the longer term effects of beaver-induced disturbance, however, will actually enhance shrub growth. Thermokarst development related to inundation, increased hyporheic and groundwater flow, channel engineering, changing water levels, beaver trails and slides, and ongoing geomorphic changes wrought by beaver activity are types of disturbances that expose mineral substrate and facilitate shrub growth (Lantz et al., 2009; Myers-Smith et al., 2011). In spite of the ongoing shrub harvest by beavers, we predict that the long-term (decadal+) effects of beavers on riparian corridors will be to widen the floodplain and facilitate disturbances, both of which promote riparian shrub growth and extent.

4.7 | Predicted beaver impacts to shrub herbivores

Prior to beaver arrival, shrubs would have functioned as forage or cover for moose, snowshoe hares, and ptarmigan. Moose, and probably snowshoe hares, colonized Arctic Alaska during the last century, concurrent with increases in willow forage (Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016), so the initial reduction in forage and habitat caused by new beavers could compromise moose and snowshoe hare's tenuous foothold in the region. Beavers cut down entire shrubs and favor willow bark, leaves, and new growth for forage, which facilitates dominance by less-palatable alder shrubs (Aleksiuk, 1970). More critically, the Alaska Hare (*Lepus othus*), whose global distribution is limited to the western tundra region of Alaska and relies on willow shrubs in winter (Cason, Baltensperger, Booms, Burns, & Olson, 2016), may be at least temporarily negatively impacted by the reduction of its habitat by encroaching beavers. The decadal and longer effects are unknown, but we believe that ultimately shrubs and shrub herbivores will thrive with the addition of disturbances like changing water levels and thawing permafrost.

The arrival of beavers and their dramatic modifications to tundra ecosystems signals a benchmark in the trajectory of arctic riparian and freshwater ecosystems. The arctic ecosystem is characterized by cold, continuous permafrost overlain by vegetation and peat, which impart resiliency during warmer periods (Jorgenson et al., 2010). Beavers are agents of disturbance that can disrupt tundra resiliency by creating wetlands (Figures 3–5) that increase winter water temperature and thaw permafrost underneath and surrounding newly inundated areas, creating thermokarst terrain (Figure 5). These physical changes create increased aquatic habitat heterogeneity and likely biological diversity. The striking changes caused by beavers create a management challenge as the ecosystem properties and resources of tundra streams are modified by the influx of beavers (Figure 8).

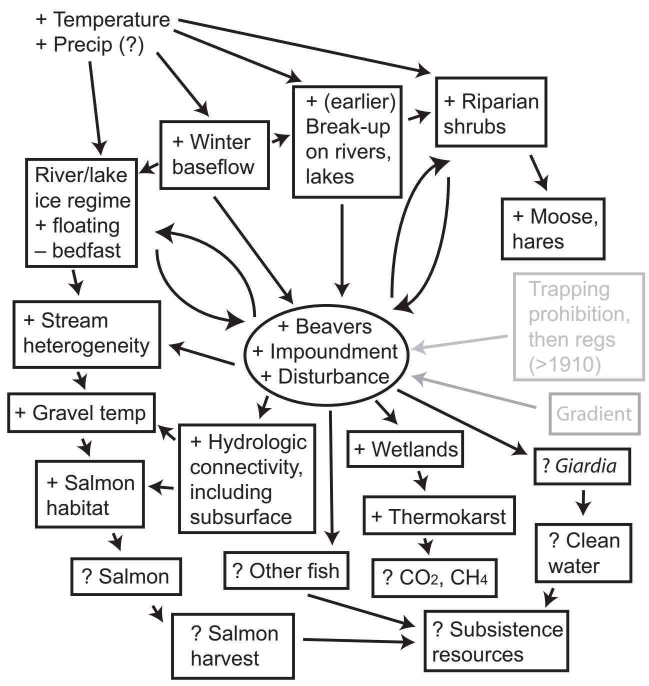

FIGURE 8 Conceptual diagram postulating the prominent role of beavers in the changing arctic ecosystem. Gray typeface denotes unchanging

ACKNOWLEDGEMENTS

KDT and CDA acknowledge support from Alaska EPSCoR NSF award #OIA-1208927 and the State of Alaska. GG and IN acknowledge support by European Research Council #338335, Helmholtz Association Initiative and Networking Fund #ERC0013, and European Space Agency GlobPermafrost. Authors acknowledge support for publication fees from the University of Alaska Fairbanks Office of Vice Chancellor for Research. We thank three anonymous reviewers and the editor for comments that improved previous versions of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

ORCID

Ken D. Tape http://orcid.org/0000-0002-1039-6868
Benjamin M. Jones http://orcid.org/0000-0002-1517-4711
Christopher D. Arp http://orcid.org/0000-0002-6485-6225
Ingmar Nitze http://orcid.org/0000-0002-1165-6852
Guido Grosse http://orcid.org/0000-0001-5895-2141

REFERENCES

Aleksiuk, M. (1970). The seasonal food regime of arctic beavers. *Ecology*, *51*(2), 264–270. https://doi.org/10.2307/1933662

Arp, C. D., Jones, B. M., Grosse, G., Bondurant, A. C., Romanovsky, V. E., Hinkel, K. M., & Parsekian, A. D. (2016). Threshold sensitivity of shallow Arctic lakes and sublake permafrost to changing winter climate. *Geophysical Research Letters*, *43*(12), 6358–6365. https://doi.org/10.1002/2016GL068506

Arp, C. D., Jones, B. M., Lu, Z., & Whitman, M. S. (2012). Shifting balance of thermokarst lake ice regimes across the Arctic Coastal Plain of northern Alaska. *Geophysical Research Letters*, *39*(16).

Bekryaev, R. V., Polyakov, I. V., & Alexeev, V. A. (2010). Role of polar amplification in long-term surface air temperature variations and modern Arctic warming. *Journal of Climate*, *23*(14), 3888–3906. https://doi.org/10.1175/2010JCLI3297.1

Bockstoce, J. R. (2009). *Furs and frontiers in the far North: The contest among Native and foreign nations for the Bering Strait fur trade* (pp. 1–472). New Haven, CT: Yale University Press.

Bouwes, N., Weber, N., Jordan, C. E., Saunders, W. C., Tattam, I. A., Volk, C., … Pollock, M. M. (2016). Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Scientific Reports*, *6*, 28581. https://doi.org/10.1038/srep28581

Bowden, W. B., Gooseff, M. N., Balser, A., Green, A., Peterson, B. J., & Bradford, J. (2008). Sediment and nutrient delivery from thermokarst features in the foothills of the North Slope, Alaska: Potential impacts on headwater stream ecosystems. *Journal of Geophysical Research*, *113*, G02026. https://doi.org/10.1029/2007JG000470

Brewer, M. C. (1958). The thermal regime of an arctic lake. *Eos, Transactions American Geophysical Union*, *39*(2), 278–284. https://doi.org/10.1029/TR039i002p00278

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*, *115*(D16), 1–16.

Brubaker, M., Bell, J., Berner, J., Black, M., Chavan, R., Smith, J., & Warren, J. (2011). *Climate change in Noatak, Alaska: Strategies for community health* (pp. 1–60). Anchorage, AK: Alaska Native Tribal Health Consortium.

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, *30*(4), 492–507. https://doi.org/10.1007/s00267-002-2737-0

Cason, M. M., Baltensperger, A. P., Booms, T. L., Burns, J. J., & Olson, L. E. (2016). Revised distribution of an Alaskan endemic, the Alaska Hare (*Lepus othus*), with implications for taxonomy, biogeography, and climate change. *Arctic Science*, *2*(2), 50–66. https://doi.org/10.1139/as-2015-0019

Coady, J. W. (1980). History of moose in northern Alaska and adjacent regions. *Canadian Field-Naturalist*, *94*(1), 61–68.

Craig, P., & Haldorson, L. (1986). Pacific salmon in the North American Arctic. *Arctic*, *39*(1), 2–7.

Craig, P. C., & McCart, P. J. (1975). Classification of stream types in Beaufort Sea drainages between Prudhoe Bay, Alaska, and the Mackenzie delta, NWT, Canada. *Arctic and Alpine Research*, *7*(2), 183–198. https://doi.org/10.2307/1550320

Daum, D. W., Rost, P., & Smith, M. W. (1984). *Fisheries studies on the north slope of the Arctic National Wildlife Refuge, 1983*. Fairbanks, AK: Fishery Resources, US Fish and Wildlife Service.

Dunmall, K. M., Mochnacz, N. J., Zimmerman, C. E., Lean, C., & Reist, J. D. (2016). Using thermal limits to assess establishment of fish dispersing to high-latitude and high-elevation watersheds. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(12), 1750–1758. https://doi.org/10.1139/cjfas-2016-0051

Ecke, F., Levanoni, O., Audet, J., Carlson, P., Eklöf, K., Hartman, G., … Futter, M. (2017). Meta-analysis of environmental effects of beaver in relation to artificial dams. *Environmental Research Letters*, *12*(11), 113002.

Fall, J. A., Brown, C. L., Braem, N. M., Ciccone, V., Holen, D. L., Hutchinson-Scarbrough, L. B., … Simeone, W. E. (2009). *Alaska subsistence salmon fisheries 2006 annual report*. Juneau, AK: Alaska Department of Fish and Game, Division of Subsistence.

Grebmeier, J. M., Overland, J. E., Moore, S. E., Farley, E. V., Carmack, E. C., Cooper, L. W., & McNutt, S. L. (2006). A major ecosystem shift in the northern Bering Sea. *Science*, *311*(5766), 1461–1464. https://doi.org/10.1126/science.1121365

Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., . . . Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States–representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*, *81*(5), 345–354.

Hood, G. A., & Bayley, S. E. (2008). Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation*, *141*(2), 556–567. https://doi.org/10.1016/j.biocon.2007.12.003

Huryn, A., & Hobbie, J. (2012). *Land of extremes: A natural history of the Arctic North Slope of Alaska* (pp. 1–311). Fairbanks, AK: University of Alaska Press.

Jorgenson, M. T., Romanovsky, V., Harden, J., Shur, Y., O'Donnell, J., Schuur, E. A., . . . Marchenko, S. (2010). Resilience and vulnerability of permafrost to climate change This article is one of a selection of papers from The Dynamics of Change in Alaska's Boreal Forests: Resilience and Vulnerability in Response to Climate Warming. *Canadian Journal of Forest Research*, *40*(7), 1219–1236. https://doi.org/10.1139/X10-060

Jung, T. S., Frandsen, J., Gordon, D. C., & Mossop, D. H. (2017). Colonization of the Beaufort coastal plain by beaver (*Castor canadensis*): A response to shrubification of the tundra? *The Canadian Field-Naturalist*, *130*(4), 332–335. https://doi.org/10.22621/cfn.v130i4.1927

Kemp, P. S., Worthington, T. A., Langford, T. E., Tree, A. R., & Gaywood, M. J. (2012). Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries*, *13*(2), 158–181. https://doi.org/10.1111/j.1467-2979.2011.00421.x

Kokelj, S. V., Lacelle, D., Lantz, T. C., Tunnicliffe, J., Malone, L., Clark, I. D., & Chin, K. S. (2013). Thawing of massive ground ice in mega slumps drives increases in stream sediment and solute flux across a range of watershed scales. *Journal of Geophysical Research: Earth Surface*, *118*(2), 681–692.

Lachenbruch, A. H., Brewer, M. C., Greene, G. W., & Marshall, B. V. (1962). Temperature in permafrost. In C. M. Herzfeld (Ed.), *TemperatureFlts measurement and control in science and industry* (pp. 791–803). New York, NY: Reinhold Publishing Co.

Langer, M., Westermann, S., Boike, J., Kirillin, G., Grosse, G., Peng, S., & Krinner, G. (2016). Rapid degradation of permafrost underneath waterbodies in tundra landscapes—Toward a representation of thermokarst in land surface models. *Journal of Geophysical Research: Earth Surface*, *121*(12), 2446–2470.

Lantz, T. C., Kokelj, S. V., Gergel, S. E., & Henry, G. H. (2009). Relative impacts of disturbance and temperature: Persistent changes in microenvironment and vegetation in retrogressive thaw slumps. *Global Change Biology*, *15*(7), 1664–1675. https://doi.org/10.1111/j.1365-2486.2009.01917.x

Liljedahl, A. K., Boike, J., Daanen, R. P., Fedorov, A. N., Frost, G. V., Grosse, G., . . . Zona, D. (2016). Pan-Arctic ice-wedge degradation in warming permafrost and its influence on tundra hydrology. *Nature Geoscience*, *9*(4), 312–318. https://doi.org/10.1038/ngeo2674

Lokteff, R. L., Roper, B. B., & Wheaton, J. M. (2013). Do beaver dams impede the movement of trout? *Transactions of the American Fisheries Society*, *142*(4), 1114–1125. https://doi.org/10.1080/00028487.2013.797497

Macfarlane, W. W., Wheaton, J. M., Bouwes, N., Jensen, M. L., Gilbert, J. T., Hough-Snee, N., & Shivik, J. A. (2015). Modeling the capacity of riverscapes to support beaver dams. *Geomorphology*, *277*, 72–99.

Malison, R. L., Kuzishchin, K. V., & Stanford, J. A. (2016). Do beaver dams reduce habitat connectivity and salmon productivity in expansive river floodplains? *PeerJ*, *4*, e2403. https://doi.org/10.7717/peerj.2403

McCulloch, D., & Hopkins, D. (1966). Evidence for an early recent warm interval in northwestern Alaska. *Geological Society of America Bulletin*, *77*(10), 1089–1108. https://doi.org/10.1130/0016-7606(1966)77[1089:EFAERW]2.0.CO;2

McNamara, J. P., & Kane, D. L. (2009). The impact of a shrinking cryosphere on the form of arctic alluvial channels. *Hydrological Processes*, *23*(1), 159–168. https://doi.org/10.1002/hyp.7199

Moerlein, K., & Carothers, C. (2012). Total environment of change: Impacts of climate change and social transitions on subsistence fisheries in northwest Alaska. *Ecology and Society*, *17*(1), 10. https://doi.org/10.5751/ES-04543-170110

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., . . . Lévesque, E. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4), 045509. https://doi.org/10.1088/1748-9326/6/4/045509

Naiman, R. J., Melillo, J. M., & Hobbie, J. E. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, *67*(5), 1254–1269. https://doi.org/10.2307/1938681

Naiman, R. J., & Rogers, K. H. (1997). Large animals and system-level characteristics in river corridors. *BioScience*, *47*(8), 521–529. https://doi.org/10.2307/1313120

Nielsen, J. L., Ruggerone, G. T., & Zimmerman, C. E. (2013). Adaptive strategies and life history characteristics in a warming climate: Salmon in the Arctic? *Environmental Biology of Fishes*, *96*(10–11), 1187–1226. https://doi.org/10.1007/s10641-012-0082-6

Nitze, I., & Grosse, G. (2016). Detection of landscape dynamics in the Arctic Lena Delta with temporally dense Landsat time-series stacks. *Remote Sensing of Environment*, *181*, 27–41. https://doi.org/10.1016/j.rse.2016.03.038

Nitze, I., Grosse, G., Jones, B. M., Arp, C. D., Ulrich, M., Fedorov, A., & Veremeeva, A. (2017). Landsat-based trend analysis of lake dynamics across northern permafrost regions. *Remote Sensing*, *9*(7), 640. https://doi.org/10.3390/rs9070640

Pastick, N. J., Jorgenson, M. T., Wylie, B. K., Nield, S. J., Johnson, K. D., & Finley, A. O. (2015). Distribution of near-surface permafrost in Alaska: Estimates of present and future conditions. *Remote Sensing of Environment*, *168*, 301–315. https://doi.org/10.1016/j.rse.2015.07.019

Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems. *BioScience*, *64*(4), 279–290. https://doi.org/10.1093/biosci/biu036

Pollock, M. M., Pess, G. R., Beechie, T. J., & Montgomery, D. R. (2004). The importance of beaver ponds to coho salmon production in the Stillaguamish River basin, Washington, USA. *North American Journal of Fisheries Management*, *24*(3), 749–760. https://doi.org/10.1577/M03-156.1

Rabung, Sam and Norton Sound Bering Straight Regional Planning Team (2015). *Norton sound bering straight regional comprehensive salmon plan: Phase II* (pp. 1–217). Juneau, AK: Alaska Department of Fish & Game.

Reist, J. D., Wrona, F. J., Prowse, T. D., Power, M., Dempson, J. B., Beamish, R. J., . . . Sawatzky, C. D. (2006). General effects of climate change on Arctic fishes and fish populations. *AMBIO: A Journal of the Human Environment*, *35*(7), 370–380. https://doi.org/10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO;2

Romanovsky, V. E., Smith, S. L., & Christiansen, H. H. (2010). Permafrost thermal state in the polar Northern Hemisphere during the international polar year 2007–2009: A synthesis. *Permafrost and Periglacial Processes*, *21*(2), 106–116. https://doi.org/10.1002/ppp.689

Serreze, M. C., & Barry, R. G. (2011). Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change*, *77*(1), 85–96. https://doi.org/10.1016/j.gloplacha.2011.03.004

Šmejkalová, T., Edwards, M. E., & Dash, J. (2016). Arctic lakes show strong decadal trend in earlier spring ice-out. *Scientific Reports*, *6*, 1–8.

Smith, M. W. (1975). Microclimatic influences on ground temperatures and permafrost distribution, Mackenzie Delta, Northwest Territories. *Canadian Journal of Earth Sciences*, *12*(8), 1421–1438. https://doi.org/10.1139/e75-129

St. Jacques, J. M., & Sauchyn, D. J. (2009). Increasing winter baseflow and mean annual streamflow from possible permafrost thawing in the Northwest Territories, Canada. *Geophysical Research Letters*, *36*(1), 6.

Sturm, M., Racine, C., & Tape, K. (2001). Climate change: Increasing shrub abundance in the Arctic. *Nature*, *411*(6837), 546. https://doi.org/10.1038/35079180

Surdu, C. M., Duguay, C. R., Brown, L. C., & Fernández Prieto, D. (2014). Response of ice cover on shallow lakes of the North Slope of Alaska to contemporary climate conditions (1950–2011): Radar remote-sensing and numerical modeling data analysis. *The Cryosphere*, *8*(1), 167–180. https://doi.org/10.5194/tc-8-167-2014

Tan, A., Adam, J. C., & Lettenmaier, D. P. (2011). Change in spring snowmelt timing in Eurasian Arctic rivers. *Journal of Geophysical Research: Atmospheres*, *116*(D3), 12.

Tape, K. D., Christie, K., Carroll, G., & O'Donnell, J. A. (2016). Novel wildlife in the Arctic: The influence of changing riparian ecosystems and shrub habitat expansion on snowshoe hares. *Global Change Biology*, *22*(1), 208–219. https://doi.org/10.1111/gcb.13058

Tape, K. D., Gustine, D. D., Ruess, R. W., Adams, L. G., & Clark, J. A. (2016). Range expansion of moose in Arctic Alaska linked to warming and increased shrub habitat. *PLoS ONE*, *11*(4), e0152636. https://doi.org/10.1371/journal.pone.0152636

Wendler, G., Moore, B., & Galloway, K. (2014). Strong temperature increase and shrinking sea ice in Arctic Alaska. *The Open Atmospheric Science Journal*, *8*(1), 7–15. https://doi.org/10.2174/1874282301408010007

Westbrook, C. J., Cooper, D. J., & Baker, B. W. (2006). Beaver dams and overbank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area. *Water Resources Research*, *42*(6).

Woo, M. K., & Waddington, J. M. (1990). Effects of beaver dams on subarctic wetland hydrology. *Arctic*, *43*(3), 223–230.

Xu, L., Myneni, R. B., Iii, F. C., Callaghan, T. V., Pinzon, J. E., Tucker, C. J., . . . Stroeve, J. C. (2013). Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change*, *3*(6), 581.

Zhu, Z., Wang, S., & Woodcock, C. E. (2015). Improvement and expansion of the Fmask algorithm: Cloud, cloud shadow, and snow detection for Landsats 4–7, 8, and Sentinel 2 images. *Remote Sensing of Environment*, *159*, 269–277. https://doi.org/10.1016/j.rse.2014.12.014

How to cite this article: Tape KD, Jones BM, Arp CD, Nitze I, Grosse G. Tundra be dammed: Beaver colonization of the Arctic. *Glob Change Biol*. 2018;00:1–11. https://doi.org/10.1111/gcb.14332