

SYNTHESIS

Perennial ice and snow-covered land as important ecosystems for birds and mammals

Jørgen Rosvold*

NTNU University Museum, Norwegian
University of Science and Technology
(NTNU), 7491 Trondheim, Norway

ABSTRACT

Aim To investigate the role of perennial ice and snow-covered land in the environment of birds and mammals, and to what degree vertebrates are parts of terrestrial glacial ecosystems.

Location Global.

Methods The synthesis was based on a review of existing literature.

Results The relationship between perennial ice and snow-covered land and birds and mammals is generally poorly known and behaviours associated with such areas are likely underreported. Nevertheless, the review revealed that a relatively large range of species actively use and spend large amounts of time on ice covered land. Foraging or seeking relief from both climatic and different biotic factors are the main behaviours associated with these landscapes, but for some species they are also important areas for food caching, water, play and travel, and even as nesting grounds. In well-used sites, birds and mammals are likely important contributors to the nutrient cycling of glacial ecosystems.

Main conclusions Despite increased global temperatures and rapid glacial melting in recent years, perennial ice and snow-covered landscapes have largely escaped management attention, likely due to them being viewed as inhospitable. It is, however, becoming increasingly clear that a large range of organisms inhabit and make use of the ice, and that these areas constitute high-quality parts of their habitats. It is therefore essential that glacierized areas are properly described, classified and managed as threatened ecosystems.

Keywords

alpine, birds, climate change, glacier, glacial melting, global warming, mammals, snow patch

*Correspondence: Jørgen Rosvold, NTNU
University Museum, Norwegian University of
Science and Technology (NTNU), 7491
Trondheim, Norway.
E-mail: jorgen.rosvold@ntnu.no

INTRODUCTION

Ice and snow have dominated large parts of the world for much of its history (Andersen & Borns, 1997). Even now, the cryosphere encompasses more than 50% of the land on a seasonal basis and around 10% of all land area is covered by perennial snow and ice (Zemp *et al.*, 2008; Vaughan *et al.*, 2013). Surface concentrations of perennial snow and ice, i.e. glaciers and snow patches (Fig. 1), are found on all continents in varying amounts and are important water reservoirs for many downstream ecosystems (Milner *et al.*, 2009; Barry & Gan, 2011; Vaughan *et al.*, 2013; Woo & Young, 2014). Annual melting influences the hydroecology and thus the biodiversity in streams, rivers and many terrestrial communities

(Prowse *et al.*, 2006; Björk & Molau, 2007; Fountain *et al.*, 2012; Jacobsen *et al.*, 2012; Finn *et al.*, 2013; Millar *et al.*, in press). Yet, we know very little about the ecology of the ice covered landscapes themselves.

Snow and ice have direct implications for the distribution and ecology of different organisms. For most animals, snow and ice covered lands are considered as limiting factors for their distribution (Helland-Hansen, 1915; Formozov, 1946). Physiological constraints in these cold environments are by themselves important for some organisms (Scholander *et al.*, 1950; Jones, 1999), and snow and ice may increase energetic demands of movement (Formozov, 1946), but most importantly permanent snow and ice are strong limiting factors for primary production (Field *et al.*, 1998; Huston & Wolverton,



Figure 1 A perennial snow patch in central Norway feeding meltwater to surrounding alpine wetlands. Note reindeer herd in the upper left corner of the snow patch.

2009) and thus food availability. Because of this, perennial ice and snow-covered environments are usually viewed as inhospitable wastelands and are not usually managed as threatened ecosystems. Many organisms are, however, very well adapted to living in cold and frozen environments (Formozov, 1946; Scholander *et al.*, 1950; Jones *et al.*, 2001) and very little is known regarding how different life-forms actually make use of glacierized lands (i.e. lands presently overlaid by perennial ice).

In recent years diverse life-forms and biological communities have been found to inhabit glacierized areas (e.g. Hartzell *et al.*, 2005; Coulson & Midgley, 2012; Uetake *et al.*, 2012; Christner *et al.*, 2014; Zawierucha *et al.*, 2015) and researchers have argued that such areas should be considered as distinct ecosystems or a separate biome (Hodson *et al.*, 2008; Anesio & Laybourn-Parry, 2012). Indeed, unexpected high levels of primary production have actually been found on glaciers from e.g. bacteria in cryoconite holes (Anesio *et al.*, 2009), surface algal mats (Takeuchi *et al.*, 2001), yeasts (Uetake *et al.*, 2012) and even moss (Coulson & Midgley, 2012), which provides a basis for the existence of other of organisms. Acknowledging this, some of the best prospects for finding life in space are even in relation to ice environments (Tranter *et al.*, 2004; Laybourn-Parry *et al.*, 2012). Thus far, however, the research focus has been on the microbiological organisms that inhabit the ice for all or most of their lives (Laybourn-Parry *et al.*, 2012). Less attention has been given to the vertebrates that use these areas as temporary habitats and little is known regarding the role of perennially ice and snow-covered land for these animals.

Ongoing and future climatic warming is expected to dramatically reduce the size and distribution of glacierized land in the future, and thereby strongly affect the organisms tied to these systems (Prowse *et al.*, 2006; Zemp *et al.*, 2008; Kivinen *et al.*, 2012; Vaughan *et al.*, 2013; Woo & Young, 2014). In order to be able to assess these areas for conservation concerns, e.g. the IUCN Red List of Ecosystems (Rodríguez *et al.*, 2015), and fully understand the implications of glacial melting on biodiversity and ecosystem services we need to understand the full variety of ecological relations to ice. This review will focus on two main questions: (1) How and why do vertebrates actively make use of perennial ice and snow-covered land? (2) To what degree are

vertebrates parts of terrestrial glacial ecosystems? The point of this discussion is to highlight the diversity of behaviours associated with the use of perennial snow and ice covered land in order to stimulate further research and reporting. The aim of this is to contribute towards further describing and identifying the terrestrial cryosphere as important and distinct ecosystems.

METHODOLOGY AND TERMS

This study is based on a review of the existing literature, with a few notes from personal field observations. The literature search was done using Web of Science and Google Scholar, as well as general glaciological books, vertebrate hand books and back-tracking of literature lists. General search terms such as 'mammal*/bird* AND glacier*' were used to some degree, but more targeted searches for a wide range of particular high-alpine and high-latitude species were also performed.

A wide range of types of perennial ice and snow-covered lands exist and are likely to have different ecological functions and uses for different organisms (Laybourn-Parry *et al.*, 2012). That said, for the sake of simplicity I use only the terms 'glacier' and 'snow patch' to cover all of these. Snow patches are relatively smaller accumulations of snow that persist over long periods of time, typically with an ice core but with too little mass to flow, and thereby become a glacier (Fujita *et al.*, 2010; Serrano *et al.*, 2011). The literature search is, however, complicated by the fact that such areas have been defined under a large variety of different names in biological studies, e.g. summer snow, permanent snowfields, snowpack, snowdrift, firn, ice sheets, ice patch, anivuat, etc. Searches were thus performed on a wide range of different search terms.

In order to qualify as being used by animals these areas have to be actively sought out, which is usually best documented during summer or early fall when seasonal snows have disappeared. The literature on this subject is quite scarce, as few studies have been designed to directly investigate these behaviours, but observations have been noted in other research. Zoological nomenclature follow Clements (2007) for birds and Wilson & Reeder (2005) for mammals. I use the definitions of ecosystems practiced by the IUCN

Red List of Ecosystems (Keith *et al.*, 2013) which largely follow the original concepts of Tansley (1935) and terms ecosystems as a complex of organisms and a particular physical environment and the interactions between and among the biotic and abiotic components.

VERTEBRATE USES OF PERENNIAL ICE AND SNOW-COVERED LAND

While several Arctic and Antarctic animals, like polar bears (*Ursus maritimus*), emperor penguins (*Aptenodytes forsteri*) and many pinnipeds (Pinnipedia), spend most or all of their time on or around sea ice (Ainley *et al.*, 2003), no vertebrates have been reported to spend their entire lives on terrestrial snow or ice. Although lizards and snakes have been found in high-alpine vegetation free areas (Swan, 1967), encounters with cold blooded herptiles are expected to be very rare in relation to perennial snow and ice. There are, however, a wide range of birds and mammals that actively visit and spend large amounts of time on glaciers and snow patches on a regular basis for different reasons (Table 1). The behaviours associated with the use of glaciers and snow patches can arguably be defined into seven broader categories as done in Table 1. *Relief* covers the use of these areas to seek reprieve or protection from both biotic and abiotic factors. *Foraging* and *caching* includes using the snow and ice to catch or store food, while *water* includes records of direct ingestion of snow. The categories *nesting*, *play* and *travel* includes instances where these behaviours have been directly associated with perennial snow and ice.

Alpine areas are, for most of the time, relatively cool areas generally inhabited by cold adapted species like pikas (*Ochotona* spp.) and ptarmigans (*Lagopus* spp.) (Martin, 2001). Temperature variations can, however, be high in the summer season and during warm summer days cold adapted animals may suffer from overheating. One well-known example is the American pika (*Ochotona princeps*) which is very sensitive to warm climates (Smith, 1974) and is often fronted in climate change discussions as a species under threat of extinction (Stewart *et al.*, 2015). In order to survive the worst of the summer heat these pikas often make use of 'rock-ice-features', e.g. rock-glaciers, to create cool burrows which represent increasingly important relief areas under climatic warming (Millar & Westfall, 2010). Glaciers and perennial snow patches have been found to cool the air down to several degrees below that of the surrounding areas and thus provides a good thermal shelter for alpine animals (Ion & Kershaw, 1989).

Daily altitudinal migrations to perennial snow or ice covered land during warm summer days have been noted in several species, but seem especially prominent among ungulates (Table 1). Probably the most iconic example of animals using such areas is the reindeer (*Rangifer tarandus*). On hot summer days, reindeer aggregate on alpine snow patches where they often lie down and stay for long periods of the day (Fig. 2a). Some of these sites have even been regularly

used for thousands of years, as evidenced from the large amount of reindeer remains and reindeer hunting related artefacts that are currently melting out of them (e.g. Fig. 2b, Farnell *et al.*, 2004; Callanan, 2012; Hare *et al.*, 2012). Similarly, white-tailed ptarmigan (*Lagopus leucura*) and rock ptarmigan (*Lagopus muta*) are often observed on warm days seeking shelter along the edges of snow patches or snow bathing in the remaining snow layer (Fig. 3, Johnson, 1968; Pedersen *et al.*, 2014).

The cool air around glacierized sites seems to have the added benefit of reducing insect harassment, especially oestrids, and the relative importance of insect versus heat relief have been much discussed for reindeer (Ion & Kershaw, 1989; Anderson & Nilssen, 1998; Hagemoen & Reimers, 2002). Relief from insect harassment has also been indicated as the reason for visits by horses (*Equus ferus*) and chiru (*Pantholops hodgsonii*) (Keiper & Berger, 1982; Schaller, 1998). Apart from reindeer there have, however, been few direct studies into these behaviours and the discussion of insect versus heat relief might as well apply to other species. Personal observations of reindeer have shown that snow patches are even used during periods of colder weather as well, indicating that they may hold additional unknown functions to the animals.

Due to the cold conditions, glaciers and snow patches often act as death traps to wind-blown arthropods, which again attract predatory arthropods that feed upon them (Kaisila, 1952; Swan, 1967; Spalding, 1979; Mann *et al.*, 1980; Edwards, 1987). This potentially creates very good foraging areas for alpine birds with highly visible and accessible prey, and indeed a relatively high number of species has been recorded foraging for arthropods on perennial snow patches and glaciers during summer (Table 1). Some species seem to use these sites only occasionally at peak insect abundance, but for some, like the horned lark (*Eremophila alpestris*), the white-winged snowfinch (*Montifringilla nivalis*) and the alpine accentor (*Prunella collaris*), this seems to be their preferred foraging areas (Edwards & Banko, 1976; Antor, 1995). The use of such sites seems to increase with altitude and higher capture rates have been found on the snow than on other substrates (Antor, 1995). Snow buntings (*Plectrophenax nivalis*) have also been observed to feed on resident ice worms (*Mesenchytraeus solifugus*) on Alaskan glaciers (Shain *et al.*, 2001), thus indicating that permanent inhabitants of glaciers may attract foragers as well.

Because of the predictable congregation of animals on snow patches during summer, these areas have been favoured hunting grounds for humans for thousands of years (Farnell *et al.*, 2004; Callanan, 2012; Hare *et al.*, 2012; Lee, 2012), and still are in some areas. Although it has, to my knowledge, not yet been reported, such areas may potentially provide good hunting grounds for alpine predators like wolverines (*Gulo gulo*) or golden eagles (*Aquila chrysaetos*) as well. It is, however, observed that wolverines make use of snow patches for caching prey (Inman *et al.*, 2012). The cool environment at these sites provides a natural refrigerator for

Table 1 Recorded uses of glaciers and perennial snow patches by birds and mammals.

Species	Common name	Relief	Foraging	Caching	Water	Nesting	Play	Travel	References
Mammals									
<i>Bison bison</i>	American bison	X							Farnell <i>et al.</i> , 2004
<i>Capra ibex</i>	Alpine ibex	X							Aublet <i>et al.</i> , 2009; Oeggli <i>et al.</i> , 2009
<i>Cervus elaphus</i>	Wapiti	X					X		Altmann, 1956
<i>Equus ferus</i>	Horse	X							Keiper & Berger, 1982
<i>Gulo gulo</i>	Wolverine			X					Bevanger, 1992; Inman <i>et al.</i> , 2012
<i>Homo sapiens</i>	Human	X	X	X	X		X	X	Carey, 2007; Gosnell, 2007; Reckin, 2013; Pers.obs.
<i>Ochotona princeps</i>	American pika	X							Millar & Westfall, 2010
<i>Oreamnos americanus</i>	Mountain goat	X			X				Stevens, 1979;
<i>Ovibos moschatus</i>	Musk ox	X							Hall, 1964
<i>Ovis aries</i>	Domestic sheep	X							Pers.obs.
<i>Ovis canadensis</i>	Bighorn sheep				X		X		Woolf, 1968; Berger, 1980
<i>Panthera uncia</i>	Snow leopard							X	Koshkarev, 1984
<i>Pantholops hodgsonii</i>	Chiru	X							Schaller, 1998; Huber, 2005
<i>Rangifer tarandus</i>	Reindeer	X			X				Ion & Kershaw, 1989; Anderson & Nilssen, 1998; Hagemoen & Reimers, 2002; Pers.obs.
<i>Rupicapra rupicapra</i>	Alpine chamois	X							Clarke, 1986
<i>Ursus arctos</i>	Brown bear	X			X		X	X	French <i>et al.</i> , 1994
<i>Ursus maritimus</i>	Polar bear	X							Schweinsburg, 1979
Birds									
<i>Anthus spinoletta</i>	Water pipit		X						Verbeek, 1970; Edwards & Banko, 1976; Mann <i>et al.</i> , 1980; Antor, 1995
<i>Aquila chrysaetos</i>	Golden eagle				X				Johnson, 1994
<i>Calcarius lapponicus</i>	Lapland longspur		X						Edwards & Banko, 1976
<i>Corvus corax</i>	Common raven		X						Edwards & Banko, 1976; Mann <i>et al.</i> , 1980
<i>Diuca speculifera</i>	White-winged diuca finch					X			Hardy & Hardy, 2008
<i>Eremophila alpestris</i>	Horned lark		X						Edwards & Banko, 1976;
<i>Junco phaeonotus</i>	Yellow-eyed junco		X						Swan, 1967
<i>Lagopus leucura</i>	White-tailed ptarmigan	X	X						Johnson, 1968; Mann <i>et al.</i> , 1980
<i>Lagopus muta</i>	Rock ptarmigan	X	X						Kaisila, 1952; Pedersen <i>et al.</i> , 2014; Pers.obs.
<i>Larus hyperboreus</i>	Glaucous gull		X						Jakubas & Wojczulanis- Jakubas, 2010
<i>Leucosticte tephrocotis</i>	Grey-crowned rosy finch		X		X	(X)			Johnson, 1965; Mann <i>et al.</i> , 1980
<i>Montifringilla nivalis</i>	White-winged snow finch		X						Antor, 1995
<i>Oenanthe oenanthe</i>	Northern wheatear		X						Edwards & Banko, 1976; Antor, 1995
<i>Phoenicurus ochurus</i>	Black redstart		X						Antor, 1995
<i>Plectrophenax nivalis</i>	Snow bunting		X						Kaisila, 1952; Shain <i>et al.</i> , 2001; Pers.obs.
<i>Pluvialis dominica</i>	American golden plover		X						Edwards & Banko, 1976
<i>Prunella collaris</i>	Alpine accentor		X						Antor, 1995
<i>Spizella arborea</i>	American tree sparrow		X						Edwards & Banko, 1976
<i>Turdus migratorius</i>	American robin		X						Edwards & Banko, 1976

preserving meat throughout the summer (Bevanger, 1992; Inman *et al.*, 2012), a fact that is also well known and used among arctic humans and alpine hunters. For wolverines,

access to cool storage sites such as these may be critical during the nursing stage of the cubs and is an essential part of their habitats (Inman *et al.*, 2012).

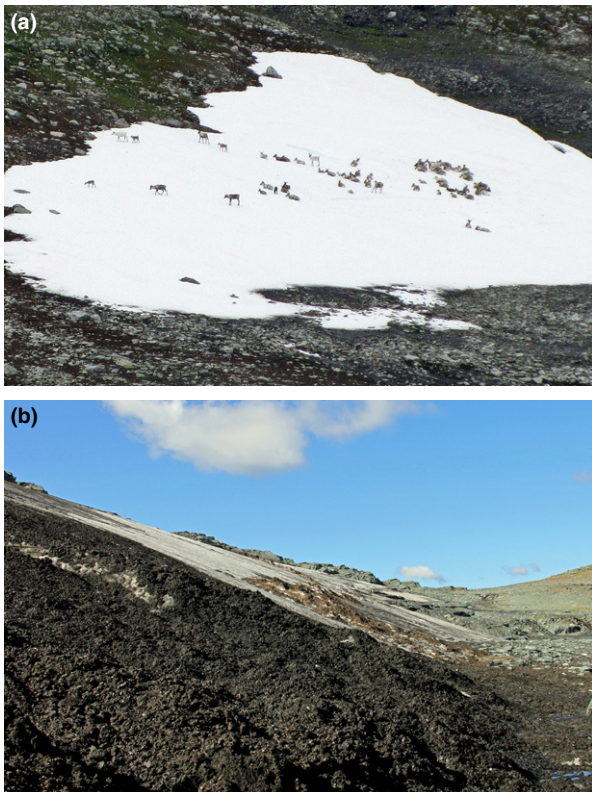


Figure 2 (a) Reindeer relaxing on an alpine snow patch. (b) Huge masses of reindeer dung have melted out and cover most of a Norwegian snow patch during an especially warm summer of 2014. Dung and wind-blown material stained most of the snow patch in the background and the masses in the foreground reached depths of up to c. 30 cm.



Figure 3 A flock of rock ptarmigan flying over an alpine snow patch. Rock ptarmigan are often found near glaciers and perennial snow patches during summer. A closer inspection of the dark layers visible in the old ice showed a mixture wind-blown dust and plant material, and animal droppings.

Ingestion of snow while spending time on glaciers and snow patches has been observed for several species (Table 1). In dry areas, these sites may act as important sources of water (Stevens, 1979; Johnson, 1994). For reindeer, it has

also been suggested that the snow eating behaviour may possibly be a part of the thermoregulatory responses on warm days to help cool down the body (Ion & Kershaw, 1989).

Several polar species use sea ice for breeding, but due to the often poorer thermoregulatory abilities of their young most birds and mammals tend to avoid snow and ice during their breeding periods. While breeding colonies of emperor penguins have been reported on inland lake ice (Kato & Ichikawa, 1999), the species is almost exclusively tied to the sea ice when rearing their young (Fretwell & Trathan, 2009). The only bird thus far reported to regularly nest on land ice is the white-winged diuca finch (*Diuca speculifera*) which, for unknown reasons, builds nests directly on or in cavities of glaciers in the Andes (Hardy & Hardy, 2008). However, although not directly on the ice, the grey-crowned rosy finch (*Leucosticte tephrocotis*) have also often been found to build their nests in cliffs close to the edges of glaciers and perennial snow patches in the Rocky Mountains which are also used for feeding (Johnson, 1965).

Some of the observed behaviours tied to glaciated grounds seem more sporadic. Perennial snow patches and small glaciers have been found to induce playing behaviour in both young and adult animals of different species (e.g. Altmann, 1956; Berger, 1980; French *et al.*, 1994), and American bison (*Bison bison*) have been seen wallowing in old dung melted out of snow patches (Farnell *et al.*, 2004). Some species, like brown bear (*Ursus arctos*) and snow leopard (*Panthera uncia*), have also been observed to prefer travelling on glacierized grounds in some areas (Koshkarev, 1984; French *et al.*, 1994). Snow patches usually form relatively smooth surfaces, compared to the scree and block-fields that often characterize mountain landscapes, and may thus provide more easy footing. How widespread such behaviours are is poorly known and is likely to be under-reported.

The collection of species and behaviours in Table 1 illustrate an important diversity of roles that perennial ice and snow-covered land has for many birds and mammals. For most of the activities associated with glaciers and snow patches there are alternative areas that can be used. Reindeer may, for example, find relief in mires or wind exposed ridges (Hagemoen & Reimers, 2002), American pikas find cool burrows in talus slopes (Millar & Westfall, 2010), wolverines may cache meat in swamps and under boulders (Bevanger, 1992) and birds find insects in other places than on snow patches. It is, however, clear that glacierized areas represent high-quality temporary habitats for many birds and mammals.

BIRDS AND MAMMALS AS PARTS OF GLACIAL ECOSYSTEMS

Although not permanent inhabitants many birds and mammals spend a large amount of time on glaciers and perennial snow patches, but can they be considered as parts of certain glacial ecosystem types?

Glacierized landscapes have convincingly been described as complex microbiological ecosystems (Hodson *et al.*, 2008; Anesio & Laybourn-Parry, 2012), harbouring a surprisingly diverse array of organic material that also contributes to the carbon cycles of downstream systems (e.g. Singer *et al.*, 2012). It has long been known that large parts of the available nutrients in glacial ecosystems come from wind-blown material and that this also sustains a variety of invertebrates and their predators (Kaisila, 1952; Swan, 1961, 1992; Edwards, 1987); some of which are highly adapted to these cold environments and spend their entire lives in snow or ice (e.g. Shain *et al.*, 2001; Hågvar, 2010). It is also clear from the above discussion that birds and mammals make use of the physical features of glacierized lands and also the available resources in these areas, by e.g. ingesting snow and invertebrates, and thus remove nutrients from the system. But are they just temporary energy drains or do they interact with the system in other ways?

By spending time on the glaciers and snow patches birds and mammals also contribute with new resources for resident organisms. Droppings, fur, feathers and even dead animals are left behind and may provide nutrients for ice-dwelling microorganisms. Glaciers are often reported as organic carbon depleted ecosystems (Singer *et al.*, 2012), thus this could be an important contribution to the carbon cycle in certain areas. Parts of this material are likely to be put into the nutrient cycling immediately, but large amounts can evidently be preserved for long periods of time (Hågvar & Ohlson, 2013). Animal remains become lodged in the ice together with wind-blown material, often forming clearly visible dark layers in the ice (Fig. 3). During warm periods with high melting this material is released and made available as nutrients for ice-dwelling organisms (e.g. Fig. 2b). Some of these nutrients will also be released to downstream ecosystems through melt water streams and can potentially be carried over long distances (Singer *et al.*, 2012). As the ice melts, organic material from well-used sites is left behind on the de-glaciated grounds and this can potentially speed up the succession of vegetation on the glacier forelands.

Birds and mammals thus partake in the energy flow and nutrient cycling of glacial ecosystems, in addition to benefiting from its direct physical properties. How large a role they play in these systems remains yet to be investigated, but is likely to be highly variable between areas and different types of glacierized lands depending on their suitability for the animals. In well-used areas, their role is likely to be substantial (e.g. Fig. 2b).

CONCLUSIONS AND FUTURE PROSPECTS

Alpine and arctic ecosystems are considered to be particularly threatened by ongoing and future climate change because resident, often cold adapted, species are pushed into smaller and more fragmented habitats with limited possibilities for dispersal (La Sorte & Jetz, 2010; MacDonald, 2010). With warmer climates glacierized areas may play an increas-

ingly important role for many birds and mammals as areas of relief, food caching, etc., but at the same time their size and distribution will diminish. This will increase the aggregation of animals on the remaining and more fragmented sites which could lead to negative impacts due to competitive interactions, spread of diseases and parasites, and possibly increased predation due to prey being easier to locate. Increased melting and eventually disappearance of glaciers and perennial snow patches will thus add to the pressure on organisms already experiencing the effects of a warmer climate. Hence, it is essential that perennial ice and snow-covered lands are properly described, classified and managed as threatened ecosystems.

We thus need more studies on the uses of glacierized land and the effects of melting. Some of the species and behaviours reported in Table 1 are represented only by occasional observations and with little knowledge of how widespread these behaviours are. It is therefore important to document such observations properly and perform more direct studies into the reasons behind these interactions with the ice.

That the use of perennial snow and ice among birds and mammals are likely unknown or underreported in many cases seems evident from the diverse collections of animal remains melting out of such areas during especially warm summers. Remains of species such as moose (*Alces alces*), snowshoe hare (*Lepus americanus*), wolf (*Canis lupus*) and several species of rodents, of which I have as yet found no reported behaviours associated with the use of perennial ice, have melted out during recent years (Farnell *et al.*, 2004; Andrews *et al.*, 2012; Hare *et al.*, 2012; Lee, 2012). There are even several reports of remains of species not normally associated with cold glacierized landscapes, such as African wild dogs (*Lycaon pictus*) and leopards (*Panthera pardus*), melting out of glaciers on Kilimanjaro and Mt. Kenya (Meyer, 1891; Guest & Leedal, 1954; Thesiger, 1970; Mizuno, 2005). Such finds may provide essential information for understanding the use of ice covered land and can potentially produce data spanning thousands of years. Glaciers and perennial snow patches may thus represent important archives of both natural and cultural history. Yet, due to the diverse uses of such areas (Table 1), and especially the caching behaviour of species such as wolverines, care must be taken in the interpretation of such finds.

As several cold adapted species show strong relations to glacierized areas today, it is likely that perennial ice and snow-covered land could have been equally or even more important features of the habitats of the rich prehistoric cold adapted fauna of the Pleistocene, especially during periods of climatic warming. This subject has thus far received little attention. Several members of the cold adapted Pleistocene mammals seem to have originated in high-altitude areas of Tibet (e.g. Deng *et al.*, 2011; Wang *et al.*, 2014). There are also indications of seasonal altitudinal migrations of some of the megafauna through high-altitude finds of species such as mammoth (*Mammuthus columbi*), mastodon (*Mammot americanum*) and short-faced bear (*Arctodus simus*) (Madsen,

2000), as well as through isotopic studies of mastodon remains (Hoppe *et al.*, 1999). The reasons for these migrations are as yet unknown. However, the massive loss of glaciated lands during the warmer interglacials, including the current one, is likely to have significantly affected many cold adapted species directly. Historically also, the areas covered by perennial ice and snow have fluctuated greatly, but most have shown a pronounced retreat during the last century (Zemp *et al.*, 2008; Vaughan *et al.*, 2013). Glacierized areas function as terrestrial 'islands' in the landscape and could thus serve as good research areas for examining aspects of the island biogeography theories (e.g. MacArthur & Wilson, 1967).

These landscapes have been important also for humans for thousands of years for subsistence, recreation and as cultural symbols (Carey, 2007; Gosnell, 2007; Reckin, 2013), and provide us with significant ecosystem services (Barry & Gan, 2011; Fountain *et al.*, 2012). With continued climatic warming and glacial melting today we risk losing several glacial ecosystems with hitherto poorly known and important ecological relationships, as well as a valuable archive of both natural and cultural history. With the exception of some key glaciological research sites, these areas are generally poorly monitored (Zemp *et al.*, 2008). Research and management actions are needed to create a more complete inventory of glacierized landscapes, document the ecological importance of different sites and perform a classification of different glacial ecosystem types.

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BIOSKETCH

Jørgen Rosvold is an ecologist with training also in archaeology and anthropology. He is particularly interested in long-term natural history, conservation biology and human-nature relationships. His current research focus is on glacial biology and the history of reindeer.

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