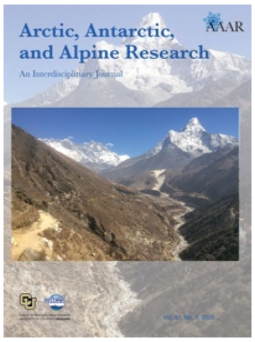

Arctic, Antarctic, and Alpine Research
An Interdisciplinary Journal

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/uaar20

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To cite this article: Martha K. Raynolds, Helga Bültmann, Shawnee A. Kasanke, Gifford Miller & Jonathan H. Raberg (2025) Recurring cycles of ice and vegetation on Baffin Island, Nunavut, Arctic, Antarctic, and Alpine Research, 57:1, 2442776, DOI: 10.1080/15230430.2024.2442776

To link to this article: https://doi.org/10.1080/15230430.2024.2442776

ARCTIC, ANTARCTIC, AND ALPINE RESEARCH
2025, VOL. 57, NO. 1, 2442776
https://doi.org/10.1080/15230430.2024.2442776

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Recurring cycles of ice and vegetation on Baffin Island, Nunavut

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ABSTRACT

Vegetation has recolonized the Arctic numerous times throughout the Holocene. The most recent retreat of glaciers on Baffin Island, Nunavut, has been since the Little Ice Age, due to anthropogenic warming. Retreating cold-based ice often uncovers ancient vegetation. Recently exposed plants can tell us about past plant communities and colonization rates, important information for parameterizing vegetation feedback in climate models. Here, we provide complete descriptions of vegetation communities recently exposed by two retreating ice caps on Baffin Island and compare them with modern vegetation in the surrounding areas. We found that the ancient vegetation was similar to current vegetation, meaning that the current vegetation had not significantly changed during the past several hundred years. Colonization of bare ground was evident and differed depending on the substrate (rock versus finer substrates), with saxicolous lichens colonizing rocks and acrocarpous mosses and liverworts colonizing areas with finer substrates. The mature communities differed at the two sites, mostly because of a warmer climate at the southern site. Vegetation colonization, especially of light-colored rocks, reduces albedo, but the process can take hundreds of years. Changes in plant community composition are likely to continue for thousands of years due to climate change and the arrival of new species.

ARTICLE HISTORY
Received 17 June 2024
Revised 8 October 2024
Accepted 18 November 2024

KEYWORDS
Arctic; Baffin Island; Nunavut; vegetation; colonization; succession; glacial retreat

Introduction

The Arctic is warming much faster than the rest of the globe (Arctic Monitoring and Assessment Programme 2021), causing increased melting of Arctic glaciers and ice caps. As the ice retreats, extensive areas that were previously buried under ice are exposed (Andrews, Davis, and Wright 1976; Locke and Locke 1977). Where glaciers were cold-based and nonerosive, ice retreat can expose ancient plant communities killed by past ice advances. It is important to understand the cycle of vegetation colonization, ice burial, re-exposure, and recolonization, because Arctic vegetation feedbacks are critical components of climate models (Pearson et al. 2013). Recolonizing vegetation also has ecological effects such as soil development and stabilization, habitat formation, and alteration of hydrological and microclimatic factors. Understanding how quickly vegetation reestablishes, and the timelines for different lifeforms in different situations, will help predict the effects of retreating glacial ice in the Arctic and improve climate models.

Baffin Island is an area that has been repeatedly glaciated during the Pleistocene (Dyke et al. 2002). At glacial maxima it was completely covered by the Laurentide Ice Sheet. Between glacial periods, it has deglaciated to various extents (Miller et al. 2022). Baffin Island's cold climate and proximity to the ocean as a water source mean that snow accumulation is extremely sensitive to temperature variations and to changes in ocean and atmospheric circulation (Margreth et al. 2014). If summers are just a few degrees cooler, winter snow accumulation does not melt during the summer and a glacial advance reestablishes (Miller et al. 2012). Feedback mechanisms, associated with both advancing and retreating ice, accelerate changes on Baffin Island (Miller et al. 2023).

Deglaciation of Baffin Island since the Last Glacial Maximum (~20,000 years ago) was interrupted by readvances around 12,000, 10,000, and 8,000 years ago (Dalton et al. 2020; Young et al. 2021). Summer cooling related to Earth's orbital irregularities starting ~10,000

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/15230430.2024.2442776

years ago led to local glacier expansion, especially in the last 2,000 years, the coldest summers of the Holocene. The maximum glacier coverage during the last 2,000 years occurred during the Little Ice Age, from 1250 to 1880 C.E. (Miller et al. 2005). At the peak of the Little Ice Age, 1780 to 1880 C.E. on Baffin Island, ice caps covered ~70 percent of northern Baffin Island (Ives 1962), including over 11,000 km^2 of north-central Baffin Island. Recent anthropogenic warming has been melting glaciers at all elevations, such that ice currently covers less than 100 km^2 of this same area (Miller et al. 2023). Approximately 12 percent of Baffin Island remains glaciated (Raynolds and Walker 2009).

Across Baffin Island, the maximum extent of the Little Ice Age glacial advance is often evident by the visual contrast between the vegetation in the areas that were recently deglaciated and adjacent surfaces that were unglaciated during the Little Ice Age. The landscape exposed when the ice cap retreats is a dark color because it is covered with dead vegetation. This vegetation soon erodes, leaving pale rocks with no vegetation in a ring around the ice cap (Figure 1). This pale band contrasts with the darker rocks covered with live lichens beyond this boundary, commonly called a “trim line.”

There have been many studies of vegetation recolonization after glacial retreat, from glacier forelands in the Alps going back to the early 1900s (e.g., von Klebelsberg 1913) to the present (e.g., Schumann, Gewolf, and Tackenberg 2016), from Scandinavia (e.g., Matthews and Whittaker 1987), from Glacier Bay, Alaska (e.g., W. S. Cooper 1923), in the Brooks Range of Alaska (e.g., Kasanke et al. 2023), in Svalbard (e.g., E. J. Cooper 2011), and elsewhere. These studies document the revegetation that occurs after erosive glaciers retreat, which leaves a reworked, barren mineral substrate that is recolonized by bryophytes, lichens, and vascular plants.

Figure 1. Photo of typical rocky landscape near ice caps on Baffin Island (near plots AFR 1–3). The retreating edge of the ice cap is in the foreground. The exposed dead, dark vegetation covering the rocks is shown in the middle. This dead vegetation dries and gets eroded by wind and water. The top of the photo shows the mostly bare pink granite that results once the vegetation is removed. Photo by S. Kasanke.

There are few vegetation colonization studies from the Canadian Arctic. Jones and Henry (2003) found that the Twin Glacier foreland in Alexandria Fjord, Ellesmere Island, was colonized by a successive series of plant communities, from mosses to vascular plants, and that the preservation of paleosols provided more favorable conditions for plant establishment and growth than bare mineral soils. Warmer areas of Alexandria Fjord supported successional communities, with species composition changing over time, whereas colder areas showed vegetation colonization and establishment, without succession (Jones and Henry 2003). In the Arctic, environmental constraints can slow down succession to the point where it proceeds on the timescale of millennia (Svoboda and Henry 1987; Kasanke et al. 2023).

In contrast to these studies of glacial forelands, this study focuses on areas that were not reworked by glaciers. Large parts of Baffin Island were covered by Little Ice Age ice caps in the late 1800s. These ice caps grew in place and were generally cold-based, frozen to their beds, and therefore mostly nonerosive. The landscapes revealed as they recede have not been reworked by moving ice, only by ice meltwater erosion and proglacial lakes, and are often covered by dead vegetation (Figure 1). These exposed landscapes have been noted in the literature on Baffin Island since the 1960s (Ives 1962) but have not yet been studied in detail.

The retreat of the cold-based ice in areas with gentle topography and minimal runoff, such as at divides between watersheds, allows the preservation of underlying vegetation that was frozen in place when the ice expanded during a previous cold period (Figure 1). On Ellesmere Island, in a warmer part of the Canadian Arctic, a dead prostrate dwarf shrub community was described emerging from a protected part of the Twin Glacier forelands (Bergsma, Svoboda, and Freedman 1984). Also on Ellesmere, the retreat of Teardrop Glacier in Sverdrup Pass exposed vegetation killed 400 years ago (La Farge, Williams, and England 2013). In less mountainous areas of Baffin Island, with finer, less rocky substrate, polygonal-patterned ground was noted emerging as ice receded (Falconer 1966). Exhumed mosses on Baffin Island have been sampled and dated to constrain the timing of various glacial advances (Anderson et al. 2008; Miller et al. 2023).

In this study we describe vegetation emerging from under ice caps in two areas of Baffin Island. We present a complete description of the vegetation communities that were killed and covered by ice and compare them with modern vegetation in the surrounding landscapes. This comparison identifies differences in both ancient and modern communities caused by variation in climate and allows some estimation of rates of colonization in these newly exposed areas. It also provides examples of the plant communities that would be expected to establish in these areas over time in some of the coldest parts of the Arctic, aiding predictions of changing vegetation structure in response to climate-induced changes.

Methods

This study describes the vegetation emerging from under the southeast edge of the Barnes Ice Cap (BRN site, 69.6° N, 71.8° W, 450 m asl), and at an ice cap in the mountains 35 km southeast of Mittimatalik (Pond Inlet) in northwestern Baffin Island (AFR site, 72.4° N, 77.4° W, 900 m asl; Figure 2). The two study sites were part of

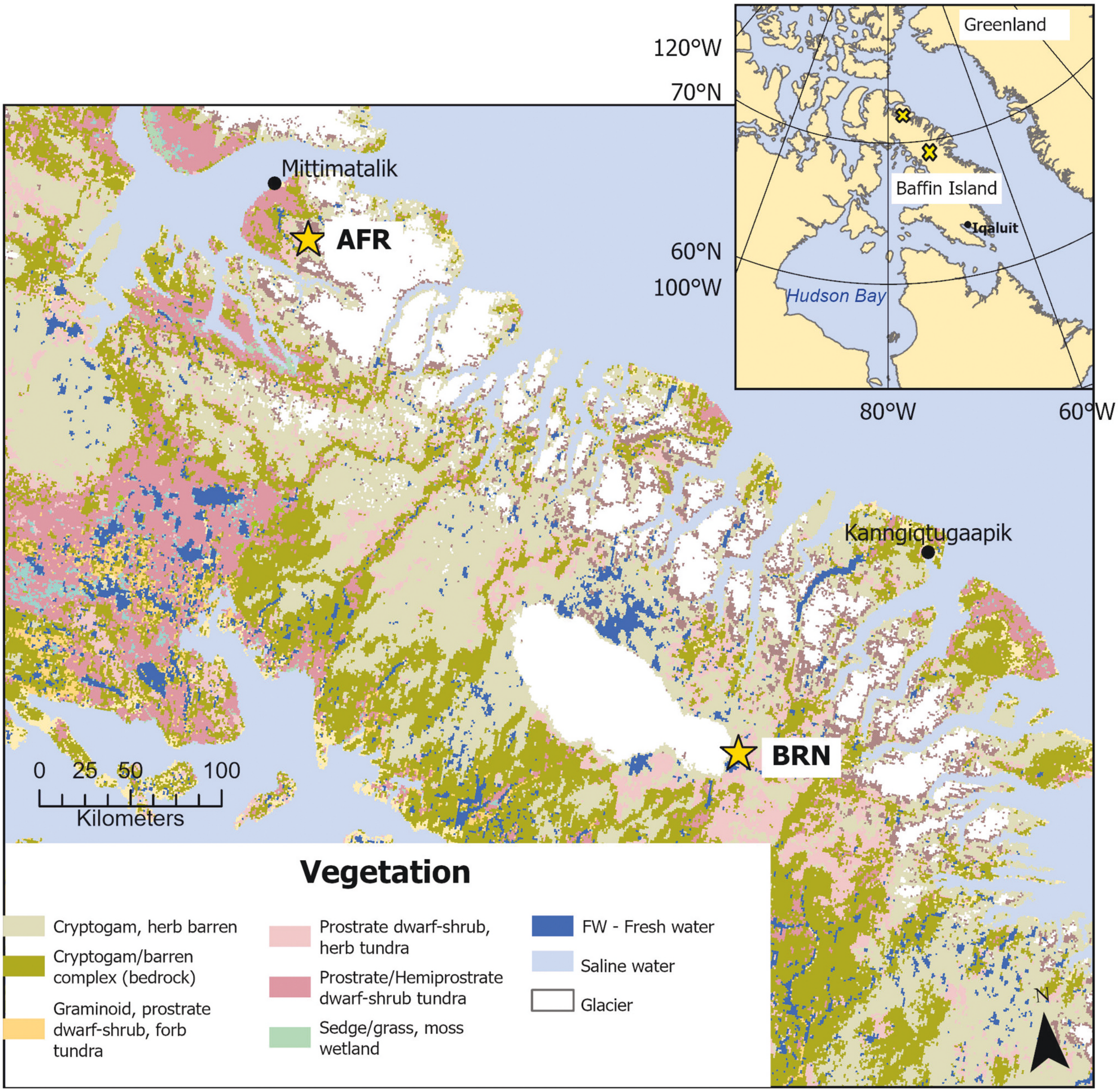

Figure 2. Map of Baffin Island showing the location of two study sites (stars) and closest communities, Mittimatalik (Pond Inlet) and Kanngiqtugaapik (Clyde River). Vegetation map from Raster CAVM (Raynolds et al. 2019).

a larger project examining past climate and vegetation in lake sediment cores at sites from treeline to the ice cap (PACEMAP, University of Colorado Boulder).

The BRN site is located near Generator Lake and the Barnes Ice Cap, the largest remnant of the Laurentide Ice Sheet (see Figure S1 for a map of all vegetation plots sampled at this site for the PACEMAP project). The site includes the Generator Lake airstrip area, which has been used as a base for studies of the Barnes Ice Cap since the 1960s. From this airstrip, we were able to sample the vegetation within walking distance and to sample near the Barnes Ice Cap by helicopter.

The AFR site was the northernmost and coldest site for the PACEMAP climate transect. The lake at this site emerged from under glacier ice around 100 years ago, and winter lake ice rarely melts completely in summer. The earliest Landsat imagery that shows this lake ice free was from 2001. The lake was ice-free in 2019 (sampling year) and 2020 but not since then, as shown by the August Landsat imagery record. The surrounding land area was snow-free in recent years for at least some of the very short summers. There are several ice caps within 2 km of the lake.

Modeled temperature data for approximately 6 × 10 km pixels that included our study sites show decadal means of annual temperature at both study sites rising over 2°C since the 1980s (Figure 3a; CanESM5 [CMIP6], SSP2-4.5, 50 percent probability, 0.0833° spatial resolution; Climatedata.ca 2023). The mean annual temperature for 2010 to 2019 was −15.5°C at the more northern, higher elevation AFR site and 4°C warmer, −11.5°C, at the more inland, more southerly, BRN site. Growing degree days, the sum of daily means >0°C, were also lower at the AFR site and have been increasing less rapidly than at the more continental BRN site (Figure 3b). The consistency of these differences in climate is demonstrated by the glacial equilibrium elevation, which are at lower elevations near AFR than BRN (Locke and Locke 1977). Annual precipitation is greater in southern Baffin Island, where the ocean is ice-free longer (361 mm at Iqaluit), compared to the north (195 mm at Mittimatalik; Environment Canada, 1990–2020 means).

Vegetation data from the AFR site were collected in August 2019 and 2023 and from the BRN site in

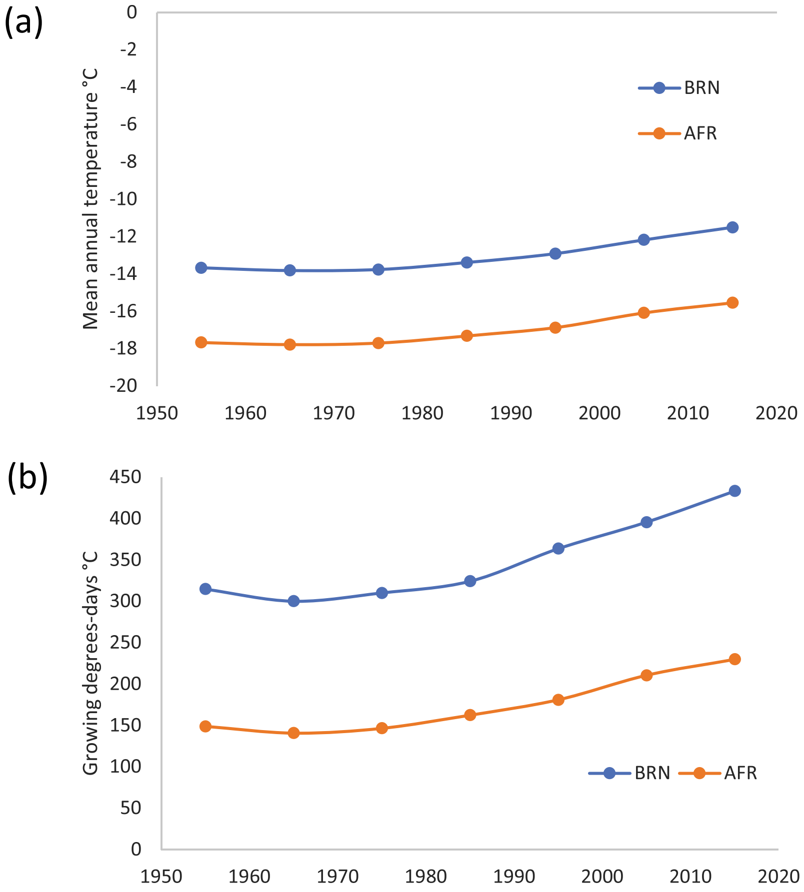

Figure 3. Modeled temperature data showing decadal means for two study sites on Baffin Island: (a) Annual mean temperature and (b) Growing degree days (sum of daily temperatures >0 °C). Data from ClimateData.ca.

August 2022. The newly uncovered vegetation at the edges of the ice caps and from older surrounding landscapes was described using the Braun-Blanquet method (Braun-Blanquet 1928). Plots (*relevés*) were subjectively chosen to best represent the vegetation at different locations near the ice edge. Well-vegetated, recently exposed locations were selected for sampling. Environmental data describing the plots, including elevation, slope, aspect, and other variables, were recorded and the plots were photographed (see Table A1 for full list of environmental variables and Figures A1–A22 for photos of all plots). Plots matching those at the ice edge, with similar environmental characteristics but with live vegetation, were selected from the set of plots sampled away from the ice edge. Within the 1 × 1 m plots, all taxa of lichens, bryophytes, and vascular plants were recorded, along with their cover values (percent). Taxa were identified to species in the field where possible and sampled and identified later if necessary. Voucher specimens were deposited with the National Herbarium of Canada. Nomenclature followed Esslinger (2021) for lichens, Leclerc (2014) for bryophytes, and the PanArctic Flora for vascular plants (Walker et al. 2016).

Plots of newly exposed vegetation were compared with plots from nearby areas that had not been buried by ice in the recent past. Shannon diversity index, species richness, Pielou's evenness, and Bray-Curtis dissimilarity were calculated in R, using the "vegan" package. Nonmetric multidimensional scaling (NMDS) ordination with Sorensen's distance measure was used to compare plot species composition as distributed in multidimensional space (McCune and Mefford 2018). A secondary matrix of environmental variables was used to investigate correlation with the ordination axes, based on Kendall's tau correlation coefficients.

Six plots were sampled at the edge of the Barnes Ice Cap (Table 1). BRN 14 to 16 documented vegetation colonization and formed a transect getting successively closer to the ice cap: 950, 425, and 350 m from the front of the Barnes Ice Cap. BRN 14 was on a hilltop beyond the Little Ice Age trim line; BRN 15 was close to, but just beyond the trim line; and BRN 16 was within the trim line (Figure 4).

In plots BRN 20, 21, and 22 vegetation was sampled at different spots along the margin of the ice cap that were 50, 10, and 2 m, respectively, from the 2022 location of the edge of the Barnes Ice Cap. These plots were compared with BRN 1 to 4, which were 10 km from the ice edge, far beyond the Little Ice Age trim line. They were selected to have similar substrate as the locations at the ice front, with some samples on rocky terrain and others on finer-grained sediments (Table 1, Figures A1–A10).

Moss samples (*Polytrichum* sp. or *Andraea* sp.) were collected along the ice margin and in a transect from the edge of the Barnes Ice Cap to beyond the trim line. Samples were prepared for radiocarbon dating at the University of Colorado Boulder and dated at the University of California, Irvine (Miller et al. 2023). Radiocarbon dates were calibrated using OxCal 4.2.4 and IntCal20 (Ramsey 2009; Reimer et al. 2020).

AFR 1, 2, and 3 were on rocky, fine-grained, and stony substrates, respectively (Table 1). They were matched in substrate with plots around the lake, AFR 12, 9, and 11, respectively. AFR 7 and AFR 23 to 27 were on older substrates, ranging from large boulders (AFR 7, 23, 27) to fine-grained/gravelly soil between boulders. Based on the size and cover of lichens. See Appendix A for photos of all plots.

Lichenometric measurements were made to estimate the ages of plant communities at both the BRN and the AFR sites. Measurements of *Rhizocarpon geographicum* thalli from the current margin of the Barnes Ice Cap and at the Generator Lake airstrip were used to estimate the duration of ice-free time, using growth rates according to Miller (1973). *R. geographicum* thalli at the AFR sites were too small to measure, so *Umbilicaria proboscidea* was used instead. The length of the longest axis of the thallus of the largest *U. proboscidea* individuals were measured in communities emerging from the AFR ice cap (AFR 1–3) and in live communities on older glacial moraines nearby (AFR 23–27). Age estimates for *U. proboscidea* were based on growth rates as defined by Calkin and Ellis (1984) from an alpine area in Alaska at similar elevation as the AFR site, using growth curves developed by others in Baffin Island, including samples from the Barnes Ice Cap, for calibration (Miller 1973; Haworth, Calkin, and Ellis 1986).

Results

Landscape ages at the Barnes site

Moss samples from a transect at the southeast front of the Barnes Ice Cap showed that plants currently emerging from the ice front were killed as long ago as 1,200 years B.P., based on ^{14}C dating (Figure 4). The vegetation kill dates decreased with increasing distance from the ice front, documenting the advance of the ice during Late Holocene cooling, with ice expanding over vegetation as recently as ~100 years ago (Figure 4 inset), and not retreating from the Little Ice Age maximum until 1960 in this area. The Little Ice Age on Baffin Island started about 800 years ago and ended around

Table 1. Most important environmental variables of plots sampled 2019 to 2023 at the BRN and AFR sites on Baffin Island.

Site	Plot	Latitude	Longitude	Emergence (years before sampling)	Date of vegetation death (years B.P.)	Elevation (m)	Slope (°)	Aspect (°)	Topographic position	Surficial geomorphology	Soil texture	Site moisture	Total cover live vegetation	Total cover dead vegetation
BRN	1	69.6066	−71.693	~4,000	N/A	490	3	10	Side slope	Stoney surface	Mixed-size rounded rocks, average 20 cm diameter	Subxeric	71	0
BRN	2	69.6056	−71.6972	~4,000	N/A	490	3	5	Side slope	Stoney surface	Coarse sand with gravel, between and over larger stones	Subxeric	68	0
BRN	3	69.6061	−71.7069	~4,000	N/A	490	2	20	Side slope	Stoney surface	Mixed size, somewhat rounded rocks, average 20 cm	Subxeric	59	0
BRN	4	69.6061	−71.7066	~4,000	N/A	490	1	20	Side slope	Stoney surface	Fine sand, some gravel and stones over rock	Subxeric	97	2
BRN	14	69.7045	−71.8349	1–2,000	N/A	670	0	none	Hill crest	Stoney surface	Coarse sand and gravel sorted out of rocks of all sizes	Xeric	71	0
BRN	15	69.6981	−71.8522	1–2,000	N/A	600	5	280	Side slope	Stoney surface	Sand and gravel sorted from average 20-cm-diameter rocks	Subxeric	60	0
BRN	16	69.7002	−71.8548	<40	N/A	600	3	300	Side slope	Sorted stripes	Sand and coarse gravel, ~40 cm over rocks	Subxeric	25	10
BRN	20	69.8323	−72.1356	1–2	110 ± 15	500	3	215	Footslope	Sorted stripes	Fibrous mat, on little sand/silt on rocks	Mesic	0	69
BRN	21	69.8318	−72.1267	1–2	110 ± 15	500	3	170	Side slope	Sorted stripes	Sand on rocks	Subxeric	10	60
BRN	22	69.7505	−71.8865	1–2	205 ± 20	550	1	90	Side slope	Flat-centered polygon	Sand on rocks	Moist	0	85
AFR	1	72.40442	−77.3992	1–2	~800	1000	20	30	Hill crest	Stoney surface	Mixed-size broken bedrock, ~10 cm diameter	Xeric	1	86
AFR	2	72.40357	−77.3995	1–2	~800	1000	0	none	Hill crest	Sorted stripes	Coarse sand and gravel sorted out of rocks of all sizes	Mesic	0	93
AFR	3	72.40368	−77.3994	1–2	~800	1000	0	none	Hill crest	Stoney surface	Broken bedrock to 40 cm size	Xeric	0	102
AFR	7	72.42123	−77.4603	~200	N/A	960	20	160	Hill crest	Stoney surface	Broken bedrock, 20 cm to 1 m	Xeric	72	0
AFR	9	72.42061	−77.4552	~100	N/A	950	5	220	Side slope	Sorted stripes	Coarse sand among 2-cm stones	Subxeric to mesic	63	0
AFR	11	72.4208	−77.4525	~100	N/A	940	3	160	Side slope	Sorted stripes	Stones (2 cm) and coarse gravel over sand	Subxeric	22	0
AFR	12	72.42128	−77.4493	~100	N/A	940	10	120	Side slope	Stoney surface	Medium to coarse sand, 4-cm stones	Xeric	4	0
AFR	23	72.42069	−77.4347	~200	N/A	960	5	210	Hill crest	Stoney surface	Broken bedrock, 20 cm to 1 m	Very xeric	83	1
AFR	24	72.42049	−77.4354	~200	N/A	950	1	210	Side slope	Featureless	Stones and coarse gravel over sand	Subxeric	90	1
AFR	25	72.42038	−77.4355	~200	N/A	950	1	210	Hill crest	Stoney surface	Broken bedrock to 40-cm size	Very xeric	63	0
AFR	26	72.42158	−77.4975	~200	N/A	970	1	210	Hill crest	Stoney surface	Stones, 10–40 cm	Xeric	101	1
AFR	27	72.42155	−77.4975	~200	N/A	970	0	none	Hill crest	Stoney surface	Mixed-size broken bedrock, ~40 cm average diameter	Very xeric	86	1

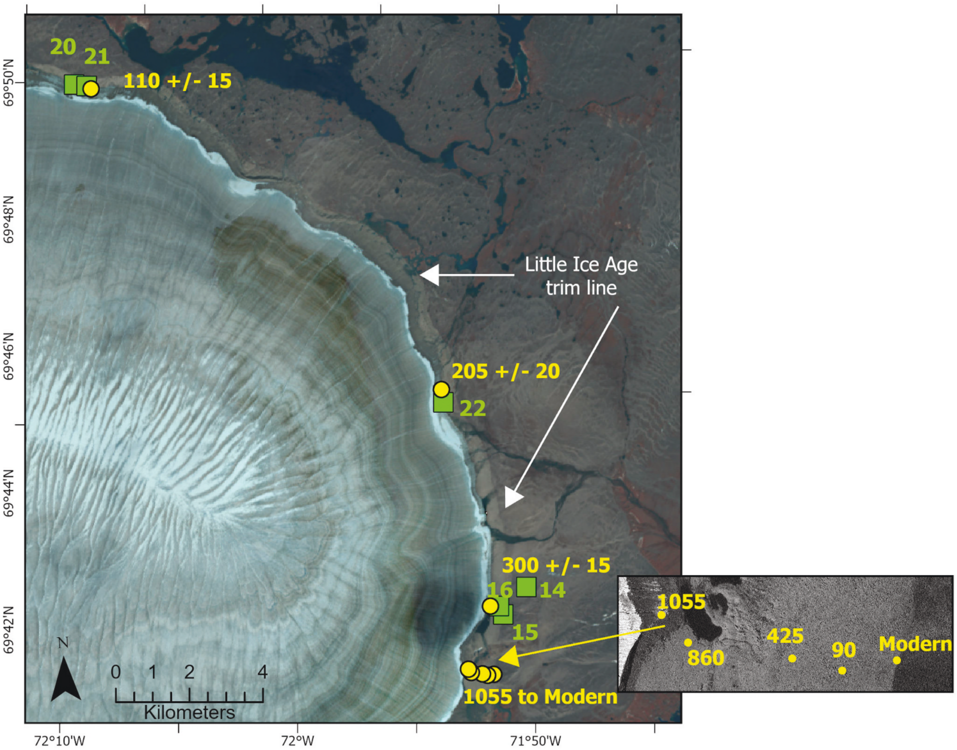

Figure 4. Location of plots (green squares) and dated samples of vegetation (yellow circles, ^{14}C dates ± SD) exposed by retreat of the Barnes Ice Cap. Landsat8 Level 2 imagery, 10 August 2022. Inset: Dates from moss samples collected along a transect, ranging from oldest closest to the ice and youngest farthest away, with modern-aged sample beyond the trim line (all ±15 years, imagery: WV01 22 August 2019, copyright Digital Globe). BRN 1 to 4 are off this image, 10 km to the east of the Barnes Ice Cap, near Generator Airstrip (see Figure S1).

150 years ago (Miller et al. 2023), but the geometry of the Barnes Ice Cap creates asymmetrical advances and retreats in different portions of the ice cap edge. The transect included one sample from beyond the Little Ice Age trim line (visible in Figures 4 and 5a), which was dated as contemporary ("modern"), meaning it incorporated carbon that matched current atmospheric ratios. Lichenometric measurements of the thallus diameter of *R. geographicum* in this area suggest that the vegetation beyond the trim line has been growing for over 2,000 years (G. Miller, pers. comm.).

The plots with emerging dead vegetation near the Barnes ice front (BRN 20–22) yielded ^{14}C dates of 110 ± 15 and 205 ± 20 years B.P. (Figure 4). These sites were buried during the most recent Little Ice Age expansion, and their vegetation was preserved under the ice for the 100 to 200 years since then. Based on Landsat imagery, they were under ice in 2020 and only emerged in the year they were sampled (2022).

BRN 14, the farthest from the ice cap, is the oldest of these plots but may be close to the same age as BRN 15, deglaciated 1,000 to 2,000 years ago. BRN 16, 350 m from the 2022 ice edge, was deglaciated <40 years ago, because it was under ice on 1985 Landsat imagery (Table 1). These plots were compared with plots near the Generator Lake airstrip, in an area deglaciated around 4,000 years ago based on cosmogenic dating of moraines (N. Young, pers. comm).

Landscape ages at the AFR site

The AFR site was originally deglaciated about 9,000 years ago (Dyke et al. 2002), and the lake was ice-free in summer until ~4,000 years ago. It then refroze, presumably due to colder summers and/or expansion of a nearby ice cap, based on radiocarbon dates in a sediment core recovered from the lake (Lake AFR; G. Miller, pers. comm.). Glaciers retreated again (Anderson et al. 2008), and around 1,000 years ago all of the AFR plots were ice-free (see ^{14}C dates below). Readvances during the Little Ice Age covered all the plots under ice once more. Ice retreat in the last several hundred years began on the ridges (see lichenometric dates below) and continued into the valleys. The lake ice has only started to melt out again in the past decades under contemporary global warming.

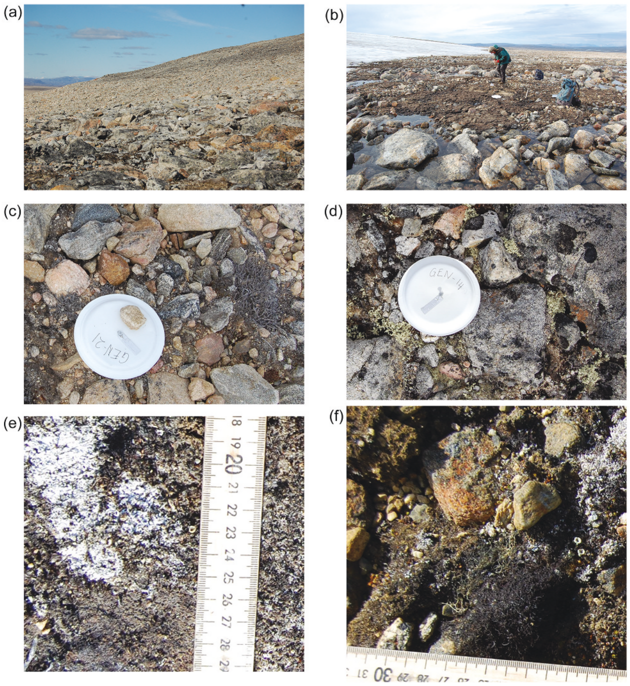

Figure 5. Photos from BRN site, central Baffin Island. (a) Darker, lichen-covered rocks beyond trim line shown in foreground and on upper hillside in background, with lighter rocks in midground within trim line. (b) Helga Bültmann sampling BRN 22, next to the Barnes Ice Cap, standing on dead cryptogamic mat. (c) Dead vegetation, including gray *Cassiope tetragona*, exposed from under ice (BRN 21). (d) Live vegetation just beyond trim line (BRN 14). (e) Close-up of dead vegetation on fine substrate, showing variety of identifiable lichen species (BRN 20). Note *Cladonia* cup at 23 cm. (f) Close-up of live vegetation on fine substrate (BRN 2). Note *Cladonia* cups on right. See Figure 4 for location of plots. Photo by M. Raynolds.

Most of the landscape is broken pink granite bedrock with very little vegetation. Some ridges are darker, with more lichen cover (Figure 6). That spectral contrast defines the distribution of deeper snow/ice that persisted through the summer in the valleys, slowing revegetation. AFR 1, 2, and 3 were sampled right next to an ice cap, in an area that was under ice in 2020, as documented by the WorldView imagery shown in Figure 6. ^{14}C dates from a nearby ice cap sampled in 2019 showed that the vegetation being exhumed from the ice in 2019 was killed 445 to 800 years ago, dating Little Ice Age advances (Figure 6).

Lichenometric measurements estimated the age of the plant communities emerging from under the ice at AFR 1, 2, 3 to be at least 174 ± 28 years and those of the nearby ridges to be at least 181 ± 8 years (AFR 23–27). *Rhizocarpon* thalli were too small to measure, indicating younger vegetation communities at time of burial relative to vegetation emerging from the Barnes Ice Cap. However, *Umbilicaria* lichenometry has also been shown to yield somewhat younger ages than *Rhizocarpon* lichenometry, suggesting that these are minimal age estimates of plant communities (Kasanke et al. 2023).

AFR 1, 2, and 3 were on rocky, fine-grained, and stony substrates, respectively (Table 1, Figure 7). They were matched in substrate with AFR 12, 9, and 11, respectively, around the lake. They emerged from under ice in the last 100 years and represent the dominant light-pink landscape. AFR 7 and 23 to 27 sampled the darker ridges around the lake (Figure 6). They were on older substrates that ranged from large boulders (AFR 7, 23, 27) to fine-grained/gravelly soil between boulders (AFR 24, 25, 26). Based on the size and cover of lichens, AFR 26 and 27, with the largest lichens, were likely the oldest. See Appendix A for photos of all plots.

Analysis of plant communities

We used NMDS ordination to compare the differences between plots based on plant species cover values and to explore the relationship to environmental factors. The NMDS ordination selected a three-dimensional solution, with a final stress of 9.60 and a final instability of 0.000 after sixty-nine iterations. The first axis correlated with plots with abundant exposed rock (Kendall's tau = −0.54) versus those with higher site moisture values (tau = 0.43) and less rock cover (Figure 8). The second axis separated plots from the two sites by elevation (tau = 0.63), latitude (tau = 0.46), and longitude (tau = −0.43). The third axis (not shown) was similar to axis 1, with the strongest correlation with cover of rock, along with cover of soil and height of vegetation. The species that correlated most strongly with axis 1 were saxicolous lichens, both the crustose lichen *R. geographicum* (tau = −0.63) and the foliose lichens *Umbilicaria torrefacta* (tau = −0.61) and *U. proboscidea* (tau = −0.55). Crustose saxicolous lichens were most strongly correlated with axis 2, including *Porpidia ochrolemma* (tau = 0.66). The third axis was correlated with a liverwort, *Gymnomitrion corallioides* (tau = 0.69), that grows on fine sediments and is a major component of cryptogamic mats.

Ordination of the species composition and cover data showed that there were two main types of plant communities. One was largely composed of saxicolous lichens growing on broken bedrock. This group of plots is on the left in Figure 8a, corresponding with increased cover of bare rock (red line indicating correlation with environmental factor). The other group growing on finer substrates such as gravel or sand, on the right side of Figure 8a, had greater moisture, was more stable, and had more soil cover. These plots were

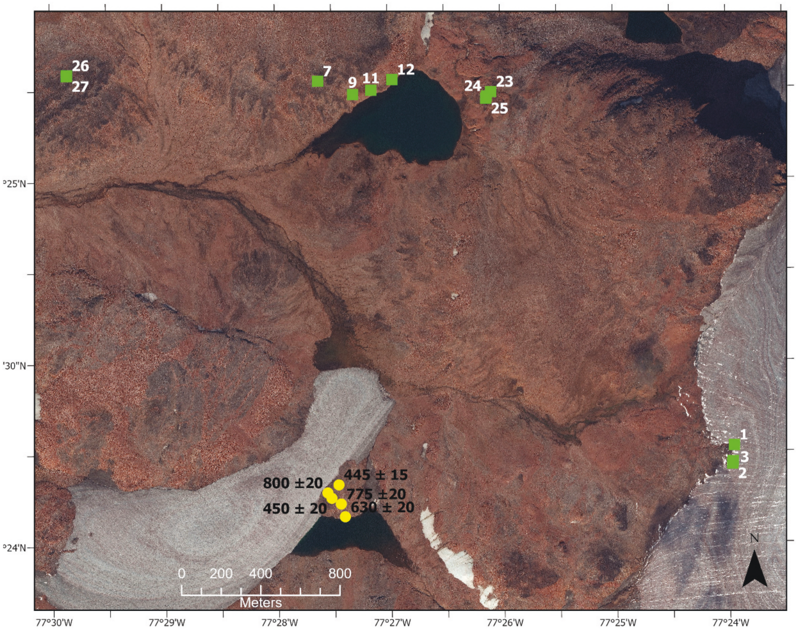

Figure 6. Location of plots (green squares) and dated samples of vegetation exposed by melting of ice caps (yellow circles, ^{14}C dates ± SD) at the AFR site in northwest Baffin Island. Lichenometric measurements were made at AFR 1–3 and 23–27. WorldView-3 imagery, 28 August 2020, copyright 2020 Digital Globe, Inc.

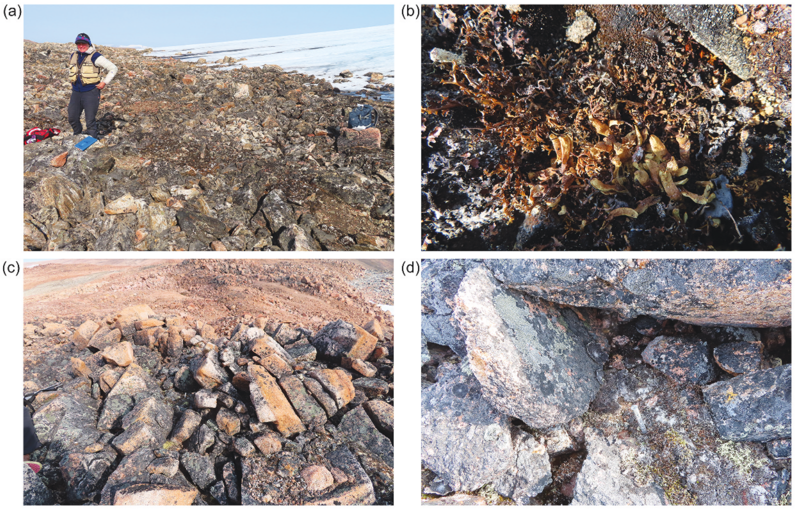

Figure 7. Photos from the AFR site, northern Baffin Island: (a) Shawnee Kasanke sampling AFR 2, on fine-grained soil adjacent to receding ice cap; (b) Same plot as in (a) (AFR 2), showing fruticose lichens with recognizable shapes and colors after being under ice for hundreds of years; (c) AFR 23, on broken bedrock. More recently exposed slopes, with less lichen cover can be seen lower down on the ridge; (d) Same plot as in (c) (AFR 23), showing live crustose and foliose lichens on rocks, and fruticose lichens between the rocks, especially in lower right. Photos by H. Bültmann.

dominated by mosses, liverworts, and terricolous lichens, with similar species at both sites and in both live and dead plant communities. Separate NMDS ordinations of plot data from each site independently (not shown) showed similar patterns separating plots by substrate.

The ordination also showed plots emerging from under the ice (orange in Figure 8) clustered in the same ordination space as mature plots from the surrounding area (shown in green), indicating the similarity of the old dead plant communities to the current live ones. Plots from the higher elevation, higher latitude AFR site were in the upper part of the ordination space, and plots from the warmer BRN site were in the lower part.

The comparison between the vegetation on the plots with dead vegetation that recently emerged from under

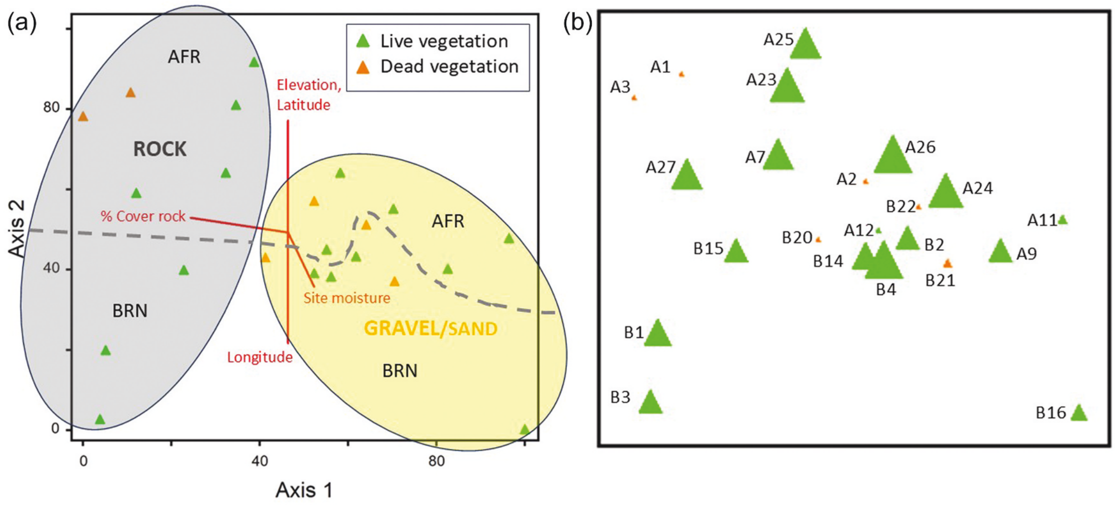

Figure 8. Ordination space showing the relationship between species composition of different plots (triangles). Those just emerging from under the ice are shown as orange triangles, others are green. (a) Strongest environmental drivers are shown in relation to ordination space with red lines. Dotted lines separate the AFR plots (upper) from the BRN plots (lower). (b) The same ordination space as in (a) but with the size of triangles proportional to live plant cover and plots labeled (B = BRN site, A = AFR site).

ice and paired plots on older substrates shows very similar total plant cover (Table 2). There was more variation in diversity measures, such as Shannon's diversity index, species richness (number of different taxa), and Pielou's evenness index. Some of the paired plots were very similar (AFR 2/24), but other pairs showed high Bray-Curtis dissimilarity (AFR 1/23 and AFR 3/26).

Sixty-one different taxa were identified in the dead vegetation emerging from under the ice at the BRN site (BRN 20–22) and sixty-six at the AFR site (AFR 1–3). See Tables A3 and A4 for complete cover data for all plots. There were no vascular plants found at these AFR plots (Table 3), though five vascular species were found in the area. In general, the BRN plots had greater cover of bryophytes than the AFR plots. There were four liverwort species in common between this set of plots from the two sites, nine acrocarpous mosses, seventeen crustose lichens, twenty-five fruticose lichens, and six foliose lichen species. The main difference in plant communities at AFR and BRN was an increase in diversity and cover of vascular plants and fruticose lichens at BRN, likely driven by the warmer climate resulting from lower latitude and elevation.

Succession in front of retreating ice caps

Plant cover was much greater beyond the Barnes Ice Cap trim line (BRN 14, 15) than within the trim line (BRN 16). BRN 16 was 50 m from the ice front and was covered by ice forty years ago. It had no recognizable old vegetation, though a patchy organic mat persisted from previous vegetation communities and was the substrate for most of the newly colonizing species. New, colonizing vegetation totaled 25 percent cover and was mostly *Psilopilum* sp. and other acrocarpous mosses (Table A3). Nearby plots beyond the trim line (BRN 14, 15) had 71 and 60 percent plant cover respectively, including 21/20 percent cover of bryophytes and 50/40 percent cover of lichens.

The plots that had just emerged from under ice had no colonizing species (BRN 20–22, AFR 1–3), but

Table 2. Comparison of diversity between paired plots of recently uncovered plots with dead vegetation versus nearby plots with live vegetation, matched for substrate and other environmental variables.

Plots	Total plant cover	Diversity index (Shannon)	Species richness	Pielou's evenness	Bray-Curtis dissimilarity
BRN 20/4	69/97	2.2/1.3	44/33	0.6/0.4	0.69
BRN 21/2	65/68	1.7/1.8	20/47	0.6/0.5	0.41
BRN 22/2	85/68	1.9/1.8	40/47	0.5/0.5	0.37
AFR 1/23	86/83	1.2/2.6	41/49	0.3/0.7	0.85
AFR 2/24	94/90	1.3/0.9	47/46	0.3/0.2	0.20
AFR 3/26	102/101	1.4/1.8	27/52	0.4/0.4	0.90

Table 3. Total cover, cover of lifeforms, and taxa with >5 percent cover in at least one plot of recently exposed dead vegetation at the BRN and AFR sites on Baffin Island.

	BRN			AFR		
Taxon	20	21	22	1	2	3
LUZNIV	10	—	—	—	—	—
Vascular total	14	2	0	0	0	0
GYMCOR	15	30	50	0.5	70	—
Liverwort total	15	30	51	1	70	0
ANDRUP	0.1	—	—	—	—	—
ANDRE	—	—	—	0.1	0.1	2
POGURN	0.1	0.1	—	—	0.1	0
POLHYP	—	0.5	—	—	—	—
POLPIL	0.1	0.1	0.1	0.1	—	—
PSILO/PSICAV	0.01	10	—	0.01	0.1	—
RACLAN	20	4	10	3	1	0.1
Moss total	21	15	13	3	2	2
ARCINC	—	—	—	0.1	—	—
CRUSTB	—	3	—	—	—	—
CRUSTGL	0.5	0.1	0.5	3	2	30
LECIDG	0.5	—	1	—	—	—
OCHFRI	5	5	2	1	2	0.1
POROCH	0.5	0.1	0.1	1	0.1	2
RHICIN	—	—	—	0.1	—	0.1
RHIGEO	7	1	0.8	3	2	50
RIM	—	—	0.1	—	—	—
Crustose lichen total	14	9	6	10	7	83
MELHEP	0.1	—	—	0.1	1	1
UMBPRO	0.5	—	0.1	2	3	10
UMBTOR	0.1	—	—	1	0.1	5
Foliose lichen total	1	0	2	5	7	16
ALEOCH	0.1	5	1	1	1	0.1
CETNIG	0.5	—	1	0.1	0.1	—
FLANIV	0.1	—	2	0.1	1	—
PSEMIN	0.1	—	—	0.1	0.1	0.1
PSEPUB	—	—	1	0.1	0.1	0.1
SPHFRA	—	—	1	65	0.1	—
STEARC	0.5	1	0.1	—	0.1	0.1
Fruticose lichen total	4	8	14	68	7	1
Total plant cover	69	65	85	86	94	102

See Table 2 for diversity indices for these plots, Table A2 for full species names, and Table A3 and A4 for all species' cover values.

recolonization began almost immediately. BRN 16, near the Barnes Ice Cap, had 25 percent cover of acrocarpous mosses (including 7 percent cover of one species, *Psilopilum* sp.) by the time it been exposed for <40 years. Plots exposed around 100 years ago at the AFR site were also colonized by acrocarpous mosses, though a different species of the same family (Polytrichaceae) was most common (*Pogonatum urnigerum*). Liverworts were important on non-rocky plots (AFR 9, 11), especially *Gymnomitrion corallioides*. Saxicolous lichens did not establish as early—they were not large enough to be visible at BRN 16 (<40 years)—and grow slowly—they had <2 percent cover at the younger AFR sites (~100 years). Lichens that were important colonizers included *R. geographicum*, *U. proboscidea*, and *Arctoparmelia incurva* (AFR 7, 23, 27). Areas exposed for on the order of 1,000 (BRN 14, 15) had many of these early colonizing species but also included more fruticose lichens (40–50 percent total lichen cover) and had 20 percent bryophyte cover. Areas that had been exposed for several thousand years (BRN 1–4) had higher cover values and higher species richness than younger areas. The increase over time in number of species and diversity was evident in the BRN transect (BRN 16, 15, 14). As age and distance from the ice cap increased, the number of plant species increased (10, 41, 40, respectively; see Table A3), as did diversity (1.56, 2.55, 2.97). The oldest rocky plots at the two sites averaged around 76 percent plant cover, with >69 percent cover of lichens. The oldest plots on finer substrates (BRN 2, 4; AFR 24, 26) had more cover, with much higher cover of bryophytes (average >65 percent) and lower cover of lichens (average <20 percent).

Discussion

Vegetation emerging from under ice caps degrades quickly when exposed to ambient conditions, due to erosion caused by wind, precipitation, freeze/thaw, and running water. Based on our experience, species are easiest to identify the same summer they first emerge, when color and textures are most distinct (e.g., Figure 7b). Dead foliose lichens on rocks, such as *Umbilicaria* spp., tend to dry and crumble after they emerge from under the ice. As we found on our transect from the Barnes Ice Cap to the Little Ice Age trim line, cover of dead plants decreases quickly with distance from the ice. Dead crustose lichens such as *Rhizocarpon* spp. exfoliated with successive freeze/thaw cycles. Dead fruticose lichens growing between rocks on finer substrates were eroded due to water runoff from precipitation and snowmelt. Bergsma, Svoboda, and Freedman (1984) also reported that plant remains were progressively more weathered with increasing distance from the ice and not suitable for sampling beyond 25 m. Dead saxicolous mosses such as *Grimmia* spp. were found clinging to protected parts of rocks even after all saxicolous lichens were eroded off the top surfaces. Similarly, dead acrocarpous mosses growing in tight clumps on cryptogamic crusts persisted longer than fruticose lichens.

On rocks emerging from under ice, saxicolous lichens last only a few years, and their loss quickly changes the color of the landscape from dark to light (Figure 9). Some persistent mosses may last for up to a decade or two but are not common enough to affect the overall color of the landscape. Thus, large areas of Baffin Island show the light coloration of recently deglaciated rocky substrates (Miller et al. 2023).

On finer substrates, the dead exhumed vegetation can last for a few years but is soon removed by erosion. Often a cryptogamic mat, composed of liverworts, algae, fungus, and cyanobacteria (Gold 1988), covers the gravel or sand substrate. The cryptogamic mat persists the longest, sometimes through glacial cycles, in protected areas (e.g., Figure 5b; Falconer 1966). This dark cryptogamic mat provides a superior surface for plant colonization, because it is warmer (Gold 1988), richer in nutrients (E. J. Cooper 2011), more stable, and less dry than the surrounding gravel or rock areas (Falconer 1966; Bliss and Gold 1999; Jones and Henry 2003). Bliss and Gold (1999) found almost ten times higher germination rates on cryptogamic crusts than on noncrusted areas, greater plant cover, and more seed production. This creates a positive feedback effect, ensuring that organic material continues to accumulate on the cryptogamic mats through each deglaciation cycle, providing a place where plant propagules can flourish and soil development can progress.

We found no evidence of regrowth from plants emerging from under the ice. However, La Farge, Williams, and England (2013) reported regrowth from some moss samples taken from emerging vegetation that had been buried for 150 to 450 years by Teardrop Glacier on Ellesmere Island. Though farther north in latitude than our study site, this area has a climate similar to our Barnes site, with a similar number of vascular species.

Once colonization begins, classic successional theory describes a series of plant communities, from initial pioneers to mature climax species. This directional replacement succession occurs in areas where plant competition is the main driving force in community development. In the Arctic, where physical constraints are usually more important than competition, directional nonreplacement or nondirectional nonreplacement are more common (Svoboda and

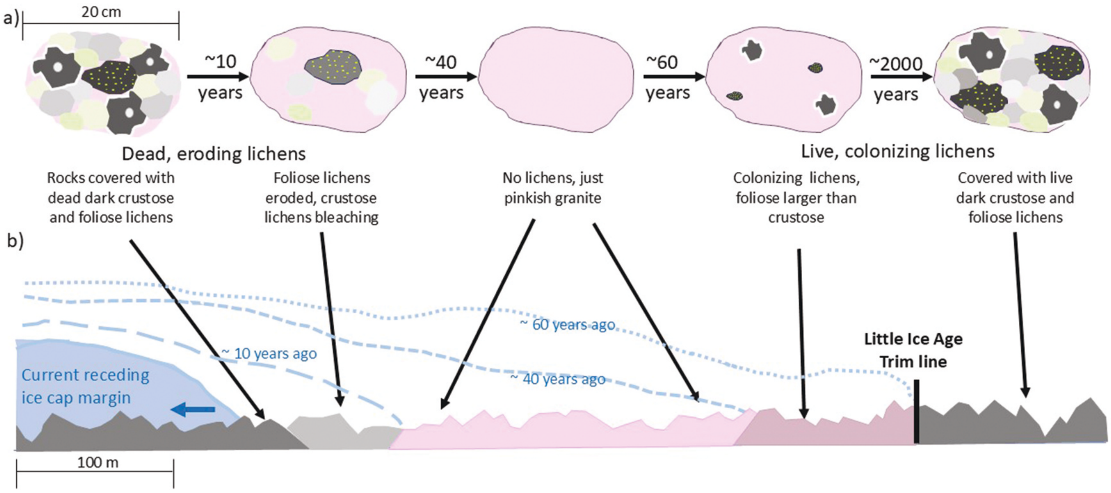

Figure 9. Conceptual diagram of the landscape next to a retreating ice cap. Dates match southeast edge of Barnes Ice Cap. (a) A typical broken bedrock cobble, showing progression from left to right over time, in loss of dead lichens and recolonization by live lichens. (b) The current landscape (note different scale from top figure), showing change in overall landscape color with distance from the ice cap margin. Blue area to the left shows current ice location, dotted lines show previous ice margins.

Henry 1987). In the former situation, colonizing plants gradually build up their populations but not to the exclusion of other species. In directional nonreplacement, which occurs only in the most extreme environments, species colonize but get stunted or killed by environmental factors, and their populations do not grow. Jones and Henry (2003) found both these situations adjacent to glaciers in Alexandria Fjord, Ellesmere Island. A similar lack of species turnover and persistence of colonizing species, especially on rocks, for over 10,000 years was found in the Brooks Range of Alaska (Kasanke et al. 2023).

Neither of our Baffin study sites showed classic succession caused by directional species replacement from initial colonizing species to mature climax species. Rather, our sites showed directional nonreplacement, with changes over time from colonization to mature communities with close to 100 percent plant cover that still included the original colonizing species. One exception was the common colonizing moss on fine-grained substrates at the BRN site, *Psilopilum* sp., which was much less common in older communities.

Early lichen colonizers on rock were similar at both sites, and these species persisted in communities on rocks that are thousands of years old (this study and Kasanke et al. 2023). Early colonizers on finer soil were more variable and are more dependent on plant propagule availability (this study and Kasanke et al. 2023). During initial colonization, the presence of plant propagules can be severely limiting in a relatively isolated, high elevation area such as AFR. In contrast, the BRN site has extensive land areas to the south with relatively flat topography. Plant propagules are much more likely to be carried by wind and birds to BRN than through the mountainous fjord area surrounding the AFR site. Many bryophytes and lichen species have very small spores that can be carried by the wind over long distances even thousands of kilometers (Longton 1988), so it is not surprising that the colonization is driven by cryptogams. Also, cryptogam spores and propagules can remain dormant for longer periods of time, giving them an advantage over less robust seeds when conditions allow for germination (La Farge, Williams, and England 2013). And there is also the potential for totipotency—regrowth from nonreproductive cells. La Farge, Williams, and England (2013) found that slurried moss stems from mosses collected from under the glacier, such as *Aulacomnium turgidum* and *Distichium capillaceum*, would grow in Petri dishes.

Once plant propagules arrive at a site, germination and survival are limited by environmental factors. It has long been documented that plant colonization depends on the climate of the area surrounding glacial forelands, with faster and more species-rich succession occurring on glaciers that reach to forested areas (von Klebelsberg 1913). Succession at Glacier Bay, at sea level at 59° N, has been documented to go from bare rock to forest in 100 years (W. S. Cooper 1923). Recolonizing vegetation also has ecological effects such as soil development and stabilization, habitat formation, and alteration of hydrological and microclimatic factors (Fastie 1995), which occur more rapidly at warmer sites.

Not only does a cold climate limit seed germination and plant viability but the limited amount of summer warmth, as summarized by degree days above zero, is directly related to the amount of time available for succession (Svoboda and Henry 1987). Establishing a plant population requires propagule arrival, their germination, seedling establishment, time for reaching maturity, population growth, and species proliferation, all of which have to occur during very short Arctic summers. At our coldest site, AFR, the summer temperature away from the ice front was not that much warmer than 0°C, and growing degree days were less than half those at BRN. AFR is in Bioclimate Subzone A, the coldest in the Arctic, with only five vascular plants found in the area. BRN, at 2.7° lower latitude and 500 m less elevation, is in Bioclimate Subzone C, with over forty-five species of vascular plants once you get away from the Barnes Ice Cap, including a low shrub (*Salix glauca*). These differences in climate and substrate lead to different succession trajectories, with the greatest contrast in species composition between the oldest communities at each site.

Our results showed that the dead vegetation communities emerging from under ice were very similar to nearby live communities. This suggests that over the several hundred years that vegetation was buried under ice, nearby unburied communities did not change much. This conclusion is supported by results from Ellesmere, where 400-year-old exhumed vegetation had similar species composition as adjacent nonburied areas, though species dominance had changed, likely due to changes in moisture availability (Bergsma, Svoboda, and Freedman 1984). Repeat sampling in Svalbard also found little change over 30 years except in pioneer communities (Moreau, Laffly, and Brossard 2009) and only minor changes after 85 years and 100 years (Prach et al. 2010; Kapfer and Grytnes 2017).

The similarities between the buried and nonburied communities at our sites highlights how well adapted these high-Arctic species are to these locations. Ice caps on Baffin Island have advanced and retreated throughout the Quaternary. Similar vegetation communities have repeatedly colonized areas that emerged as ice receded. Despite the very different ages of the vegetation communities discussed here, from ones killed over a thousand years ago at the Barnes Ice Cap to current vegetation that has been growing on sites for several thousand years, the same major species were found. What this means for the future is that, given enough time, we would expect similar communities to reestablish themselves on these newly exposed northern Arctic sites.

However, recent colonization has taken place under the relatively cool conditions since the Little Ice Age. With ongoing climate change, vegetation communities are likely to change to resemble ones currently growing in warmer locations. One wonders how long it might take before vegetation at the AFR site resembles the current BRN site. Climate modeling shows the AFR site reaching the same mean annual temperature that the BRN site had in the 1950s by the 2030s and the same growing degree days by the 2050s (Figure 3; ClimateData.ca). Fickert, Grüninger, and Damm (2017) showed that vegetation colonization in the Alps is accelerated compared to 100 years ago due to a warmer climate. However, plant propagule availability is currently limited at the AFR site due to its geographically isolation. Even looking at a very large area—all of Scandinavia—colonization by new species continued for over 3,000 years after deglaciation (Alsos et al. 2022). The combination of limited plant propagules; the extended time period required for arctic colonization and growth (thousands of years); directional non-replacement succession, which is dependent on stochastic events; and the complex effects of past history on edaphic conditions (Schumann, Gewolf, and Tackenberg 2016) means that though AFR is likely to have complete plant cover within a few thousand years, it will probably have similar major species but not the same plant communities as BRN.

In terms of changes in albedo and the feedbacks to climate models, our study confirmed the importance of substrate in controlling plant communities, as also shown by Kasanke et al. (2023). Areas with fine substrate often have residual dark cryptogamic mats (Falconer 1966) and recolonize quickly with pioneer mosses and liverworts, keeping their albedo low. However, most of Baffin Island is rocky, especially at higher elevations around ice caps, so the colonization and growth of saxicolous lichens is the limiting factor in changing the dominant high-albedo, light-pink granite and other light-colored rocks to a vegetated, dark surface (Figure 9). Although it is generally accepted that many saxicolous lichen species colonize rocks quickly, it can take up to thirty years before they are even visible (Calkin and Ellis 1984). Even when well established, growth rates can be quite slow. One of the most common species, *R. geographicum*, a dark crustose lichen, has an initial radial growth rate of 0.1 mm/year (Haworth, Calkin, and Ellis 1986), slowing to 0.03 mm/year after about 200 years (Miller 1973). *Umbilicaria* spp., dark, foliose, saxicolous lichens, grow much more rapidly (~1.7 mm/year from 0 to 30 mm in diameter), slowing to approximately 0.21 mm/year after reaching approximately 60 mm in diameter (Calkin and Ellis 1984). *Umbilicaria* spp. also have shorter life spans of only around 500 years compared to *R. geographicum*, which can reach thousands of years of age (Haworth, Calkin, and Ellis 1986).

There are areas around ice caps on Baffin Island that have been ice-free since the earliest aerial imagery (1949) that still show as light rings compared to the areas beyond the Little Ice Age trimlines. This shows that it will require at least a century for ice-killed landscapes to revegetate to the point where they are spectrally similarly to non-ice-covered landscapes. In Svalbard, it took 1,000 to 1,500 years to establish climax vegetation communities on terminal moraines and about 3,000 years for beach ridges and salt marshes (Tishkov 1986). Alsos et al. (2022) found a break point in functional diversity ~2,000 years after deglaciation in Scandinavia, shifting from a state of ecosystem buildup to a state where most habitat types and biotic ecosystem components were in place. Truelove Lowland beaches on Devon Island, Nunavut, continued to show increases in plant community diversity from 2,000 to 9,000 years of age (Svoboda and Henry 1987). Changes in species composition were even found after 25,000 years on fine-grained substrates and up to 125,000 years on rocky substrates in the Alaska Brooks Range (Kasanke et al. 2023).

A circumpolar analysis of a satellite vegetation index (Normalized Difference Vegetation Index, NDVI) and landscape age confirmed this time frame, using space for time. An analysis of Arctic landscapes of different ages showed rapid increases in NDVI during the first several thousand years after deglaciation. After the initial rise in NDVI, values stayed relatively constant for areas deglaciated 2,000 to 20,000 years ago. This is the timescale at which paludification and peat accumulation occur. Peatland initiation generally occurred 1,000 to 2,000 years after deglaciation and peaked after 10,000 years (Gorham et al. 2007). Tens of thousands of years is the time frame required for soil development in the Arctic (Birkeland 1978). So despite rapidly changing climate, we can expect that Arctic vegetation communities will continue to change at a slower time frame, on the scale of thousands of years, rather than centuries or decades.

Conclusion

This study of vegetation emerging from under two ice caps on Baffin Island found that, if sampled within the first summer of exposure, detailed plant community composition data can be collected to characterize these ancient communities. The emerging vegetation, killed by Little Ice Age advances 100 to 800 years ago, was very similar to adjacent areas that had not been covered by ice. However, far older vegetation is likely entombed under the ice of the cold-based glaciers on Baffin Island, especially under the Barnes Ice Cap, which may prove to be different from current plant communities.

Our two sites had different climates, with fewer vascular plants found at the colder site. Younger plots at the two sites were more similar than older plots. Though species composition differed between the sites for the older plots, the species richness at the two sites was similar due to the diversity of bryophytes and lichens. Ordination results showed the importance of substrate (rock versus finer-grained) on plant community composition.

The timescale for vegetation change in the Arctic is very long. Light-colored rings from retreating Little Ice Age ice caps on Baffin Island persist since the earliest aerial photographs. Recolonization of rocks by dark lichens will change this spectral signature, but the process will take hundreds of years. Changes in species composition are expected to continue for thousands of years.

Acknowledgments

We acknowledge and thank the Inuit people who live on the lands where this research took place, especially the people of Kanngiqtugaapik (Clyde River) and Mittimatalik (Pond Inlet). Their gracious welcome and support facilitated this research. Thanks also to the Nunavut Research Institute and Polar Continental Shelf Project for logistical support.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Office of Polar Programs [#1737750, #1737712, #1927148, #1927153, #1928237].

Data availability

The *relevé* data are available from the authors. The complete set of *relevés* from the PACEMAP project will be submitted as part of the Arctic Vegetation Archive (www.geobotany.uaf.edu/ava/).

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