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Abstract

Snow covers Arctic and boreal regions (ABRs) for approximately 9 months of the year, thus snowscapes dominate the form and function of tundra and boreal ecosystems. In recent decades, Arctic warming has changed the snowcover's spatial extent and distribution, as well as its seasonal timing and duration, while also altering the physical characteristics of the snowpack. Understanding the little studied effects of changing snowscapes on its wildlife communities is critical. The goal of this paper is to demonstrate the urgent need for, and suggest an approach for developing, an improved suite of temporally evolving, spatially distributed snow products to help understand how dynamics in snowscape properties impact wildlife, with a specific focus on Alaska and northwestern Canada. Via consideration of existing knowledge of wildlife-snow interactions, currently available snow products for focus region, and results of three case studies, we conclude that improving snow science in the ABR will be best achieved by focusing efforts on developing data-model fusion approaches to produce fit-for-purpose snow products that include, but are not limited to, wildlife ecology. The relative wealth of coordinated *in situ* measurements, airborne and satellite remote sensing data, and modeling tools being collected and developed as part of NASA's Arctic Boreal Vulnerability Experiment and SnowEx campaigns, for example, provide a data rich environment for developing and testing new remote sensing algorithms and retrievals of snowscape properties.

1. Introduction

Snow covers Arctic and boreal regions (ABRs) for approximately 9 months of the year, thus snowscapes dominate the form and function of tundra and boreal ecosystems. In recent decades, Arctic warming has changed the snowcover's spatial extent and distribution, as well as its seasonal timing and duration, while also altering the physical characteristics of the snowpack (Brown and Mote 2009, Callaghan *et al* 2011, Winski *et al* 2017). To date, a small amount of research has highlighted the consequences of these changing snowscape properties on the biogeochemistry, hydrology, and energy balance of ABRs (Callaghan *et al* 2011), while far fewer have focused on the effects of shifting snowscape dynamics on wildlife. Despite their specific adaptations to snow, in many cases, these species rely heavily on favorable snow conditions for their fitness (survival and reproductive success). Since ABRs host some of the last remaining pristine regions of the planet with intact wildlife communities—and are home to such spectacles as the longest overland migration in the world (i.e. caribou)—understanding the effects of changing snowscapes on its wildlife communities is critical given that they are experiencing pronounced alterations due to shifting temperature and precipitation regimes associated with global climate change.

There is growing appreciation of the effects of snowscape properties on wildlife within the ABR, yet snow data available to assess these effects often have insufficient spatial and temporal resolutions and extents. Furthermore, many of the specific physical properties of snowscapes most relevant to wildlife ecology in ABRs remain unquantified over large spatial and temporal scales. Current ABR-wide datasets are limited to what can be estimated from established space-borne sensors or models for climate and hydrologic applications; they include snow variables such as snow-covered area, snow-cover duration, snow albedo, snow–water equivalent (SWE), and snow surface temperature and freeze-thaw state. Other snowscape properties such as depth, density, stratigraphy, ice layers, and snow-layer hardness are significant factors affecting wildlife (Laperriere and Lent 1977, Skogland 1978, Collins and Smith 1991, Forchhammer and Boertmann 1993); yet observations of these variables are sparse and ABR-wide datasets do not exist. Furthermore, ABR wildlife biologists are frequently confronted with a lack of available snow products at suitable spatial and temporal scales, and this a major limiting factor in their research efforts. Therefore, our ability to understand, predict, and respond to snow-wildlife interactions is limited by the inadequate spatial snow products that are currently available.

Given the rapid rate at which climate change is altering ABR snowscapes, the goal of this paper is to demonstrate the urgent need for, and suggest an approach for developing, an improved suite of temporally evolving, spatially distributed snow products to help understand how dynamics in snowscape properties impact wildlife, with a specific focus on Alaska and northwestern Canada. Our objectives are to:

- highlight the proven importance of snowscape dynamics to wildlife ecology as demonstrated by previous studies conducted in snow dominated ecosystems, including ABRs (section 2)
- summarize and describe the snow-related spatial products currently available for studying snowscape dynamics in ABRs of Alaska and northwestern Canada (section 3)
- demonstrate that new and improved snow spatial products are required to reveal, understand, and quantify snow-wildlife interactions in ABRs (section 4)
- provide a future prospectus for how to create fit-for-purpose snow spatial products for understanding wildlife responses to the changes in snowscape properties that are expected to continue as climate continues to warm in ABRs (section 5).

2. The Importance of snowscapes to wildlife

In snow-dominated ecosystems, the amount, distribution and physical characteristics of snow have significant impacts on wildlife populations (Formozov 1946). Snowscape properties can either negatively or positively influence wildlife movements (e.g. Pruitt 1959), Predator–prey dynamics (e.g. Sokolov *et al* 2016), access to food (e.g. Fancy and White 1985), thermal insulation (e.g. Kausrud *et al* 2008), and, ultimately, their reproductive success and survival (as reviewed in Berteaux *et al* 2017). While most species wade through the snowpack, some species require the insulation provided by the subnivean environment to den, burrow, move, forage, take cover from predators, and ultimately survive and reproduce. As demonstrated in the paragraphs below, a broad suite of snow properties must be explicitly considered in order to understand how ABR wildlife are being affected by and responding to rapid, ongoing changes in snowscape conditions caused by climate warming.

Variability in snow cover duration—defined as the period between snow cover onset in the fall and the snowpack disappearance date in the spring or early summer—has important implications for a wide range of wildlife species. Several studies have found that migratory shorebirds and passerines breeding in the Arctic alter the timing of egg-laying in years with early or late snowmelt dates (Meltofte *et al* 2007, Smith *et al* 2010, Grabowski *et al* 2013, Liebezeit *et al* 2014, Boelman *et al* 2017). Since the timing of clutch initiation can affect clutch size, opportunity for re-nesting, timing of autumnal migration, and the size and skill of young of the year by the onset of winter conditions, snow disappearance dates can influence reproductive success in these birds (Meltofte 1985, 2000, Nol *et al* 1997, Sandercock *et al* 1999). The timing of spring and fall snow cover also directly influences Predator–prey dynamics. For example, in years with early snow disappearance dates, rodents that overwinter in the subnivean environment (such as voles and lemmings, *Arvicolinae*) are exposed to avian predators earlier in the season relative to years with later snow disappearance (Duchesne *et al* 2011, Bilodeau *et al* 2013, Berteaux *et al* 2016). In early snowmelt years, snowshoe hares (*Lepus americanus*) show little phenotypic plasticity in the phenology of their spring coat color change from white to brown (Zimova *et al* 2014). As such, models predict that as snow cover duration continues to decrease with climate warming, the seasonal mismatch between their persistently white coat color and the increasingly snow-free landscape will strengthen. The diminishment of their seasonal camouflage will markedly increase the susceptibility of the hares to predation (Mills *et al* 2013). In fact, similar seasonal mismatches between animal coat and landscape color phenologies are predicted to develop in several other Arctic-boreal species as the snow-covered season continues to shorten (Mills *et al* 2013, Henden *et al* 2017). In summary, migration patterns, Predator–prey relationships, and physical adaptations to snow-covered landscapes are strongly influenced by the timing and duration of the snow season, and thus changes in snowscape seasonality will lead to cascading effects on a wide range of animal species.

In addition to snow-cover duration, a suite of other physical snowpack characteristics is critical to wildlife movement, habitat selection, survival, and reproduction. Multiple studies have shown that deep, soft snow, as well as wet snow, impede animal movements and increase energy expenditure demands (Fancy and White 1987, Nicholson *et al* 2016), potentially affecting demographic rates (Parker *et al* 2009). Body mass, limb length, and foot loading (body weight divided by total foot area contacting snow) strongly influence the effect of snow depth on locomotion energetics (Kelsall and Telfer 1971, Kelsall and Prescott 1971, Mech *et al* 1971, Telfer and Kelsall 1984). For this reason, northern ungulates (hooved mammals) tend to select areas of shallow snow to overwinter (Stelfox and Taber 1968, Duquette 1988). Le Corre *et al* (2017) reported that spring caribou migration was earlier following mild winters, and was later when April snowfall was high, suggesting that the animals may adjust migration timing in response to more favorable snow conditions along their migration routes. Large ungulates, such as elk (*Cervus canadensis*), moose (*Alces alces*), mountain goats (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis*), tend to avoid deep snow that they sink in easily (Parker *et al* 1984, Dailey and Hobbs 1989). Species-specific responses to variations in snowscape properties can also play a significant role in shaping Predator–prey interactions during the snow season. Rates of predation on deer and moose are highest when snow is deepest (Mech and Frenzel 1971, Peterson and Allen 1974, Haber 1977, Lendrum *et al* 2017), largely because ungulates have a higher foot load than wolves, making them slower in deep, soft snow, and thus less able to escape wolf predation (Nelson and Mech 1986).

Accessibility of ground forage is also influenced by the physical snowpack properties. For example, caribou, reindeer, and sheep forage where snow is shallowest and least dense (Hoefs and McTaggart-Cowan 1980, Fancy and White 1985, Duquette 1988, Nichels and Bunnell 1999, Johnson *et al* 2001, Beumer *et al* 2017). When and where snow depth, density, hardness, and ice layers limit access to ground lichen, woodland caribou shift to feeding on arboreal lichen (Johnson *et al* 2001). More generally, the increasing occurrence of rain and snowmelt freeze events—which create hard ice layers on, within, or beneath the snowpack—inhibit access to forage, causing catastrophic die-offs in northern ungulate populations (Putkonen *et al* 2009, Rennert *et al* 2009, Stien *et al* 2010, 2012, Hansen *et al* 2011, 2013). These snowpack-induced die-off events can have cascading effects that ripple through the food web. Sokolov *et al* (2016) documented such an event that created an abundance of ungulate carcasses which produced a resource pulse the following summer, thereby supporting an abundance of red fox (*Vulpes vulpes*) and hooded crows (*Corvus cornix*), which in turn increased predation pressure on rodents and ground-nesting bird species the following spring and summer. In addition, species of ptarmigan (*Lagopus*)—the smallest bird in the grouse family—migrate across ABRs and are active throughout winter, browsing on the buds of shrubs such as willow and birch that protrude from the snowpack. They depend on snow for their burrows, but deep snowpacks may inhibit their browsing access to shrubs. Their browsing habits affect shrub architecture and height, thereby creating a feedback between browsing and snow accumulation (Liston *et al* 2002, Tape *et al* 2010).

The quality of overwintering habitat for species that den, hibernate, or remain active in the subnivean environment is generally highest in deep, low density snow because the insulative capacity of snow increases with depth and decreases with density (Pomeroy and Brun 2001). For this reason, studies conducted in Yellowstone National Park show that grizzly bears (*Ursus arctos)* tend to choose hibernation den sites on slopes where prevailing winds cause deep snow to accumulate, insulating dens from outside frigid air temperatures as low as −45 °C (Craighead and Craighead 1972, Vroom *et al* 1980). Several small mammal species are able to remain active within the subnivean layer throughout the winter due to these insulative properties. In a field study conducted at three Canadian Arctic sites, Reid *et al* (2012) found that lemmings used areas with deeper snow (i.e. more thermal insulation) more frequently than areas with shallower snow (i.e. less insulation). As the frequency of winter rain and snowmelt freeze events continue to increase in the Arctic due to changing climate regimes (Kim *et al* 2015), resulting increases in snow density, hardness, and presence of ice layers will reduce the snowpack's insulating properties on which these species depend (Kausrud *et al* 2008, Berteaux *et al* 2017, Penczykowski *et al* 2017). Due to their numerical dominance and central position in ABR food webs, dynamics in the survival and reproductive success of voles and lemmings affects numerous plant and predator species by altering trophic interactions (Ims and Fuglei 2005).

3. Current spatial snowscape products for ABRs

Scientists quantify and monitor variations and trends in snowscape properties using *in situ* measurements, remotely-sensed observations, numerical modeling, and by integrating these approaches through model-data assimilation and reanalysis products. We have listed and summarized the attributes of the spatial snow products that are—to the best of our knowledge—currently available for the ABRs of North America (table S1 is available online at stacks.iop.org/ERL/14/010401/mmedia). These products were produced for a number of purposes, ranging from operational earth observations to studies of ecosystem processes at various scales. While these data are used when and where they are available, they are often inadequate for wildlife studies. The three sub-sections that follow summarize the types of ABR snow-related products that are available for wildlife studies.

3.1. *In-situ* measurements of snowscape properties

The ABR is a vast and geographically diverse region with sparsely distributed *in situ* observations of snow and other weather-related station observations; the spatial distribution of these measurements are generally inadequate to accurately represent environmental gradients that influence snow such as altitude, latitude, and the distance from the coast. During the snow cover season, the temporal resolution of *in situ* snow measurements in ABRs are typically hourly at automated meteorology and snow measurement stations and monthly at manual snow course sites. These measurements typically lack the spatial coverage required to quantify variability in snowscape properties across the range of spatial scales relevant to wildlife behavior. While interpolated data from reanalysis or physical and statistical models are widely used, the utility of such data in wildlife studies remains limited by the sparse *in situ* observations available for calibration and validation.

Relative to the snow cover of the western conterminous United States, which has <50% snow covered area for less than 6 months per year, Alaska has >95% snow covered for 7–10 months of per year (Liston and Hiemstra 2011, Robinson *et al* 2018). When compared to the Western states of the conterminous United States, Alaska has <1/8 the density of *in situ* snow-cover observations. Figure 1 highlights this, showing the number and density of active Natural Resource Conservation Service (NRCS) snow measurement sites in the combined area of Washington, Oregon, California, Arizona, Nevada, Utah, Idaho, Montana, Wyoming, and New Mexico (mean February snow covered area = $1.31 \times 106\,km^2$) compared with Alaska (mean February snow covered area = $1.72 \times 106\,km^2$) (wcc.nrcs.usda.gov/snow/). The limited periods of record and sparse spatial distribution of *in situ* data in Alaska further constrain calibration and validation of both remote-sensing observations and spatial models of snowscape properties (Bokhorst *et al* 2016). While many of the snow observing sites in the ABR measure SWE, snow depth, air temperature, and total precipitation, other variables critical to understanding wildlife behavior are rarely measured, including snow hardness and ice-layers, and local scale spatial heterogeneity in these and the other snow properties.

In addition to readily accessible snow data, other public and private stakeholders (e.g. United States Department of Agriculture Forest Service, United States National Park Service, petroleum and mining companies) collect limited *in situ* snow observations in Alaska. These data are also sparsely distributed and may be reported using different formats or, in the case of private industry, unavailable to the public, making them more difficult to discover, access, and utilize. In recognition of the need for coordinated management and archiving of ABR data, some notable efforts have emerged to locate and consolidate these data such as the NSF Arctic Data Center (arcticdata.io/) and NOAA's Sustaining Arctic Observing networks (arcticobserving.org/).

3.2. Remotely sensed retrievals of snowscape properties

The use of satellite data for global mapping of snow-cover extends over the modern satellite era. However, it was not until the launch of the daily-orbiting Moderate Resolution Imaging Spectroradiometer (MODIS) sensors on the NASA EOS Terra (1999) and Aqua (2002) satellites, and more recently the reanalysis of satellite passive microwave sensor records, that daily snow products describing the extent, albedo, grain size, and relative ice and water content have become available (Tedesco *et al* 2013). The spatially continuous nature of satellite information complements *in situ* observations that are spatially limited. Unfortunately, effective remote-sensing techniques to map and monitor snow properties at the spatial and temporal resolutions required to understand wildlife behavior are still lacking (Nolin, 2010, Dietz *et al* 2012, Bokhorst *et al* 2016). As shown in section 4, the spatial resolution of snow-related information required to characterize wildlife behavior can range from meters (e.g. polar bear (*Ursus maritimus*) denning habitat) to kilometers (e.g. caribou migration timing). Similarly, regular daily observations that capture transient snowscape conditions and anomalous events are also required (e.g. snow-free date and water or ice content of the snowpack). Another major challenge for remotely derived snow assessments is that wildlife respond to a broad range of ecosystem-specific snowscape properties that are not available from current remote-sensing observations and data products.

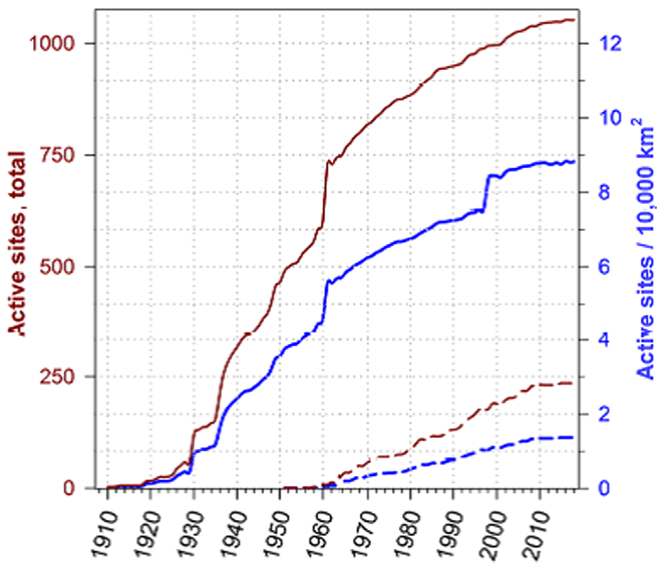

Figure 1. Total number (brown) of active snow measurement sites 1910–2017 and mean Feb. snow covered area per site (blue) for Washington, Oregon, California, Arizona, Nevada, Utah, Idaho, Montana, Wyoming and New Mexico combined (solid) and Alaska (dashed).

Existing satellite-derived snow products meet some snow-wildlife study requirements (table S1), but no single sensor or data record provides consistent and reliable observations of all of the relevant snow variables at the required spatial and temporal scales. Most available satellite records are limited by one or more factors, including the trade-off between spatial resolution and temporal frequency; where more frequent sensor scans (e.g. Passive Microwave and MODIS) have coarser footprints when compared to those scanning smaller areas that can resolve information at finer spatial resolution (e.g. Landsat) but are only available at much coarser temporal resolution (e.g. 16 d). Each sensor type also has limitations causing other data gaps and uncertainties. Optical and infrared sensors are limited by low solar illumination, polar night, and persistent cloud cover. The signal strength of microwave energy emitted from Earth's surface, complex terrain, vegetation cover, and snow-cover properties (e.g. stratigraphy, grain size) likewise complicate data retrieval by microwave sensors (Nolin 2010, Dietz *et al* 2012).

Airborne or satellite image retrievals are also used to create high resolution digital elevation or surface elevation models (DEM and SEM, respectively) that are in turn input into physical snowpack evolution models to study snow-wildlife interactions (see *Model simulations of snowscape properties*). Unfortunately, much of the digital elevation and surface mapping of the ABR is of relatively low spatial resolution, with two notable exceptions: the Alaska Interferometric Synthetic Aperture Radar DEM (5 m resolution), and the SEM called the ArcticDEM, created using stereo pairs of high resolution optical imagery (2 m resolution) (LPDAAC, 2017, Polar Spatial Center, 2017). Higher resolution airborne LiDAR and structure from motion products are also available in a few locations (as described in case study 1) and provide the opportunity to conduct wildlife relevant snowscape research by mapping snow depth through differencing (Deems *et al* 2013, Nolan *et al* 2015).

3.3. Model simulations of snowscape properties

Temporally varying snowpack properties can be extrapolated over landscapes using process-based models that implement snow physics within the context of a numerical modeling system (e.g. Durand *et al* 1999, Bartelt and Lehning 2002, Lehning *et al* 2006, Liston and Elder 2006a). These models input time-invariant variables such as topography and land-cover, and time-evolving meteorological forcing such as air temperature, humidity, precipitation, wind, and radiation, and simulate the evolution of variables such as SWE, snow albedo, and snow density. Existing snow-evolution models faithfully represent key snow-related processes; including snow–water-equivalent accumulation of snowfall, redistribution by wind, snow-forest-canopy interactions, snow-vegetation interactions, and snowmelt. In addition, these snow modeling tools appropriately handle the spatial-distribution and temporal-evolution aspects of snowpack growth and decay. Often these models have been developed for a specific application (e.g. climate studies, water resource management, avalanche risk assessment), and the details of the model configuration (e.g. grid increment, time step, and represented physical processes) reflect that focus. To date, because the focus has rarely been on wildlife applications, model configurations have rarely met the needed criteria to produce snow products that are directly applicable to understanding wildlife-snow interactions (Liston *et al* 2007).

Modeling approaches for characterizing snowscape properties can be developed to produce a large suite of wildlife-relevant snow variables over large spatial and temporal extents, and over a wide range of spatial and temporal resolutions. In this way, modeled snowscape products can be tailored to fit the specific needs of wildlife studies (e.g. Vikhamar-Schuler *et al* 2013, Eaton and Businger 2014, Northrup *et al* 2016, Ouellet *et al* 2016, Rasmus *et al* 2016, Lendrum *et al* 2017, Reinking *et al* 2017). While current snow-evolution models can make valuable contributions to snow-wildlife interaction studies, the majority are not yet up to the task because they do not simulate the required snow variables that are often most critical to wildlife dynamics studies, although there are some notable exceptions (see table S1).

Other weaknesses associated with snow-evolution models limit their ability to simulate or estimate snowscape properties, which in turn limits their efficacy in studies of wildlife-snow interactions. For example, the models are only as good as the meteorological forcing inputs; these data can suffer from deficiencies in data quality or resolution. Currently the most problematic meteorological input is the precipitation forcing; the available data on water-equivalent precipitation (i.e. total precipitation of various forms falling from the sky and reaching the ground) are often of insufficient quality to exactly reproduce observed snow distributions (Goodison *et al* 1981, Yang *et al* 1998, Liston and Sturm 2002, Pan *et al* 2003, Liston *et al* 2008, 2016, Girotto *et al* 2014, Margulis *et al* 2015, Wrzesien *et al* 2017). Often times there are no validation data to compare the model outputs to, and available topography and vegetation datasets may be inadequate. In addition, it has been challenging to develop snow models that are general enough to consistently and accurately simulate snow properties throughout the entire ABR for the entire scope of processes found within the domain. This is because of the wide range of processes found in warm-wet, cold-dry, tundra, and forested environments. The existing models almost always produce qualitatively reasonable snow-property distributions when driven with realistic forcing data. However, their outputs may include biases when compared to *in situ* observations of snow properties made at a given location and time.

4. Case studies: the importance of wildlife-relevant snowscape products at appropriate analysis scales

This section presents three case studies that demonstrate the need for new, wildlife-relevant snow variables, at spatial and temporal scales that are generally not available in existing spatial snow products. These examples highlight our use of specialized snowscape products to understand current snow-wildlife interactions and how those interactions may change in the future.

4.1. Case study 1: mapping polar bear den habitat requires fine-scale snow depth estimates

Pregnant polar bears typically den in snowdrifts found on sea ice or land (Amstrup 2003). As sea ice has become progressively thinner and unstable (Comiso *et al* 2008, Kwok and Rothrock 2009, Maslanik *et al* 2011, Polyakov *et al* 2012), the proportion of land-based dens has increased from 42% (in the 1980s) (Amstrup and Gardner 1994) to 63% (in the early 2000s) (Fischbach *et al* 2007). Coupled with concurrent increases in human activity in the coastal regions of Alaska's Beaufort Sea, the potential for human-bear interactions has heightened. To minimize interactions, as well as disturbance to denning bears, it is critical to identify active dens (MacGillivray *et al* 2003, Stirling and Derocher 2012). As such, Liston *et al* (2016) developed, applied, and tested a physically based numerical model (SnowDens-3D) to map land and barrier-island polar bear snowdrift den habitat along the Beaufort Sea coast.

Liston *et al* (2016) found that snowdrift dens are not randomly distributed, but are the direct result of wind blowing snow into topographic snowdrift traps. They used SnowDens-3D to simulate the year-specific physical interactions of concurrent snow, wind, and topographic dynamics. The model was run annually from 1995 through 2012, on a 2.5 m × 2.5 m horizontal grid; a grid sufficient to resolve the snowdrifts that polar bears den in. The minimum snow-depth required for a viable den was defined and applied to the SnowDens-3D simulated snow depths. This yielded annual maps of potential polar bear den habitat locations, which change every year depending on wind speed and direction, and snowfall amounts. They found that 97% of observed maternal den locations were correctly identified in the simulated snowdrifts modeled by SnowDens-3D (figure 2). The model's high level of accuracy is due to its use of high resolution (2.5 m) topographic data and its ability to account for the influences of year-specific snowfall and wind speed and direction. Given that the existing suite of widely available spatial snow products does not include snow depth data with comparable accuracy nor spatial resolution (see table S1), this case study illustrates the clear need for a highly specialized snow product for identifying polar bear denning habitat, and provides an example of a wildlife-relevant snow-related variable that is not available by field or remote sensing methods alone. Because of SnowDens-3D's basis in snow and weather physics, it can be incorporated into climate scenario simulations to explore how shifts in early-winter meteorological conditions are likely to impact the formation and availability of polar bear snowdrift den habitat.

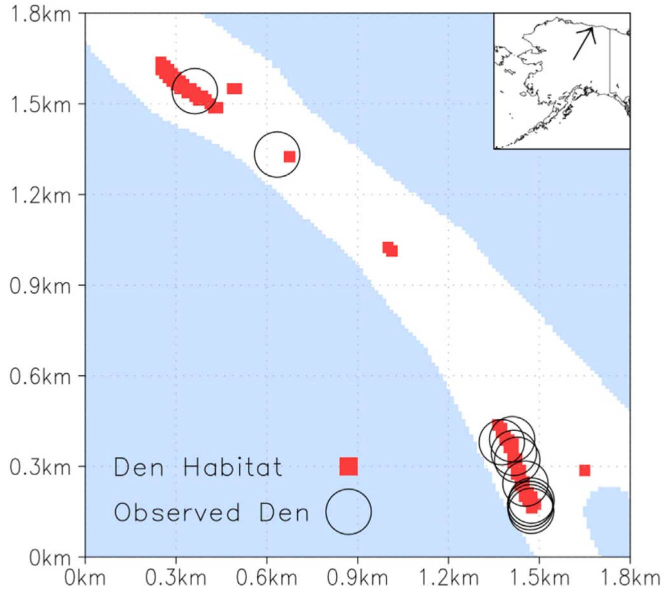

Figure 2. Polar bear den habitat locations simulated with SnowDens-3D over Cottle Island on Alaska's Arctic coast using a 2.5 m grid (Liston *et al* 2016). Snow depths over 1.5 m are displayed in red and the snowdrift edges have been widened by 12.5 m to improve visibility. Polar bear dens, which change locations each year, were observed at the centers of the large open circles during from 1995 through 2012. Blue is ocean, white is land.

4.2. Case study 2: understanding Dall sheep movement behavior requires fine- and course-resolution snowscape products

The Dall sheep (*Ovis dalli dalli*) is an iconic northern wildlife species endemic to the mountain ranges of Alaska and northwestern Canada. Range-wide, Dall sheep populations have declined by at least 20% during the past decade, with some areas declining up to 70% and causing emergency harvest closures (Koizumi *et al* 2011, Alaska Department of Fish and Game 2014). Dall sheep may be particularly sensitive to changing snow conditions, because sheep occur at both high elevations and high latitudes, and average temperature increases and the associated changes are likely amplified due to reductions in the cold regions' temperature inversions (Callaghan *et al* 2011).

Dall sheep exhibit seasonal movements that may be tied to seasonal changes in snow conditions, including use of wind-exposed patches of forage along ridgelines during peak snow coverage and short-distance elevational migrations (Simmons 1982, Nichols and Bunnell 1999). Mahoney *et al* (2018) evaluated the efficacy of MODIS snow-cover fraction and SnowModel (Liston and Elder 2006a) snow depth and density products in predicting Dall sheep movements at multiple spatial and temporal scales, finding that adding a snow covariate, regardless of type, substantially improved model predictions of sheep movements (figure 3(a)). However, the relative performances of snow products were scale-dependent. At higher resolutions (25 and 500 m), SnowModel products that included blowing-snow redistribution, snow-density evolution, orographic precipitation increases, and slope-aspect snowmelt relationships, outperformed MODIS at predicting the finest movement scales (i.e. the distances traveled over 7–56 h).

However, the 500 m MODIS fractional snow cover outperformed SnowModel's grid-averaged snow products at coarser resolutions and movement scales (>112 h), likely because the coarser resolution SnowModel outputs did not include the sub-grid snow information reflected in the MODIS data (figure 3(a)). At fine movement scales (i.e. 7 h), Dall sheep generally selected low density, shallow snow (figures 3(b), (c)), likely to facilitate access to forage and reduce energy expenditure (Dailey and Hobbs 1989). However, they selected for higher snow density at or above the mean threshold of support (329 kg m^{-3}, SE = 18; Sivy *et al* in press) when traveling through deep snow above mean chest height (54 cm; figures 3(b), (c)), likely to reduce snow hoof penetration and improve efficiency of movement (Parker *et al* 1984). At coarse scales, Dall sheep selected for areas with lower fractional snow cover (figure 3(d)), indicating sheep may be detrimentally affected if regional trends of increased winter precipitation continue (Olsen *et al* 2011, Winski *et al* 2017).

These scale-dependent differences in snow product performance indicate that use of a snowpack evolution model such as SnowModel may be necessary to obtain critical insights regarding fine-scale responses of animals to changing snow properties, whereas MODIS fractional snow cover data may be able to provide insight into the effects of snow on movements at broader scales. Although MODIS products are readily available and relatively easy to use, incorporating snow cover in this case required removing a substantial proportion of animal location data due to cloud cover

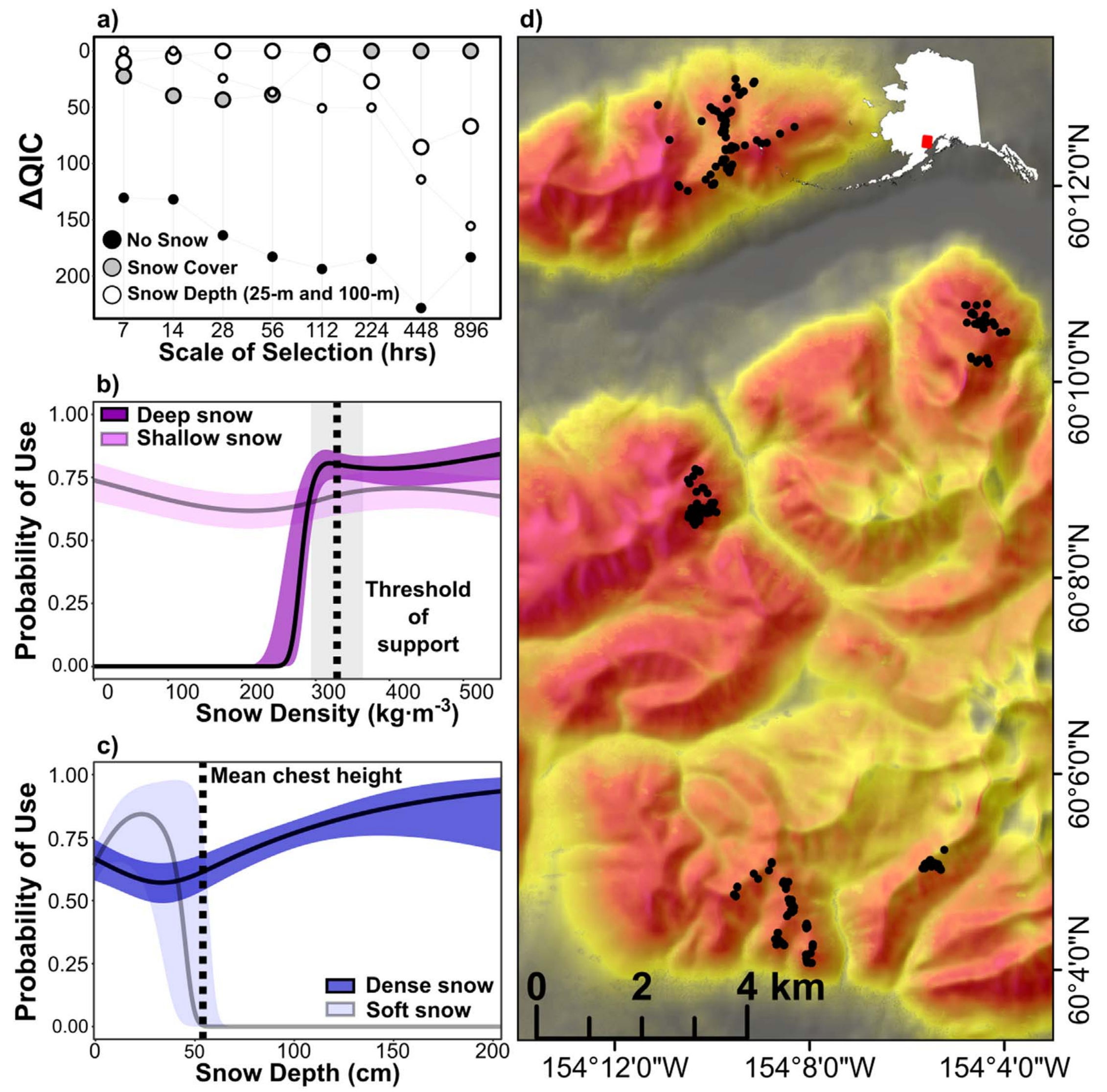

Figure 3. The relative fit of models (quantified using the QIC (Quasilikelihood under the Independence model Criterion)) with MODIS fractional snow cover (grey circles), SnowModel snow depth at 25 m (small white circles) and 500 m (large white circles), and no snow metrics (black circles) (a). The best-fitting model of fine-scale (7 h time step only) resource selection in sheep predicted nonlinear responses to snow density and depth (b), (c). This best fitting snow model was used to produce a heat map of predicted space use for 1 April 2006 in Lake Clark National Park (d); darker reds equate to higher probability of use. Included with the map is an overlay of observed sheep locations (black circles) from 26 March to 4 April 2006 as a visual representation of model performance. Adapted from Mahoney *et al* 2018.

inhibiting image acquisition (82.1% of used locations removed), which reduced the statistical power and the ability to characterize complex movements in response to fine-scale spatial processes.

4.3. Case study 3: caribou migrate well in advance of snow cover melt

During their spring migrations to calving grounds, barren-ground caribou (*Rangifer tarandus* spp.) travel up to one thousand kilometers within only weeks. There is considerable variability in the timing of the spring migrations across years, but relatively few large-scale studies have explored the environmental drivers of these variations (though see LeCorre 2017). The amount of spring snow is even more variable across years, but has shown a steady negative trend in high northern latitudes for several decades (Derksen and Brown 2012). In temperate zones, snowmelt precipitates spring green-up, which has been shown to be an important driver of ungulate migrations (Aikens *et al* 2017). It therefore seems reasonable to hypothesize that the timing of snowmelt might drive spring migration phenology of caribou, as well.

To explore these relationships, we analyzed caribou movement data collected during 15 consecutive spring migrations (2000–2014) from the Bathurst herd in central Canada that has historically been one of the largest migratory herds in the world. To quantify the timing of snowmelt, we computed *snow disappearance day* (SDD) for each 500 m MODIS pixel, averaging neighbors in space and time to fill gaps. Caribou generally started migrating more than three weeks prior to

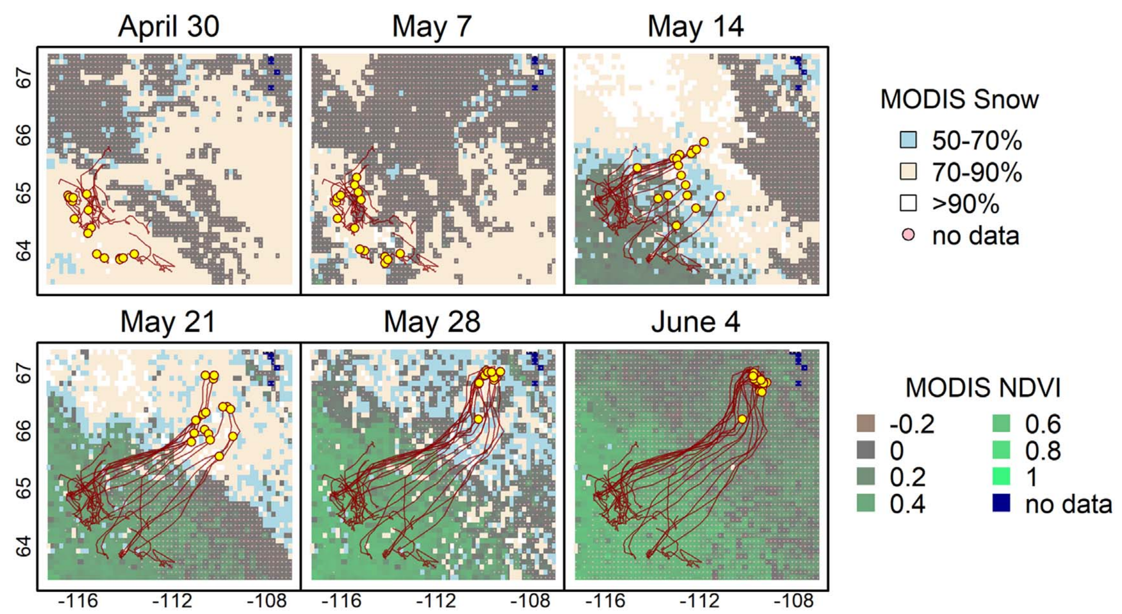

Figure 4. Snapshots of Bathurst caribou movements (circles) over a two-month period in 2011 encompassing the spring migration. Background colors represent MODIS snow cover (pink-light blue-white) and NDVI (brown-green tones). The pink circles illustrate the missing data (e.g. all of 4 June and most of 11 June) obscured by cloud cover.

snowmelt, with high variability among years (mean DAS = 21.9 d, standard deviation 17.5), and arrived at the calving grounds one week before snowmelt (mean 7.3 d, s.d. 12).

Spring migration for collared caribou in 2011 overlaid on MODIS snow-cover data (MODIS/Terra Snow Cover Daily L3 Global 500 m Grid, Version 6—table S1, item 19) is presented in figure 4. The 2011 migration began well before snowmelt and continued until well ahead of the melting snow front, which was the case in all years of the migration. We investigated whether the inter-annual variation in migration timing was explained by timing of snowmelt, as indexed by the median SDD in the entirety of the wintering and calving ranges, respectively. These exploratory analyses indicate that caribou do not migrate in a consistent way with respect to MODIS-derived snowmelt timing. While caribou tended to move ahead of the snowmelt front, they were as likely to move anywhere from one day to three weeks ahead of the retreating snow front. Our findings suggest that if snow-related drivers are important to the timing of migration, snow properties other than cover—the most readily accessible of remotely sensed snow data—are more important. For example, local snow *quality*, including snow variables such as depth, hardness, and finer-scaled spatial patterns of snow cover and timing of ice cover melt on the tundra's many waterbodies, may be more important. To more fully explain the spring phenology of caribou migration a combination of more sophisticated snow products and more ecologically driven combinations of climatic variables (e.g. temperature and precipitation to assess snow quality) need to be taken into account.

5. A future prospectus for improving wildlife-specific snowscape products for ABRs

The snowscape-related questions being asked by the wildlife community span a wide range of spatial and temporal scales and a comprehensive suite of wildlife-relevant snow variables. As demonstrated in the case studies above, spatial and temporal resolution requirements range from meters to kilometers, and from hours to decades. The snow-related variables of interest include depth, density, hardness, collapse pressure, thermal resistance, snow-onset date, snow-free date, length of snow-covered season, and many others depending on the particular application. Recent advances in Arctic snow monitoring and modeling have indeed been made (reviewed in Bokhorst *et al* 2016), yet the development process of these snow products lacks inter-disciplinary cooperation, which can lead to snow datasets inappropriate for, e.g. wildlife applications. In what follows, we offer a future prospectus for improving wildlife-specific snowscape products for the ABR that focuses on enhancement and integration of existing observations and modeling approaches.

5.1. Ground-based measurements of snowscape properties

Given the sparseness of existing *in situ* snow and snow-related observations (see figure 1), improvement of the existing ground-based observing network should focus primarily on improving the spatial coverage and representativeness of the measurements. When selecting where to locate new stations, under-represented landscape types and areas identified by snow models as particularly difficult to characterize should be prioritized. Areas that are most underrepresented include locations that are farthest from existing road networks and higher elevations. Unfortunately, the current trend in the total number of snow monitoring stations is flat and agencies operating them have tightening budget constraints. However, there may be opportunities to leverage existing infrastructure to meet the need for *in situ* data through greater collaboration across management agencies. For example, Alaska Transportable Array infrastructure (usarray.org/alaska#after-2018), located in underrepresented areas, could be identified, augmented with sensors, and operation supported to collect snowscape relevant data. Further, it is critical that augmented networks are equipped with sensors that measure the most critical variables required to make characterize snowscape properties: total precipitation, snow depth, snow water equivalence, and snow surface temperature.

Finally, we suggest a complimentary, ground-based observational approach to collecting information on snowscape properties—deployment of animal-borne sensors. The state of the art in movement ecology includes several miniaturized data logging sensors, including video, audio, biological, and atmospheric data (Kays *et al* 2015). When combined with GPS units, these sensors allow scientists to spatially and temporally reference a suite of co-registered data. For example, cameras have been used to record short videos on pre-programmed schedules, yielding qualitative data on ground conditions (Thompson *et al* 2012), with potential for remote documentation of a suite of vegetation and snowpack characteristics. In an analogous application, oceanographic sensors have been deployed on narwhals (*Monodon monoceros*) to make deep-water observations in Arctic waters that were otherwise unobtainable (Laidre and Heide-Jørgensen 2007). Animal-borne cameras could not only serve to augment traditional ground measurement networks, but also contribute to validation of remotely sensed snow products. Further, biotelemetry sensors that provide data on activity (e.g. accelerometers) and physiology (e.g. heart-rate or body temperature data loggers), can inform empirical relationships between snowscape properties and wildlife movement, activity, and physiological metrics. These empirical relationships can then, in turn, enable those fine-scale metrics to be used as indirect indicators of localized snow conditions throughout remote ABRs.

5.2. Remotely sensed retrievals of snowscape properties

Developing more effective snow retrievals for wildlife studies will likely involve the use of different sensor combinations, including passive optical-IR, lidar, gamma radiation, and active and passive microwave remote sensing. Promising approaches include the fusion of satellite optical-IR and multi-frequency active and passive microwave sensor observations for delineating landscape freeze-thaw heterogeneity and wet snow conditions (Podest *et al* 2014, Kim *et al* 2015). In addition, the use of multi-frequency satellite radar data for landscape level SWE retrievals (Rott *et al* 2010) shows promise and, when combined with a measure of snow density, could be used to calculate the more wildlife-relevant snow depth. These products will offer the greatest benefit when combined with emerging high resolution land surface and digital elevation models that will provide better scaling and modeling opportunities (e.g. Noh and Howat 2015).

New developments in airborne remote sensing offer the potential for significant advances in the remote sensing of snowscapes using coordinated observations from different sensors to develop and test new algorithms for more effective snow retrievals (Deems *et al* 2013, Witz, 2016). For example, airborne observations of snow depth can be obtained through differencing snow-on and snow-off lidar observations (Bolton *et al* 2013, Kirchner *et al* 2014, Painter *et al* 2016, Zheng *et al* 2016), or less expensive structure from motion DSMs (Hopkinson *et al* 2004, Trujillo *et al* 2007, Mott *et al* 2011, Deems *et al* 2013, Nolan *et al* 2015). These methods are especially viable for small to medium scale (10–100 km^2), un-forested areas where a few seasonal data collections (e.g. peak snow depth and bare earth) are sufficient (Nolan *et al* 2015, Harder *et al* 2016) Larger areas with tree cover, rugged topography, and the need for multiple observations quickly add to mission complexity and cost. Airborne activities such as these offer a path forward for developing next generation satellite-based methods to monitor snowscapes at wildlife-relevant spatial and temporal scales using data such as that expected from the Advanced Topographic Laser Altimeter System to be launched aboard the NASA ICESat-2 platform (see Treichler and Kaab 2017). Because snowscape properties in ABRs are inherently very different than those in other snow landscapes (Sturm *et al* 1995), an ABR-specific airborne snow campaign, conducted concurrent with ground observations—similar to NASA's SnowEx campaign focused on mapping SWE in Colorado's forested ecosystems (https://snow.nasa.gov/snowex)—will be essential to developing effective snow retrievals for the region.

5.3. Model simulations of snowscape properties

To satisfy the needs of wildlife studies, existing snow-evolution models that were initially designed for climate, hydrologic, and/or avalanche applications should be modified and enhanced to include new wildlife-relevant snow variables such as snow depth, snow hardness, and ice-layer thickness, and vertical distribution within the snowpack. These models must also have the ability to be run at a wide range of spatial resolutions, depending on the wildlife application of interest; for example, as shown in our case studies, simulations of polar bear den habitat likely require much finer resolution than studies of caribou migration timing and routes.

5.4. Data-model fusion: combining snow products for wildlife-snow interaction studies

While it is true that each meteorological input, each ground observation, each remote sensing instrument, and each snow modeling tool includes some valuable information on snow-property distribution and evolution, each of these contributions also comes with their own collection of weaknesses. We contend that a combined approach, using atmospheric forcing from meteorological stations (re)analyses, and/or climate scenario datasets; ground-based snow measurements; remote-sensing datasets; and modeling tools is required to answer the breadth of snow science and management questions being asked by the wildlife community. In such a synthesis, each meteorological dataset, ground measurement, remote sensing observation, and model result, contributes toward unveiling the 'snow puzzle'. We call this 'data-model fusion', as opposed to 'data assimilation', because it embodies a synergetic extracting and merging of information obtained from different sources, in an effort to produce an outcome that is better than the outcome obtained by using the different sources independently. By merging data from meteorological, ground *in situ*, remotely sensed, and/or modeled data sources, the data-model fusion approach—if carefully applied—dynamically offsets weakness in any individual component dataset at any given point in space and time, while including the strength of other component datasets. Under conditions where, or when, a given data source is known to have certain limitations or has missing data, another data source can fill in. For example, given that snow-evolution models suffer often from precipitation inputs that are inadequate to reproduce observed snow distributions (see section 3), integration of snow-on-the-ground observations using data-model fusion can correct those precipitation deficiencies (e.g. Liston and Sturm 2002, Liston *et al* 2008, Pedersen *et al* 2017). As another example, snow-depth datasets are often available instead of the more hydrologically important SWE data (Sturm *et al* 2010), this information can be used to add information to data-model fusion efforts. Collectively, the data-model fusion system should ultimately return a well-informed and valued product.

Data-model fusion is a multi-step process, where at each step there are interactions and feedbacks between (1) the observations, (2) the model configuration and representations, and (3) the modeling team (Williams *et al* 2009, Keenan *et al* 2011). Inherent in this process is the requirement that the model developers have intimate knowledge of the observational datasets, how they were collected, what features and processes they represent, what they contribute, and their limitations. The model developers must also have intimate knowledge of the modeling systems and how those systems relate to, and merge with, the various data inputs. This knowledge is particularly important to reduce the ultimate amount of error and uncertainty during product development.

The data-model fusion system that we are advocating includes three basic and practical requirements, which emerge from limitations in current (and likely future) snow-related datasets. All of these requirements can be met with modifications to existing snow-evolution modeling tools, and with inputs from ground and remote-sensing observations. The system should:

1. Add physical properties to basic snow information and datasets (e.g. convert SWE data from a remote sensing instrument to snow depth, by adding model-simulated snow density data).
2. Using our physical understanding and model representations of snow-evolution processes, fill in missing data between snow measurements sparsely distributed in space and/or time.
3. Account for a wide range of snow-related observational datasets provided by both ground observations (e.g. SWE, snow depth, snow surface temperature), and remote sensing (SWE, snow presence or absence, fractional snow-covered area, grain size, albedo, snow surface temperature, snow wetness, and icing).

Figure 5 provides an example of the data-model fusion approach we used to simulate snow depth in the Arctic National Wildlife Refuge (ANWR) for 1 April 2015. We merged snow-on-the-ground observations (figure 5(a)) with the MicroMet (Liston and Elder 2006b), SnowModel (Liston and Elder 2006a), and SnowAssim (Liston and Hiemstra 2008) snow-evolution modeling tools. The models were run over the 400 km × 400 km domain using a 500 m grid increment and 3 h time step (figure 5(b)). MicroMet ingested atmospheric reanalysis data, SnowAssim assimilated end-of-winter (pre-melt) SWE observations, and SnowModel performed the spatial and temporal interpolations and evolutions and added the higher-resolution physics to the distributions, including conversion from SWE to snow depth (figure 5(b)).

Figure 5(a) displays the spatially interpolated observations (no physically based adjustments have been applied). Figure 5(b) shows the value added when the physics in the models are used to distribute and convert the SWE to snow depth. The data-model fusion snow-depth distribution (figure 5(b)) includes features such as (1) thinner snow along the lowlands in the south of the domain and along the Arctic coast (the purple areas), (2) less snow in the bottoms of the drainage basins, (3) deeper snow in the higher elevations,

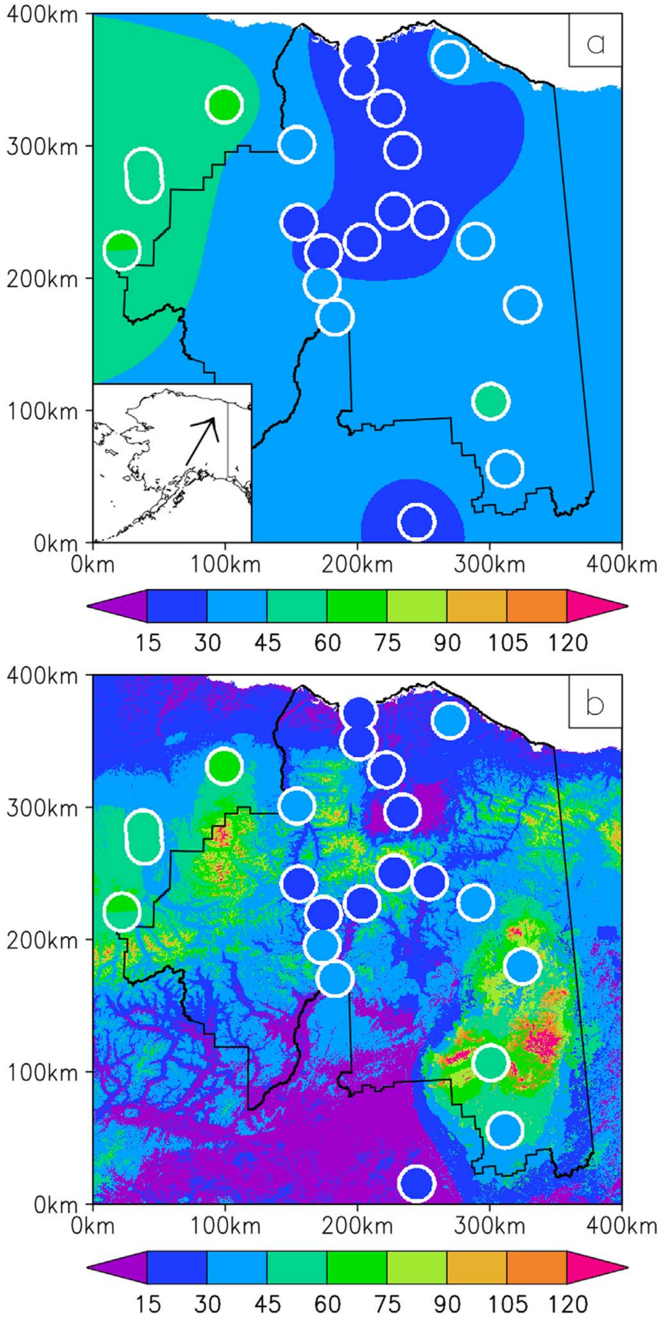

Figure 5. (a) Snow depth (cm) observations (solid-color dots surrounded by white borders) collected during March–April 2015 in the Arctic National Wildlife Refuge (ANWR) and spatially interpolated over the ANWR domain (color shades). (b) Snow depths (cm; color shades) simulated by SnowModel on 1 April 2015, while assimilating the snow depth observations using SnowAssim. Observed snow depth sites and values are included as solid-color dots surrounded by white borders. The ANWR boundary is also included (black line).

(4) precipitation-shadow effects south of the Brooks Range, and (5) vegetation-related snow distributions (e.g. forests versus tundra). All of these important snow-distribution features are largely absent in the observations (figure 5(a)).

The data-model fusion example shown in figure 5(b) produced spatially- and temporally-continuous snow-property distributions that match our physical understanding of snow processes (e.g. snowfall/precipitation distributions, conservation of mass and energy, layer development within the snowpack, snow-canopy interception progression, blowing snow redistribution, snow-vegetation interactions, melt rates and timing, snow-covered-area evolution, etc) and the available field observations. Only one time (day; 1 April 2015) is shown, but the model simulated the snow-depth distribution every 3 h from 1 September 2014 through 31 August 2015. In addition, while this simulation example only assimilated snow-on-the-ground observations, remote sensing observations could have also been included in the data-model fusion.

This data-model fusion approach promises to be broadly applicable to a wide range of ecosystem studies in the ABR, but it is a particularly attractive option for studying wildlife-snow interactions because we expect it to deliver on all of our most pressing needs via one, consistent and effective approach. In fact, we believe there is no other option. There is no evidence to suggest we have the financial resources or ability to modify existing snow monitoring technologies (i.e. ground-based or remote-sensing systems) such that comprehensive and complete mosaics of wildlife-relevant snow variables are available for the purposes of wildlife science and management research. This forces us to turn to models. But it is also clear that these models can benefit from the observations we are making. The logical next step, and the solution to our data-deficiency problem, is to merge the data with the models and create something more than exists without this coupling. The data-model fusion approach can produce spatially detailed and temporally continuous datasets of multiple snowscape properties and variables relevant to wildlife over large areas. It can do this by merging (1) the detailed temporal coverage of snow and meteorological data from ground observations, (2) the vast spatial coverage offered by remotely sensed observations, and (3) the large suite of simulated snowscape variables from wildlife-relevant snow modeling tools.

Other ABR research efforts will also benefit from this data-model fusion approach. The spatial snow products that are critical to understanding wildlife behavior and fitness are also essential to understanding the influence of snow dynamics on people in the ABR. Humans are affected by the same suite of snowscape properties as wildlife. For example, dynamics in snowscape properties influence travel by residents of rural subsistence communities, and thus impact the ease and safety of access to provisioning ecosystem services such as fish, wild game, drinking water, hydro power, and firewood (Callaghan *et al* 2011, Brinkman *et al* 2016). As other examples, changes in snowscape conditions in wildlife habitat may alter availability of wild game to subsistence communities (Tyler 2010, Langlois *et al* 2017), or limit skiing opportunities and snowmobile operation, thus affecting winter tourism (Abegg *et al* 2007). At the same time, reported experiences and qualitative observations made by people working and living in ABRs can be formally included in our understanding of human-snow interactions. Currently, however, there is a dearth of information on the topic because the spatial and temporal resolution of data on both humans and snow are insufficient to estimate causal relationships. The data-model fusion approach we advocate herein is a viable mechanism to correct this data void.

6. Conclusions

Although a large suite of ABR-wide spatial snow products is available, these products often have insufficient spatial or temporal resolutions, coverage, or lack specific snowpack properties that are most relevant to wildlife behavior. Given that snow depth, collapse pressure, layer hardness, and other wildlife-relevant factors significantly affect wildlife in snowscapes, the development, improvement, and availability of spatial products for each of these variables should be a clear and well defined focus of future wildlife-snow studies. It is equally important that the spatiotemporal resolution of collected wildlife data is well-matched to that of the spatial snow products that are proposed herein. In fact, rapid technological advances in animal-borne sensors are enabling measurements of animal behavior at increasingly finer spatial and temporal resolutions, and over larger areas (Kays *et al* 2015). This means that wildlife biologists are increasingly able to ask and test questions relevant at scales and resolutions that surpass those of the existing suite of widely available environmental covariates—such as snow properties—that influence the movement and behavior they seek to understand.

As a specific and urgent example of this need, the NASA Arctic Boreal Vulnerability Experiment (ABoVE) is an intensive multi-year field campaign recently inaugurated across Alaska and northwestern Canada that involves coordinated observations from airborne and satellite remote sensing in context with detailed field studies and modeling (Goetz *et al* 2011). A major ABoVE science objective is to quantify how changes in the spatial and temporal distribution of snow impacts ecosystem structure and function, including wildlife habitats across ABR environmental gradients. The ABoVE design provides a framework for coordinating ground and remote sensing observations with modeling approaches for producing snowscape products at multiple spatial resolutions and temporal scales. With these data sources, ABoVE could lead the way in improving snow science in the ABR by focusing its efforts and developing data-model fusion approaches to produce fit-for-purpose snow products, with particular emphasis on the, to date, underserved needs of Arctic and boreal research scientists. The relative wealth of coordinated *in situ* measurements, airborne and satellite remote sensing data, and modeling tools being collected and developed as part of ABoVE and NASA's SnowEx campaign, provide a data rich environment for developing and testing new remote sensing algorithms and retrievals of snowscape properties that may provide a testbed for developing next generation satellite missions able to monitor ABR snowscape dynamics relevant to wildlife.

To accomplish this requires active development and contributions from all three constituents of the data-model fusion system: *in situ* ground, remotely sensed observations, and models. By working together these groups will define and make new types of measurements to develop snow-evolution modeling systems that ingest observing system variables and create wildlife-relevant outputs. Immediate investment into improving the availability of specialized, fit-for-purpose spatial snow products for the ABR is required to expand our knowledge and improve our ability to answer key snow-related wildlife science and management questions.

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