

CONSERVATION

Glacial ice supports a distinct and undocumented polar bear subpopulation persisting in late 21st-century sea-ice conditions

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Polar bears are susceptible to climate warming because of their dependence on sea ice, which is declining rapidly. We present the first evidence for a genetically distinct and functionally isolated group of polar bears in Southeast Greenland. These bears occupy sea-ice conditions resembling those projected for the High Arctic in the late 21st century, with an annual ice-free period that is >100 days longer than the estimated fasting threshold for the species. Whereas polar bears in most of the Arctic depend on annual sea ice to catch seals, Southeast Greenland bears have a year-round hunting platform in the form of freshwater glacial mélange. This suggests that marine-terminating glaciers, although of limited availability, may serve as previously unrecognized climate refugia. Conservation of Southeast Greenland polar bears, which meet criteria for recognition as the world's 20th polar bear subpopulation, is necessary to preserve the genetic diversity and evolutionary potential of the species.

The impact of human-mediated climate warming on biodiversity is a global conservation concern (1). Shifts in species phenology, distribution, and abundance are altering ecological communities and increasing extinction risk (2). Understanding how life history strategies affect species persistence, including the role of within-species diversity at multiple spatial scales, is critical for conservation (3, 4).

The ongoing and predicted decrease in Arctic sea ice (1) raises concerns for ice-dependent species such as polar bears (5), whose survival will depend on establishing populations in fragmented habitats and maintaining genetic connectivity among them (6). Recent forecasts of reduced polar bear distribution and abundance (7) are based on broad-scale climate projections and the estimated number of days that bears can fast without sea ice, which they require for hunting. These forecasts do not consider the role of small-scale habitat features

that, although of limited availability, could serve as climatic refugia. Here, we combine 36 years of movement, genetic, and demographic data to describe a genetically distinct and functionally isolated group of polar bears in Southeast Greenland. We use these data to explore the prospects for polar bear survival in a warmer, ice-free Arctic.

The East Greenland subpopulation, one of 19 recognized subpopulations of polar bears, occupies a marine area of ~700,000 km² along a mostly uninhabited ~3200-km coastline (8, 9). In 2011, we initiated a multiyear project to assess the status of East Greenland bears using movements, genetics, and demography (Fig. 1 and figs. S1 and S2). Intriguingly, satellite telemetry revealed that bears living south of 64°N, hereafter Southeast Greenland ($n = 27$ adult females, 2015–2021; table S1), did not interact with bears living north of 64°N, hereafter Northeast Greenland ($n = 56$ adult females, 1993–2021; Fig. 2A). Instead, female bears in Southeast Greenland made localized movements in fjords and at marine-terminating glacier fronts (Fig. 2B) with a median 4-day movement rate of 10 km (8.4 to 13.1 km, 25 and 75% quartiles; fig. S3). Some bears remained in one fjord for years, while others moved between adjacent fjords, traveling over mountains via the ice sheet and peripheral glaciers (fig. S4). In contrast, the median 4-day movement rate of female bears in Northeast Greenland was 40 km (30.0 to 49.0 km; fig. S3), with annual movements of >1500 km on the offshore sea ice. Recaptures of males indicated similar movement patterns (10). The degree of geographic isolation of Southeast Greenland bears distinguishes them from other subpopulations (11).

Current sea-ice conditions in Southeast Greenland, like those projected for the late 21st century in the High Arctic, appear unsuitable to support polar bears. Pack ice (freely floating sea ice) is intermittently flushed into fjords but is largely unusable owing to its low concentration and transience (Fig. 2C and figs. S5 to S10). Southeast Greenland bears use fast ice (sea ice frozen to the coastline) when it is available in winter and spring (figs. S11 to S15), but the number of days per year with fast-ice coverage is low and variable (between 0 and 153 days; mean: 89 days) (fig. S15 and table S2). Fast ice typically forms in February and disappears by late May, so the region is sea ice-free for more than 250 days per year, exceeding polar bears' estimated seasonal fasting threshold of 100 to 180 days (7). Our data show that Southeast Greenland bears use glacial mélange (freshwater ice at glacier fronts) as a platform for hunting during the sea ice-free season (Fig. 2, D and E), whereas in most parts of the Arctic, polar bears must move onto land or track the receding sea ice northward into the less productive polar basin (11).

Southeast Greenland bears appear to have adapted their movements to the region's specific physical geography. The high-velocity East Greenland Coastal Current (12) seasonally brings a narrow band of low-concentration pack ice south of 64°N and around the southern tip of Greenland (figs. S8 to S10) (13). All tracked Southeast Greenland bears that moved out of the fjords ($n = 11$) became caught in this current's drift ice and were transported southward toward Cape Farewell, drifting an average of 189 km in <2 weeks (fig. S4). Notably, all swam ashore and walked via land to their home fjord within 1 to 2 months, demonstrating high site fidelity. Bears in Southeast Greenland must remain inside fjords or risk export to human-inhabited areas of South Greenland or into the North Atlantic.

Southeast Greenland bears are the most genetically isolated polar bears in the Arctic (figs. S16 to S25 and tables S3 to S8). Principal components analyses showed a distinct Southeast Greenland cluster across 20 microsatellite loci isolated from 372 bears (Fig. 3A, fig. S16, and table S3), 40 whole genomes (Fig. 3B, fig. S21, and table S7), and whole-blood transcriptomic data from 16 bears (Fig. 3C and table S8) (10). In a Bayesian clustering analysis of 3064 bears from all subpopulations except the Arctic Basin, Southeast Greenland bears were distinct from all subpopulations across the species' circumpolar range when the model assumed four clusters (Fig. 3D and figs. S18 to S20) (10). Norwegian Bay bears, previously identified as the most distinct subpopulation (14–16), emerged at five clusters. Southeast Greenland bears also have the lowest levels of heterozygosity across microsatellites (table S4) and whole genomes (fig. S25), as well as the

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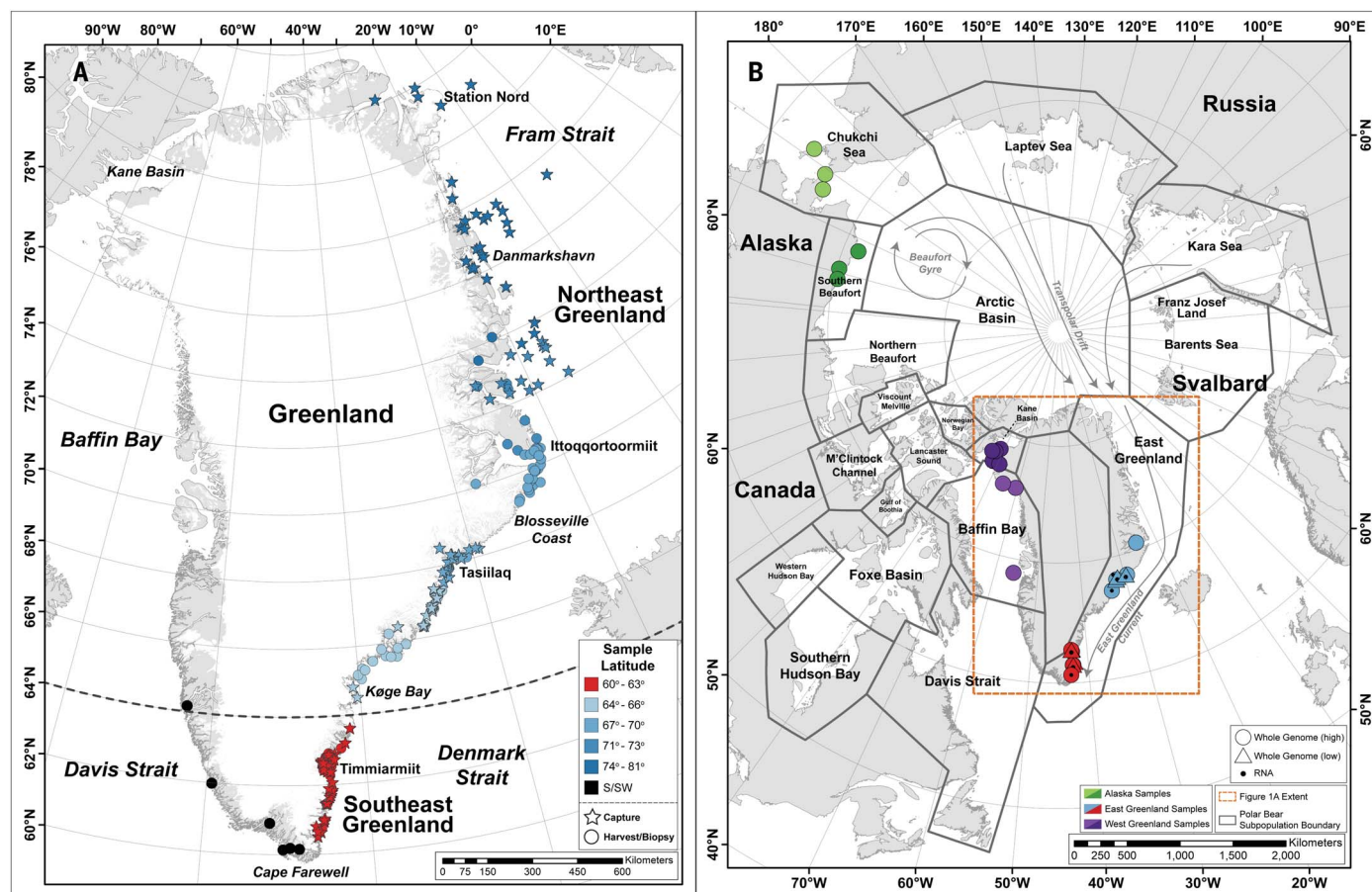


Fig. 1. Place names and distribution of samples. (A) Locations of physical captures, biopsies, and subsistence harvest samples used for genetic (1983–2017) and movement (1993–2021) analyses from polar bears collected within Southeast Greenland and Northeast Greenland, separated by 64°N. (B) Geographic locations of whole-genome and RNA samples (2015–2017) and subpopulation boundaries.

highest proportion of their genomes in runs of homozygosity (fig. S25) compared with other polar bear subpopulations.

Estimates of genetic divergence measured as F_{ST} showed that Southeast Greenland bears are more genetically diverged from neighboring groups of bears [in Northeast Greenland ($F_{ST} = 0.059$) and the Davis Strait subpopulation ($F_{ST} = 0.086$)] than any other neighboring subpopulation pair (table S5). The pair with the next-highest F_{ST} (M'Clintock Channel and Foxe Basin, $F_{ST} = 0.039$) are separated by a land boundary, which is less conducive to polar bear movement than a water-ice boundary. Norwegian Bay has even lower F_{ST} values with its neighbors (Kane Basin, $F_{ST} = 0.026$; Lancaster Sound, $F_{ST} = 0.027$). The genetic distinctiveness of Southeast Greenland bears may be due in part to the rapid directional flow of the East Greenland Coastal Current, which limits both northward emigration and southward immigration. In support of this hypothesis, bears genotyped from South and Southwest Greenland did not cluster with Southeast Greenland, their nearest neighbor. Instead, they clustered with Northeast

Greenland bears (Figs. 1 and 3A), suggesting that they originated in Northeast Greenland and were subsequently transported south on the sea ice, past Southeast Greenland's fjords and around Cape Farewell. Davis Strait bears also were more similar to Northeast Greenland bears than to Southeast Greenland bears (table S5), suggesting gene flow from Davis Strait around the northern coast of Greenland.

Demographic data are consistent with Southeast Greenland bears functioning as a distinct subpopulation. Birth rates were low compared with Northeast Greenland and most other polar bear subpopulations (10, 17). We found no differences in litter sizes between Southeast Greenland and Northeast Greenland subpopulations, which suggests similar cub survival (tables S9 and S10). Adult female body mass, an important determinant of cub production and survival (18), was lower in Southeast Greenland than in several other subpopulations but was similar to that of Northeast Greenland bears and the Barents Sea subpopulation (fig. S26 and table S11), both of which use glacial fjords (19). It is possible that low birth rates are influenced by highly fractured fjord and moun-

tain habitats that reduce bear movements and impede breeding pair formation (20).

The distinctive movement, genetic, and demographic patterns of Southeast Greenland bears may have evolved over several hundred years of isolation. The earliest reference to polar bears in South Greenland dates to the 1300s (21), and the first written Western record of bears in Southeast Greenland fjords is from the 1830s (22). These records are consistent with analyses of rare single-nucleotide polymorphisms [maximum allele frequency of 5%; (10)] in the whole-genome data, which suggested that sampled Southeast Greenland bears share a common ancestor ~200 years ago (95% confidence interval: 189 to 264 years ago; fig. S22) and thus have been genetically isolated for at least this long.

Southeast Greenland bears have few opportunities for dispersal. Their habitat comprises steep coastal topography with fjords separated by >2000-m mountains and narrow glaciers. To the west, dispersal is restricted by the Greenland Ice Sheet. To the east is the open water of the Denmark Strait. Northward movement is limited by the East Greenland Coastal

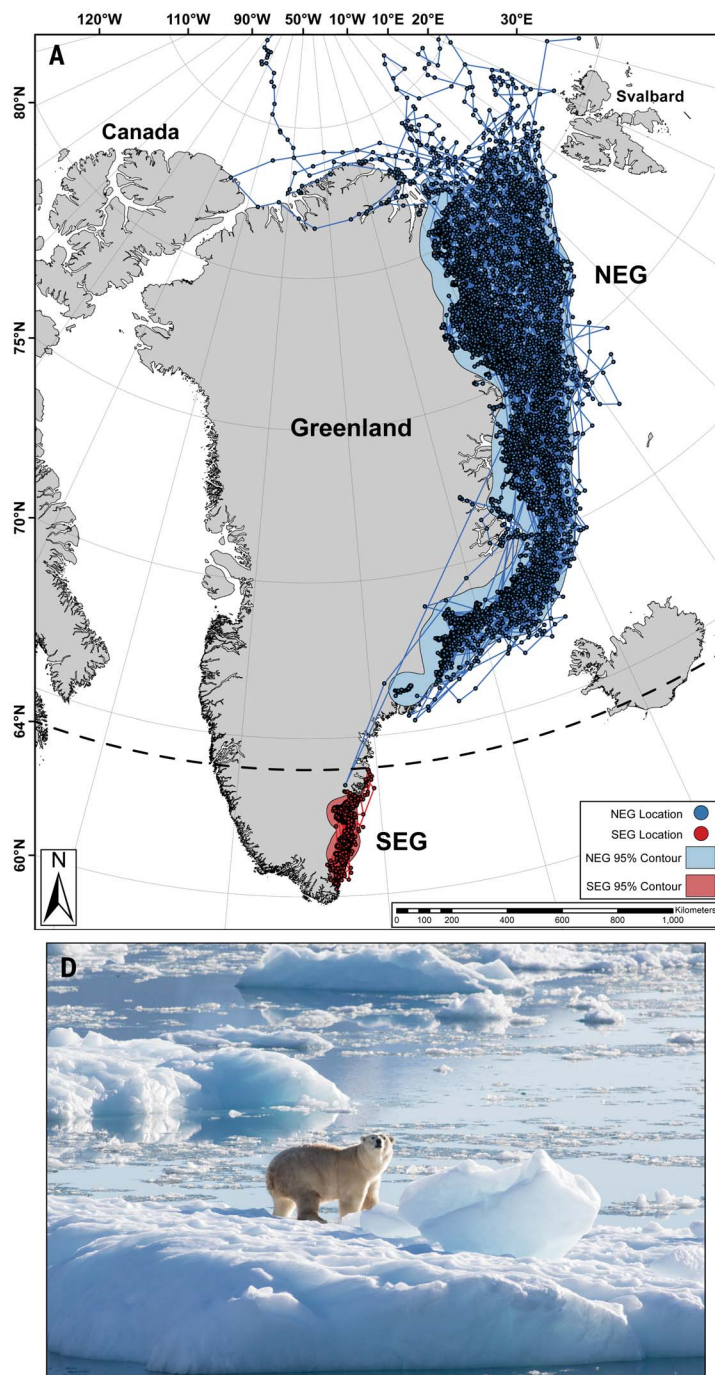


Fig. 2. Polar bear movements and habitat types. (A) Area use for Northeast Greenland (NEG) and Southeast Greenland (SEG) polar bears based on satellite telemetry from 1993 to 2021. SEG bears range over ~400 linear km of mountainous and glaciated coastal habitat (~27,749 km² within 95% probability contours), whereas NEG bears range over >2000 linear km of pack

ice and fast ice and 671,208 km² (95% probability contours). NEG and SEG are separated at about 64°N latitude. (B) Fjord fast-ice habitat in SEG, present <4 months per year. (C) Low-concentration drift ice with open water on the horizon in Denmark Strait. (D) SEG polar bear using glacial ice at 62°N in September 2016. (E) Polar bear with a fresh seal kill at 61°N in September 2016.

Current (12), by katabatic winds that flush the region of sea ice around Køge Bay (65°N), and by subsistence hunting around the community of Tasiilaq. To the south, polar bear habitat disappears at the southern tip of Greenland, and both South and Southwest Greenland are inhabited by humans who hunt polar bears.

Despite limited options for dispersal, Southeast Greenland bears occasionally capture genetic diversity from other subpopulations, and our observations suggest that immigrants can adapt to the distinctive environment. Research-marked bears have been observed in Southeast and Southwest Greenland after being tagged

in Franz Josef Land (Russia), Svalbard, Baffin Island, and the eastern Beaufort Sea (9). Our whole-genome dataset identifies two individuals as potential immigrants: one that clusters closer to the Southern Beaufort Sea and Chukchi Sea subpopulations in Alaska, and another that clusters closer to Northeast Greenland (Fig. 3B).

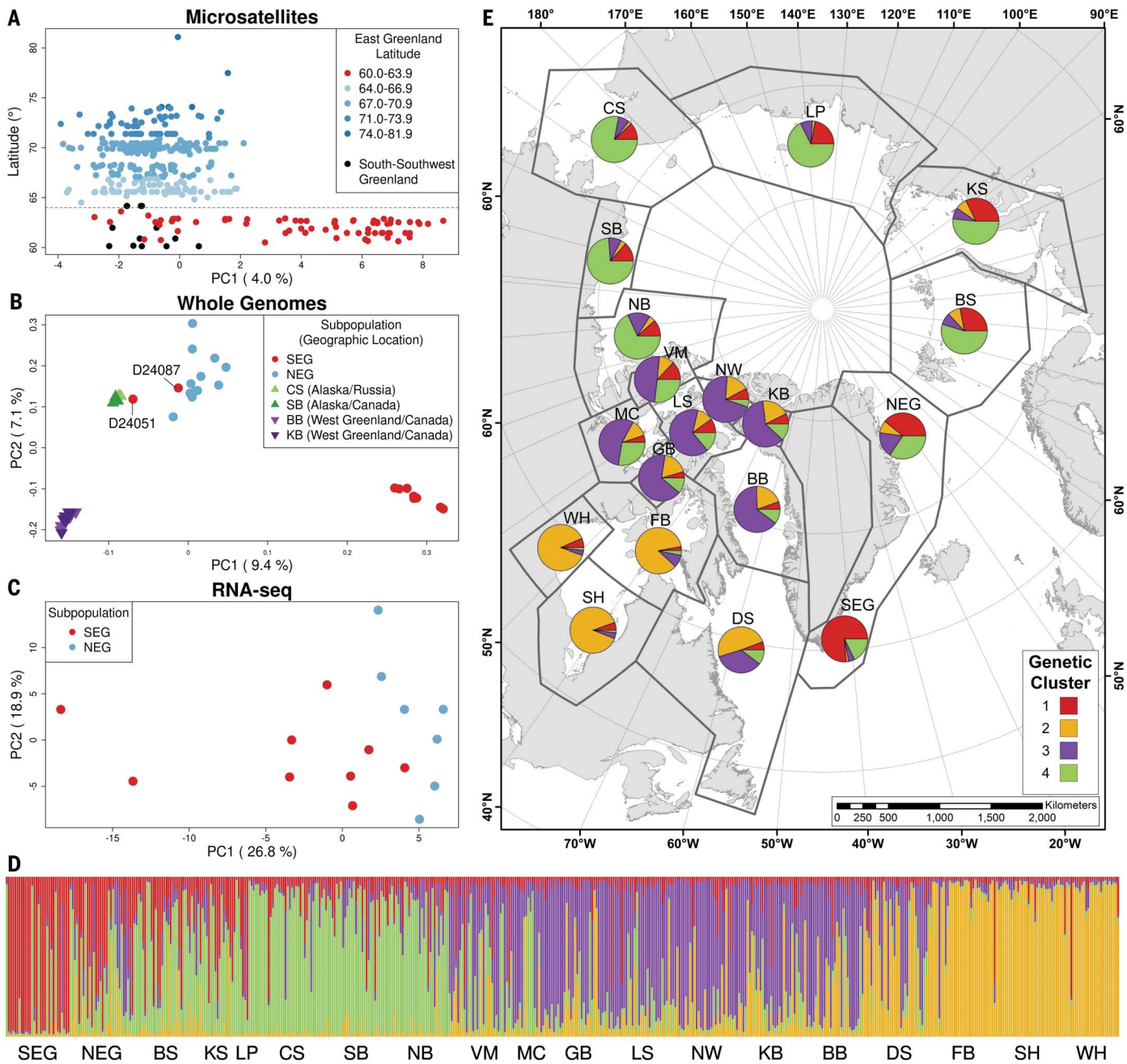


Fig. 3. Population structure. (A) Primary axis of genetic principal components analysis (PCA) versus latitude of Greenland bears. Most SEG bears (red) cluster separately from NEG bears (blue). Bears from South and Southwest Greenland (black) cluster with NEG bears. (B) Genomic PCA showing that SEG bears cluster separately from other subpopulations, except individuals D24051 and D24087, which cluster with Chukchi Sea (CS)/Southern Beaufort (SB) and NEG bears, respectively. (C) Transcriptomic PCA of East Greenland samples. SEG (red) and NEG (blue) bears show different gene expression profiles. Axes

in (A) to (C) show the percentage of variation explained. (D) Bayesian clustering assuming four clusters. Each column represents a sample. (E) Summary by subpopulation of the individual-based results from (D). SEG bears are genetically distinct from other subpopulations. BS, Barents Sea; KS, Kara Sea; LP, Laptev Sea; NB, Northern Beaufort Sea; VM, Viscount Melville Sound; MC, M'Clintock Channel; GB, Gulf of Boothia; LS, Lancaster Sound; NW, Norwegian Bay; KB, Kane Basin; BB, Baffin Bay; DS, Davis Strait; FB, Foxe Basin; SH, Southern Hudson Bay; WH, Western Hudson Bay.

We detected little evidence of admixture in either bear (Fig. 4 and fig. S23). Combined with ancestry analysis (fig. S22), this suggests that these individuals were recent immigrants into Southeast Greenland. While these data do not establish successful gene flow into Southeast Greenland, microsatellites identify

some Southeast Greenland bears with mixed ancestry (Fig. 3A and figs. S18 to S20), suggesting that immigrant bears adapt sufficiently to interbreed with resident bears.

Although our study was not designed to estimate abundance, data from marked individuals suggest that a few hundred animals currently

inhabit Southeast Greenland, similar to other small polar bear subpopulations (10, 11). Human-caused mortality is unlikely to limit the numbers of Southeast Greenland bears. Human settlements in the Skjoldungen-Timmiarmiit area were abandoned in the mid-1960s. Small numbers of subsistence hunters lived along

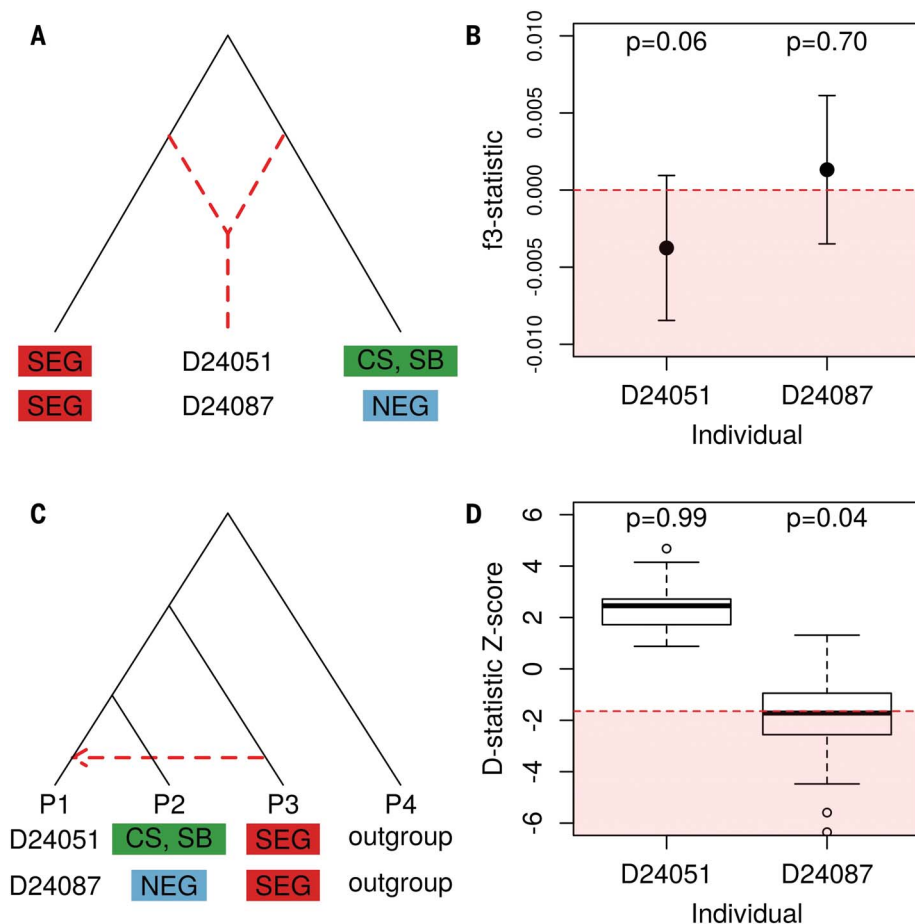


Fig. 4. Genomic tests of admixture in D24051 and D24087. (A) The f_3 statistics explore whether D24051 and D24087 are mixtures of two source populations. (B) We find no statistical evidence at ± 1.96 SE that either individual is admixed. Negative values (red region) indicate admixture. (C) The D-statistics investigate whether either D24051 or D24087 has excess ancestry from SEG as compared with the subpopulations they cluster with genetically. (D) Box plots showing all combinations of individuals from the specified subpopulations show little evidence that either individual is admixed. The region of statistical significance for a single comparison is highlighted in red.

the coast until the late 1970s (23), but it is uncommon for polar bear hunters to go to Southeast Greenland today (24).

We propose that Southeast Greenland polar bears are a resident, functionally and demographically isolated group that warrants consideration as the 20th subpopulation of polar bears by the International Union for Conservation of Nature. Southeast Greenland bears are distinct according to the same lines of evidence used to delineate other subpopulations, most of which exhibit substantially more genetic mixing (11, 16). Maintenance of the distinctive Southeast Greenland lineage is necessary to preserve the genetic diversity of the species.

The existence of the Southeast Greenland subpopulation has implications for conservation. In most of the Arctic, glacial mélange habitats are uncommon, and the future of polar bears will be closely tied to the availability of sea ice (5–7). However, in Greenland

and Svalbard, glacial mélange habitat is available and occupied year-round by ringed seals, the polar bear's primary prey (25) (Fig. 2, D and E). We show that some polar bears can become established and adapt to this distinctive environment, which, in some areas, may provide a buffer to sea-ice loss. The long-term role of refugia in the persistence of polar bears is unknown (26). Even glacial mélange habitat is changing, because the Greenland Ice Sheet coastal margin is undergoing widespread reconfiguration (27). Continued monitoring of Southeast Greenland bears will be critical to understand how the species will be affected by, and respond to, anthropogenic climate warming.

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The authors declare that they have no competing interests. **Data and materials availability:** Detailed lists of samples are provided in the supplementary materials. Microsatellite genotypes are available in Dryad (28). Genomic data are available at NCBI under BioProject ID PRJNA669153. **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S26
Tables S1 to S11
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Glacial ice supports a distinct and undocumented polar bear subpopulation persisting in late 21st-century sea-ice conditions

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A new hope

Polar bears are one of the most mentioned—and iconic—potential victims of climate change. Most polar bears rely on sea ice to hunt, so the current and predicted reductions in sea ice occurrence and persistence are likely to have major impacts on their survival. Laidre *et al.* describe the discovery of an isolated population of polar bears from southeastern Greenland that is much less reliant on sea ice, instead existing at the terminal end of a glacier and relying on resources from this glacial-freshwater mélange (see the Perspective by Peacock). Discovery of this population suggests both that such environments might serve as refugia for polar bears and that conservation of this new population is essential. — SNV

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