REVIEW ARTICLE

Five decades of terrestrial and freshwater research at Ny-Ålesund, Svalbard

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Abstract

For more than five decades, research has been conducted at Ny-Ålesund, in Svalbard, Norway, to understand the structure and functioning of High-Arctic ecosystems and the profound impacts on them of environmental change. Terrestrial, freshwater, glacial and marine ecosystems are accessible year-round

Keywords

Biogeochemical cycles; climate change; ecosystem structure and functioning; environmental change; High Arctic; human impacts; soil

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from Ny-Ålesund, providing unique opportunities for interdisciplinary observational and experimental studies along physical, chemical, hydrological and climatic gradients. Here, we synthesize terrestrial and freshwater research at Ny-Ålesund and review current knowledge of biodiversity patterns, species population dynamics and interactions, ecosystem processes, biogeochemical cycles and anthropogenic impacts. There is now strong evidence of past and ongoing biotic changes caused by climate change, including negative effects on populations of many taxa and impacts of rain-on-snow events across multiple trophic levels. While species-level characteristics and responses are well understood for macro-organisms, major knowledge gaps exist for microbes, invertebrates and ecosystem-level processes. In order to fill current knowledge gaps, we recommend (1) maintaining monitoring efforts, while establishing a long-term ecosystem-based monitoring programme; (2) gaining a mechanistic understanding of environmental change impacts on processes and linkages in food webs; (3) identifying trophic interactions and cascades across ecosystems; and (4) integrating long-term data on microbial, invertebrate and freshwater communities, along with measurements of carbon and nutrient fluxes among soils, atmosphere, freshwaters and the marine environment. The synthesis here shows that the Ny-Ålesund study system has the characteristics needed to fill these gaps in knowledge, thereby enhancing our understanding of High-Arctic ecosystems and their responses to environmental variability and change.

To access the supplementary material, please visit the article landing page

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Abbreviations

β-HCH: β-hexachlorocyclohexane
C: carbon
CH_4: methane
CO_2: carbon dioxide
DFG: German Research Council
Hg: mercury
ITEX: International Tundra Experiment
K: potassium
N: nitrogen
N_2: atmospheric nitrogen
N_2O: dinitrogen oxide
Na: sodium
NPI: Norwegian Polar Institute
O_2: oxygen
P: phosphorus
PCB: polychlorinated biphenyl
POP: persistent organic pollutant
ROS: rain-on-snow
SOC: soil organic carbon

Introduction

The Arctic tundra is one of the world's largest terrestrial biomes, with a set of abiotic characteristics that result in one of the most extreme environments on Earth (CAFF 2013). The structure and functioning of the biome are currently challenged by global climate change, which is accentuated by the effects of Arctic amplification (Serreze & Barry 2011), with profound impacts on tundra ecosystems already being evident (Post et al. 2009; Hansen et al. 2013; Legagneux et al. 2014). Climate model projections suggest continued seasonal temperature increases, with climatic conditions changing to the extent that novel ecosystems are formed (Williams & Jackson 2007). To understand how these changes affect whole ecosystems, mediated through multiple impacts on different species and their ecological functions and interactions, ambitious ecosystem-level approaches are essential, with coordinated and multidisciplinary efforts integrating research and long-term monitoring (Ims & Yoccoz 2017). Combining observational research and experiments with long-term monitoring data, the availability of which is currently limited in the Arctic, provides a powerful tool to link observed patterns with underlying processes. In doing so, a more complete and mechanistic understanding of ecosystems and their responses to human perturbations can be gained (Ims & Yoccoz 2017; Schmidt et al. 2017; Christensen et al. 2020). Moreover, substantial flows of energy and a range of trophic interactions between terrestrial, freshwater and marine ecosystems (Post et al. 2013) necessitate large-scale holistic approaches to understand and predict ecological change in the Arctic (Dietze et al. 2018).

Situated on Brøggerhalvøya, a peninsula in northwestern Spitsbergen, the largest island of the High-Arctic archipelago of Svalbard, the Ny-Ålesund Research Station and settlement (78.9°N, 11.8°E) is the northernmost site for international year-round ecosystem research and long-term environmental monitoring (Fig. 1). The archipelago is currently exposed to some of the most rapid climatic changes on Earth (Førland et al. 2011; Nordli et al. 2020) and, during recent years, has also experienced increased research and tourism activities. This makes it a unique hotspot for studying the consequences of environmental change for the High Arctic and a 'canary in the coalmine' that highlights the risks being faced by ecosystems across the entire Arctic (Chapin et al. 2005; CAFF 2013). Compared with other Arctic ecosystems, Svalbard has relatively simple (i.e., species-poor) plant and animal communities (Descamps et al. 2017). However, the physical proximity and coupling between the terrestrial, marine, glacial and freshwater ecosystems in the vicinity of Ny-Ålesund result in considerable environmental heterogeneity along physical, chemical, hydrological, climatic and ecological gradients.

This review aims to synthesize scientific knowledge gained from five decades of research and monitoring at Ny-Ålesund. It integrates a broad cross-section of the terrestrial and freshwater research undertaken in the area,

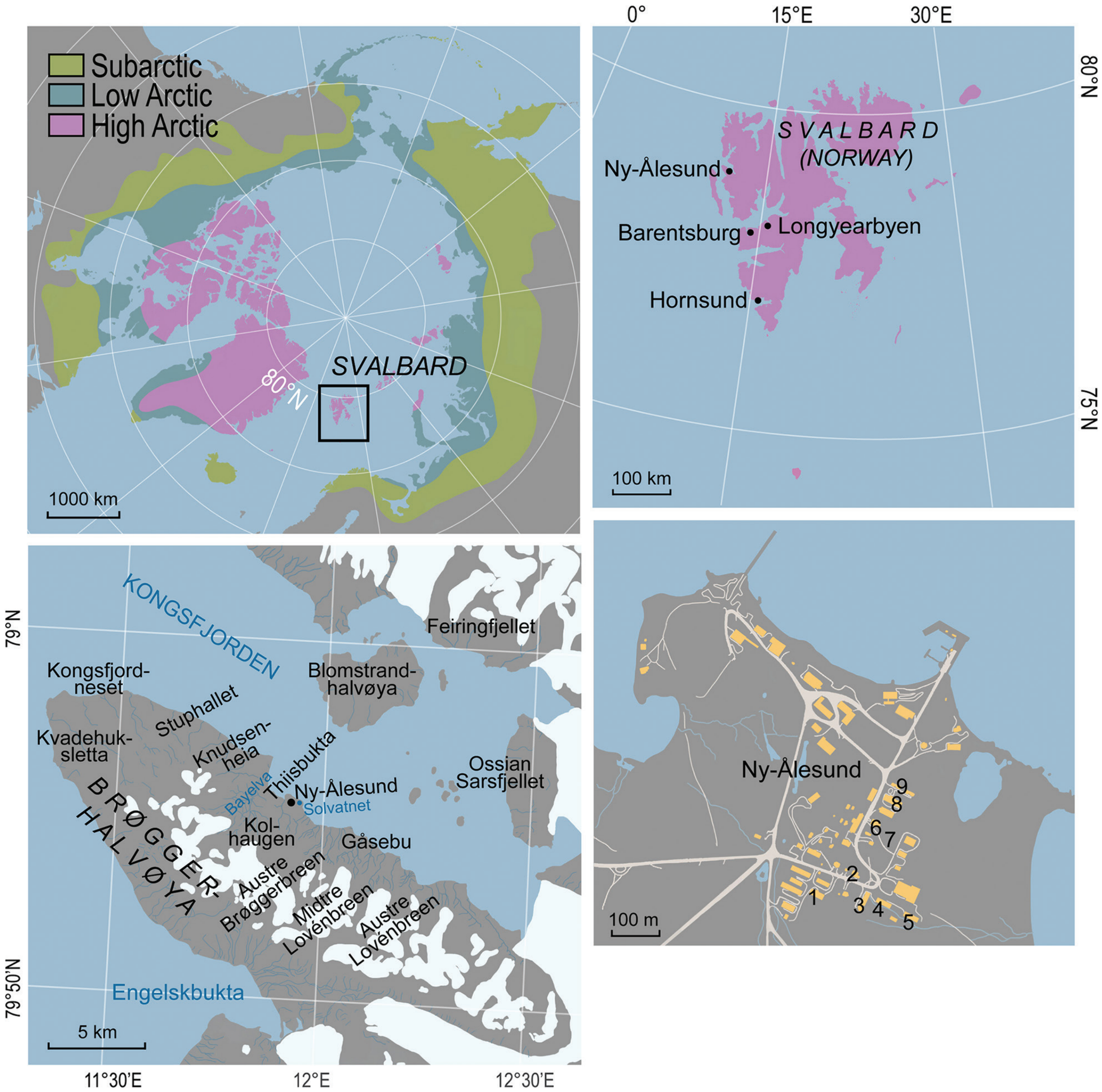

Fig. 1 The location of Svalbard, Brøggerhalvøya and Ny-Ålesund in the circumpolar Arctic. In Ny-Ålesund, the nine research stations are as follows: (1) National Research Council (Italy); (2) Alfred Wegener Institute for Polar and Marine Research (Germany) and the Polar Institute Paul Emile Victor (France); (3) Norwegian Polar Institute; (4) Korea Polar Research Institute; (5) Polar Research Institute of China; (6) National Centre for Polar and Ocean Research (India); (7) National Institute of Polar Research (Japan); (8) Natural Environmental Research Council (UK); (9) University of Groningen (Netherlands). (Figure by S.M. Kristiansen.)

highlighting and identifying key knowledge gaps and future research priorities that this unique location is especially suited to address. Our review highlights the role that research and long-term monitoring have played in unravelling the complexities of ecosystem responses to climate change and other environmental perturbations and, more broadly, contributes to understanding the structure and functioning of High-Arctic terrestrial ecosystems.

The Ny-Ålesund study system

Ny-Ålesund, which covers approximately 0.25 km^2 (Fig. 1), was originally established as a Norwegian coal mining settlement, operated by the Kings Bay Kull Company from 1916 to 1962. Mining operations ceased after a major accident in 1962, and regular scientific observations began in 1967 when the European Space

Research Organisation established a satellite telemetry station at Ny-Ålesund. Since then, the settlement has developed into a hub for international polar research, with more than 20 institutions from more than 15 countries currently engaged in research and long-term monitoring programmes (Supplementary Table S1). The station's wider surrounding environment, which is easily accessed on foot or by small boat or snowmobile, is generally pristine and is at present protected and managed by the Governor of Svalbard, with a focus on providing support and opportunities for scientific research.

Research at Ny-Ålesund is focused on the natural sciences within the framework of the Svalbard Environmental Protection Act and the Ny-Ålesund Research Station Strategy (Research Council of Norway 2019). Ny-Ålesund is accessible year-round by air or sea and hosts accommodation, laboratory buildings, logistical facilities, automated instrumentation, and a high-speed internet connection. The settlement's small size and the large numbers of visiting researchers from many different institutions and countries act together to enhance the cross-disciplinarity and internationalization of research carried out in and around Ny-Ålesund. The Research in Svalbard database (www.researchinsvalbard.no) provides a complete overview of all research projects conducted in the region.

The landscape of Brøggerhalvøya is characterized by striking geological and glaciological features, with mountainous terrain divided by numerous glaciers, and substantial variation in elevation, vegetation and habitat types (Fig. 2). The total area of the peninsula is approximately 221 km², approximately a quarter of which is covered by glaciers, with approximately half of the area consisting of exposed rock, boulder fields and scree, and marine clay, soils and rivers accounting for the remaining land area. Periglacial features, such as frost boils, polygons, sorted

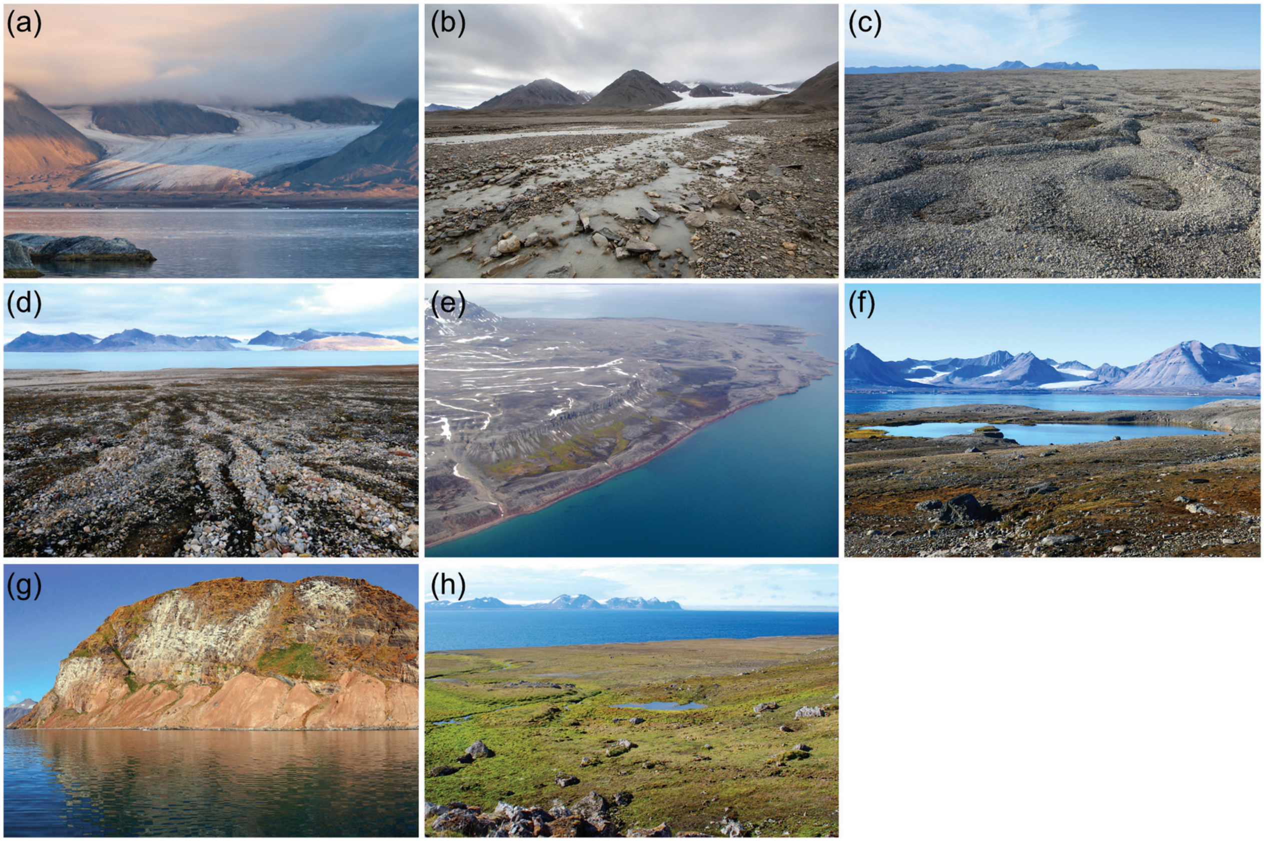

Fig. 2 Dominant landforms and habitats close to Ny-Ålesund. (a) The Midtre Lovénbreen glacier. (b) Moraine with braided streams below the Midtre Lovénbreen glacier. (c) Sorted stone circles at Kvadehuksletta. (d) Sorted stone stripes at Stuphallet. (e) View of the north-western peninsula, showing the plateaued landscape and the bird cliffs at Stuphallet, where nesting seabirds introduce marine-derived nutrients, leading to extensive plant growth. (f) Inland lake on Blomstrandhalvøya, where shorebirds and waterfowl breed. (g) Ossian Sarsfjellet, a bird cliff, where summertime nutrient inputs from nesting black-legged kittiwakes (*Rissa tridactyla*), coupled with an exceptionally mild microclimate, lead to high diversity of vascular plants and bryophytes. (h) Moss tundra habitat in flat lowlands beneath bird cliffs at Simlestupet. (Photo a by F. Samuelsson; b by E.M. Biersma; c and h by Å.Ø. Pedersen; d, f and g by J. Mosbacher; and e by P. Convey).

circles and stone stripes (Fig. 2), are frequent. Approximately 45 km^2 (ca. 20%) of Brøggerhalvøya is significantly vegetated (Johansen et al. 2012), with the peninsula hosting a range of High Arctic plant community types (described in detail below), typified by bryophytes, lichens, dwarf shrubs, forbs and graminoids (Elvebakk 1994; Williams et al. 2017; Table 1). Brøggerhalvøya also hosts a species-poor high-latitude vertebrate community, with only three widespread vertebrate species permanently resident in terrestrial habitats, namely the Svalbard reindeer (*Rangifer tarandus platyrhynchus*), the Svalbard rock ptarmigan (*Lagopus muta hyperborea*) and the Arctic fox (*Vulpes lagopus*). Voles and lemmings are absent. Polar bears (*Ursus maritimus*) are also occasionally present on land. During spring and early summer, considerable numbers of migratory birds arrive—ducks, geese, seabirds, snow bunting (*Plectrophenax nivalis*) and shorebirds—that breed in tundra and freshwater habitats, on shorelines and on bird cliffs (Descamps et al. 2017).

The climate of Svalbard, and particularly that of Spitsbergen, is influenced by the West Spitsbergen Current, a branch of the North Atlantic Current derived from the Gulf Stream, which delivers relatively warm water to the region's western shores (Cottier et al. 2005; David & Krishnan 2017). Consequently, the climate of western Svalbard is typically warmer and wetter than that of other landmasses at the same latitude. Ny-Ålesund has a mean annual air temperature of -5.7 °C, and a total

Table 1 Common species of lichens, mosses, other plants, invertebrates and vertebrates in and around Ny-Ålesund.

Lifeform	Frequent species[a]
Lichens[b]	*Acarospora* spp., *Bellemerea subsorediza*, *Caloplaca cerina*, *Cetraria islandica*, *Cetrariella delisei*, *Cladonia arbuscula*, *Cladonia* spp., *Flavocetraria nivalis*, *Lecidea* spp., *Nephroma* spp., *Ochrolechia frigida*, *Peltigera canina*, *Protoblastenia cyclospora*, *Rhizocarpon geographicum*, *Rhizocarpon hochstetteri*, *Stereocaulon* spp.
Liverworts[b]	*Blepharostoma trichophyllum*, *Cephaloziella varians*, *Lophoziopsis excisa*, *Odontoschisma macounii*, *Ptilidium ciliare*, *Schljakovianthus quadrilobus*, *Sphenolobus minutus*, *Trilophozia quinquedentata*
Mosses[b]	*Aulacomnium turgidum*, *Bryum pseudotriquetrum*, *Ditrichum flexicaule*, *Hylocomium splendens*, *Philonotis tomentella*, *Pohlia cruda*, *Polytrichastrum alpinum*, *Tomentypnum nitens*, *Racomitrium lanuginosum*, *Sanionia uncinata*
Vascular plants[c]	Shrubs: Arctic bell-heather (*Cassiope tetragona*), polar willow (*Salix polaris*) Herbs: alpine bistort (*Bistorta vivipara*), *Draba* spp., drooping saxifrage (*Saxifraga cernua*), longstalk (*Stellaria crassipes*), moss campion (*Silene acaulis*), mountain avens (*Dryas octopetala*), mountain sorrel (*Oxyria digyna*), polar cress (*Cardamine pratensis*), polar horsetail (*Equisetum arvense*), purple saxifrage (*Saxifraga oppositifolia*), pygmy buttercup (*Ranunculus pygmaeus*), tufted saxifrage (*Saxifraga cespitosa*) Graminoids: Alpine hair-grass (*Deschampsia alpina*), *Festuca* ssp., *Poa* spp., *Luzula* spp.
Invertebrates[d]	Crustacea: water-flea (*Daphnia pulex, Chydorus sphaericus* and *Macrothrix hirsuticornis*), copepod (*Cyclops abyssorum*), various rotifers, tadpole shrimp (*Lepidurus arcticus*) Insects: dungfly (*Scatophaga furcata*), nonbiting midges (e.g., *Paratanytarsus austriacus*, *Psectrocladius barbimanus*, *Cricotopus tibialis* and *Diamesa* spp.), brown knot-horn moth (*Pyla fusca*), mosquito (*Aedes nigripes*), caddisfly (*Apatania zonella*) Mites: *Diapterobates notatus, Camisia* spp. Spiders: *Erigone arctica palaearctica* Springtails: *Folsomia quadrioculata, Hypogastrura viatica, Megaphorura arctica* Worms: nematodes, Enchytraeidae Water bears: tardigrades (*Hypsibius pallidus*)
Non-migratory birds[e]	Svalbard rock ptarmigan (*Lagopus muta hyperborea*)
Migratory birds[e]	Ducks/geese: barnacle goose (*Branta leucopsis*), common eider (*Somateria mollissima*), long-tailed duck (*Clangula hyemalis*), pink-footed goose (*Anser brachyrhynchus*) Divers: red-throated diver (*Gavia stellata*) Sea birds: Arctic tern (*Sterna paradisae*), Atlantic puffin (*Fratercula arctica*), black guillemot *(Cepphus grylle)*, black-legged kittiwake (*Risa tridactyla*), Brünnich's guillemot (*Uria lomvia*), glaucous gull (*Larus hyperboreus*), little auk (*Alle alle*), northern fulmar (*Fulmarus glacialis*) Passerines: snow bunting (*Plectrophenax nivalis*) Shorebirds: purple sandpiper (*Calidris maritima*), red phalarope (*Phaloropus fulicarius*), ringed plover (*Charadrius hiaticula),* ruddy turnstone (*Arenaria interpres*) Skuas: Arctic skua (*Stercorarius parasiticus*)
Mammals[d]	Arctic fox (*Vulpes lagopus*), polar bear (*Ursus maritimus*), Svalbard reindeer (*Rangifer tarandus platyrhynchus*)

[a] There is no formal threshold of frequency for inclusion. [b] Arnell & Mårtensson (1959), Elvebakk & Prestrud (1996), Øvstedal et al. (2009), Zhang et al. (2015) and Inoue et al. (2019). [c] Rønning (1996), www.svalbardflora.net. [d] Coulson et al. (2014). [e] Kovacs & Lydersen (2006).

precipitation of 409 mm, mainly falling as snow. Mean winter and summer air temperatures (1971–2000) are -12.7 and 3.7 °C, respectively (Hanssen-Bauer et al. 2019; see also Maturilli et al. 2019). However, during recent decades, the ecosystems around Ny-Ålesund have experienced dramatic changes in climate (Hanssen-Bauer et al. 2019; Maturilli et al. 2019), with consequent impacts on ecosystems, which are described in detail below. Annual air temperature and precipitation, especially rain, have increased significantly, but with large variation across seasons (Hanssen-Bauer et al. 2019). Of particular significance are ROS events, associated with extreme warm spells in winter, which increased markedly in frequency around the turn of the millennium (Hansen, Pedersen et al. 2019; Peeters et al. 2019).

Glacial retreat on Brøggerhalvøya has been extensive in recent decades (Schuler et al. 2020), resulting in the exposure of new ground for weathering and colonization processes, providing a focus for multicentury research into plant and soil microbial community succession (e.g., Hodkinson et al. 2003; Cooper et al. 2004; Rozema et al. 2006; Moreau et al. 2008; Gwiazdowicz et al. 2020). Similarly, the timing of spring snowmelt has advanced, and the active layer of the underlying permafrost is warming and deepening (Westermann et al. 2009; Boike et al. 2018). Hydrological cycles have also undergone radical changes, with new patterns emerging in the storage and distribution of water resources (e.g., more persistent rivers and groundwater bodies), which may profoundly affect ecosystem development (Doveri et al. 2019). Importantly, many of these changes can be partly linked to the marine fjord system, where sea-ice extent and duration have substantially declined (Pavlova et al. 2019).

These examples of past environmental and ecosystem changes call for a synthesis of scientific knowledge to identify the future research directions that will generate knowledge relevant to both science and ecosystem management and conservation in Svalbard, as well as in other Arctic regions.

Furthermore, we summarize the wealth of research and monitoring—covering abiotic and biotic components of freshwater and above-ground and below-ground terrestrial ecosystems—that has been conducted at Ny-Ålesund during the last five decades. We present the status of current scientific knowledge and identify key gaps to guide future research priorities that can be addressed in the region. The synthesis arises from three workshops held by the Ny-Ålesund Terrestrial Flagship in 2018–19. These workshops hosted experts from 15 countries, mainly within the fields of biology, geology, snow physics and climatology, all of whom have long-term research experience in the Ny-Ålesund area. The synthesis includes literature listed in the Web of Science, the online database of peer-reviewed scientific articles, and other published sources identified by the authors.

Terrestrial ecosystems

Landforms and soils

The dominant landforms of Brøggerhalvøya include glaciers, moraines, glacial outwash plains (sandurs), unconsolidated rock debris beneath cliffs (colluvial fans), raised beaches and bedrock outcrops, with their integral habitats and patterned ground, including solifluction lobes on gently sloping terrain and sorted circles on level ground (Fig. 2a–d). Plant cover varies considerably and is strongly influenced by periglacial processes, especially frost heave and creep, gelifluction and ice segregation, giving rise to a mosaic of microhabitats sharply contrasting in physical properties and microclimate (Cannone et al. 2004; Dallmann & Elvevold 2015; Miccadei et al. 2016; Wojcik et al. 2019).

The dominant soil types are weakly developed orthent and entisols, typically lithic haplorthels, derived from Upper Carboniferous and Permian rocks with quartzite and carbonates (Wojcik et al. 2019). The soil active layer is underlain by permafrost within 100 cm of the ground surface (Hugelius et al. 2013). Radiocarbon dating indicates soil C ages of 2000–31 000 calibrated years before present at 11–31 cm depths (Wojcik et al. 2019). Quartz is the dominant mineral in soils (34–74% of dry mass), followed by dolomite (5–32%) and calcite, muscovite, biotite, chlorite, Na-plagioclase and K-feldspar (all <13%) (Kern et al. 2019). Other than in historical coal mining areas, soils are typically weakly acidic to alkaline, with pH values in the vicinity of Ny-Ålesund ranging between 6.0 and 8.5 (Zhang, Wang, Liu et al. 2016). The coarse mineral fraction and often high sand content of the soils result in rapid nutrient leaching and limitation. The slow decomposition of plant litter and other C sources, caused by low temperatures and aridity, leads to soil organic matter accumulating in tundra soil (Robinson et al. 1995; Uchida et al. 2016; Kotas et al. 2018). Compared with other Arctic soils, SOC concentrations at 0–100 cm depths on Brøggerhalvøya are low, at around 1 kg per m^{-2}, with little evidence of significant SOC storage in permafrost (Wojcik et al. 2019). However, in vegetated soils, SOC storage in the upper soil layers may exceed 30%, with a potential release of CO_2 from the active layer (Cannone et al. 2016). Pyrolysis-field ionization mass spectrometry shows that SOC components are dominated by lipids/sterols, alkylaromatics and phenols/lignin monomers, with a chemical signature different from soils in other climatic zones (Pushkareva et al. 2020).

As in many other Arctic regions, concentrations of N and P in the soils of the peninsula are typically low, with strong N- and P-limitation of plant growth in areas not influenced by guano or other sources of fertilization (Wookey et al. 1993; Baddeley et al. 1994). In contrast, vegetation development beneath bird cliffs (Fig. 2e, g) provides a clear visual demonstration of the effects on bryophytes and vascular plants of the transfer of marine-derived nutrients by vertebrates to land (Odasz 1994). These nutrients can lead to more than tenfold increases in soil nitrate and ammonia concentrations and high denitrification potentials (Hayashi et al. 2018), with strong stimulatory effects on plant growth, biomass and seed production, key leaf enzymes (e.g., nitrate reductase) and invertebrate population densities (Arnell & Mårtensson 1959; Cooper et al. 2004; Zmudczynska-Skarbek et al. 2015). Vertebrates other than birds also provide sources of fertilization, through feces and carcasses (Robinson et al. 1995), which may locally stimulate plant litter decomposition, resulting in enhanced C and/or N concentrations in soil that can have prolonged (>20 years) effects on plant communities (Bekku et al. 2004; Yoshitake et al. 2007; Street et al. 2018). Besides nutrients being transferred from sea to land, soil–water interactions in coastal areas are also a potential source of nutrients for surrounding fjord and coastal ecosystems (Doveri et al. 2019). For instance, snowmelt chemistry in glacial catchments is largely influenced by the presence of meltwater derived from stored glacial ice and snow and the substantial contribution of solutes released during the weathering and leaching of the underlying rock and glacial tills (Hodson et al. 2005).

Soil microbial communities

Brøggerhalvøya soils are inhabited by diverse microbial communities, which, as in all soils, play key roles in the biogeochemical cycling of C, N, P and other elements, soil organic matter decomposition, greenhouse gas emissions to the atmosphere and various food web interactions (Tveit 2014; Tveit et al. 2015; Söllinger et al. 2016). Studies of the soil microbial communities of the peninsula have been carried out across a range of habitats, from polar desert through various types of vegetated tundra and enriched bird cliff-associated vegetation, to moraines, disturbed periglacial ground, glacier forelands and wetlands (Tveit et al. 2013; Zhang, Wang, Zhang et al. 2016; Borchhardt et al. 2017; Lim et al. 2018). Physiological adaptations of specific microbial taxa to the High-Arctic environment have been studied using multiple approaches, including comparative genomics (Lee et al. 2012; Shen et al. 2017), high-throughput sequencing and bioprospecting for cold-active enzymes (Kim et al. 2010; Singh et al. 2012) and have targeted, for example, unsaturated fatty acids (Srinivas et al. 2009), carotenoids (Kim, Rim et al. 2016) and poly-beta-hydroxybutyrate and polyphosphate compounds (Kim, Kang et al. 2016). However, there are no long-term monitoring data sets recording soil microbial diversity (Supplementary Table S1).

A study of the microalgal communities that form biological soil crusts in the Ny-Ålesund region indicates the presence of at least 102 taxa, the majority being green algae (chlorophyta; Borchhardt et al. 2017). However, the application of molecular and integrated taxonomic techniques suggests that microalgal and cyanobacterial genus richness may be an order of magnitude higher than previously estimated (Rippin et al. 2018). The most abundant cyanobacteria in soils around Ny-Ålesund are members of the orders Synechococcales, Oscillatores and Nostocales (Rippin et al. 2018; Jung et al. 2019). Cyanobacteria, either free living or as photobionts of lichens, are a primary source of N input in Arctic terrestrial ecosystems owing to the ability of specific clades to fix atmospheric N_2 (Liengen & Olsen 1997; Stewart et al. 2011), with fixation rates being correlated with water availability, temperature, light (Chapin et al. 1995; Elster et al. 2012) and grazing intensity (Zielke et al. 2004).

Studies using high-resolution molecular methods have documented diverse microbial communities in soils around Ny-Ålesund. The dominant bacterial phyla are the Chloroflexi, Actinobacteria, Proteobacteria, Acidobacteria and Bacteroidetes (Tveit et al. 2013; Lim et al. 2018). The domain Archaea is mainly represented in wetland soils by CH_4-producing groups in the orders Methanobacteriales, Methanomicrobiales, Methanosarcinales and Thermoplasmatales (Tveit et al. 2014; Tveit et al. 2015; Söllinger et al. 2016), whose communities exhibit both taxonomic and metabolic shifts in response to changes in temperature and humidity (Høj et al. 2006; Høj et al. 2008; Tveit et al. 2015). Emissions of CH_4 from wetland soils are limited by an efficient community of CH_4-oxidizing bacteria (methanotrophs), dominated by species closely related to *Methylobacter tundripaludum* (Wartiainen et al. 2006; Graef et al. 2011; Svenning et al. 2011; Rainer et al. 2020). Metazoa and protists, which graze on bacterial cells and fungal hyphae, also occur in the peninsula's soils and exhibit responses to temperature changes, with subsequent effects on ecosystem function (Tveit et al. 2013; Geisen et al. 2015; Tveit et al. 2015).

As in other High Arctic ecosystems, symbiotic arbuscular mycorrhizal fungi are infrequent in the roots of grasses and forbs on the peninsula (Newsham et al. 2017), but the vascular plant species *Salix polaris*, *Cassiope tetragona*, *Bistorta vivipara* and *Dryas octopetala* consistently form ectomycorrhizal or ericoid mycorrhizal symbioses with soil fungi (Geml et al. 2012; Blaalid et al. 2014; Mundra, Halvorsen et al. 2015). These symbioses promote plant growth primarily by enhancing the acquisition of limiting nutrients (typically N and P) from the soil. However, frequent soil freeze–thaw events may limit their beneficial effects (Tibbett & Cairney 2007; Mundra, Bahram et al. 2015). In addition to mycorrhizal fungi, saprotrophic microfungi, important soil organic matter decomposers, are also frequent in Brøggerhalvøya soils (Zhang, Wang, Liu et al. 2016), and mushroom-forming macrofungi are present at elevations up to 100 m (Jalink & Nauta 2004).

Vegetation

Vegetation performs key terrestrial ecosystem functions, including primary production, habitat provision, moisture retention, gas exchange with the atmosphere and the prevention of erosion (e.g., Muraoka et al. 2002; Nakatsubo et al. 2005; Yoshitake et al. 2010; Luers et al. 2014; Hayashi et al. 2016; Uchida et al. 2016; Wojcik et al. 2019). The extent of terrestrial plant cover on the peninsula varies considerably and is strongly influenced by periglacial processes (Welker et al. 1993; Wookey et al. 1993; Elvebakk 1994; Rieley 1994; Cannone et al. 2004), thermal sums (Brossard et al. 2002; Joly et al. 2003), snow cover (Beck et al. 2005), grazing pressure (Cooper & Wookey 2001; Kuijper et al. 2006; Hansen et al. 2007; Kuijper et al. 2009), soil nutrients (Robinson et al. 1998; Ohtsuka et al. 2006) and succession following glacial retreat (Hodkinson et al. 2003; Moreau et al. 2008; Yoshitake et al. 2011). Fertilization from seabirds provides an important source of marine-derived nutrients to vegetation, facilitating lush growth and seed production (Odasz 1994; Cooper et al. 2004; Cooper et al. 2011; Hayashi et al. 2018).

Cryptogams dominate the vegetation on Brøggerhalvøya (Arnell & Mårtensson 1959; Williams et al. 2017; Kern et al. 2019). Cryptogamic cover, which is strongly influenced by water availability (Cooper et al. 2001; Uchida et al. 2002; Uchida et al. 2006; Kern et al. 2019) and also by soil fertility and bacterial diversity (Duran et al. 2021), encompasses a range of community types, such as biological soil crusts, composed of various micro-organisms (algae, protists, bacteria and fungi; Yoshitake et al. 2010), with lichens and bryophytes dominating later successional stages (Fig. 2h). Lichens growing on rocks, soil and bryophytes are widespread and include several species common across Svalbard (Elvebakk & Prestrud 1996; Øvstedal et al. 2009; Zhang et al. 2015; Inoue et al. 2019; Table 1). The biomass of lichens in the vicinity of Ny-Ålesund declined after the re-introduction of reindeer in 1978, particularly that of fruticose species that form part of the reindeer's diet or are susceptible to trampling and selective removal (Cooper & Wookey 2001; Cooper 2006; Hansen et al. 2007; Øvstedal et al. 2009). Mosses are the most abundant bryophytes, with approximately 130 species occurring on the peninsula, and about 55 species of leafy liverworts are also present (Arnell & Mårtensson 1959; Elvebakk & Prestrud 1996; Table 1), many of which are pan-Arctic taxa, occurring in the Canadian High Arctic and Greenland (Damsholt 2013; Hassel et al. 2014). In comparison with cryptogams, vascular plant cover is typically low to moderate (Kern et al. 2019), except in habitats with mild microclimates, such as the west-facing bird cliff at Ossian Sarsfjellet (Fig. 2g), which is one of the warmest locations around Kongsfjorden (Daniel et al. 2010). Around 184 vascular plant species have been reported from Svalbard (Elvebakk & Prestrud 1996; www.svalbardflora.net), with the peninsula hosting many of them, although local standardized lists are lacking. *Saxifraga oppositifolia* and *S. polaris* are common in mesic areas, with *Dryas octopetala* and *Luzula* spp. growing on well-drained rocky ridges. *Cassiope tetragona* is found in more sheltered areas toward the inner fjord, and late-lying snowbed vegetation is common throughout (Table 1).

Early research on vegetation was largely descriptive, providing species lists and distributions (Rønning 1963; Nimis 1985; Elvebakk & Prestrud 1996) and vegetation maps (Brattbakk 1981; Brossard et al. 1984; Brossard & Joly 1994; Spjelkavik 1995; Nilsen et al. 1999). Detailed studies of vegetation composition and plant reproduction were subsequently made along successional gradients following glacial retreat (e.g., Naoya 1999; Kume et al. 2003; Cooper et al. 2004; Moreau et al. 2008; Nakatsubo et al. 2010; Müller et al. 2011). However, in the 1990s, process-based ITEX studies were initiated to determine plant responses to environmental perturbations. These studies focused on the effects of simulated climate change on vegetation, which are summarized below in the section on climate change impacts. Studies of plant ecotypes in differing habitats, together with transplant experiments, have also increased knowledge about Arctic plant adaptations to their environment (Prock & Körner 1996; Kume et al. 1999). A better understanding of plant molecular diversity and physiological processes, for example, tolerance to freezing and anoxia (Crawford et al. 1993) and the effects of temperature on gas exchange (Schipperges 1992; Uchida et al. 2002; Cooper 2004; Uchida et al. 2006; Muraoka et al. 2008; Yoshitake et al. 2010), has been derived from combinations of field and laboratory studies. Such studies have indicated that interspecific interactions in plant communities are important in Svalbard, where the harsh environment causes facilitation to play a larger role than at lower latitudes (Dormann & Brooker 2002).

Investigations focused on the effects of grazing pressure on terrestrial vegetation close to Ny-Ålesund have shown that herbivory strongly influences vegetation dynamics (van der Wal & Brooker 2004; Cooper 2006; Hansen et al. 2007; van der Wal & Hessen 2009; Sjögersten et al. 2011; Sjögersten et al. 2012). Grazing by barnacle geese (*Branta* *leucopsis*) and Svalbard reindeer reduces flower density, the germinable seed bank, dwarf shrub cover, lichen cover and moss layer thickness (van der Wal et al. 2001; Cooper & Wookey 2003; van der Wal & Brooker 2004; Cooper 2006; Kuijper et al. 2006; Little et al. 2017), potentially benefiting graminoid communities, which may partly compensate for the loss of above-ground biomass to grazers through compensatory growth (Bakker & Loonen 1998; Cooper et al. 2006; van der Wal 2006). Selective foraging by Svalbard reindeer and barnacle geese is common in the area around Ny-Ålesund (Cooper & Wookey 2003; Hansen et al. 2007; Kuijper et al. 2009). Both of these herbivores may alter the abundance of various plant species, consequently modifying interspecific competition, vegetation composition and nutrient availability. The largest impacts of these herbivores are through direct grazing (Kuijper et al. 2006; Hansen et al. 2007), but fertilization and trampling effects can also be substantial (van der Wal & Brooker 2004). Large herbivores can accelerate nutrient cycling and redistribute nutrients, most importantly N, via the excretion of feces and urine (van der Wal et al. 2004; Mosbacher et al. 2016), which can affect plant growth and vegetation composition. Exclosure experiments have been used to mechanistically investigate the impacts of resident and migratory herbivores, with Svalbard reindeer having been found to reduce lichen and vascular plant cover and the germinable seedbank (Cooper & Wookey 2001; Cooper 2006). Such enclosure experiments also indicate that preventing barnacle goose access to wet moss meadows leads to rapid vegetation recovery, switching the meadows from a C source to a C sink (Sjögersten et al. 2012).

Invertebrate communities

Invertebrates play key roles in Arctic terrestrial ecosystem functioning. The first records of terrestrial invertebrates on Brøggerhalvøya, which predominantly consist of insects, mites, springtails and worms (Table 1), originate from the 1860s (Boheman 1865). In recent years there have been numerous sampling surveys or short-term experiments applied to terrestrial invertebrate communities on the peninsula (e.g., Hågvar 1971; Nurminen 1973; Halvorsen & Gullestad 1976; Coulson et al. 1996; Sømme & Birkemoe 1999; Coulson et al. 2000; Coulson, Hodkinson & Webb 2003a, b; Ávila-Jiménez & Coulson 2011; Zawierucha et al. 2013; Pilskog et al. 2014; Zawierucha et al. 2017; Walseng et al. 2018; Tiusanen et al. 2019; Kankaanpää et al. 2020), but, as for the circumpolar Arctic, current knowledge of this crucial element of Svalbard's fauna is limited because of a lack of long-term monitoring programmes (Gillespie, Alfredsson, Barrio, Bowden, Convey, Coulsen et al. 2020; Gillespie, Alfredsson, Barrio, Bowden, Convey, Culler et al. 2020).

The terrestrial invertebrate fauna of Brøggerhalvøya is diverse. More than 900 terrestrial and freshwater invertebrate species have been recorded in Svalbard, with the majority most probably occurring in the Kongsfjorden region (Coulson et al. 2014). Among the most abundant terrestrial macro-invertebrates in the area are spiders, predominantly the Linyphiidae, which occur in rocky, vegetated habitats (Aakra & Hauge 2003), but are also present in glacial forefields (Hodkinson et al. 2001; Hawes 2008). Diptera, particularly Chironomidae (midges), may be frequent and especially active on warm, calm days (Hodkinson et al. 1996). Several species of Coleoptera are known to occur (Hågvar 1971), but, as for other locations in Svalbard, the Coleoptera fauna is poor in both species diversity and abundance. Lepidoptera are uncommon around Kongsfjorden although there are populations of the relict species the brown knot-horn (*Pyla fusca*; Pyralidae) and the exile or northern arches (*Apamea zeta*; Noctuidae) on Ossian Sarsfjellet (Coulson, Hodkinson, Webb & Convey 2003). The vagrant *Plutella xylostella* is occasionally observed at locations along the west coast (Coulson, Hodkinson, Webb, Mikkola et al. 2002). Nematoda, Tardigrada and Rotifera are also present in soil (Coulson et al. 2014) although few studies have been made on these soil animals at Ny-Ålesund specifically. True earthworms (Lumbricidae) are not naturally present on Svalbard, but annelids are represented by the smaller enchytraeids, which perform similar functions (Coulson et al. 2014).

In terms of abundance, the microarthropod groups of springtails (Collembola) and mites (Acari) dominate soil habitats, with densities of up to at least several tens of thousands of individuals per square metre regularly being recorded (Gwiazdowicz et al. 2020). In habitats that are moist and nutrient rich, such as beneath bird cliffs, the abundance of mites and springtails can reach >240 000 individuals per square metre (Bengtson et al. 1974). The life histories of springtails and mites have been studied on account of the importance of these invertebrates in the below-ground food web and nutrient cycling (Birkemoe & Sømme 1998; Søvik et al. 2003; Søvik 2004). Moreover, owing to their abundance and the absence of earthworms, springtails also connect above- and below-ground food webs by serving as prey items for bird species, such as the purple sandpiper (*Calidris maritima*; Leinaas & Ambrose 1992).

There have been several experimental field studies of the terrestrial invertebrate fauna around Ny-Ålesund. These have, for instance, applied metapopulation theory to investigate the movement of springtails in patchy habitats (Ims et al. 2004), and have looked at the impacts of winter basal ice formation and the effects of accidental fuel oil release on soil fauna (Coulson et al. 2000). Several invertebrates from the region have also been the focus of laboratory studies investigating adaptations to Arctic conditions.

These studies have addressed, for example, freeze tolerance and avoidance (Worland et al. 2000), freeze-desiccation (Bahrndorff et al. 2007; Sørensen & Holmstrup 2011), physiology (Aunaas et al. 1983; Block et al. 1994), dispersal (Coulson, Hodkinson, Webb & Harrison 2002; Coulson, Hodkinson, Webb, Mikkola et al. 2002; Coulson, Hodkinson & Webb 2003a; Ávila-Jiménez & Coulson 2011), hatching (Pasquali et al. 2019), melanization and UV protection (Hessen et al. 2002; Leinaas 2002), drought stress (Hertzberg 1997; Hertzberg & Leinaas 1998), diet (Hodkinson, Bird et al. 2004) and biological rhythms (Pasquali et al. 2017). However, our ability to make predictions about the responses of terrestrial invertebrates to environmental pertubations is currently restricted by a lack of long-term studies and limited knowledge of the natural inter-annual variability of many invertebrate populations (Taylor et al. 2020). To address the lack of monitoring of invertebrate communities, Gillespie, Alfredsson, Barrio, Bowden, Convey, Culler et al. (2020) make several recommendations, principally that (1) research on invertebrates needs a substantial effort with wider international collaboration to collate available data on a pan-Arctic scale and (2) terrestrial invertebrates must be given higher priority within long-term research plans, with more statewide commitments to their monitoring.

Vertebrate communities

The terrestrial food web of the Arctic tundra around Ny-Ålesund is relatively simple because of the lack of small rodents and specialist predators (Ims et al. 2013; Descamps et al. 2017; Table 1). Only a few herbivore species are present in significant numbers, including the resident Svalbard reindeer and the Svalbard rock ptarmigan, as well as the migratory barnacle goose and pink-footed goose (*Anser brachyrhynchus*). The predator/scavenger guild consists of the Arctic fox, glaucous gull (*Larus hyperboreus*) and skuas (mainly the Arctic skua [*Stercorarius parasiticus*]), which impact the breeding success of many ground-nesting birds (e.g., Steen & Unander 1985; Fuglei et al. 2003; Layton-Matthews et al. 2019). Migratory snow buntings, red-throated divers (*Gavia stellata*) and a range of shorebirds add to the species diversity but have generally been less studied in the region when compared with seabirds, which link marine and terrestrial ecosystems (Hop et al. 2002; Kovacs & Lydersen 2006; Gabrielsen et al. 2020). Importantly, polar bears are increasingly visiting the peninsula during summer, where, despite their classification as a marine mammal, they predate on the eggs of ground-nesting birds (Prop et al. 2015).

Studies of the vertebrates of Brøggerhalvøya span a wide range of resident and migratory species and research topics, including physiological and behavioral adaptations to the High-Arctic environment (Gabrielsen et al. 1985; Unander & Steen 1985; Steen & Gabrielsen 1988; Gabrielsen et al. 1991; Frafjord 1992; Fuglei 2000; Sandström et al. 2014), growth and body size (Steen & Unander 1985; Bishop et al. 1995; Tombre et al. 1996; Loonen et al. 1997), population ecology and dynamics (Steen & Unander 1985; Prestrud 1992; Hansen et al. 2011; Pedersen et al. 2014; Unander et al. 2016; Hansen, Pedersen et al. 2019; Layton-Matthews et al. 2019), diseases and parasites (Prestrud 1992; Dolnik & Loonen 2007; Prestrud et al. 2007; Sandström et al. 2013), spatial ecology (Stahl & Loonen 1998; Fuglei & Tarroux 2019; Pedersen et al. 2021), trophic interactions (e.g., van der Wal & Loonen 1998; Fuglei et al. 2003; Dabert et al. 2015; de Jong et al. 2019; Layton-Matthews et al. 2020) and climate change impacts (Hansen et al. 2011; Hansen, Pedersen et al. 2019; Layton-Matthews et al. 2020; Layton-Matthews et al. 2021). Some of the most extensive time series available for vertebrate populations in Svalbard originate from Ny-Ålesund and Brøggerhalvøya (Supplementary Table S1). These have provided information on, for instance, the abundance, demography, phenology and spatial ecology of barnacle geese (Alsos et al. 1998; Loonen et al. 1998; Layton-Matthews et al. 2019; Layton-Matthews et al. 2020; Layton-Matthews et al. 2021), Arctic fox (Fuglei et al. 2003) and Svalbard reindeer (Aanes et al. 2000; Hansen et al. 2011; Hansen, Pedersen et al. 2019).

The longest time series for vertebrates around Ny-Ålesund has tracked the abundance of Svalbard reindeer (Fig. 3a, Supplementary Table S1), a species eradicated from the peninsula for more than a century. However, the re-introduction of 15 individuals (of which 12 survived) from Adventdalen in central Spitsbergen in 1978 was followed by rapid population growth to 360 individuals (Aanes et al. 2000). In 1994, the population crashed and was reduced to 80 individuals, and some emigrated to the nearby Sarsøyra and Kaffiøyra peninsulas and became established there. Population densities on Brøggerhalvøya have subsequently fluctuated but have remained generally low since the crash, with a slight, but significant, decline in population size between 1995 and 2020 (Aanes et al. 2000; Hansen, Pedersen et al. 2019). The 43-year time series has revealed that plant–herbivore interactions, in the absence of predation, are characterized by a dynamic combination of bottom-up effects and top-down control (Hansen et al. 2007). Thus, density dependence, winter weather variability and the interactions between these factors have been found to shape the population dynamics of Svalbard reindeer (Aanes et al. 2000; Aanes et al. 2002; Kohler & Aanes 2004; Hansen et al. 2011; Hansen, Pedersen et al. 2019).

Barnacle geese started breeding on the shores and on the islands of Kongsfjorden in the early 1980s. The estimated number of adults in the local breeding population

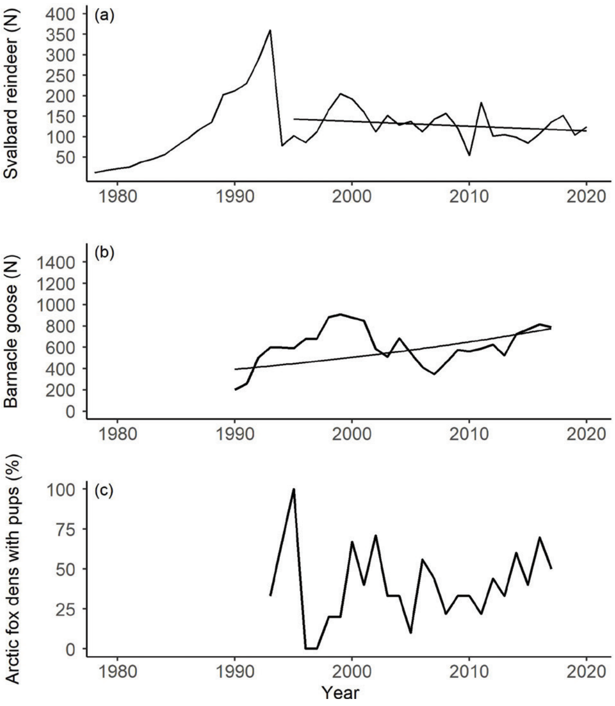

Fig. 3 Time series of the abundances of three key vertebrate species at Ny-Ålesund and Brøggerhalvøya. (a) Late winter population size of Svalbard reindeer (modified from Hansen et al. 2019; Pedersen et al. 2021). (b) Summer population size of adult barnacle goose (modified from Layton-Matthews et al. 2020). (c) Arctic fox dens with pups (modified from Layton-Matthews et al. 2020). There is no trend line in (c) because of lack of statistical significance.

of barnacle goose show that the population size of the species increased between 1990 and 2016 (Layton-Matthews et al. 2019; see also Fig. 3b, Supplementary Table S1), with most of the population using Ny-Ålesund and its surrounding islands as breeding sites. The proximity to Ny-Ålesund of brood rearing and molting barnacle geese has made behavioral studies possible (e.g., Loonen et al. 1999; Stahl et al. 2001). Age-structured population modeling, based on a combination of population censuses and capture–mark–recapture data since 1990, suggests a recent molting population size of ca. 600–800 adults (Layton-Matthews et al. 2019; Layton-Matthews et al. 2021). Adult overwinter survival rates are mainly influenced by winter temperatures in the temperate wintering grounds and total flyway population size, while reproductive parameters, such as egg numbers, hatching rates and fledging success, are shaped by a combination of density dependence, local weather and the effects of Arctic fox predation (Layton-Matthews et al. 2019; Layton-Matthews et al. 2020; Layton-Matthews et al. 2021) and polar bears (see Prop et al. 2015 for an example).

The Arctic fox, which is the most important terrestrial predator and scavenger in the region, is another species that has been subject to long-term monitoring (Fuglei et al. 2003; Layton-Matthews et al. 2019; Supplementary Table S1). The fox population shows considerable inter-annual variation in den occupancy rate, ranging from 0 to 100%, with no long-term trend in the proportion of dens with pups (Layton-Matthews et al. 2019; Fig. 3c). Arctic fox population dynamics are driven by a strong bottom-up effect through the availability of Svalbard reindeer carcasses in winter, with a 1-year time lag due to the effects of carcasses on pup production in the following year (Loonen et al. 1998; Fuglei et al. 2003; Hansen et al. 2013).

Freshwater ecosystems

A range of freshwater habitats is present in the Ny-Ålesund area, such as snowmelt pools (Stibal & Elster 2005; Stibal et al. 2007), cryoconite holes (Kaštovská et al. 2005; Vonnahme et al. 2016), ponds on glacier surfaces (Kaštovská et al. 2005) and small streams and rivers draining glaciers (Elster et al. 2001; Kubečková et al. 2001), through to ephemeral or permanent ponds and deeper lakes (Fig. 2f). Part of the meltwater that penetrates to glacial beds also supplies groundwater systems below the permafrost, returning to the surface as springs (Kaštovská et al. 2007; Haldorsen et al. 2012) or discharging directly into Kongsfjorden (Sundfjord et al. 2017). Hydrological data from Arctic regions are generally limited (Bring et al. 2016), and for the Ny-Ålesund area, the only data available are from the Bayelva river catchment. The first systematic runoff measurements commenced in 1974 (Repp 1988; Bogen & Bonsnes 2003; Krawczyk et al. 2003), with some further information available from a small catchment on Blomstrandhalvøya (Krawczyk & Pettersson 2007).

Freshwater communities in glacial habitats

Given the numbers of glaciers close to Ny-Ålesund, snow surface and cryoconite holes are locally important, with those of Midtre Lovénbreen being among the world's most thoroughly studied glacial surface habitats (Edwards et al. 2011; Telling et al. 2012). Cryoconite holes are an extreme aquatic ecosystem formed of water-filled holes on the glacier surface, where cryoconite, consisting of microbes, small stone particles and other debris, becomes concentrated. These systems have a distinct biogeographical structuring and unique species assemblages adapted to the extreme conditions (Anesio & Laybourn-Parry 2012; Stibal et al. 2012; Vonnahme et al. 2016). The microbial assimilation of atmospherically deposited N in these ecosystems may also be important when terrestrial soil microbes remain inactive (Hodson et al. 2010). The ice and subglacial water on three glaciers on Brøggerhalvøya have been screened for fungi and bacteria, revealing the presence of 109 fungal strains belonging to 30 mostly basidiomycete yeasts, with abundant Actinobacteria (typically *Micrococcus*) and Proteobacteria in glacial and sub-glacial ice (Perini et al. 2019).

Pond and lake communities

Shallow ponds are the most common freshwater bodies in the area, with only a few deeper lakes. The generally clear water of these lentic water bodies permits deep light penetration (Ellis-Evans et al. 2001), allowing phytoplankton primary production in the entire water column, and particularly strong development of extensive epibenthic microbial mats containing micro-eukaryotic algae and phototrophic bacteria (Rautio & Vincent 2006). Knowledge of the chemical features and the occurrence of plankton in ponds and lakes near Ny-Ålesund is scarce. Kim et al. (2011) document freshwater algae in the area, whilst Hessen & Leu (2006) report that nutrient-poor Lake Storvatnet has relatively low phytoplankton biomass dominated by small chrysomonads and microalgae, whereas nutrient-rich Lake Solvatnet has higher biomass dominated by chlorophytes (*Scenedesmus* cf. *linearis)*, small chrysomonads and microalgae. While bryophytes may occur in and around waterlogged ground, ponds and lakes in the area, other aquatic macrophytes have not been reported from Svalbard (Elvebakk & Prestrud 1996). Food webs in freshwater bodies are simple and typically consist of microbes, phyto- and zooplankton and invertebrate and vertebrate consumers. Except for two records of three-spined stickleback (*Gasterosteus aculeatus*) in freshwater bodies around Isfjorden, the anadromous Arctic char (*Salvelinus alpinus*) is the only fish species found in freshwaters on Svalbard. Most shallow water bodies in the vicinity of Ny-Ålesund freeze to their bottoms in winter and therefore lack char. However, *S. alpinus* occurs in lakes and rivers on other peninsulas in the archipelago (Svenning et al. 2015) and has been a focus of studies into its life-history traits (Gulseth & Nilssen 2001). Owing to the absence of fishes, the omnivorous Arctic tadpole shrimp (*Lepidurus arcticus*) is the dominant consumer species in freshwater lakes and ponds on Brøggerhalvøya (Walseng et al. 2018). The shrimp is relatively abundant and its presence is strongly linked to climatic and environmental variables (Calizza et al. 2016; Pasquali et al. 2019).

The freshwater invertebrate fauna is less species rich than that of the terrestrial environment (Halvorsen & Gullestad 1976). Important zooplankton species include the water fleas *Daphnia pulex, Chydorus sphaericus* and *Macrothrix hirsuticornis*, the copepod *Cyclops abyssorum* (Walseng et al. 2018) and a number of rotifers (Coulson et al. 2014). Chironomids dominate the macrobenthos, with common species including *Paratanytarsus austriacus*, *Psectrocladius barbimanus* and *Cricotopus tibialis*, and the caddisfly *Apatania zonella* also being common (Walseng et al. 2018; Table 1). Nematodes, tardigrades, ostracods and harpacticoid copepods dominate the meiofauna (Walseng et al. 2018). An inventory of the freshwater invertebrate fauna in ponds in western Svalbard, including the Ny-Ålesund area, has recently become available (Chertoprud et al. 2017; Dimante-Deimantovica et al. 2018; Walseng et al. 2018). However, broad taxonomic surveys have not been performed, and the few studies of freshwater micro-organisms have mainly focused on microscopy-based identification or isolation campaigns targeting functional groups (Kim et al. 2008; Graef et al. 2011; Kim et al. 2011). Studies of specific micro-eukaryotes, such as the alga *Zygnema* (Pichrtova et al. 2016; Pichrtova et al. 2018) and the cyanobacterium *Phormidium* (Tashyreva & Elster 2016), have also been performed.

Freshwater bodies on the peninsula are important as a molting and foraging habitat for birds and for transporting water, sediments and nutrients from the terrestrial to the marine ecosystem. Increasing air temperatures and changes to soil microbial activity and the length of the drainage period can increase the overall losses of organic C and N in drainage waters (Tye & Heaton 2007), with occasional algal blooms being observed (Pichrtova et al. 2016; Tashyreva & Elster 2016). In ponds and lakes in western Svalbard, the impacts of increasing goose populations in aquatic ecosystems (Hessen et al. 2017; Jensen et al. 2019) result in elevated nutrient concentrations, leading to increased microbial biomass (Mindl et al. 2007), altered phytoplankton and invertebrate communities (Jensen et al. 2019) and shifts in the genetic diversity of *Daphnia* spp. (Alfsnes et al. 2016). However, algal biomass typically does not increase in lakes impacted by geese, possibly because of top-down control in some systems from grazing crustaceans (Van Geest et al. 2007).

Stream and river communities

The streams and rivers of the region are also characterized by relatively low diversity and simple food webs. Primary producers in running waters in Svalbard are epiphytic algae and, to a lesser extent, bryophytes. Cyanobacteria and diatoms predominate in the epiphyton (Skulberg 1996). Kubečková et al. (2001) studied the epiphytic communities in two glacial-fed streams and one snow-fed stream in the Ny-Ålesund area, distinguishing a group of cyanobacteria and algae that are important in primary succession owing to their ability to colonize new substrates rapidly. The lotic invertebrate fauna in Svalbard is dominated by chironomids (Chertoprud et al. 2017). Lods-Crozet et al. (2007) compared the chironomid assemblages of the glacier-fed stream Bayelva and the nonglacial stream Londonelva near Ny-Ålesund. Environmental conditions (discharge, water temperature, suspended sediment) differed between the glacial and nonglacial systems, likely explaining differences found in the chironomid communities. The glacial-fed stream had lower abundances of chironomids and was characterized by the species *Diamesa aberrata* and *D. bohemani*. In contrast, the nonglacial stream had higher abundances of chironomids, typified by *D. arctica* and *D. bertrami* (Lods-Crozet et al. 2007).

Human impacts

Despite its remote location, the Ny-Ålesund area is impacted by current and past human activity. In this section, we review studies concerning pollution, disturbance and non-native species. Impacts of anthropogenic climate change are reviewed in the subsequent section.

Local pollution

The coal mining that took place around Ny-Ålesund prior to 1962 led to anthropogenic pollution in and close to the settlement. Foci for research into the effects of local pollution have been the old landfill and dumping sites, former mining and fuel storage areas, wastewater system, airport and the harbour (e.g., Skei 1994; Breedveld et al. 1999; Breedveld & Skedsmo 2000; Børresen 2003; Sulej et al. 2011, 2012; Granberg et al. 2017; Dekhtyareva et al. 2018). During the coal mining period, mining waste was mainly deposited close to the mines in spoil heaps, which are still visible today. Sulfuric acid production in the heaps, caused by high spoil sulfur content, has led to metal dissociation and accumulation in runoff. This acidic metal-enriched runoff, known as acid mine drainage (Askaer et al. 2008), is released during spring thaw, after which it enters the surrounding terrestrial environment, where it causes soil pH values to decline to <4 and leads to reductions in plant cover and substantial changes to microbial communities (Kerfahi et al. 2022). Close to former mine sites, coal dust is also detectable in several abiotic matrices and is associated with elevated polyaromatic hydrocarbon concentrations (Breedveld et al. 1999; Vecchiato et al. 2018). Concentrations of Hg in soil and vegetation are also significantly higher in the vicinity of mine sites compared with more distant areas (van den Brink et al. 2018). Experiments with captive barnacle goose goslings showed significant effects of trace elements from coal mining on stress physiology and behavior (Scheiber et al. 2018). Microplastics and other pollutants have also recently been documented in both marine and freshwater ecosystems close to Ny-Ålesund (Iannilli et al. 2019; González-Pleiter et al. 2020; von Friesen et al. 2020).

Long-range pollution

Terrestrial ecosystems in Svalbard are influenced by the long-range atmospheric transport of volatile and semi-volatile POPs and heavy metals from industrial areas at lower latitudes that can accumulate in Arctic biota (Wania & Mackay 1996; Burkow & Kallenborn 2000; Berg et al. 2013). The northern regions of Svalbard, and in particular Ny-Ålesund, have been key in monitoring and research on the long-range atmospheric transport of anthropogenic pollutants (Kylin et al. 2015). In addition to relatively rapid atmospheric transport, water-soluble contaminants, such as β-HCH and per- and polyfluoroalkyl substances, are transported to the Arctic by ocean currents (Li et al. 2002; Stemmler & Lammel 2010). As documented in other Arctic regions, these contaminants can be transported from sea to land, for instance by migratory seabirds, where they become concentrated in higher trophic levels through biomagnification (Blais et al. 2005; Evenset et al. 2007).

Heavy metals, especially Hg, have been recorded in soils, vegetation and seabirds around Kongsfjorden (Savinov et al. 2003; Halbach et al. 2017; Aslam et al. 2019; Hitchcock et al. 2019; Kristiansen et al. 2019). High concentrations of a range of contaminants in soil and vegetation under bird cliffs, and in the droppings of birds such as black-legged kittiwake, glaucous gull and Brünnich's guillemot (*Uria lomvia*), illustrate the role of seabirds in transferring contaminants between marine and terrestrial ecosystems (Headley 1996; Evenset et al. 2007; Kristiansen et al. 2019). In principle, this mechanism can lead to the transfer of contaminants from marine food sources in both local and remote areas, since these seabirds spend the winter season at lower latitudes.

POPs, such as PCBs and per- and polyfluoroalkyl substances, have also been documented in soils and various biota around Ny-Ålesund, with levels generally being low, except for around bird cliffs (Zhang et al. 2014; Aslam et al. 2019; Hitchcock et al. 2019). One study demonstrated higher concentrations of PCBs in vegetation than in the underlying organic soil and showed a correlation with atmospheric sources (Aslam et al. 2019). However, contaminant concentrations in tundra were not correlated with those measured in springtails (Kristiansen et al. 2019). Contrasting with the generally low organic pollution levels documented in the terrestrial environment, Arctic foxes can accumulate high levels of several POPs derived from the marine components of their diet (Andersen et al. 2015). Importantly, Svalbard reindeer and birds are also impacted by long-range marine debris pollution, namely fishing nets and other waste washed ashore on beaches, in which they become entangled, leading to mortality (Hallanger & Gabrielsen 2018).

Disturbance

Human traffic in Svalbard has increased during the last few decades, leading to damage to vegetation (Hagen et al. 2012; Thuestad et al. 2015), alien seed dispersal (Ware et al. 2012) and disturbance of wildlife (e.g., Gabrielsen 1984; Gabrielsen et al. 1985; Gabrielsen & Smith 1995; Madsen et al. 2009; Hansen & Aanes 2015). However, only a few studies into the effects of human disturbance have been made at Ny-Ålesund. Thuestad et al. (2015) surveyed the impact of recent human activities on the natural environment and cultural heritage at a location near Ny-Ålesund and found a sharp increase in trampled vegetation between 1990 and 2009 (1.3% and 12.6% of surveyed areas, respectively). Hansen and Aanes (2015) showed that local Svalbard reindeer habituate to human presence at small spatiotemporal scales through individual learning. Arctic foxes have also become habituated to the presence of humans and regular food supplies at Ny-Ålesund and have consequently bred in the settlement between 2003 and 2011 (E. Fuglei & M.J.J.E. Loonen, unpubl. data). Studies of birds, such as Svalbard rock ptarmigan, common eider and seabirds, generally show negative effects of human disturbance on reproduction and survival rates (Gabrielsen 1984, 1987; Gabrielsen et al. 1985). Various studies have themselves had long-term effects on the environment in and around Ny-Ålesund, such as experiments applying N and P fertilizers to vegetation (Baddeley et al. 1994) or those simulating oil spills (Sendstad 1980).

Alien and vagrant species

Other than a single record of the dock *Rumex longifolius* being found in the settlement in 2017 (Bartlett et al. 2021), there are no known non-native vascular plant, terrestrial vertebrate, or invertebrate species in the Ny-Ålesund area (Coulson 2015). However, non-native species documented in other settlements in Svalbard could potentially invade habitats on Brøggerhalvøya (Coulson 2015; Sysselmannen på Svalbard 2017). Vascular plants are the most frequent non-native species on Svalbard, with 38 species found in a recent survey (Bartlett et al. 2021). Vagrants from landmasses at lower latitudes also occur in the vicinity of Ny-Ålesund, as evidenced by occasional observations of the moth *Plutella xylostella* and other Lepidoptera (Coulson, Hodkinson Webb, Mikkola et al. 2002).

Climate change and its impacts on ecosystems

Climate models predict continued rapid warming of the Arctic, with increased frequency of rainfall, more extreme weather events and altered seasonality (Bintanja & Andry 2017; Hanssen-Bauer et al. 2019). Such changes are already evident in the terrestrial ecosystems surrounding Ny-Ålesund. During the last few decades, annual precipitation and mean temperatures have increased dramatically (Førland et al. 2011; Maturilli et al. 2015; Hanssen-Bauer et al. 2019; Maturilli et al. 2019; Peeters et al. 2019). This has resulted in glacial recession and thinning (Kohler et al. 2007; Schuler et al. 2020), a regime shift toward more rain in winter (Peeters et al. 2019); changes in snow characteristics, depth, extent and duration (Brown et al. 2017; Peeters et al. 2019); increased depth of the permafrost active layer (Boike et al. 2018); and reductions in sea-ice cover and thickness in Kongsfjorden (Pavlova et al. 2019). Mean annual air temperature increased at a mean rate of +0.71 °C/decade from 1971 to 2017. However, the greatest rate of increase in air temperature has been recorded during winter (+1.35 °C/decade; Hanssen-Bauer et al. 2019), with mean winter temperature rising significantly (Fig. 4a), associated with an upward trend in the Arctic Oscillation (Maturilli & Kayser 2017). Precipitation has also increased (+7.1% and +14.4% for the same yearly and winter time period, respectively; Hanssen-Bauer et al. 2019), with winter melt events now occurring more frequently (Graham et al. 2017; Peeters et al. 2019). There is now occasionally severe winter rainfall (Vikhamar-Schuler et al. 2016), such as the record-breaking ROS event in late January 2012, when 98 mm of rain (equivalent to 25% of mean annual precipitation) fell in one day (Hansen et al. 2014). During the last five decades, there has been a substantial increase in the amount of rain falling on snow at Ny-Ålesund, from close to zero in some years from 1975 to 1998 and to up to 170 mm in 1999–2021 (Fig. 4b). A recent model-based study, using long-term monitoring data of snowpack on Brøggerhalvøya, further suggests that rainfall events and associated basal ice formation have increased in frequency (Peeters et al. 2019). Results indicate that, since 1998, mild and rainy winters with basal ice formation have occurred annually, whereas in the previous decades, they occurred on average every 3–4 years (Peeters et al. 2019). Snow cover duration is highly variable from year to year, but is generally declining both at Ny-Ålesund and more widely in Svalbard, resulting in earlier spring onset (four days/decade; Brown et al. 2017) and changes in patterns of snowmelt (van Pelt et al. 2016; Hanssen-Bauer et al. 2019). Furthermore, based on air temperature data, winter length at Ny-Ålesund has become shorter, with the onset of winter being delayed and spring becoming advanced (Fig. 4c). On glacier surfaces in Svalbard, autumn snow onset has

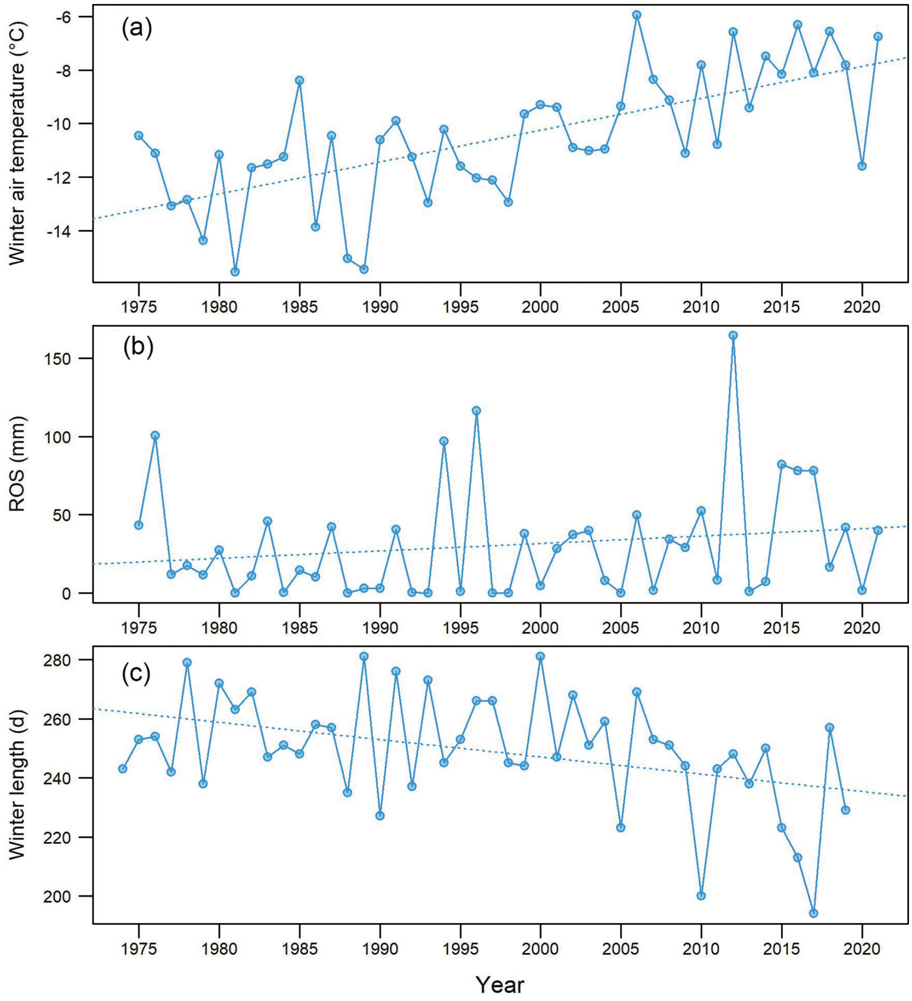

Fig. 4 Time series of winter weather recorded by the meteorological station at Ny-Ålesund, 1974/75–2020 (Norwegian Centre for Climate Services 2020). (a) Mean winter (November–April) air temperature. (b) Rain on snow (mm), calculated as the amount of precipitation falling when the daily average air temperature was ≥1 °C. There was a significant change around 2000 in the amount of precipitation falling as rain in winter (see Peeters et al. 2019). (c) Winter length, calculated as the number of days between winter onset and spring onset. Winter onset was estimated as the day from which the 10-day running mean daily air temperature in autumn remained below 0 °C for a minimum of 10 consecutive days, and spring onset was estimated as the time in spring when the 10-day running mean daily air temperature exceeded 0 °C for a minimum of 10 consecutive days (see Hansen, Gamelon et al. 2019 for methods).

been delayed by two days/decade between 1961 and 2012 (van Pelt et al. 2016). Local glaciers are consistently retreating, opening up forelands for biological colonization (Bradley et al. 2017; Schuler et al. 2020). Sea-ice formation has become restricted to the northern part of Kongsfjorden (Pavlova et al. 2019) and tidewater glacier melting patterns have also changed (Sundfjord et al. 2017). The thickness of sea ice has decreased (from an average of 0.6 m in 2003 to 0.2 m in 2016), as has the depth of snow cover on sea ice (from 0.2 m to <0.05 m over the same period [Pavlova et al. 2019]). There is therefore strong evidence that the climate of the Ny-Ålesund area is changing rapidly, with substantial implications for ecosystems. Moreover, we provide an overview of the effects of these changes on different components of the terrestrial and freshwater ecosystems in the region.

Impacts on permafrost, soils and soil microbes

As for elsewhere in the Arctic (Biskaborn et al. 2019), long-term permafrost and biological soil crust monitoring programmes, established in the Ny-Ålesund area in the 1990s, indicate significant annual and seasonal warming (0.08–0.25 °C yr^{-1} between 1998 and 2017) in the active layer at depths of 4–58 cm and at the top of the permafrost at 138 cm depth (Boike et al. 2018). Permafrost degradation associated with climate warming is expected to have profound and complex effects on biological and biogeochemical processes, including, as documented in other Arctic regions, ground collapse and habitat destabilization (Christensen et al. 2019; Parmentier et al. 2019). Moreover, permafrost thaw potentially affects local freshwater systems because of the increased release of nutrients into these systems (see below). Whether warmer Arctic ecosystems will become C sinks or sources is uncertain because trends in CO_2 fluxes depend on the interaction between abiotic (e.g., soil temperature, soil moisture and photosynthetically active radiation) and biotic (e.g., vegetation type, phenology, leaf area index, photosynthetic capacity, state of the soil microbial community, grazing [Falk et al. 2015]) factors. Transition seasons (spring and autumn) play a key role in the potential for ecosystems to move from being C sinks to C sources (Cannone et al. 2016). Shifts in the growing period to later in the season are evident from experiments in Adventdalen near Longyearbyen on Svalbard that use snow fences to reduce the effects of summer drought, allowing C fixation to continue for longer (Blok et al. 2015). However, given the spatial variability of SOC concentrations in the active layer of permafrost on Brøggerhalvøya, there is uncertainty about the amount of C potentially released to the atmosphere from permafrost thawing, as vegetated sites could release comparatively greater amounts than barren ground (Cannone et al. 2016; Wojcik et al. 2019). Although warming may enhance soil respiration at sites with high permafrost SOC content, overcoming C fixation to produce a net source effect, the lower rates of respiration in soils with low SOC content will probably be offset by C fixation from increased plant biomass, with a consequent sink effect (Cannone et al. 2019; Wojcik et al. 2019).

The retreat of glaciers on Brøggerhalvøya has enabled chronosequence studies of colonization and succession of multiple microbial, plant and invertebrate groups in newly exposed forelands (e.g., Hodkinson et al. 2003; Hodkinson, Coulson et al. 2004; Kaštovská et al. 2005; Nakatsubo et al. 2005; Yoshitake et al. 2007; Moreau et al. 2008; Pessi et al. 2019; Gwiazdowicz et al. 2020). In the Midtre Lovénbreen and Austre Brøggerbreen glacier forelands, the areas exposed in the first 100 years after deglaciation initially became colonized by biological soil crusts, which stabilized the soil surface and increased soil nutrient concentrations (Hodkinson 2003; Yoshitake et al. 2011). Microbial community structure, although highly variable, displays clear overall changes along chronosequences (Tsuji et al. 2016; Kim et al. 2017; Yoshitake et al. 2018), as does soil CO_2 flux (Bekku et al. 2004) and the diversity of ectomycorrhizal fungi (Fujiyoshi et al. 2011). Laboratory-based studies indicate effects of temperatures of up to 30 °C on the activity and community composition of methanogenic soil microbes (Høj et al. 2005; Tveit et al. 2015), but data on the responses of soil microbes to warming in the natural environment at Ny-Ålesund are sparse.

Impacts on terrestrial vegetation

Starting in the early 1990s, ITEX process-based research investigated the sensitivity of polar semi-desert and heath communities on Brøggerhalvøya to elevated summer temperature, moisture and nutrient availability (Wookey et al. 1993; Wookey et al. 1994; Robinson et al. 1995; Wookey et al. 1995; Robinson et al. 1998; Weijers et al. 2012). Both community types exhibited rapid advances in the phenology of vascular plants in response to warming, while fertilization led to decreased coverage of vascular plants, increased moss cover and only small effects on lichen abundance (Robinson et al. 1998). Analyses of satellite images show that the timing of the onset of the plant growing season varies greatly between years on Brøggerhalvøya (Karlsen et al. 2014), likely due to interannual variation in spring temperature and snowmelt (Karlsen et al. 2018). However, overall, spring onset has advanced, particularly during the last decade (Layton-Matthews et al. 2019; Le Moullec et al. 2020). Some plant species also show advanced senescence at the end of the growing season (Semenchuk, Gillespie et al. 2016). However, the mechanisms controlling the timing of plant senescence, especially in the Arctic, are still poorly understood and remain debated (Estiarte & Penuelas 2015). Studies at Ny-Ålesund have yet to document mismatches between flowering phenology and pollinators, as are evident in other regions of the Arctic (Gillespie et al. 2016; Schmidt et al. 2016). Changes in plant phenology and in growing season length also provide feedback to biogeochemical cycles, in particular to CO_2 fluxes, with potential impacts on the regional CO_2 balance (Cannone et al. 2016).

Changes to winter precipitation, especially the incidence of rainfall and the cover, depth and density of snow, have major effects on Arctic vegetation. For instance, studies using snow fences on Brøggerhalvøya and also in Adventdalen indicate major consequences for vegetation and nutrient cycling of increased snow depth (e.g., Rieley et al. 1995; Morgner et al. 2010; Foster et al. 2016). These include altered leaf traits and delayed phenology (Rieley et al. 1995; Cooper et al. 2011; Semenchuk, Gillespie et al. 2016), higher leaf and whole plant N contents (Semenchuk et al. 2015; Mörsdorf et al. 2019) and changes in plant community composition, with, for instance, loss of dwarf shrub dominance in some areas (Cooper et al. 2019). ROS events lead to extensive dieback of vascular plants, such as *C. tetragona* and *D. octopetala*, on Brøggerhalvøya (Bjerke et al. 2017). In a recent study, Le Moullec et al. (2020) showed that the annual growth of the shrub *Salix polaris* at Ny-Ålesund is inhibited by ROS events but is positively affected by snow amount, with less clear impacts of summer temperature. Changes in the depth and distribution of snow cover can lead to both increased insulation and exposure of terrestrial plants to freezing and temperature extremes (e.g., Ávila-Jiménez & Coulson 2011; Semenchuk et al. 2013; Cooper 2014; Convey et al. 2015; Foster et al. 2016; Convey et al. 2018). For instance, temperatures close to and even above 0 °C under deep snow cover lead to a continuation of biological activity and depletion of energy reserves (Convey et al. 2015; Semenchuk, Christiansen et al. 2016; Natali et al. 2019). In severe winters, vegetation experiences frost damage, caused by either lack of insulation from snow, ambient temperature fluctuations, or ROS events leading to basal ice accumulation (Bjerke et al. 2017). Furthermore, snowpack with ice layers conducts heat more efficiently than dry snow, which affects the thermal regime of the underlying permafrost, with consequences for its C content (Gouttevin et al. 2012). As the frequency and reproduction of plant pathogens are also responsive to precipitation (Hoshino et al. 2009; Masumoto et al. 2018; Cooper et al. 2019), climate change could also influence host–pathogen interactions, such as those between *S. polaris* and the tar spot fungus (*Microbotryum bistortarum*; Tojo & Nishitani 2005) and mosses and *Globisporangium* spp. (Hoshino et al. 2011; Tojo et al. 2012).

Impacts on terrestrial invertebrates

The effects of predicted climate change on terrestrial invertebrate communities in the Ny-Ålesund area have also been investigated using ITEX methodologies. These studies have demonstrated positive effects of soil warming on the abundance and reproductive performance of some, but not all, terrestrial soil invertebrates (e.g., Strathdee & Bale 1995; Coulson et al. 1996). Soil moisture has been identified as having a key role in the responses of microarthropods to experimentally elevated summer temperatures (Coulson, Hodkinson & Webb 2003b), with the densities of drought-susceptible springtails declining in warmed, and consequently drier, soils (Coulson et al. 1996). Experiments mimicking winter basal ice formation have demonstrated taxon-specific consequences for the soil fauna, with springtail abundances declining, but with no detectable effects on oribatid mite populations (Coulson et al. 2000). Increases in tick (*Ixodes uriae*) infestation rates of seabirds have been linked to recent increases in winter temperatures (Descamps 2013) and interannual differences in chironomid emergence patterns have also been attributed to summer temperature variations (Hodkinson et al. 1996).

The soil microarthropod fauna is tolerant of current winter conditions (Coulson et al. 2014; Convey et al. 2015), but changes to the depth and distribution of snow cover affect insulation and the exposure of invertebrates to freezing and temperature extremes. The aphid *Acyrthosiphon svalbardicum*, which occurs along the southern coast of Kongsfjorden, has been the focus of studies into its responses to warming. It is predicted to expand its range to currently unoccupied habitat patches, possibly through windborne dispersal of winged alate morphs (Simon et al. 2019), in response to increased local temperatures and longer summer periods. Field warming experiments also lead to an order of magnitude increase in overwintering eggs of the aphid through completion of an extra summer generation (Strathdee & Bale 1995). The range of the species on the Brøggerhalvøya was mapped in 1992 (Strathdee & Bale 1995) and on a microscale in 2010 (Ávila-Jiménez & Coulson 2011). During the latter study, the importance of winter snow accumulation, timing of melt and the duration of the summer period in determining the local distribution of the aphid was established. Another endemic Svalbard aphid, *Sitobion calvulum*, has complex interactions with its host, *S. polaris*. Increases in temperature and goose grazing, as well as disease transmission, can lead to deleterious impacts on the aphid, with cascading impacts in the food web (Gillespie et al. 2013). Several recent Arctic studies have also shown drastic changes in invertebrate species abundance, community composition and phenology associated with climate change, particularly in relation to mismatches with the flowering season (Schmidt et al. 2016; Koltz et al. 2018; Loboda et al. 2018; Høye et al. 2020). Given the rapid rate of climate change at Ny-Ålesund, these observations reinforce the conclusion of Gillespie, Alfredsson, Barrio, Bowden, Convey, Culler et al. (2020) and Taylor et al. (2020) that terrestrial invertebrates must be given higher priority for funding within long-term research.

Impacts on terrestrial vertebrates

The Svalbard reindeer reintroduction and barnacle goose colonization in the late 1970s and early 1980s, respectively, have been the dominant drivers of change in the abundance of terrestrial vertebrates and vegetation communities on Brøggerhalvøya. However, both direct and indirect effects of climate warming now play an increasingly important role. The marked increase in winter ROS events (Peeters et al. 2019), which lead to the frequent encasement of plants in ice, limits Svalbard reindeer population abundance through negative density-dependent effects on body mass, survival and reproduction (Hansen et al. 2011; Hansen, Pedersen et al. 2019). In the mid-1990s, an extreme ROS event on Brøggerhalvøya was a major contributor to the largest known Svalbard reindeer population crash on Svalbard, with the population declining from 360 to 78 individuals (Aanes et al. 2000; Kohler & Aanes 2004). The effects of forage suppression, amplified by an over-abundance of reindeer, also triggered a substantial dispersal event, most likely across sea ice, and the subsequent establishment of new populations on coastal plains south of Brøggerhalvøya (Aanes et al. 2000). ROS events have also led to increased reliance on marine food resources (e.g., marine kelp and seaweed [Hansen & Aanes 2012; Hansen, Pedersen et al. 2019]) and the use of steep mountainous grazing grounds (Hansen et al. 2009; Pedersen et al. 2021). Svalbard reindeer movements have recently been severely restricted by a lack of fjord ice during winter, which can limit gene flow and contribute to further genetic differentiation among coastal subpopulations (Peeters et al. 2020). More indirectly, climate change is also altering the food resource base for herbivores in the tundra ecosystem, through its effects on primary production, plant biomass, community composition, phenology and nutrient availability (Box et al. 2019).

Recent modeling of the barnacle goose population at Ny-Ålesund, based on extensive capture–mark–recapture studies initiated in the 1990s, has demonstrated a clear impact of climate warming on several reproductive parameters (Fjelldal et al. 2020; Layton-Matthews et al. 2020). For instance, earlier onset of breeding has been observed (Lameris et al. 2019), and an increasingly earlier spring onset has led to enhanced egg production (Layton-Matthews et al. 2020) and a younger age at first reproduction (Fjelldal et al. 2020). This is most likely due to earlier access to forage plants and snow-free nesting sites. Higher summer temperatures also appear to increase hatching success (Layton-Matthews et al. 2020). However, although these climate-driven changes in important life history traits may have cumulative impacts on population trajectories and might even have evolutionary consequences, density-dependent mechanisms in temperate wintering grounds suppress overwinter survival, which, along with predation of goslings by Arctic foxes and polar bears, restricts population growth (Layton-Matthews et al. 2019; Layton-Matthews et al. 2020).

The impact of climate change on Arctic foxes is predicted to be mediated through mostly indirect pathways (Ims et al. 2013). Lack of sea ice has a negative impact on fox populations by restricting both migration and exploitation of marine resources in winter (Prestrud 1992; Fuglei & Tarroux 2019). The abundance of two key terrestrial food resources, geese and Svalbard reindeer (in the form of carcasses), along with marine subsidies, also determines fluctuations in local Arctic fox reproduction and abundance, which follow reindeer population dynamics (Fuglei et al. 2003; Hansen et al. 2013). This, in turn, may lead to higher predation rates on ground-breeding birds, which reduces the population growth rate of, for instance, barnacle goose (Loonen et al. 1998; Layton-Matthews et al. 2020). These lines of evidence indicate that fluctuations in the overwintering vertebrate community are largely driven by winter climate change and ROS events (Hansen et al. 2013), which may cascade through the terrestrial food web, with impacts on migratory geese and plant communities.

Impacts on freshwater systems

Very few studies have addressed the impacts of climate change on freshwater ecosystems at Ny-Ålesund. At the ecosystem level, Jiang et al. (2011) demonstrated climate change impacts on both contemporary and historical time scales. Their study indicated that recent climate warming has increased nutrient inputs to lakes, which, together with reduced ice cover, has increased primary production and altered diatom communities. Moreover, keystone species, such as the Arctic tadpole shrimp, appear to be responding to the changing climate. A recent study showed a significant effect of water temperature on the hatching of this species, with no hatching occurring at elevated temperatures, suggesting that climate change may impact the life cycle of this species (Pasquali et al. 2019), with potential implications for the freshwater food web. Furthermore, glacial retreat is thought to induce strong changes in environmental conditions downstream (Milner et al. 2017), with impacts on biodiversity (Jacobsen et al. 2012) and ecosystem functioning (Brown et al. 2018). Although this has not been addressed directly in the Ny-Ålesund area, the study of Lods-Crozet et al. (2007) nevertheless suggests that reduced glacial impact is also likely to affect lotic communities. As known from temperate regions, increased temperatures in Arctic freshwater systems may be associated with increased cyanobacterial biomass (Przytulska et al. 2017), which can produce toxins (Kleinteich et al. 2013; Trout-Haney et al. 2016). Such impacts could be accelerated by synergistic effects of climate change and waterfowl-mediated eutrophication of Arctic freshwaters. Furthermore, permafrost thaw may result in increased loadings of C and nutrients to Arctic freshwaters, increasing their C content and productivity (Vonk et al. 2015). This may affect microbial activity and C-sequestration in the freshwater environment (e.g., Mindl et al. 2007), but may also impact higher trophic levels (Chin et al. 2016; Roberts et al. 2017), although no such studies have been carried out at Ny-Ålesund. A major impact of climate change on freshwaters is its influence on ice dynamics,

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specifically the change in the timing of ice cover, ice thickness and amount of snow/rain on ice. For example, changes to the timing of ice formation and break-up can have large implications for community phenology, such as the length of the growing season and the timings of insect emergence and fish migration and reproduction (Hampton et al. 2017). Although we know of no specific studies of the subject from Svalbard, in Greenland lakes, higher water temperatures linked to earlier ice break-up are associated with a higher biomass of phytoplankton and abundances of copepods and *Daphnia*. However, the abundance of rotifers is lower in years with earlier ice-off (Christoffersen et al. 2008). In general, more local and site-specific studies are required to allow robust interpretations of climate change impacts on freshwater systems in Ny-Ålesund.

Future perspectives

As is evident from the previous section, many components of terrestrial and freshwater ecosystems close to Ny-Ålesund have already been affected by climate change. However, there remains a lack of mechanistic understanding of linkages and patterns in the food webs of these ecosystems (Ims & Yoccoz 2017; Schmidt et al. 2017; Gillespie, Alfredsson, Barrio, Bowden, Convey, Culler et al. 2020). In this section, we highlight potential topics for future research using long-term monitoring approaches, which align with international calls for ecosystem-based monitoring in the Arctic (Ims & Yoccoz 2017; Christensen et al. 2020). While many separate ecosystem components have been studied and monitored in Ny-Ålesund over the past five decades, they have hitherto not been combined in a holistic, integrated, ecosystem-based monitoring effort. Individual research projects have often been short-term and/or taxon specific, with limited focus on how different trophic levels are interlinked or potentially differentially impacted by climate change. We strongly recommend that the international research community working at Ny-Ålesund more effectively harmonizes its studies to achieve a fully integrated ecosystem monitoring effort, building on currently available data sets and time series (Supplementary Table S1).

Above-ground terrestrial interactions and processes

Understanding the resilience of terrestrial ecosystems to environmental change requires integration across all biological scales (individual, species, population, community and ecosystem) and the availability of appropriate data at the relevant resolution on the drivers of change. Seasonality in resource availability may be altered, highlighting the need for whole season and year-round studies (CAFF 2013) and the study of, for instance, phenological mismatches (Gillespie et al. 2016; Henden et al. 2017). Despite our growing understanding of the impacts of climate change on many components of High-Arctic food webs, the impacts of nutrient dynamics and availability and their associated consequences for vertebrates remain poorly understood. Basic knowledge of the trace mineral contents of plant tissues, and the drivers and processes that control their availability and utilization, is limited, as is our knowledge of how climate change might affect nutrient dynamics and consequently the availability of elements critical to above- and below-ground biota (but see Oster et al. 2018). Changes in habitat or resource availability may influence interspecific competition, which is rarely studied in natural systems. The Ny-Ålesund region, with its many long-term data sets, provides a natural system for addressing these issues (Ims et al. 2013). Owing to their close proximities, it is also especially well suited to studying the multiple interactions among glacial, terrestrial, freshwater and marine ecosystems.

In order to facilitate improved model development and prediction of ecological consequences of changes in food web interactions and ecosystem dynamics, it is vital that environmental variability is studied at appropriate temporal and spatial scales (see Convey et al. [2018] for an example), as suggested by the adaptive ecosystem-based monitoring approach (Ims & Yoccoz 2017). Many of the topics outlined in this synthesis require long-term time series spanning different environmental and ecological gradients. Some of the longest time series available in the Arctic originated from the Ny-Ålesund area, although, as emphasized here, some key ecosystem components, such as invertebrates, have yet to be included in long-term monitoring programmes (see also below). A recent review identified five micro-arthropod functional groups, namely pollinators, decomposers, herbivores, predators and parasites (Gillespie, Alfredsson, Barrio, Bowden, Convey, Culler et al. 2020), as focal ecosystem components that should be addressed in long-term monitoring programmes. Thus, by harmonizing sampling design, methods and classification criteria, research at Ny-Ålesund provides unique opportunities to answer questions using state-of-the-art food web and/or ecosystem-based models (Ims et al. 2013; Ims & Yoccoz 2017). However, given the rapidity of climate change on Brøggerhalvøya, these model frameworks may only have the ability to predict responses in the near future (Dietze et al. 2018).

Below-ground terrestrial interactions and processes

Knowledge of the biodiversity and distribution of below-ground ecosystem components in the Ny-Ålesund area is currently limited, as is our understanding of the effects of the changing climate on soil microbial communities. Microbes are pivotal to the functioning of terrestrial and freshwater ecosystems through their effects on decomposition, nutrient cycling, primary production and the release of greenhouse gases to the atmosphere, yet field experiments into the effects of warming and water availability on microbial diversity and function on the Brøggerhalvøya are sparse (Supplementary Table S1). To fully and accurately predict the responses of terrestrial and freshwater ecosystems to environmental change, the physiological responses of microbes to rising temperatures need to be assessed, as do the responses of the soil microbial community to altered water availability. Moreover, energy and C flows between above- and below-ground food webs, which are closely linked and fundamental to many Arctic ecosystems, should be a focus for future research, as should the processes and climatic drivers that influence decomposition and the release of greenhouse gases to the atmosphere by the microbial community (Tveit et al. 2015; Lim et al. 2018; Rainer et al. 2020).

Freshwater interactions and processes

This review has highlighted that, other than in glacial habitats (Hodson et al. 2005; Hodson et al. 2010), there has been a shortage of studies in freshwater ecosystems close to Ny-Ålesund (e.g., Lods-Crozet et al. 2007; Walseng et al. 2018), reflecting the paucity of freshwater monitoring activities across the Arctic (Culp et al. 2012). We strongly recommend an increased focus on freshwaters and the potential impacts of climate change on these systems. At present, predictions have to be inferred from research in other, often ecologically divergent, Arctic sites. Enhancement of integrated ecological and physico-chemical monitoring programmes (e.g., Doveri et al. 2019), including the measurement of freshwater discharge from glaciers to the sea, is key to understanding the interactions of freshwaters with, and their impacts on, terrestrial and marine ecosystems. Research focus is also required on the presence and behavior of groundwater and its interaction with surface waters, as well as its role in tundra. The use of palaeolimnological approaches to reconstruct long-term changes in freshwater environments in the Ny-Ålesund area also needs to be expanded (Jiang et al. 2011).

Integrating data across trophic levels and ecosystems

The proximity of terrestrial, marine, glacial and freshwater ecosystems to Ny-Ålesund makes the region suitable for studies focusing on interactions within and between ecosystems, although at present such studies are almost entirely lacking. A centrally important requirement, both for Ny-Ålesund and for the Arctic in general, is to integrate long-term monitoring studies, particularly addressing terrestrial and freshwater invertebrates (Gillespie, Alfredsson, Barrio, Bowden, Convey, Coulsen et al. 2020; Gillespie, Alfredsson, Barrio, Bowden, Convey, Culler et al. 2020), trophic cascades, soil-associated microbial communities and biogeochemical cycling, with field manipulations to identify potential responses to future climate change (but see Layton-Matthews 2020; Supplementary Table S1). Currently, few studies integrate across different groups of organisms or, for instance, identify changes in the dynamics of key species and trophic cascades, and the subsequent effects on ecosystems. Even less attention has been given to cross-ecosystem interactions, such as the flows of C, nutrients and pollutants among marine, glacial, terrestrial and freshwater ecosystems, key priorities that are also recognized in the Svalbard marine flagship programme (Bischof et al. 2019).

Concluding remarks

Its long history of environmental research, large international research community and focus on cooperation and coordination make the Ny-Ålesund Research Station uniquely suited to develop further key monitoring and research activities. Addressing the scientific knowledge gaps and research priorities identified in this comprehensive review, which are based on more than five decades of research, will make a fundamental contribution to achieving the overall goals of the Ny-Ålesund Research Strategy (Research Council of Norway 2019). Specifically, we further recommend developing current monitoring efforts at Ny-Ålesund to become fully ecosystem-based, and to integrate the monitoring of microbial, invertebrate and freshwater communities. We further recommend gaining an understanding of the effects of environmental change on food webs, identifying trophic cascades within and across ecosystems, and measuring C and nutrient fluxes between soils, atmosphere, freshwaters and the marine environment. These goals require the multidisciplinary research approaches that characterize the four Ny-Ålesund flagship programmes (Gabrielsen et al. 2009; Coulson et al. 2010; Neuber et al. 2011; Svalbard Science Forum 2012) and the adaptive ecosystem-based ecological monitoring approach of the Climate-ecological Observatory for Arctic Tundra (Ims et al. 2013; Ims & Yoccoz 2017; Mellard et al. 2021). By focusing on these research needs, the international research community at Ny-Ålesund will provide globally relevant contributions to understanding the functioning of, and changes to, High-Arctic terrestrial and freshwater ecosystems, and their linkages with climate, glacial habitats and marine ecosystems.

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Note: the references below include sources cited in the supplementary file that are not cited in the main article. The reference library (compiled by Silje Marie Kristiansen, Ingrid M.G. Paulsen and Åshild Ønvik Pedersen) can be downloaded in EndNote format as a supplementary file.

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