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Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times[1]

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Abstract: The change of water phase around 0 °C has considerable impacts on wildlife ecology because liquid and solid water strongly differ in their insulating capability, mechanical resistance, and light reflectance. Freeze and melt events thus have strong ecological relevance, particularly in the Arctic where snow and ice are omnipresent and their conditions are changing due to climate warming. We first review the mechanisms linking water phase transitions to wildlife ecology, with emphasis on seven key processes. These processes are illustrated with examples or detailed case studies, such as snowmelt and icing events affecting herbivore populations, thaw-induced collapse of structures used by wildlife for reproduction, and thermal erosion of ice wedges reducing waterfowl habitat. We infer that water phase transitions generate some critical places and critical times that play a disproportionate role in the ecology of tundra wildlife. We map these critical places and times to help structure future research on the effects of climate change on tundra wildlife in a context where changing permafrost and snow conditions might trigger abrupt ecological responses in the Arctic tundra.

Key words: ice, permafrost, snow, tundra, wildlife.

Résumé : Le changement de phase de l'eau autour de 0 °C a des impacts considérables sur l'écologie de la faune parce que l'eau liquide et l'eau solide diffèrent fortement dans leur capacité d'isolation, leur résistance mécanique et leur réflectance à la lumière. Les événements de gel et de dégel ont ainsi une grande pertinence écologique, particulièrement dans l'Arctique où la neige et la glace sont omniprésentes et leurs conditions changent en raison du réchauffement climatique. Nous passons d'abord en revue les mécanismes liant les transitions de phase de l'eau à l'écologie de la faune, l'accent étant mis sur sept processus clés. Ces processus sont illustrés par des exemples ou des études de cas détaillées, tels que des événements de fonte des neiges et de gel ayant un effet sur les populations herbivores, l'écroulement provoqué par le dégel des structures utilisées par la faune pour la reproduction et l'érosion thermique des fentes de glace réduisant l'habitat du gibier d'eau. Nous déduisons

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que ces transitions de phase de l'eau produisent quelques endroits critiques et temps critiques qui jouent un rôle disproportionné dans l'écologie de la faune de la toundra. Nous dressons la carte de ces endroits et temps critiques afin d'aider à structurer la recherche future sur les effets du changement climatique sur la faune de la toundra, dans un contexte où les conditions changeantes du pergélisol et de la neige pourraient déclencher des réponses écologiques brusques dans la toundra arctique.

*Mots-clés :* glace, pergélisol, neige, toundra, faune.

Introduction

A key finding of the Arctic biodiversity assessment (CAFF 2013) is that climate change is by far the most serious threat to Arctic biodiversity and exacerbates all other threats. Two important mechanisms are at play. First, the polar amplification of the last 50 years has resulted in larger changes in temperature in the Arctic than the planetary average (McBean et al. 2005). Second, this change in temperature has considerable impacts on snow and ice (Vaughan et al. 2013), with extensive effects on ecological systems, including wildlife (Post et al. 2009; Hansen et al. 2011; Gauthier et al. 2013). This context has contributed to the emergence of a sense of global stewardship toward Arctic wildlife, with a clear need to better monitor, understand, predict, and manage the relations between Arctic wildlife, humans, and their common polar environment.

The change of water phase from liquid to solid and vice versa has far-reaching consequences for wildlife given that liquid water, snow, and ice strongly differ in their physical properties (Marchand 1987; Halfpenny et al. 1989). The growing body of literature describing the effects of climate change on Arctic wildlife recognizes this central role of water phase transitions (Klein et al. 2005; Post et al. 2009; Gilg et al. 2012; CAFF 2013; Hansen et al. 2013). Examples range from earlier onset of the spring melt advancing bird egg laying (Høye et al. 2007) to winter ground-icing blocking access to food plants by reindeer (or caribou) (*Rangifer tarandus*) (Hansen et al. 2011). Yet no coherent framework exists as to the various pathways linking climate change, water phase transitions, and wildlife. Understanding the biological mechanisms involved in climate change effects is vital to design robust ecosystem-based monitoring plans (Christensen et al. 2013; Ims et al. 2013), to predict some of the changes yet to come (Berteaux et al. 2006), and for sustainable management of human–wildlife relations. Indeed, several of the wildlife species included in this review represent important values (ecosystem services) to people in the Arctic and beyond, and an important role of science should be to provide knowledge that can aid in preserving these values in an uncertain future.

The Canadian Arctic Development and Adaptation to Permafrost in Transition (ADAPT) project has studied the mechanisms and consequences of permafrost degradation within an interdisciplinary framework (Vincent et al. 2013). We draw on this effort to review the links between Arctic wildlife and the terrestrial cryosphere in a climate change context. We concentrate on tundra wildlife, the nondomesticated birds and mammals living primarily in natural habitats of the Arctic terrestrial environment (after Klein et al. 2005). Virtually all of the Arctic is underlain by continuous permafrost and for this synthesis, we use a conceptual model of the permafrost system modified from Vincent et al. (2013), which involves, from top to bottom, the snow–vegetation layer (or buffer layer), the soil surface interface, the active layer, the transient layer (Shur et al. 2005), which is the interface between the active and the permafrost layers (the depth of this interface depends on year to year variations in the active layer depth), and the permafrost layer itself (Fig. 1).

We first summarize the main characteristics, seasonal changes, and longer-term changes of snow and ice in the Arctic tundra. We then review the mechanisms linking the permafrost system to the ecology of tundra wildlife, with emphasis on the impacts of

Fig. 1. Graphical model of the permafrost system, shown here after the first snowfall in autumn. The ground is considered as a three-layer system with transition zones in which the bottom permafrost layer extends from beneath the active layer (the seasonal thaw zone) into bedrock or sediments. The uppermost buffer layer contains mostly snow and vegetation. The thickness of the layers varies in the Arctic depending on local climate and in the landscape depending on site conditions and soil thermal properties.
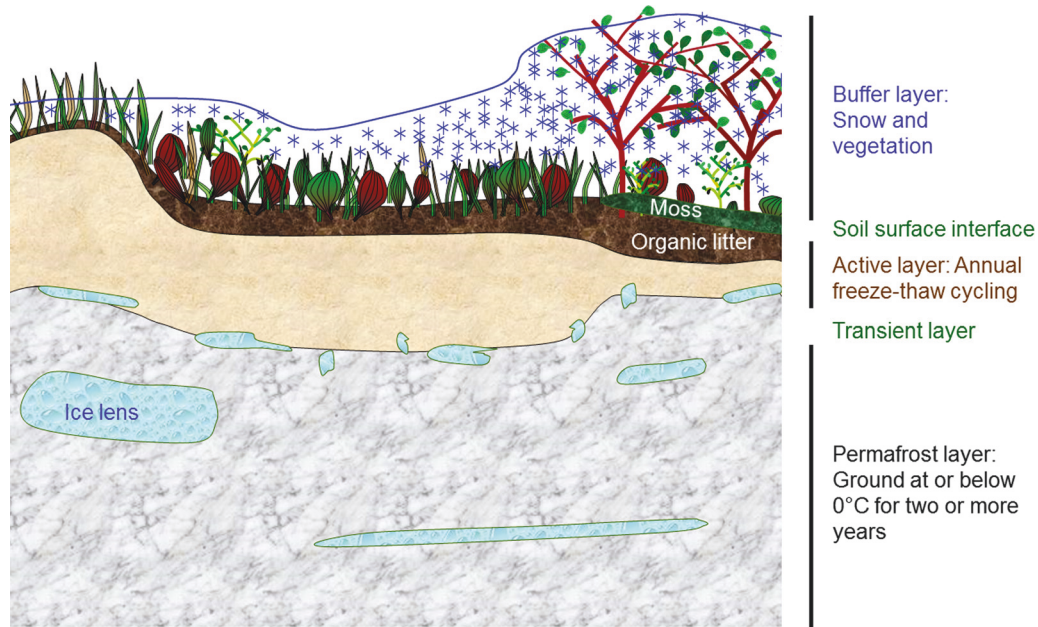
water phase transition. Examples and case studies demonstrate that there are some critical places and critical times that play a disproportionate role in the ecology of tundra wildlife. We provide a map of these critical places and times and conclude by summarizing the main knowledge gaps and research directions at the interface between the permafrost system and tundra wildlife ecology.

Snow and ice in the Arctic tundra

For tundra wildlife, the most important changes occurring in the buffer layer of the permafrost system are the transitions between liquid water and snow, whereas the most important changes occurring in the active layer are the transitions between liquid water and ice. This section gives wildlife ecologists the background information needed to understand the relationships between Arctic terrestrial wildlife, snow, and ice. We first describe the buffer layer characterized by its seasonal snowpack and follow up with the active layer characterized by its seasonal ground ice.

The buffer layer: establishment and transformations of the snowpack

As the air temperature nears 0 °C in late summer, precipitation changes from rain to melted snow to snow. Whereas the form of precipitation reaching the ground depends first and foremost on air temperature, it is also affected by the temperature gradient in the atmosphere and by snow crystal aerodynamic properties, which determine their fall velocity (Barthazy and Schefold 2006). A snow cover, which sometimes contains liquid water, rapidly forms on the ground, with pronounced consequences for the surface energy budget, hydrology, vegetation, and wildlife of the tundra. Snow reflects 70%–90% of incoming solar radiation in the 300–2500 nm range, i.e., it has an albedo over the solar spectrum of 0.7–0.9 (Gardner and Sharp 2010). In the visible wavelength range (380–760 nm), snow albedo

increases to 0.9–0.98, depending on snow grain size and impurity content, so that snow is the most reflective surface on Earth. By comparison, Arctic vegetation has a broadband albedo around 0.12 (0.06 in the visible) (Loranty et al. 2011), bare ground around 0.25 (0.15), and water bodies around 0.03 (0.06) (Varotsos et al. 2014). The high albedo of snow is to a large extent responsible for the cold climates of polar regions. With climate warming, the extent and duration of snow cover decrease, and the replacement of highly reflective snow surfaces by much more light-absorbing surfaces generates a positive feedback (Hall 2004), which partly explains why polar regions warm up faster than lower latitudes (Pithan and Mauritsen 2014).

Another impact of the formation of the snow cover is that it provides a thermally insulating layer for the ground, vegetation, and wildlife living in the subnivean space. The thermal conductivity of snow ranges from 0.025 $W \cdot m^{-1} \cdot K^{-1}$ for fresh snow and light depth hoar (the large-grained crystals occurring at the base of the snowpack) to about 0.65 $W \cdot m^{-1} \cdot K^{-1}$ for hard wind slabs and melt–freeze crusts (Sturm et al. 1997).

The physical properties of snow such as its albedo, thermal conductivity, density, and permeability to air are not stable during winter, but rather vary widely through time as the structure of snow changes with meteorological conditions (Sturm et al. 1995). These changes in snow structure involve changes in the size and shape of snow crystals and in the strength of bonds between grains through recrystalization processes referred to as snow metamorphism (Sommerfeld and LaChapelle 1970; Colbeck 1983). The main processes involved in metamorphism are phase transitions, that is changes from ice to water vapor (sublimation), from ice to liquid water (melting), from water vapor to ice (condensation), and from liquid water to ice (freezing). Melting and freezing only take place at 0 °C. Therefore, in the Arctic, sublimation and condensation are dominant because the snowpack is well below 0 °C most of the time, whereas melting and freezing are observed at the beginning and end of the snow season and during warm spells.

At the beginning of Arctic snow season, a temperature gradient reaching 300 $°C \cdot m^{-1}$ can establish itself in the 5–10 cm thin snowpack between the ground still at 0 °C and the atmosphere, which can be as cold as –15 °C. Since the water vapor partial pressure very strongly depends on temperature (it is 165 Pa at –15 °C and 611 Pa at 0 °C; Marti and Mauersberger 1993), this extreme temperature gradient generates water vapor fluxes from the base to the top of the snowpack, with the top part of snow crystals sublimating, and the water vapor thus produced condensing on the bottom part of the crystals above them. Water vapor is thus carried vertically from one crystal to the next in a process called "hand to hand delivery of water vapor" (Yosida 1955). This leads to rapid grain growth and to the formation of large (>10 mm) hollow striated snow crystals that form very soft uncohesive layers of low density (typically 200–250 $kg \cdot m^{-3}$) called depth hoar layers (Domine et al. 2016a). Depth hoar crystals, despite their name, form near the surface at the beginning of the snow season and because of their size are unlikely to be eroded and transported by wind.

Later in the season, once the ground has cooled and the snow cover is thicker, the temperature gradient in the snowpack is much lower. This results in a reduced water vapor flux that cannot lead to depth hoar formation anymore. Grains stop growing and hard wind slabs made of small, rounded, and well-sintered grains form instead. The density of these layers sometimes exceeds 500 $kg \cdot m^{-3}$ (Dalerum et al. 2002; Domine et al. 2016a) and contrary to depth hoar, they easily support travel by large animals. On Arctic tundra, the snowpack therefore generally consists of two main layers: a hard wind slab that supports travel by humans and wildlife and, below it, a soft depth hoar layer offering shelter to subnivean species (Fig. 2) (Domine et al. 2016b).

Fig. 2. Snow stratigraphy at Bylot Island (73°05′N, 80°00′W) in May 2015 showing the two-layer structure typically encountered in the Arctic: a 8 cm soft depth hoar layer made of large grains is overlaid by a 17 cm harder wind slab made of small, well sintered rounded grains, which supports travel by humans and wildlife.
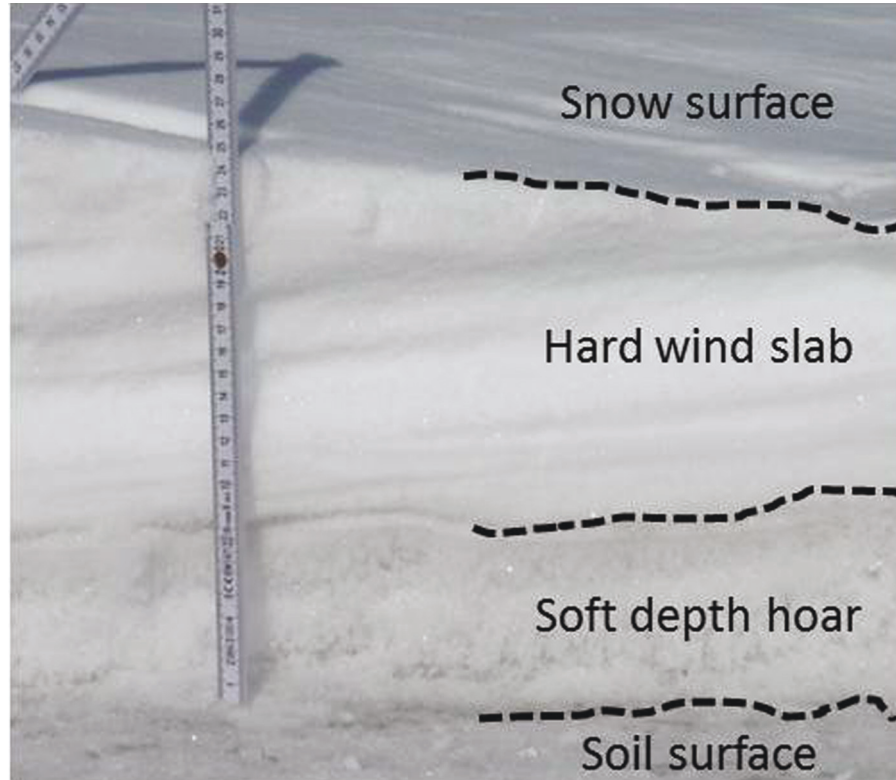
This mode of formation of the Arctic snowpack illustrates how physical processes governed by meteorological conditions determine snow physical properties. With climate change, this type of snowpack may be affected by several perturbations, three of them being particularly relevant to wildlife ecology. First, increases in temperature and precipitation induce both a reduction in the temperature difference between the ground and the atmosphere and an increase in snow thickness, which reduce the temperature gradient in the snowpack and limit the formation of the soft depth hoar layer at the bottom of the snowpack. Second, changes in wind speed modify the hardness of wind slabs and their ability to support travel (Kotlyakov 1961). Since wind speeds have overall been observed and predicted to increase in the coastal Arctic (Steiner et al. 2015; Stopa et al. 2016), partly because of the late freezeup that increases the thermal contrast between land and ocean, snow hardness is expected to increase. Third, episodes of temperatures above 0 °C lead to the formation of melt–freeze crusts at the top of the snowpack (Jamieson 2006). Domine et al. (2007) gave a more exhaustive account of the impact of warming on snow physical properties, whereas Bokhorst et al. (2016) reviewed recent developments and assessed future needs regarding observations, modelling, and impacts of changing Arctic snow cover.

A key message for wildlife biologists is that changes in weather patterns, including total precipitation and seasonal and annual variability, as well as changes in wind speed, are likely to have strong influences on snow characteristics that are likely to favor harder snow at

the beginning of the snow season. However, so far, attempts to predict these changes have not been fully successful (Overland et al. 2015).

The buffer layer: effects of shrubs on the snowpack

Shrub distribution in the tundra is patchy at multiple spatial scales but is increasing as climate warms up (Sturm et al. 2001; McManus et al. 2012; Fraser et al. 2014). Shrub abundance has far-reaching effects on the formation and properties of the snowpack. In particular, the dense networks of twigs of species such as willows (*Salix* spp.) and dwarf birch (*Betula* spp.) considerably limit snow compaction. This creates a thicker snow layer of low density and therefore low thermal conductivity, which helps keep the ground warm, lengthening the depth hoar formation season and allowing depth hoar to develop throughout the height of the shrubs (Domine et al. 2016*a*).

Strong differences exist between the insulating property of a snowpack established on top of a herb layer and that of a snowpack established among shrubs (Fig. 3). The insulating property of a layered material is conveniently expressed by its thermal resistance R_T:

$$(1) \quad R_T = \sum_i \frac{h_i}{k_{eff,i}}$$

where h is the thickness of each layer and k_{eff} is its thermal conductivity (Domine et al. 2012). The heat flux F through the snow can then be expressed as

$$(2) \quad F = \frac{T_{base} - T_{top}}{R_T}$$

where $T_{base} - T_{top}$ is the temperature difference between its base and its surface. The thermal resistance of the snowpacks observed at Bylot Island (Nunavut, Canada) represented in Fig. 3 were 4.1 m^2 $K \cdot W^{-1}$ (herb tundra) and 10.1 m^2 $K \cdot W^{-1}$ (shrub tundra), indicating that shrubs more than doubled the insulating property of the snowpack (Domine et al. 2016*a*). In mid-May 2015 on Bylot Island, this resulted in a basal snow temperature of −12.8 °C in the shrub tundra and −17.2 °C in the adjacent herb tundra. Such a shrub-induced warming of 4.4 °C illustrates the impact of vegetation on subnivean life and potentially on nutrient cycling and permafrost thaw.

The active and permafrost layers: heat exchanges with the atmosphere

The active layer and underlying permafrost layer play an important role in how seasonal conditions evolve in the tundra. Permafrost is defined as ground material that remains frozen for two or more years and may form in any earth material, including peat, mineral soil, sediment. and rock (French 2007). The distribution of permafrost across the Arctic varies substantially and ranges from thin (0–25 m thickness) and spatially discontinuous in the boreal region to thick (250 to >600 m thickness) in the High Arctic (Smith and Riseborough 2002). These differences in permafrost extent reflect climatic conditions and the balance between summer heat gains and winter heat losses at the land surface (French 2007). This heat exchange with the atmosphere results in a progressive reduction in seasonal heat exchanges with soil depth and a lower annual amplitude of temperature with depth (Fig. 4). Seasonal variations in surface heating from solar irradiance and convective heat exchange with the atmosphere are conducted vertically through the soil with increased time lag as depth increases (Romanovsky and Osterkamp 1995). Horizontal heat exchange can also be important, particularly adjacent to streams, rivers, and surface water bodies (Bonnaventure and Lamoureux 2013). Additionally, physical disturbance of the landscape through thermo-erosional incision (Bowden et al. 2008) and slope failures can result in abrupt increases in horizontal heat flux and perturbation of active layer dynamics.

Fig. 3. Typical stratigraphy of snowpacks at Bylot Island (Nunavut, Canada) in May 2015. Over herb tundra, the snowpack is thin and the depth hoar layer is 5–10 cm thick. Herbaceous vegetation is mostly flattened by snow and has little effect on its structure. In *Salix richardsonii* bushes, the snow is thicker and the 20–30 cm thick depth hoar layer rises to shrub height. Hard wind slabs are nearly absent in willows.
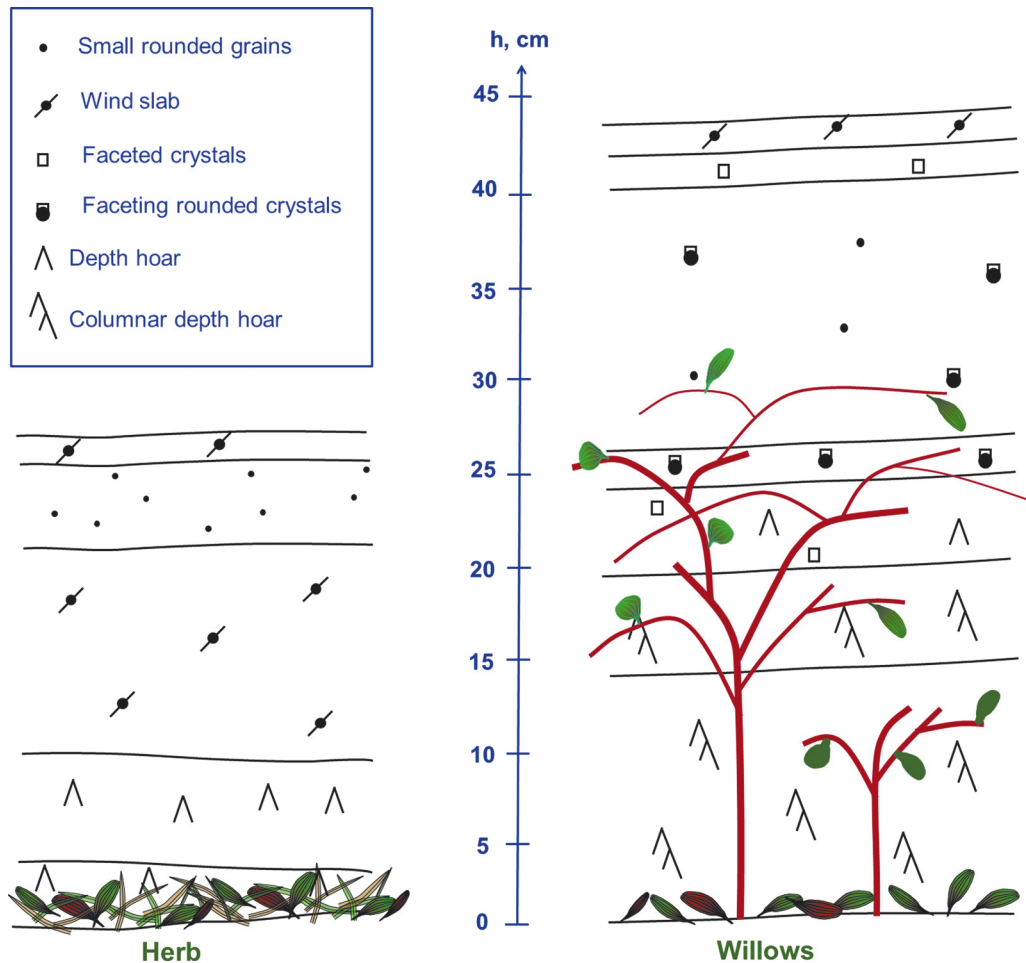
During the summer melt season, energy from the climate system progressively thaws the soil from the surface to depth, generating the seasonal active layer. The active layer depth varies each year depending on climate conditions, with greater depths associated with warmer conditions, but other factors such as snow cover duration and thickness can play an important modifying role by altering autumn and winter heat loss and, conversely, spring and early summer warming of the soil (Lafrenière et al. 2013). The active layer typically reaches maximum depth in late summer but varies substantially over small spatial scales. Factors other than climate control thaw depth, primarily those related to thermal conductivity of the surface and soil materials, especially soil water content, soil texture, and mineral composition (French 2007).

Low thermal conductivity soil materials include vegetation, leaf litter, moss, and unsaturated soil organic matter. The presence of these materials substantially slows conductive heating of the underlying material and is frequently associated with shallower active layer development (French 2007). However, it is important to note that when saturated, these

Fig. 4. A typical depth–temperature profile (or "trumpet" diagram) illustrating soil and permafrost thermal state at seasonal extremes of winter (blue line) and summer (red lines). Due to varying seasonal melt, the active layer depth may vary with increasingly less frequency at depth and represents the transient layer. The transient layer (Shur et al. 2005) is shown by the colored rectangle. Modified from Bonnaventure and Lamoureux (2013).
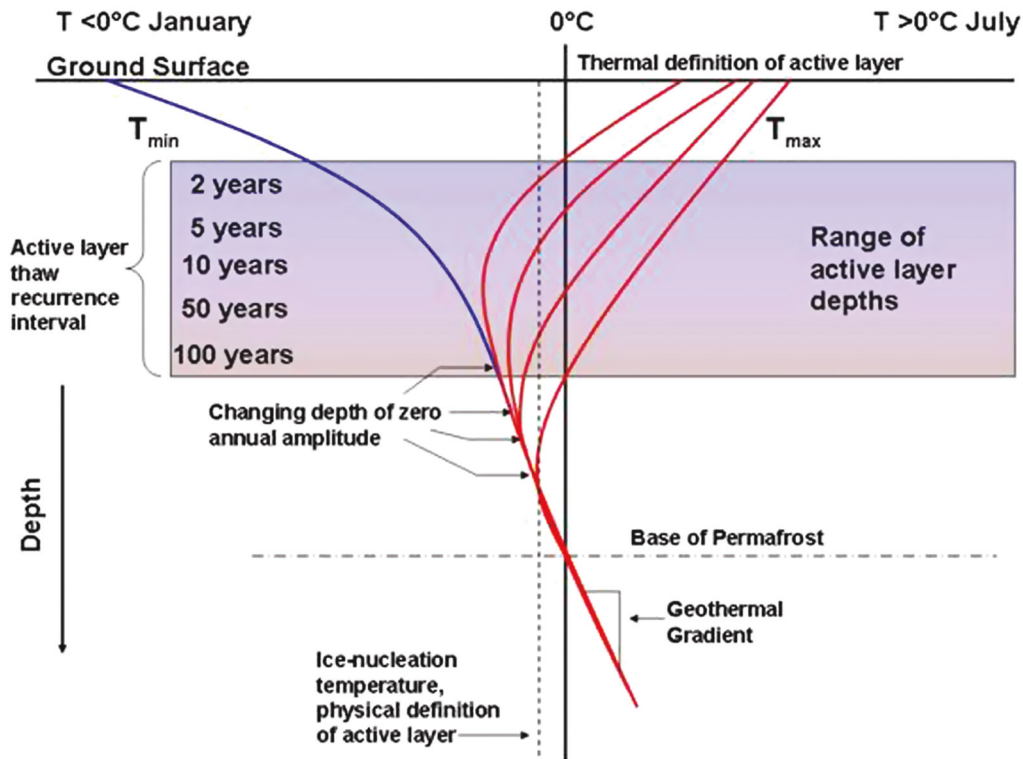
organic materials have substantially higher thermal conductivity. By comparison, minerogenic soil has higher thermal conductivity and thaws more deeply for a given set of climatic inputs. Hence, variations in the surface buffer (vegetation, snow cover), soil structure, and soil water content result in substantial variations in active layer depth, both at small and large spatial scales. For example, relatively barren minerogenic High Arctic soils with a limited surface buffer may develop active layer depths of 60–100 cm, while Low Arctic soils with thick organic matter accumulations may develop active layer depths of <50 cm, despite greater potential heat inputs from the climate system (Shur et al. 2005). As we have seen above, increased shrub cover tends to increase snow cover accumulation and is associated with reduced heat loss in the winter (Sturm et al. 2001). It is, however, also associated with reduced heat gains in the summer because it shields the ground from direct radiation absorption. Both of these processes affect active layer depth.

Surface processes and properties are expected to be substantially altered by climate change, with attendant impacts on the heat balance of the active layer and upper permafrost. Broadly, the snowpack is expected to increase in Arctic regions along with increased air temperatures (AMAP 2012). The timing of increased snowpack will result in different thermal effects in the soil, with early (autumn) snow helping to retain heat in the active layer and delaying freeze-up. By contrast, late snowpack accumulation (winter, early spring) will slow heat gain, resulting in later and shallower active layer development (Lafrenière et al. 2013). Increased summer rainfall is also an important mechanism

for delivering heat to the active layer and accelerating thaw (Carey and Woo 2002). In addition, the expansion of shrub cover is expected to cause deeper snowpack with consequences for the heat budget and active layer development (Sturm et al. 2005; AMAP 2012).

The active and permafrost layers: water phase transitions

Soil water and ice play a critical role in the development of the active layer. Percolation of water through the soil results in comparatively rapid heat delivery to depth and can accelerate thaw. Summer rainfall is a key mechanism contributing to active layer development (French 2007). On the other hand, soil ice represents a substantial thermal barrier to thaw due to latent heat requirements for ice melt (Bonnaventure and Lamoureux 2013). Soils that develop segregated ice bodies during the autumn freeze period have a slower thaw advancement during the following melt period. Water and ice content in soils varies considerably, as discussed below.

The melt season generates a typical sequence of active layer development. Initially, some snow meltwater can percolate into frozen soils, refreeze, and release latent heat that warms the upper soil (Woo 2012). After snow has melted, the exposure of lower albedo vegetation and soil increases absorption of solar radiation, warming the surface soil and initiating progressive heat conduction and thaw with depth. By midsummer, the combination of surface warming and warm atmospheric conditions results in maximum soil temperatures at the surface and a progressive cooling with depth (Fig. 4) (Bonnaventure and Lamoureux 2013). This cooling gradient reaches 0 °C at depth (the base of the active layer) and continues to cool with depth into the permafrost. As a result, the amplitude of annual soil temperature is highest at the surface and decreases with depth, until the depth of zero amplitude is reached in the upper permafrost and corresponds to constant temperatures throughout the year (Fig. 4).

As the atmosphere cools and solar radiation intensity and duration wanes in autumn, the thermal gradient in the soil reverses and heat is conducted towards the surface where it is lost to the atmosphere as infrared radiation and convective exchanges. The rate of heat loss is greatest at the surface, and as a result, the soil typically freezes from the surface down as heat is conducted vertically towards the surface (Fig. 4). As the freezing isotherm (often referred to as the freezing plane) advances down through the active layer, soil water becomes a critical modifying factor. Liquid water that freezes releases latent heat, offsetting conductive heat loss to the surface and slowing or temporarily halting the progression of freezing. In fine-grained soils such as clays and silts, water is drawn by capillary cryosuction to the freeze plane, resulting in a period of ice accumulation and delay in the advance of the freeze plane until soil water supply is no longer available or cryosuction is insufficient to maintain ice formation and latent heat release (French 2007). The stabilization of the freeze plane is referred to as the frost curtain effect and can slow the refreezing of the active layer for days, and in some cases weeks, during the autumn (Bonnaventure and Lamoureux 2013). Considerable amounts of ice may form under these conditions, leading to the formation of segregated ice bodies that may be continuous layers (1 to >20 cm thickness) or laterally discontinuous lenses (Figs. 1 and 5). Once the ground is frozen, the ice contained near the surface can sublimate because of the temperature gradient between the ground and the colder atmosphere. The water vapor thus generated accelerates ground cooling because of latent heat consumption and is released to the snowpack and possibly the atmosphere through the soil pores (Sturm and Benson 1997). Thus, the thermal effects of water phase transitions are complex and can play an important role in soil thaw and water conditions in a given season.

Fig. 5. Exposed segregated soil ice layer in a wetland located near Iqaluit, Baffin Island. In this setting, abundant water availability during autumn freeze-up generates a thick ice layer and slows the depth progression of the freeze plane (photo credit: Scott Lamoureux).

There is a growing body of evidence that climate change is causing deeper active layer development and thaw of both the transient layer and the upper permafrost in many Arctic regions (Shur et al. 2005; AMAP 2012; Bonnaventure and Lamoureux 2013). This has resulted in substantial changes to surface stability that has resulted in altered surface drainage and ponding (Liljedahl et al. 2016), slope failures and thermo-erosional features (Bowden et al. 2008; Lantz and Kokelj 2008; Lamoureux and Lafrenière 2009), and loss of permafrost in the Low Arctic (AMAP 2012). Climate projections indicate both increased air temperatures and precipitation, especially in winter, and model results suggest widespread active layer deepening and further permafrost loss (Shur and Jorgenson 2007; Lawrence et al. 2008; AMAP 2012).

Importance of snow and ice for tundra wildlife

The state (liquid or solid) of water contained in the buffer and active layers of the permafrost system has major consequences for the behavior, reproduction, and survival of tundra wildlife. Building on the above summary of the physical properties of snow and ice, we now review the main mechanisms through which water phase impacts wildlife ecology. As we will see, the greater insulation capacity, mechanical resistance, and light reflectance of snow and ice compared to liquid water have cascading effects on wildlife ecology.

Insulation: snow protects subnivean species from temperature extremes

The small body size of lemmings (*Lemmus* spp. and *Dicrostonyx* spp.), voles (e.g. *Microtus* spp. and *Myodes* spp.), shrews (*Sorex* spp.), and their mustelid predators (*Mustela* spp.) put them at an energetic disadvantage during the long and cold Arctic winter. These small mammals have high thermoregulatory requirements because of their elevated lower

critical temperature and thermal conductance (McNab 2002), and they show little adaptation to Arctic climates in that respect (Klaassen et al. 2002). In addition, small mammals must remain active throughout the winter because, with the exception of Arctic ground squirrels (*Spermophilus parryii*) living in the low Arctic, they cannot store enough fat reserves to hibernate (Humphries et al. 2002).

During winter, small mammals are largely confined to the soil surface and bottom of the buffer layer, as they cannot dig into the frozen active layer and are exposed to predation above snow (Pruitt 1984). The soft depth hoar, through which they can easily tunnel for foraging, is their critical microhabitat. The insulating properties of the snowpack are determined by its thickness and thermal conductivity. Collared lemmings (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) studied in the High Arctic prefer areas with a snowpack ≥60 cm (Duchesne et al. 2011) and are very apt at finding snow drifts (usually called snowbeds by ecologists; Reid et al. 2012), often located on the leeward side of slopes or terrain with a rugged microtopography (Duchesne et al. 2011) or in habitats where erect shrubs capture drifting snow. Although these areas may occupy a small proportion of the landscape, they are critical for the winter survival of these species. Domine et al. (2016*a*) showed at Bylot Island, in the Canadian High Arctic, that the highest snowpack thermal resistances were found in drifts and in willow shrubs, thus explaining quantitatively their suitability as a habitat for subnivean life. The temperature under deep snow is both higher and less fluctuating than under shallow snow (Duchesne et al. 2011; Reid et al. 2012), and temperature stability better predicts lemming presence than temperature per se (Duchesne et al. 2011).

Thermal protection offered by snow can influence small mammal population dynamics. In Arctic Canada, summer abundance of brown lemmings was higher following winters with deep snow and a low density of the bottom 5 cm of the snowpack (Bilodeau et al. 2013*b*). Given that snow density is correlated with its thermal conductivity, this demographic response was presumably caused by increased survival or winter reproduction due to reduced thermoregulatory costs (Duchesne et al. 2011). Moreover, since density and shear strength are positively correlated (Domine et al. 2011), dense snow may also increase the energetic costs of tunneling to access food. Winter reproduction is an important prerequisite for high-amplitude cyclic peaks in lemmings (Ims et al. 2008; Fauteux et al. 2015).

Spring snow melt is a critical transition period for small mammals. First, the subnivean space gradually becomes colder than above the snowpack as the air temperature increases (Bilodeau et al. 2013*a*). Second, surface meltwater starts to percolate through the snowpack and refreezes at the bottom upon reaching the permafrost (Woo et al. 1982) (Fig. 6). This process may follow a diurnal cycle and persist over several days or weeks. Finally, water starts accumulating in snowbeds due to meltwater and surface runoff, as these are often located in depressions. All of these factors destroy the subnivean microhabitat of small mammals and reduce their access to food, forcing them to move out of these areas.

The fall transition period, when snow and ice progressively invade the buffer and active layers, is also a critical time for small mammal populations. Weather conditions during the establishment of the snowpack may largely determine the physical properties of the bottom snow layer throughout the winter. For instance, melt–freeze events can form hard refrozen crusts or even ice layers near the ground and wind storms can form hard wind slabs. Both of these snow types form hard depth hoar upon metamorphism (Domine et al. 2016*b*). On the contrary, snow falling in the absence of wind and snow not subject to melting favor the formation of soft depth hoar. These initial conditions could therefore have a lasting impact on the quality of the subnivean space of small mammals for the whole winter (Domine et al. 2016*b*).

Fig. 6. Impact of snow conditions on food accessibility for lemmings. Left: In a dry snowpack that has never been subjected to wetting and refreezing, the basal depth hoar is soft and lemmings can travel and access food easily. Middle: If wetting and refreezing has taken place, hard melt–freeze clusters, ice layers, and percolation fingers render the depth hoar harder, thus limiting food access. Right: Extensive wetting can lead to the formation of a basal ice layer that covers the vegetation and limits or completely prevents access to food.
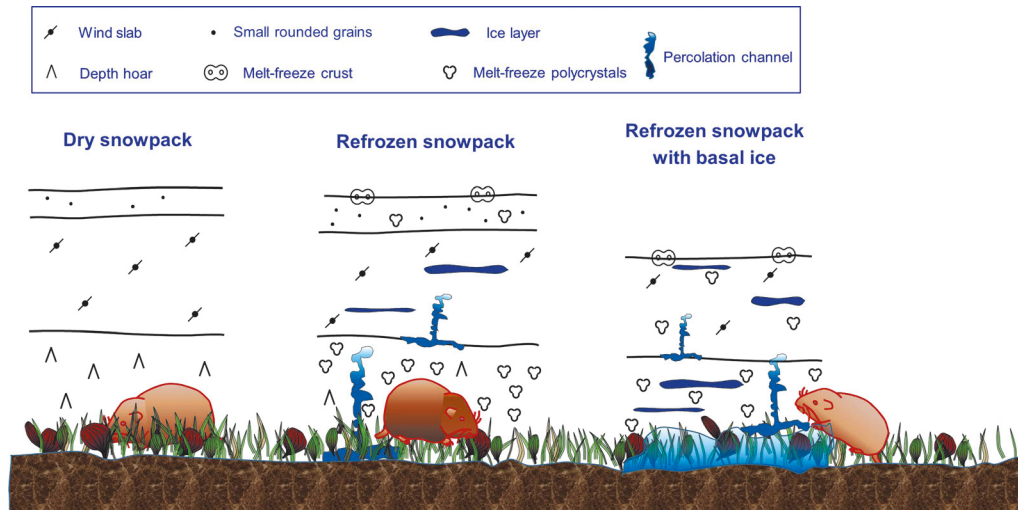
Whereas small mammals spend the entire winter below the snow and may benefit the most from its thermal protection, larger species such as foxes (*Vulpes* spp.) and ptarmigans (*Lagopus* spp.) may also occasionally incur thermal benefits from the snowpack (Korhonen 1980). For example, ptarmigans normally evade exposure to severe cold by roosting in the snow, where ambient temperature usually exceeds their lower critical temperature (Stokkan 1992).

Mechanical resistance-1: snow protects subnivean species against herbivores and predators

The snowpack provides important protection to subnivean plants from damage by snow abrasion and wind (Pereg and Payette 1998). Plants are also protected, however, by the physical barrier that snow provides against digging by herbivores living above the snow. Protection from herbivory varies according to herbivore species, snow depth, and snow density. Ptarmigans, hares, and muskoxen have a limited ability to dig into the snow and thus forage on plants emerging through the snowpack or growing in wind-blown areas (Schaefer and Messier 1995; Tape et al. 2010). Caribou have enlarged hooves making them better adapted to dig through the snow and reach snow-covered plants (Klein 1992), at least where snow is relatively shallow and soft. Yet, snowbed vegetation is entirely protected from large ungulates during winter (Ims et al. 2007).

Interestingly, plants are better protected from small mammal herbivory in areas with shallow snow such as at ridges with prostrate vegetation than in depressions with erect shrubs and deep snow, where small mammals concentrate in winter. If abundant, lemmings can have a considerable impact on snowbed vegetation locally and they can even girdle shrubs, with long-term effects on plant composition (Virtanen et al. 1997; Johnson et al. 2011; Olofsson et al. 2014). However, high abundance of small mammals in snowbeds can also benefit plants through the fertilizing effect of their urine and feces (Johnson et al. 2011).

Snow also offers small mammals some mechanical protection against many predators, although the amount of protection depends on predator species. Snow can effectively protect small mammals from avian predators such as the rough-legged hawk (*Buteo lagopus*)

and, to a lesser extent, the snowy owl (*Bubo scandiacus*) (Gilg et al. 2009; Therrien et al. 2015). Protection offered to small mammals by snow is more limited for predators that can easily dig through the snow, like the Arctic fox (*Vulpes lagopus*). In Arctic Canada, Bilodeau et al. (2013*a*) found that deep and hard snow did not hamper the ability of foxes to dig through the snow to catch lemmings, but did limit their use of the alternative hunting technique of jumping through the snow. Ovsyanikov (1993) reported that Arctic foxes dug holes up to 70–80 cm deep to reach lemmings under the snow. Finally, the ability of least weasels (*Mustela nivalis*) and ermines (or stoats) (*Mustela erminea*) to catch lemmings does not appear to be affected by snow depth or hardness (Bilodeau et al. 2013*a*), probably because their small size allows them to move under the snow through the tunnels created by their small rodent prey.

An interesting question is whether the snow conditions that best protect subnivean species from their predators are also those providing the best insulation. This is probably true for snow depth, such that subnivean species face no tradeoff between thermoregulation costs and predation risks with respect to this variable, at least when considering predators living above the snow. The answer is more complex, however, regarding snow density. When the snowpack is thin, a single, high-density snow layer (we admit this rarely occurs in the Arctic) offers weak insulation but good protection against predators. When the snowpack is thick and heterogeneous, a layer of hard snow or ice on top of a layer of soft snow yields benefits for both thermoregulation and predator protection. Finally, poor snow conditions at the soil interface may force small mammals to move toward the surface of the snowpack in search of food, thereby increasing predation risk.

Whether different herbivores react similarly or differently to changes in snow properties is likely to vary depending on species-specific biological characteristics. For instance, large High Arctic herbivores such as muskoxen (*Ovibos moschatus*) that are relatively invulnerable to predation are likely to benefit from a longer snow-free season. In contrast, lemmings will be affected negatively through a longer period with more intense predation. Even biologically similar herbivores like lemmings and voles are suspected to have different sensitivities to altered physical snow properties (Ims et al. 2011).

Mechanical resistance-2: impact of freeze–thaw or rain-on-snow events

In addition to its negative effects on the insulating properties of snow, the appearance of the water phase in snow can have dramatic consequences for wildlife habitats because of the induced changes in the mechanical resistance of the snow layer (Fig. 6). Alternating periods of freeze–thaw or rain-on-snow events are occurring regularly in some parts of the Arctic with relatively mild and humid maritime winter climate such as on Svalbard, while they are still sufficiently rare to become characterized as extreme events in continental areas with cold and dry winter climate such as Siberia and northeastern Canada. In large parts of the Arctic, winter precipitation is low and rain-on-snow events usually only form thin melt–freeze crusts. When this happens at the beginning of the snow season, they can be transformed into depth hoar (Domine et al. 2009), so their impact is limited. Profound freeze–thaw or rain-on-snow events, however, are likely to have pervasive effects on snow physical properties (Kausrud et al. 2008).

Episodes with heavy rain cause flooding in the subnivean space and subsequent freeze-up of a thick layer of ice at the soil surface (Hansen et al. 2014; Sokolov et al. 2016). Both rain-on-snow events and freeze–thaw cycling strengthen bonds between snow grains, which increases snow thermal conductivity and hardness and decreases snowpack thickness (Colbeck 1982; Sturm et al. 1997). Snow thermal resistance is then reduced, sometimes dramatically, leading to a cooling of the basal layer. Increased snow hardness makes subnivean travel and foraging much more difficult for small mammals or, in the worse situation,

renders food totally inaccessible (even to large herbivores) if plants are encapsulated in ice (Fig. 6). On Svalbard, rain-on-snow events of >50 mm are not uncommon in winter despite the high latitude of the site and are linked to specific weather patterns such as low sea level pressure extending from the southwest (Serreze et al. 2015). The formation of ice at the soil surface following large rain-on-snow events (Hansen et al. 2014) and the ensuing reduction in forage availability negatively affects all herbivores (voles, reindeer, and ptarmigans) (Hansen et al. 2013). The most extreme rain-on-snow events in Svalbard cause massive reindeer mortality (Hansen et al. 2014). Such phenomena have also been observed in western Siberia, a region with a much more continental climate (Sokolov et al. 2016), and in Canada (Miller and Barry 2009). In Svalbard, more moderate rain-on-snow events may not cause abnormal reindeer mortality, but still impact the condition of females to the extent that fecundity is reduced (Stien et al. 2012). Consequently, snow conditions during the winter will affect the growth rate and the demographic structure of reindeer and caribou populations, both of which are important to account for when deciding on harvest quotas. Indeed, prudent harvesting strategies may improve a population's resilience to rain-on-snow events by targeting sex and age categories that are most sensitive to difficult snow conditions as well as by keeping population size at levels where negative density-dependent responses (e.g. reduced body condition) are weak (Solberg et al. 2001; Tveraa et al. 2007).

In Norway, Aars and Ims (2002) found a strong inverse relationship between the winter survival of tundra voles (*Microtus oeconomus*) and the number of days with temperature >0 °C in winter. They attributed the increase in mortality to both a reduction in thermal insulation and a reduction in food availability due to the formation of ice on the ground. In some areas of Greenland and Fennoscandia, lemming and vole populations have become less cyclic and populations have remained low for a decade or more (Hörnfeldt 2004; Kausrud et al. 2008). Changing snow conditions due to climate warming, with the associated negative consequences for small mammals explained above, was invoked as a potential cause for the disappearance of population cycles (Hörnfeldt et al. 2005; Kausrud et al. 2008; Gilg et al. 2009). Opinions differ, however, about what mechanisms are decisive, perhaps because these mechanisms, as well as the direction and magnitude of impacts, vary among study locations. While Gilg et al. (2009) emphasized the impact of changing season length (in particular, shorter winters offering lemmings less snow cover protection from predators) in a relatively dry and cold site in the High Arctic, Kausrud et al. (2008) found snow density to be most important in a relatively mild and humid alpine site in Norway.

Considering that the frequency and magnitude of extreme events such as winter warm spells and rain-on-snow are predicted to increase with climate warming, the ecological effects of extreme meteorological events clearly deserve more attention in future years. Indeed, persistent low populations of small mammals, such as those reported in eastern Greenland for the past 15 years, can have a considerable impact on the numerous predators that depend upon lemmings for their survival (Schmidt et al. 2012). On Svalbard, the impact of rain-on-snow events on herbivores had a cascading positive impact on the Arctic fox, the only resident predator in this simple food web, due to increased carrion resulting from reindeer mortality (Hansen et al. 2013).

Mechanical resistance-3: snow and ice affect traveling abilities of wildlife
Water freezing can both increase and decrease the traveling ability of tundra wildlife. Water freezing has negative effects on wildlife mobility when deep and soft snow impedes movement of supranivean animals. Indeed, traveling costs of running species increase with snow depth, snow softness, and foot-load (ratio of body mass to foot area; Murray et al. (1994)), so that even well-adapted species like caribou significantly increase their energy expenditure when walking in the snow (Fancy and White 1987; Duquette 1988).

Cold water bodies such as large rivers, lakes, and seas can represent formidable barriers impossible to cross by many species. For nonaquatic mammals, walking requires less energy per unit distance than swimming (Alexander 2002), while thermoregulation requires less energy expenditure in air than in water. Accordingly, seasonal ice-bridges have great ecological importance in the Arctic, as they give many tundra wildlife species access to some habitats otherwise impossible to reach.

In their review, Gaston et al. (2012) reported dispersal distances across ice of 380 km for caribou, 100 km for Grizzly Bear (*Ursus arctos*), >50 km for muskox, wolf (*Canis lupus*), wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*), and Arctic hare (*Lepus arcticus*), and >10 km for smaller species such as ermine, brown lemming, and collared lemming. Such distances would be impossible to swim in cold water for these animals. Some species such as the Arctic fox have specialized into using the seasonal sea ice as a foraging platform (Lai et al. 2015) and can travel thousands of kilometres over land and ice (Tarroux et al. 2010). Migrating caribou in northern Quebec regularly cross large lakes when they are frozen (Leblond et al. 2016), and spring ice breakup is a critical time when impassable barriers, such as flooded rivers, can arise even for strong swimmers like caribou. Ice cover may thus have important impacts on daily movements, seasonal migrations, and dispersal events of tundra wildlife, with far-reaching consequences on their foraging behavior, population dynamics, and species distributions.

Mechanical resistance-4: ground ice supports and constrains structures used for wildlife reproduction

In many wildlife species, adults must provide intensive care to their newly born young, as they have little capacity to escape predators, maintain their body temperature, or obtain food on their own. Such altricial species, like the snowy owl, rough-legged hawk, peregrine falcon (*Falco peregrinus*), gyrfalcon (*Falco rusticolus*), Arctic wolf, and Arctic fox, raise their young for extended periods of time in structures such as nests and dens built on the tundra.

When selecting appropriate sites to build their nests or dens, Arctic wildlife must cope with the constraints imposed by the permafrost and its associated geomorphological hazards. Three broad situations can be distinguished. First, birds such as snowy owls and mammals such as lemmings primarily breed in lowland tundra and do not use the same nests in successive years. They face minimal constraints related to ground ice for their breeding site. Second, mammals such as wolves and foxes give birth in dens made of one or several burrows. Because the permafrost layer itself is very difficult to dig through unless it is made of dry sand (Tannerfeldt et al. 2003), burrows are mostly restricted to the active layer. For this reason, Arctic foxes prefer denning sites with low snow cover in spring, high ground temperature, deep active layer, and steep and southerly exposed slopes (Dalerum et al. 2002; Szor et al. 2008). Third, birds such as rough-legged hawks and falcons build more elaborate nest structures along steep slopes or cliffs and reuse them for many years (Swem 1996; Wightman and Fuller 2005; Burnham et al. 2009). They often prefer sites protected from rain and terrestrial predators. These sites improve reproductive success and thus become highly valuable resources (Anctil et al. 2014; Beardsell et al. 2016). This strategy exposes nests, however, to geomorphological hazards related to slope stability and type of ground material, which are especially severe over permafrost (Beardsell et al. 2017).

The rough-legged hawk is an abundant raptor of the circumpolar regions (Bechard and Swem 2002) and offers an excellent example of the strong interactions that can exist between ground ice, structures used for wildlife reproduction, and changing climate conditions. Among 82 nesting structures monitored on Bylot Island, 23 were destroyed over a 9 year period, 20 (24%) of which were destroyed due to geomorphological hazards, primarily nest collapse due to slope failure and nest burial due to rock falls (Beardsell et al. 2017) (Fig. 7). Nests on unconsolidated or poorly consolidated material (primarily sand, gravel,

Fig. 7. Photographs documenting the complete destruction of a rough-legged hawk nest on Bylot Island (Nunavut, Canada) in 2014. (*a*) Intact nest with five live chicks on the 28th of July. (*b*) Collapsed nest on the 5th of August following 2 days of heavy rain (6.0 and 7.5 mm). (*c*) Buried nest with three dead chicks on the 8th of August. White arrows show the locations of the slope failures that caused the nest destruction (photo credit: Andréanne Beardsell).

soft sandstone, or silt) were at higher risk of being destroyed than those on consolidated material (such as sandstone or shale). Among the 59 nesting structures still intact at the end of the study, 31% had a moderate probability (0.25–0.5) and 22% a high probability

Fig. 8. Extreme impact of thermo-erosion on Bylot Island (Nunavut, Canada). (*a*) Low-centered polygons seen from the air and showing signs of thermo-erosion. A gully network illustrates the scale of impact (photo credit: Gilles Gauthier). (*b*) Geese grazing in intact low-centered polygons (photo credit: Dominique Berteaux). (*c*) Snow melt runoff finds a cavity in the ground and is channeled into an ice wedge (photo credit: Dominique Berteaux). (*d*) Large, recently open gully showing exposed and quickly eroding ice wedge (photo credit: Gilles Gauthier). (*e*) New drainage channels have completely changed the local hydrology, with cascading effects on soil moisture, plant communities, and waterfowl habitat quality (photo credit: Dominique Berteaux). A blue backpack and a walking stick give scale on Figs. 8*c* and 8*e*.
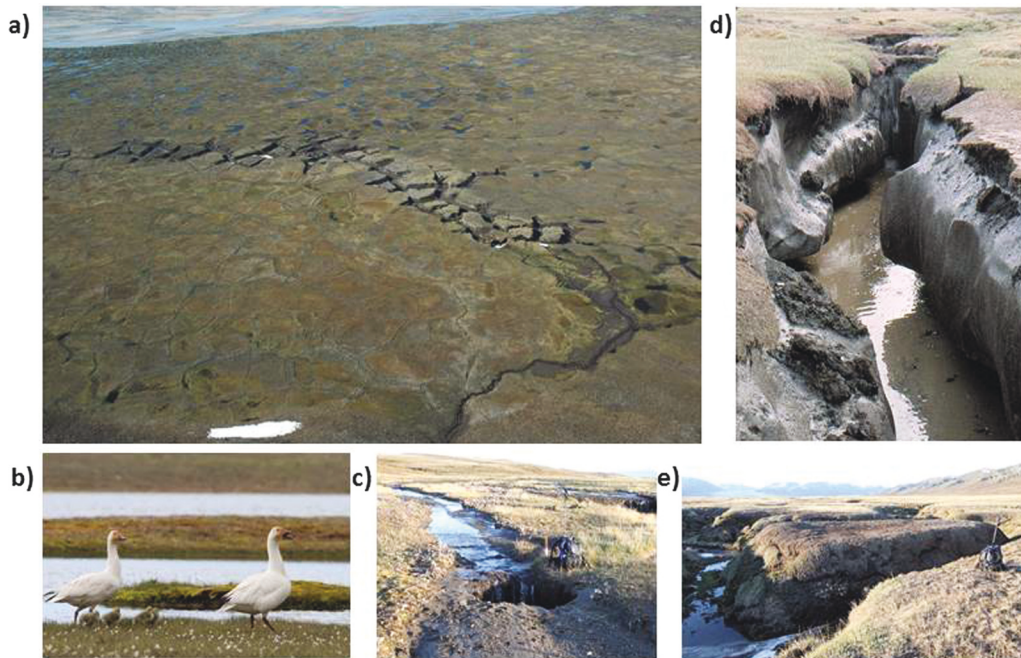
(>0.5) of being destroyed by a geomorphological hazard. Slope failure was also reported as a major cause of breeding failure in rough-legged hawks nesting in northern Yukon, Canada (Gauthier et al. 2011) and in Alaska (Swem 1996).

On Bylot Island, the probability of collapse of a hawk nesting structure was positively related to the number of rain events >7 mm since the last visit (Fig. 7; Beardsell et al. 2017). Active layer detachment slides resulting from permafrost thawing are known to be triggered by high rainfall (Lewkowicz and Harris 2005; Lamoureux et al. 2014). The interface between the active layer and permafrost is thus a critical place for the stability of raptor nesting structures, and infiltration of liquid water at this interface may be a major factor affecting their stability along steep slopes. Because episodes of high rainfall are predicted to increase with climate warming (AMAP 2012; IPCC 2014), such phenomena may be exacerbated in the future and threaten the reproduction of Arctic avian predators.

Mechanical resistance-5: ground ice sustains waterfowl habitats

In the Arctic, ground ice and ice wedges strongly influence local hydrology in flat terrain by limiting water percolation and lateral flow, which promotes the formation and maintenance of wetlands (Woo 2012). These wetlands provide high-quality habitats for numerous waterfowl species throughout the Arctic (Gauthier et al. 1996). Ice wedges, the dominant massive ice type in Arctic tundra, develop near the surface in regions where winter temperatures enable thermal contraction cracking (Fortier and Allard 2005; Jorgenson et al. 2015). Over decades or even centuries, ice wedges grow from water that fills the cracks

and refreezes, a process that heaves the soil and disturbs the surface drainage favoring the formation of small catchment basins typical of low-centered polygons (Fig. 8a) (French 2007). Such periglacial processes can generate a diversity of wetlands ranging from small lakes and shallow ponds to rich fens in low-center polygons (Billings and Peterson 1980; Gauthier et al. 1996), which are prime breeding and brood-rearing habitats for geese, a dominant summer herbivore in many Arctic regions (Fig. 8b). Goose families can forage on high-quality graminoid plants in the fens, whereas water bodies provide protection against predators like foxes (Hughes et al. 1994; Gauthier et al. 1996). Likewise, ducks use ponds to forage on aquatic invertebrates and to rest. These landforms, however, are not static but rather result from dynamic processes operating over decades to centuries (Billings and Peterson 1980; Fortier and Allard 2004; French 2007). As such, changes in drainage can have profound effects on waterfowl habitat, as demonstrated in the following example.

The stability of wetlands in periglacial landscapes such as low-center polygons critically depends upon the integrity of the frozen ground underneath, and especially ice wedges. These ice wedges are particularly sensitive to thermal erosion when surface water penetrates the soil (Jorgenson et al. 2015). In flat terrain, ice wedge degradation can initially favor the formation of thermokarst troughs that redistribute water from low-center polygons into deeper linear features; this can lead to a transient increase in water bodies', area as demonstrated by Jorgenson et al. (2015) in Alaska. Over time, however, degradation increases connectivity and drainage of these troughs, especially in sloping terrain (Liljedahl et al. 2016). Although wetland plants can grow at the margin of these troughs (Jorgenson et al. 2015), their distribution is often more limited than in low-center polygons. The overall impact on wetland habitats of these slow processes involving habitat loss in low-center polygon fens and habitat gain along trough margins has not been properly quantified and deserves further attention.

Thermal erosion can also rapidly transform waterfowl habitat through catastrophic erosion of ice wedges. This process can be initiated on gently sloping surfaces when a large amount of snowmelt runoff penetrates cavities (Fig. 8c) and is channelled into underground tunnels running in ice wedges and surrounding sediments (Fortier et al. 2007). Running water can rapidly erode these ice wedges and the enclosing frozen ground, leading to the collapse of the soil on top of them and the formation of large open gullies, often several metres wide and deep (Fig. 8d). These gullies can create, over a period of only a few years, new drainage channels and completely change the local hydrology (Fig. 8e), which has cascading effects on the surrounding landscape, including change in the topography, snow cover, maximum active layer thaw depth, and ground moisture content (Godin et al. 2015).

The formation of a network of gullies due to the thermal erosion of ice wedges can have dramatic effects on the local plant communities. Over a period of 5–10 years after the apparition of such gullies on Bylot Island, Perreault et al. (2015) documented a 40% decrease in soil moisture in affected polygons and a shift in vegetation from wet to mesic as graminoids such as *Dupontia fisheri*, *Eriophorum scheuchzeri*, and *Carex aquatilis* were replaced by *Arctagrostis latifolia* and *Salix arctica*. This resulted in a fivefold decrease in the aboveground biomass of grasses and sedges that are the preferred foraging plants of snow geese (*Chen caerulescens*) in the area. Perreault et al. (2017) found that gullies created by thermal erosion led to 55 m^2 of disturbed area per metre of gullying, leading to a significant loss of wetlands in a major brood-rearing area used by snow geese on Bylot Island. Climate warming has a strong potential to enhance and accelerate these processes, which could have far-reaching consequences for the habitat of geese and possibly other wildlife species of the tundra. This is a prime example of how the rapid transition from snow to liquid water at a critical time (snow melt season) can have a considerable impact on the cryosphere with cascading effect on ecological processes.

Fig. 9. Seasonal color variation of Arctic fox on Bylot Island (Nunavut, Canada) and color matching with tundra habitat. (*a*) Good matching: Arctic fox in its white winter coat over a white snow background (photo credit: Dominique Berteaux). (*b*) Good matching: Arctic fox in its brown summer coat (note ear tags) over a brown tundra background (photo credit: Nicolas Bradette). (*c*) Poor matching: Arctic fox in its white winter coat (note ear tags and radiocollar antenna) over a brown tundra background (photo credit: Nicolas Bradette).
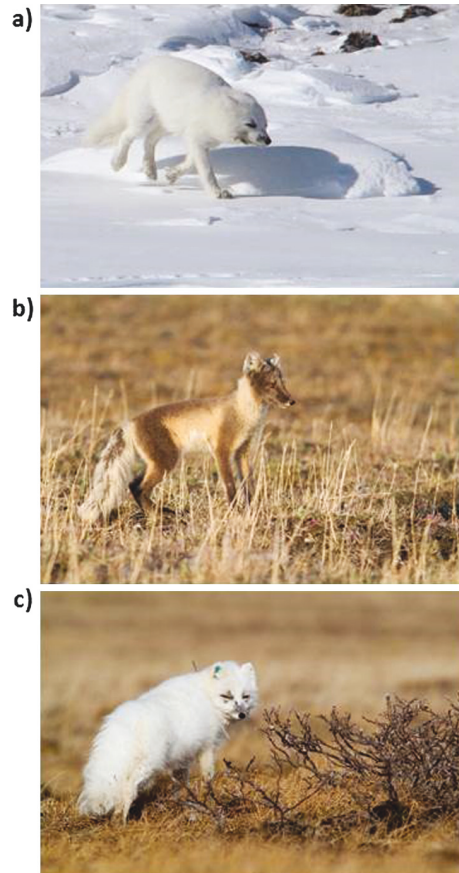
Light reflectance: snow provides camouflage opportunities to predators and prey and hides prey from predators

Camouflage is the single most important evolutionary force explaining overall coloration in mammals, whereas sexual selection plays a prominent role in birds (Caro 2005). Yet most mammal and bird species present in the Arctic during at least part of the snow season have a white coloration matching the color of their snow-dominated habitat (e.g., snowy owl, greater snow goose, Arctic wolf). Matching a white coat to a snowy background has obvious benefits for both predators approaching prey and prey avoiding predators (Caro 2005). Many tundra species (e.g., rock ptarmigan (*Lagopus muta*), Arctic fox, collared lemming, stoat, least weasel, mountain hare (*Lepus timidus*), Arctic hare) molt seasonally from brown to white so that coat color tracks the presence of snow (Fig. 9) (Mills et al. 2013).

One critical aspect of camouflage in habitats seasonally dominated by snow is how animals manage the abrupt transition in background color generated by snow melt. Whereas the seasonal changes in coat color are likely regulated by photoperiod, the decrease in the number of days with snow on the ground is one of the most pervasive effects of climate warming in the Arctic (McBean et al. 2005). This creates the potential for a phenological

Table 1. Critical places and critical times where water phase transitions play a major role in shaping the ecology of tundra wildlife.

Phenomenon (process involved; see relevant section in text)	Location or timing	Scale	Reference(s)
Critical places			
Increased snow hardness prevents subnivean travel and feeding (Insulation, Mechanical resistance-2)	Soil-snow interface	Microhabitat– landscape	Kausrud et al. 2008; Domine et al. 2016b
Freezing of water body surfaces increases mobility of mammals (Mechanical resistance-3)	Lakes, rivers, and seas	Landscape	Tarroux et al. 2010; Lai et al. 2015
Permafrost thawing collapses nests and dens through slope detachment (Mechanical resistance-4)	Cliffs	Microhabitat	Gauthier et al. 2011; Beardsell et al. 2017; Lamoureux and Lafrenière 2009
Thermal erosion of ice wedges can reduce waterfowl habitats (Mechanical resistance-5)	Polygonal soils	Habitat	Godin et al. 2015; Perreault et al. 2015, 2016
Critical times			
Snow melt triggers flooding and thermo-erosion, removes insulating/protecting snow cover, and changes habitat reflectance (Insulation, Mechanical resistance-1, Light reflectance)	Spring	Weeks	Godin et al. 2015; Gilg et al. 2009; Bilodeau et al. 2013a, 2013c; Zimova et al. 2016
Weather conditions during fall onset of the snowpack have long-lasting effects on its insulating properties (Insulation)	Fall	Weeks	Domine et al. 2016b
Icing events lock herbivore forage (Mechanical resistance-2)	Winter	Hours or days	Hansen et al. 2011, 2014

mismatch between a white coat color and a nonsnowy background (Fig. 9) (Mills et al. 2013; Zimova et al. 2016).

Snow also creates a visual screen lowering the probability of prey detection by predators. For example, Therrien et al. (2015) showed that snowy owls tracked in the Canadian Arctic during their prebreeding movements concentrated their searching time in areas with thinner or reduced snow cover. They suggested that a thinner and sparser snow cover increased snowy owls' ability to detect signs of lemming presence and thus facilitated prey detection.

Critical places and critical times of changing permafrost and snow conditions

The above-described mechanisms and associated examples linking snow and ice to tundra wildlife suggest that water phase transitions generate multiple critical places and times that play a disproportionate role in the ecology of tundra wildlife. Building from McClain et al. (2003), we thus define critical places as locations that have, due to freezing of water or melting of snow and ice, a disproportionate influence on wildlife ecology relative to the surrounding matrix. Similarly, critical times are short periods of time that have, due to freezing of water or melting of snow and ice, a disproportionate influence on wildlife ecology relative to longer intervening time periods. Table 1 provides a simplified list of these critical places and times, focusing on spatial scales ranging from microhabitat to landscape and on temporal scales ranging from hours to centuries.

Knowledge gaps and research needs

Water phase transitions generate abrupt changes in the physical environment of all wildlife species living in the tundra. These abrupt modifications in snow and permafrost conditions translate into similarly abrupt physiological, behavioral, and ecological changes for animal species. Our review identifies the buffer layer, particularly its snow component, as the most influential part of the permafrost system for the ecology of tundra wildlife.

On a temporal scale, seasonal transitions from water to snow and back to water (i.e. the fall and spring shoulder seasons) come up as the most critical time periods for wildlife. The following questions, however, still need to be answered to fully address the many connections that exist between snow, climate change, and wildlife ecology.

- What physical parameters of the snow layers are the most critical to wildlife? At what temporal and spatial scales should they be measured? How do they vary across climatic regimes?
- Can we accurately predict these physical parameters from variables derived from climate models, in order to translate climate change scenarios into ecologically relevant snow change scenarios?
- Can we predict species-specific responses to changing snow properties using biological traits such as diet, body size, morphology, or migratory behavior?
- Can prudent management of harvested species like reindeer and caribou improve the resilience of populations to adverse meteorological events like rain-on-snow?
- Can we predict how species-specific responses to changing snow influence population, food web, and ecosystem level dynamics in a warming terrestrial Arctic?
- How, and at what pace, will increases in liquid water modify the permafrost system and transform wildlife habitats?
- Given the large spatial heterogeneity of Arctic climates, how should we design a network of observation systems to monitor the interactions between weather, snow, and wildlife?

These questions must form an important backbone of future research programs in Arctic wildlife ecology, given that the timing, location, and speed of water phase transitions will all be modified under new climatic regimes. Although we have mostly explored the likely negative consequences of cryospheric change to tundra wildlife, it is important to keep in mind that there will also be "winners" after most forms of cryospheric change, especially among species recruited from boreal regions.

We close by emphasizing that the Arctic is vast and its climates are heterogeneous (Mernild et al. 2015). For example, during winter, Svalbard receives more precipitation than Bylot or Barrow (Alaska, USA), less than western or southwestern Greenland (Mernild et al. 2015), but as much as eastern or northwestern Greenland (Wong et al. 2015). It is tempting for any literature review to simplify this reality and generalize across the Arctic a situation documented at one or a few sites. However, large differences among sites, including differences in vegetation structure (Walker et al. 2005), often make it impossible to predict the future conditions at a given site from the current conditions at another site. In other words, substituting space for time rarely works (Krebs and Berteaux 2006). Therefore, although sophisticated climate and biological models are required to build future scenarios of change, and ecologists must continue looking for the general rules that explain the distribution and abundance of species, real-time, on-the-ground monitoring will always remain a critical part of Arctic wildlife biology (Ims et al. 2013).

Acknowledgements

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