Assessing the risk of climate maladaptation for Canadian polar bears

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Abstract

The Arctic is warming four times faster than the rest of the world, threatening the persistence of Arctic species. It is uncertain if Arctic wildlife will have sufficient time to adapt to such rapidly warming environments. We used genetic forecasting to measure the risk of maladaptation to warming temperatures and sea ice loss in polar bears (*Ursus maritimus*) sampled across the Canadian Arctic. We found evidence for local adaptation to sea ice condition and temperature. Forecasting of genome-environment mismatches for predicted climate scenarios suggested that polar bears in the high Arctic had the greatest risk of becoming maladapted to climate warming. While bears in the high Canadian Arctic may be most likely to become maladapted, all polar bears face potentially negative outcomes to climate change. Given the importance of the sea ice habitat to polar bears, we expect that the increased risk of maladaptation to future warming is already widespread.

Introduction

Climate change is a major contributor to the biodiversity crisis, with many species threatened with extinction due to habitat loss (IPCC 2023). The vulnerability of species to climate change is determined by multiple interacting factors, including population size, dispersal capabilities, genetic background, and adaptive capacity (Thomas et al. 2004; Pacifici et al. 2015). Adaptive capacity can help species cope with climate change; however, the pace of environmental change may prove to be too rapid for some species to adapt (Berteaux et al. 2004). Spatial variation in environments adds an additional layer of complexity to species responses to climate change. Identifying the spatial and environmental drivers of local adaptation supports assessments of a species' potential for maladaptation to future environments under climate change.

The Arctic is warming at 2-4x the global average (Cohen et al. 2014; Previdi et al. 2021; Rantanen et al. 2022). Increased temperatures have led to significant changes in sea ice conditions. Annual sea ice forms later and melts earlier in the year compared to previous decades, creating sea ice with reduced thickness and less spatial coverage (Comiso et al. 2008; Screen and Simmonds 2010; Stroeve et al. 2014; Kwok 2018; Laidre et al. 2018). Even under moderate emission scenarios, the Arctic could become ice-free in the summer as early as the mid-2030s (Docquier and Koenigk 2021; Kim et al. 2023; Shen et al. 2023). The high Arctic (>68 °N) is predicted to experience some of the largest environmental changes associated with climate change, as warming temperatures have reduced the extent of multiyear sea ice (i.e., ice that has survived at least two years of summer melt) by more than 90% (Kwok 2018; Stroeve and Notz 2018). The loss of sea ice has significant implications for the Arctic ecosystem, particularly for species that depend on sea ice for survival.

Climate-mediated reductions in the extent of sea ice habitat represents the single greatest threat to the persistence of Arctic species (Amstrup et al. 2008; Marcot et al. 2023). Polar bears (*Ursus maritimus*) are ice-adapted predators that rely on sea ice for hunting, migration, and mating (Regehr et al. 2016; Stern and Laidre 2016). Polar bears forage intensively on sea ice, hunting ringed (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) as their primary food source (Stirling and Archibald 1977; Wiig et al. 2008). Sea ice loss due to climate warming influences habitat use and connectivity among polar bears (Durner et al. 2009; Laidre et al.2018). When seasonal sea ice melts in southern regions of the Arctic, polar bears are restricted to land and typically fast until the sea ice returns. Accelerating sea ice loss increases the time polar bears spend on land (Rode et al. 2015; Atwood et al. 2016; Lunn et al. 2016; Laidre et al. 2018), elevating their exposure to disease pathogens (Pilfold et al. 2021) and anthropogenic food sources (Smith et al. 2023; Stimmelmayr et al. 2023), and exacerbating human-bear conflict (Wilder et al. 2017; Heemskerk et al. 2020). Extended fasting periods lead to declines in body condition, reproductive output, and survival of polar bears (Regehr et al. 2007; Stirling and Derocher 2012; Lunn et al. 2016). As the ice-free period continues to increase, polar bears may face local extirpation as they are pushed beyond their physiological fasting limits (Molnár et al. 2020).

Despite extensive knowledge of the effects of sea ice loss on polar bear ecology, there are relatively few studies on the evolutionary responses of polar bears to climate change. Modern polar bears have lower levels of genetic diversity than their nearest relatives, grizzly bears (Miller et al. 2012; Liu et al. 2014, Lan et al. 2022). Some polar bears have experienced additional genetic diversity losses and increased genetic isolation associated with recent sea ice loss (Maduna et al. 2021). These findings suggest that changes in ice availability may alter

patterns of gene flow and genetic drift (Laidre et al. 2022), potentially limiting the ability of polar bears to adapt to climate change. However, the adaptive capacity of polar bears to warming climates in the Arctic remains unknown.

Genetic forecasting is a tool that can be used to inform predictions of whether polar bears can adapt to a warming Arctic. These predictive models can be used to assess if mismatches exist between current population allele frequencies and the future environments those populations are likely to experience (Capblancq et al. 2020). Populations with a higher degree of mismatch (genetic offsets *sensu* Fitzpatrick and Keller 2015) are at risk of maladaptation to climate change, particularly if they are genetically isolated or have low fitness (Láruson et al. 2022). Quantifying genetic offsets at the population level allows us to assess potential vulnerability to climate change across polar bear management-designated populations, known as subpopulations.

We assessed the risk of maladaptation to climate change in polar bears across the Canadian Arctic. We asked 1) how does standing genetic variation and population structure vary among subpopulations?; 2) do sea ice loss and warming air temperatures affect allele turnover in polar bears?; and 3) are genetic offsets to future environments variable among subpopulations? We predicted that polar bear subpopulations that face the greatest amount of environmental change (i.e., those in the high Arctic) will have the greatest genetic offsets to future environments, leading to an increased risk of maladaptation.

Materials and methods

Study system and genotype processing

Polar bears are distributed across the Arctic in 19 subpopulations recognized by the International Union for the Conservation of Nature (IUCN; Obbard et al. 2010). Subpopulation boundaries

were determined by satellite telemetry data, ecological and genetic differences among bears, and regional differences in management policy (Obbard et al. 2010). There are 14 polar bear subpopulations within Canada's borders (Figure 1A), some of which are shared with Greenland and the USA. These subpopulations range in abundance from 160-2800 individuals (Table 1; IUCN/SSC 2021). We categorized the Canadian subpopulations included in our study as high Arctic (>68 °N), low Arctic (55-68 °N), and sub-Arctic (<55 °N) following the Arctic Biodiversity Assessment Arctic Zones guideline (Table 1; Meltofte et al., 2013).

Two single nucleotide polymorphism (SNP) arrays have been developed for polar bears and used to assess population structure, heritability, and hybridization (Malenfant et al. 2015, 2018; Miller et al. in review at Conservation Genetic Resources, inlcuded in supporting information). A total of 1,450 polar bears were genotyped on the *Ursus maritimus V1* SNP chip, a 9K Illumina Infinium Bead Chip containing a combination of transcriptome-derived and RAD-derived SNPs (Malenfant et al. 2015). Bears genotyped on the *Ursus maritimus V1* SNP chip primarily originated from the Hudson Bay and were sampled between 1985-2012. Another 628 polar bears were genotyped on the *Ursus maritimus V2* SNP chip, an 8K Illumina Infinium Bead Chip containing loci from the *V1* SNP chip augmented to include species diagnostic loci (Miller et al. in review). Bears genotyped on this chip originated from the circumpolar Arctic and were sampled between 1975-2015. Additional sampling and harvesting details can be found in Malenfant et al. (2015) and Miller et al. (in review). Bears that were genotyped on both chips have a 99% genotyping concordance (Miller et al. in review), and thus we are confident in the genotypes of individuals from both chips.

We used the genotype files generated by Miller et al. (in review) for our analyses. We selected SNPs present on both SNP chips (N = 4,723 SNPs) and removed individuals that were

not georeferenced. To avoid uneven sample sizes and improve the performance and speed of the genetic offset models, we selected a maximum of 50 bears per subpopulation. For subpopulations which contained more than 50 sampled bears, we preferentially selected bears with a complete set of environmental data points and with no missing genotype calls. We also removed the single individual that was sampled from the Arctic Basin subpopulation. We quality filtered on our final sample set using PLINK v1.90 (Chang et al. 2015) to remove SNPs with a genotyping rate below 90% (*--geno 0.1*), a minor allele frequency below 1% (*--maf 0.01*), and that were in linkage disequilibrium (*--indep-pairwise 10 1 0.1*). For the genetic diversity and differentiation analyses, we also removed SNPs that were out of Hardy-Weinberg equilibrium (HWE; *--hwe 0.001 midp*).

Genetic diversity and differentiation

We assessed standing genetic variation and differentiation among polar bear subpopulations. We used the *--het* call in PLINK to calculate individual per-locus level estimates of observed heterozygosity (H_O), and inbreeding (F), then averaged values across subpopulations. We used the *pi* function from the R v4.3.0 (R Core Team 2023) package radiator v1.2.8 (Gosselin et al. 2020) to calculate nucleotide diversity (π) for each subpopulation (Nei and Li 1979). The transcriptomic loci on the SNP chips were ascertained using the Western Hudson Bay (WH) subpopulation which can inflate estimates of genetic diversity for WH relative to other subpopulations. To account for this inflation, we repeated the calculations if H_O and π on the transcriptomic-derived (N = 1,381 SNPs) and RAD-derived loci (N = 2,304 SNPs) separately.

We calculated pairwise F_{ST} among subpopulations using the *stammpFst* function in the StaMMP v1.6.3 R package (Pembleton et al. 2013). We bootstrapped across loci 100 times to generate 95% confidence intervals for each pairwise F_{ST} value to determine if subpopulations

were significantly differentiated from one another. Lastly, we calculated the number of private alleles per subpopulation using the *gl.report.pa* function from the R package dartR v2.9.5 (Gruber et al. 2018).

Population structure analyses

Given that polar bears have been grouped into subpopulations for management purposes, we were interested in determining if the genetic structure of individuals corresponded to their subpopulation designation. We used two complementary methods to assess population structure. First, we estimated individual ancestry coefficients using sparse non-negative matrix factorization (sNMF; Frichot et al. 2014), implemented with the *snmf* function from the R package LEA v3.12.2 (Frichot and François 2015). sNMF takes an unsupervised approach to estimate individual admixture coefficients from multilocus genotype data comparable to those from STRUCTURE and ADMIXTURE (Frichot et al. 2014). We identified the optimal number of clusters by comparing the fit of each model with K = 1-13 clusters. We ran each model 10 times and selected the value of K with the lowest cross-entropy score. We generated admixture plots to visualize how individuals formed clusters, and then mapped the results on to each subpopulation location. Lastly, we extracted the cluster assignment for each bear for later use in the genetic offset analysis. We assigned an individual to a cluster if it had an ancestry proportion greater than 0.75 to any single cluster. If ancestry to any cluster was lower than 0.75, the individual was assigned as admixed.

We conducted a spatial principal component analysis (sPCA) to identify spatial patterns in genetic variation among individuals. sPCA uses an ordination-based approach to maximize the variation between allele frequency and spatial autocorrelation estimated with Moran's I (Jombart and Ahmed 2011). The eigenvectors generated by the sPCA are mapped onto geographic

coordinates, allowing for clines in genetic structure to be evaluated (Jombart and Ahmed 2011). We used the function *chooseCN* from the adegenet v2.1.10 package (Jombart and Ahmed 2011) to create a Delauney's triangulation connection network and account for continuously distributed individuals across the range (Jombart et al. 2008). We first ran a sPCA model that included all axes using the *spca* function from adegenet. We ran permutation tests with 999 permutations to identify if a significant effect of global structure existed in the data. We retained the first five positive (global) eigenvalues which contributed most strongly to variance in the final model. We visualized genetic similarity among individuals using the *colorplot* function from adegenet to plot the lagged principal component (PC) scores on a map.

Environmental variable selection

We quantified present and future conditions for sea ice and air temperature across the Canadian Arctic. We extracted mean annual ice thickness (m) and ice cover (%) from the Bio-ORACLE v2.0 database (Assis et al. 2018). Annual sea ice thickness is a measure of how thick the ice is at a given sampling area averaged across the year, whereas annual sea ice cover is a measure of how much of the sampling area is covered by ice throughout the year. Bio-ORACLE marine layers are available as monthly and annual averages for present conditions (2000–2014) at a spatial scale of 9.2 km at the equator (5 arcmin; Assis et al. 2018). We used the R package sdmpredictors v0.2.14 (Bosch and Fernandez 2021) to extract values at each sampling location with a 50 km^2 buffer surrounding each site to account for bear movement. We also extracted ice thickness values from future (2040-2050 and 2090-2100) conditions that were forecasted under RCP8.5 (IPCC 2014). Forecasted ice thickness was sourced from three coupled Atmosphere–Ocean General Circulation Models (AOGCM) provided by Coupled Model Intercomparison Project Phase 5 (CMIP5; Assis et al. 2018). We selected RCP8.5 because this level of climate

warming is predicted to occur if no mitigation practices are put into place (Brown et al. 2020). Ice concentration has not yet been included in the future climate scenarios dataset in Bio-ORACLE, so we did not include this predictor in our future environment dataset.

We followed a similar approach to extract near-surface air temperature averaged from 2000-2014 from each sampling location. We used the StableClim database (Brown et al. 2020) to extract mean annual temperature surrounding 50 km^2 from each sampling location. Air temperature under RCP8.5 was sourced from all 19 AOCMs from CMIP5 (Brown et al. 2020). StableClim has at a spatial scale of 278 km at the equator (150 arcmin, so we used the R package raster v3.6-20 (Hijmans 2023) to match the extent of the temperature layer to the ice condition layers. We extracted values under the same timelines (present and future) and climate scenario as the ice condition layers.

Gradient Forest predictions of maladaptation

We assessed the risk of genetic maladaptation to climate warming using Gradient Forests (GF), a nonparametric machine learning approach that can be used to assess changes in allele frequencies across environmental and spatial gradients (Fitzpatrick and Keller 2015). GF builds regression trees using Random Forests (Breiman 2001) and creates turnover functions that determine how well environmental change along the gradients explains changes in individual allele frequencies. A goodness-of-fit measure (R^2) is generated from each regression tree and used to weight predictors in proportion to their accuracy and importance in explaining allele turnover (Ellis et al. 2012). Importantly, the relative importance of predictors on allele turnover can be interpreted even when R^2 are small.

Turnover functions can be aggregated across alleles to generate a cumulative importance curve for the entire genome (Láruson et al. 2022). The slope of the importance curve describes

the rate of change in allele frequency across the environmental gradient; steeper curves indicate greater allele turnover. The underlying assumption of this method is that populations are locally adapted to their current environment; any shift in allele frequency along the environmental gradient is presumed to be maladaptive. Maladaptation can be quantified with genetic offset scores, which are the Euclidean distance between current and future allele frequencies under current and future environmental gradients (Ellis et al. 2012). The greater the distance, the greater the mismatch between current allele frequencies and future environments, and the greater the risk of maladaptation.

We implemented the GF with the gradientForest v0.1-34 package in R (Smith and Ellis 2013) using the sea ice and air temperature as environmental predictors. We ran separate models for sea ice thickness and cover because these variables were highly correlated (r = 0.82). Both models included temperature as a co-factor. We imputed missing SNPs with the *impute* function from the LEA package using the most likely genotype value computed from the genotype matrix. To account for spatial variation in population abundances and genetic structure, including isolation-by-distance (IBD), we included a matrix of uncorrelated spatial variables in the models (Láruson et al. 2022). We calculated distance-based Moran's eigenvector maps (PCNMs) with the *pcnm* function in the R package vegan v2.6-4 (Oksanen 2015). We retained the first half of the positive PCNMs ($N = 62$) in the model, which represent broad-scale spatial autocorrelation patterns (Fitzpatrick and Keller 2015). We set the number of trees to 500 (*ntree* = 500) with 201 bins to compact splits (*nbin* = 201) and a predictor correlation threshold above 0.5 (*corr.threshold* = 0.5). We assigned the maximum number of splits using the default settings for gradientForest (Smith and Ellis 2013). We visualized the environmental change in our study area with PCA biplots and mapped the compositional distribution of alleles across the area.

We used the GF model output to calculate genetic offset scores for each polar bear under ice thickness and temperature conditions in 2050 and 2100. We created raster maps of the offset score for each pixel, then extracted offset score for each sampling location. We ran a generalized linear model with a quasi-binomial distribution to test for differences in individual genetic offsets among polar bears. We included location in the Arctic (high, low, and sub-Arctic), genetic cluster (Clusters 1-5, or admixed), subpopulation abundance, and climate projection year (2050 or 2100) as predictor variables. We assessed the assumptions of the model by plotting residuals and examining collinearity between predictors. We tested the significance of predictors using the *anova.glm* function from the R stats v4.3.0 package (R Core Team 2023).

Results

Population genetic diversity

The HWE-filtered dataset contained 3,685 SNPs from 411 bears sampled from 13 subpopulations in Canada between 1985-2016. Subpopulations contained an average of 32 individuals (range: 10-50; Table 1). Across all SNPs, mean H_O was 0.263 and mean F was 0.037 (Table 1, Figure S1). Norwegian Bay (NW) had the lowest heterozygosity and highest inbreeding values (H_O = 0.240, F = 0.121), whereas Kane Basin (KB) had the highest heterozygosity and lowest inbreeding values (H_O = 0.271, F = 0.017). Nucleotide diversity for the entire population was 0.137 (Table 1). As with H_O, nucleotide diversity was lowest in NW (π = 0.118) but was greatest (π = 0.133) in Foxe Basin (FB), Davis Straight (DS), and Western Hudson Bay (WH). Genetic diversity was ~50% higher in transcriptomic-derived SNPs relative to RAD-derived SNPs as expected (Table S1) but was lowest in NW for both sets of SNPs, consistent with observations from the HWE-filtered dataset.

297 Global F_{ST} was 0.035. Pairwise F_{ST} ranged from 0.001 to 0.089 (Table S2) and were
298 significantly differentiated from one another ($p < 0.05$) except for Kane Basin and Baffin Bay (p
299 $= 0.29$). Lastly, we identified a mean of 420 private alleles per subpopulation (Table 1), with the
300 greatest number being found in NW ($N = 747$ alleles).

301 **Population genetic structure**

302 We identified K = 5 genetic clusters of polar bears as the best fitting model with a cross-entropy
303 score of 0.648 (range 0.671-0.648; Figure S2). The Norwegian Bay (NW) subpopulation formed
304 a unique genetic cluster (Cluster 3; Figure 1). The Hudson Bay subpopulations formed a single
305 cluster (Cluster 5), which included Western Hudson Bay (WH), Southern Hudson Bay (SH), and
306 Foxe Basin (FB), as did the Southern and Northern Beaufort Sea (SB and NB, respectively)
307 subpopulations (Cluster 4). Viscount Melville Sound (VM) and M'Clintock Channel (MC)
308 formed a cluster (Cluster 1), while the remaining subpopulations shared ancestry (Cluster 2) with
309 some degree of admixture.

310 Polar bears were most likely to share genetic variation with those in closest proximity to
311 them, suggesting that IBD contributes to genetic structure across the Canadian Arctic. The
312 permutation test from the sPCA analysis identified a significant effect of global structure (p-
313 value < 0.01), indicating that genetic structure is best explained by the positive spatial
314 autocorrelation among individuals. Visualization of the lagged PC scores confirmed patterns of
315 IBD, where genetic similarity gradually declined with distance (Figure S3).

316 **Gradient Forest model of allele turnover**

317 Ice thickness and near surface air temperature were among the top five most important predictors
318 of allele turnover ($N = 3,830$ linkage-pruned SNPs) across all samples. Mean weighted R^2 of the
319 GF model was 0.0018. The top ranked predictor variables were two spatial variables that

accounted for turnover in alleles associated with latitude, population abundance, and genetic structure (PCNM-2: $R^2 = 0.014$; PCNM4: $R^2 = 0.008$; Figure S4). Ice thickness was the third ranked predictor ($R^2 = 0.008$). The largest turnovers in allele frequency along the ice thickness gradient occurred between 2-3 m of ice depth (Figure 2a). Temperature was the fifth ranked predictor ($R^2 = 0.004$), with the largest turnover in alleles occurring at -5 °C (Figure 2a). We found similar results for the model with ice cover and temperature, with the largest turnover in alleles occurring at 60% ice cover (Fig. S5; Supplementary Results).

PC scores generated from the environmental variables mapped into geographic space demonstrate a split in genetic composition between high Arctic polar bears and the rest of the population (Figure 2b). The PCA biplot indicates that ice thickness and temperature were uncorrelated but had similar loading magnitudes, suggesting that while they both contribute to the genetic similarity among bears, the predictors explain different components of the variation (Figure 2b inset). Changes in ice thickness explained variation between the Beaufort Sea and the rest of the bears, whereas changes in temperature contributed to variation across the entire sampled range.

Genetic offsets

Genetic offsets were predicted to be highest in the high Canadian Arctic (Figures 3 and S6). We found that offset scores differed between location ($F_{2,796} = 64.01$, $p < 0.001$), genetic cluster ($F_{5,796} = 20.11$, $p < 0.001$), and abundance ($F_{1,796} = 33.17$, $p < 0.001$). Offset scores were greatest in bears in the high Arctic (Figure 3a, c), particularly Viscount Melville Sound (VM) and Norwegian Bay (NW). Polar bears from the Hudson Bay and Davis Strait (DS) had the lowest offset scores. Genetic offsets declined as subpopulation abundance increased ($b = -1.96 \times 10^{-4}$, Figure 3b). Offset scores were greater under the climate projections for 2100 compared to 2050

343 ($F_{1,796} = 74.74$, $p < 0.001$), but the effect of location and population size remained consistent
344 between projection years.
345
346 **Discussion**
347 We examined genetic offset scores under projected climate warming to assess the potential for
348 maladaptation to climate change in polar bears in Canada. We identified turnover in allele
349 frequencies that corresponded to changes in sea ice and temperature gradients. Polar bear
350 subpopulations in the Canadian high Arctic and those with low population abundances had the
351 highest genetic offset scores, suggesting that these subpopulations may be the most vulnerable to
352 climate change. We also found that the Norwegian Bay (NW) subpopulation in the high Arctic
353 had the lowest levels of standing genetic variation and was genetically isolated from other
354 subpopulations. Our findings can help inform science-based conservation and harvesting
355 strategies with the capacity to target specific subpopulations (Peacock et al. 2011) and shed light
356 on the difficulties ice-adapted Arctic species will have in response to climate warming.
357 We identified points along the ice and temperature gradients associated with large turnover
358 in allele frequencies. Allele frequency turnover peaked at approximately 2 m of ice thickness,
359 60% ice cover, and at -5 °C. Allele turnover points at 2 m thickness are consistent with those
360 found in the high Arctic, whereas 60% ice cover and -5 °C temperatures occur more frequently in
361 the low and sub-Arctic. Ice condition was the strongest environmental driver of allelic turnover,
362 likely reflecting differences in regions of the Arctic with thick multiyear sea ice versus thin
363 seasonal sea ice. Consequently, our analysis may be capturing different aspects of local
364 adaptation between low/sub-Arctic subpopulations and high Arctic subpopulations. Ice thickness

365 may be a more influential predictor for high Arctic polar bears that are experiencing rapid
366 thinning of multiyear ice compared to bears farther south (Stroeve and Notz 2018).
367 The reliance on multiyear sea ice may explain why we observed greater genetic offsets in
368 the high Arctic. Declines in ice thickness likely contribute to allelic mismatch in some high
369 Arctic subpopulations, such as Viscount Melville Sound (VM) and Norwegian Bay (NW), which
370 had the highest offset scores. However, decreasing sea ice thickness may provide temporary
371 benefits to some subpopulations due to increased marine productivity in areas that were
372 previously covered by multiyear sea ice (Yool et al. 2015). Between 1990 and 2010, Kane Basin
373 (KB) transitioned from a multiyear ice habitat to a seasonal ice habitat (Laidre et al. 2020). Polar
374 bears in KB have shown improvements in body condition and increased range sizes, suggesting
375 that they are benefitting from sea ice loss (Laidre et al. 2020). We found that KB had higher
376 genetic diversity than many other subpopulations, but also had high offset scores, suggesting that
377 continued sea ice loss may become problematic for the subpopulation. Interestingly, Southern
378 Hudson Bay (SH), the only sub-Arctic subpopulation, had the lowest genetic offsets and
379 increased in abundance between 2016-2021 (Northrup et al. 2021), potentially indicating some
380 degree of robustness to climate change.
381 Variation in genetic offset scores across the Arctic suggests that subpopulations differ in
382 their potential for adaptation to climate change (Fitzpatrick et al. 2021). Adaptation depends on
383 the strength of selection imposed by the environment, standing genetic variation within each
384 population, and the rate of gene flow between populations. The efficacy of selection is weaker in
385 small populations and when standing genetic variation is reduced (Barrett and Schluter 2008;
386 Charlesworth 2009). We found that genetic offset scores were negatively correlated with
387 subpopulation abundance, consistent with the hypothesis that small population sizes reduce

388 adaptive capacity (Charlesworth 2009). This trend was observed even after accounting for spatial
389 variation in population abudance with the PCNMs. We also identified the lowest genetic
390 diversity in NW, which combined with its small abundance, suggests that NW may have less
391 capacity to adapt to climate warming than other subpopulations.
392 We identified two spatial predictors as the most influential drivers of allele turnover. These
393 predictors corresponded to variation in latitude and population abundance and suggest the
394 presence of IBD among polar bears. If bears from the southern Arctic migrate north, they may
395 introduce alleles adapted to warmer conditions into high Arctic subpopulations. For example, a
396 small, isolated population of polar bears in southeastern Greenland that relies on glacial ice
397 rather than sea ice may could serve as a critical source of adaptive alleles for populations farther
398 north (Laidre et al. 2022). Although polar bears are capable of long-distance dispersal (Durner
399 and Amstrup 1995), the effects of climate change on dispersal rate are variable (Ferguson et al.
400 2002; Pagano et al. 2021). Our sPCA identified evidence of IBD among polar bears, suggesting
401 that while dispersal does occur, it is limited by the distance. Consequently, the rate of gene flow
402 may be insufficient to prevent maladaptation of Canadian high Arctic polar bears.
403 In addition to patterns of IBD, we identified five genetic clusters of polar bears. This
404 number is consistent with those identified by other studies conducted in Canada (Malenfant et al.
405 2016; Jensen et al. 2020), although we did not find a unique cluster corresponding to SH
406 (Viengkone et al. 2016). The clusters we identified correspond approximately to the four polar
407 bear ecoregions that are based on life-history and sea-ice dynamics, both of which contribute to
408 genetic structure among bears (Amstrup et al. 2008). The NW subpopulation formed a unique
409 genetic cluster that is not accounted for in the ecoregions. Previous research has examined the
410 genetic structure of NW, but low samples sizes have limited the power for drawing robust

411 conclusions (Jensen et al. 2020). We found that the NW subpopulation had the greatest number
412 of private alleles despite low genetic diversity, suggesting that many of the present genetic
413 variants are unique to this subpopulation. The distinctive genetic attributes indicate that NW may
414 require special consideration when designing management plans.

415 Some caution is required when applying our results to conservation. The SNPs in our
416 analysis contained few highly differentiated loci, which contributes to the low R^2 values from the
417 models and could reduce our ability to detect variation in allele frequency that is driven by
418 natural selection. However, our primary goal was to rank the predictors of allele turnover, which
419 does not require interpreting the magnitude of the R^2 values. Additionally, climate change
420 vulnerability assessments typically require that phenotypic and genetic changes associated with
421 climate change are correlated with fitness measures (Pacifici et al. 2015; Foden et al. 2019). A
422 preliminary analysis of the lifetime reproductive success of the 50 Western Hudson Bay (WH)
423 polar bears found that individual offsets score was negatively associated with reproductive
424 success ($p = 0.08$; Figure S7). Studies that tie genome-wide measures of genetic offsets with
425 patterns of selection, gene flow, and fitness estimates are needed to fully investigate the
426 vulnerability of polar bears to climate change (Capblancq et al. 2020).

427 In this study, we have identified Canadian high Arctic polar bears as being at greater risk of
428 maladaptation to climate change. As the Arctic moves towards being ice-free in the summer,
429 polar bears must adapt quickly, disperse to lower quality habitat, or risk extirpation. Our work
430 suggests that bears that already face ice-free summers in the low and sub-Arctic are potentially
431 better suited for life in the warming Arctic. Given the extent of sea ice loss that has already
432 occurred, it is unlikely that most polar bears are adapted to current environmental conditions in
433 the Arctic. Designing conservation and management strategies for the polar bear subpopulations

that have the greatest capacity for adaptation may be important (Nicotra et al. 2015). However, the high Arctic contains a substantial portion of standing genetic variation that is absent or rare in most of the Canadian range, and conserving this unique genetic variation may improve persistence across the range. Ultimately, all polar bears, and indeed all ice-adapted Arctic species, are likely to face negative outcomes to climate warming. Reductions of greenhouse gas emissions and protection of the remaining habitat may facilitate the long-term persistence of polar bears.

Statements and Declarations

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Conflicts of interest/Competing interests

Not applicable

Consent for publication

All authors have read the manuscript and approve of its submission for publication.

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Tables and Figures

Table 1. Subpopulation names, location in the high, low, and sub-Arctic, most recent abundance estimates, and year they were censused. Sample size (*N*) of each subpopulation included in this study is also provided, along with the primary genetic cluster assignment (see Figure 1 for visualization of cluster assignments), mean observed heterozygosity (H_O), inbreeding (F), nucleotide diversity (π), and the number of private alleles per subpopulation. Subpopulation abundance was obtained from the IUCN/SSC (2021).

Subpopulation	Location	Census Year	Abundance	*N*	Cluster	H_O	F	π	Private alleles
Southern Hudson Bay (SH)	sub	2016	780	37	5	0.264	0.036	0.131	469
Western Hudson Bay (WH)	low	2016	842	50	5	0.269	0.017	0.133	429
Foxe Basin (FB)	low	2010	2,585	28	5	0.269	0.016	0.133	405
Davis Strait (DS)	low	2007	2,158	32	2	0.267	0.022	0.133	295
Gulf of Boothia (GB)	low	2017	1,525	13	2	0.270	0.012	0.129	551
Baffin Bay (BB)	high	2013	2,826	28	2	0.268	0.019	0.131	336
Kane Basin (KB)	high	2014	357	10	2	0.271	0.009	0.128	667
Lancaster Sound (LS)	high	1997	2,541	30	2	0.265	0.033	0.131	315
Northern Beaufort Sea (NB)	high	2006	980	50	4	0.263	0.039	0.130	245
Southern Beaufort Sea (SB)	high	2010	900	50	4	0.259	0.054	0.130	296
M'Clintock Channel (MC)	high	2016	716	27	1	0.259	0.052	0.128	453
Viscount Melville Sound (VM)	high	1992	161	39	1	0.259	0.053	0.131	261
Norwegian Bay (NW)	high	1997	203	17	3	0.240	0.121	0.118	747

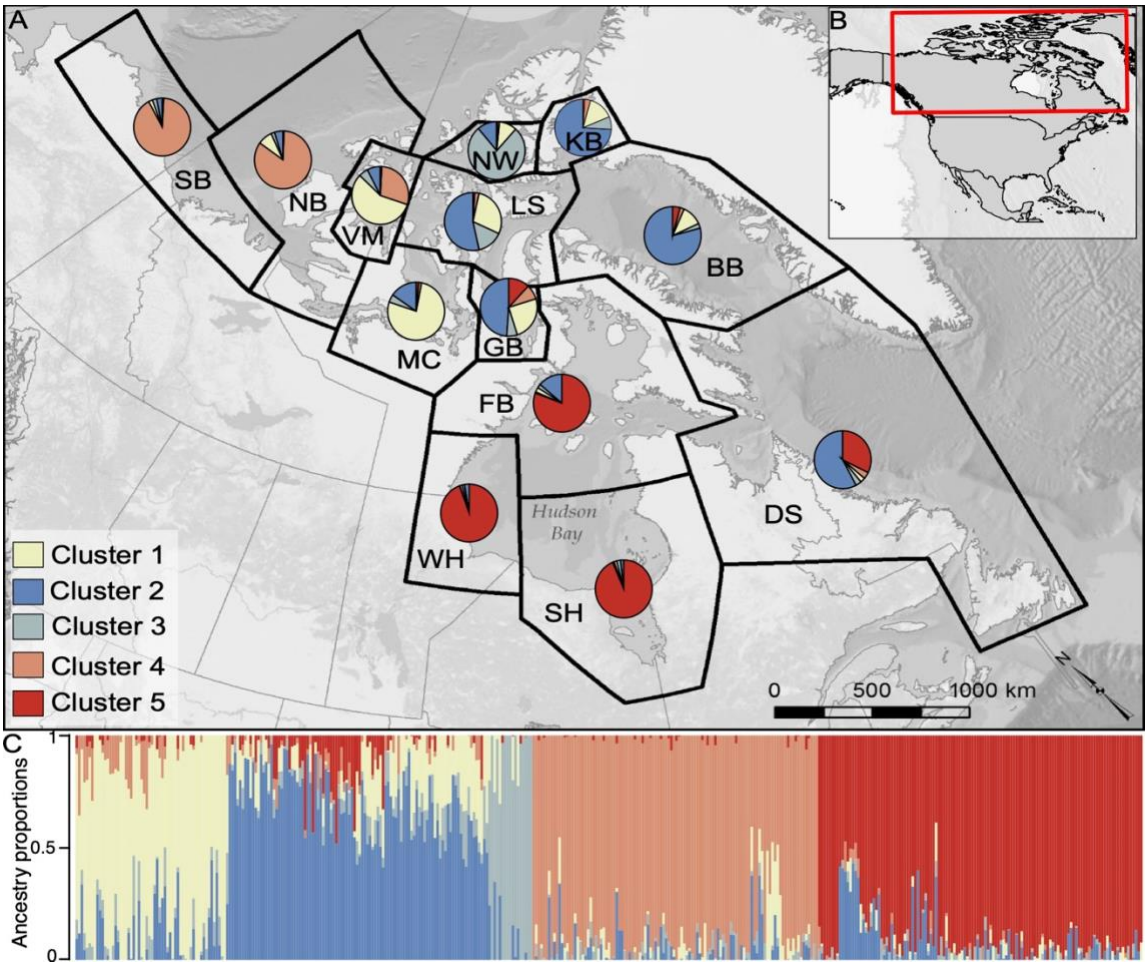

Figure 1. A) Map of ancestry coefficient proportions (K = 5 clusters) for each subpopulation (*N* = 411 polar bears, 3,685 SNPs). Each cluster has a subpopulation abbreviation (high Arctic: Kane Basin (KB), Lancaster Sound (LS), M'Clintock Channel (MC), Northern Beaufort Sea (NB), Norwegian Bay (NW), Southern Beaufort Sea (SB), Viscount Melville Sound (VM), Baffin Bay (BB); low Arctic: Davis Strait, (DS), Foxe Basin (FB), Gulf of Boothia (GB), Western Hudson Bay (WH); sub-Arctic: Southern Hudson Bay (SH)). Subpopulation borders recreated from Obbard et al (2022). B) Map of North America with study region highlighted in red. C) Individual ancestry proportions, where each bar represents a single individual and similar colors represent shared ancestry.

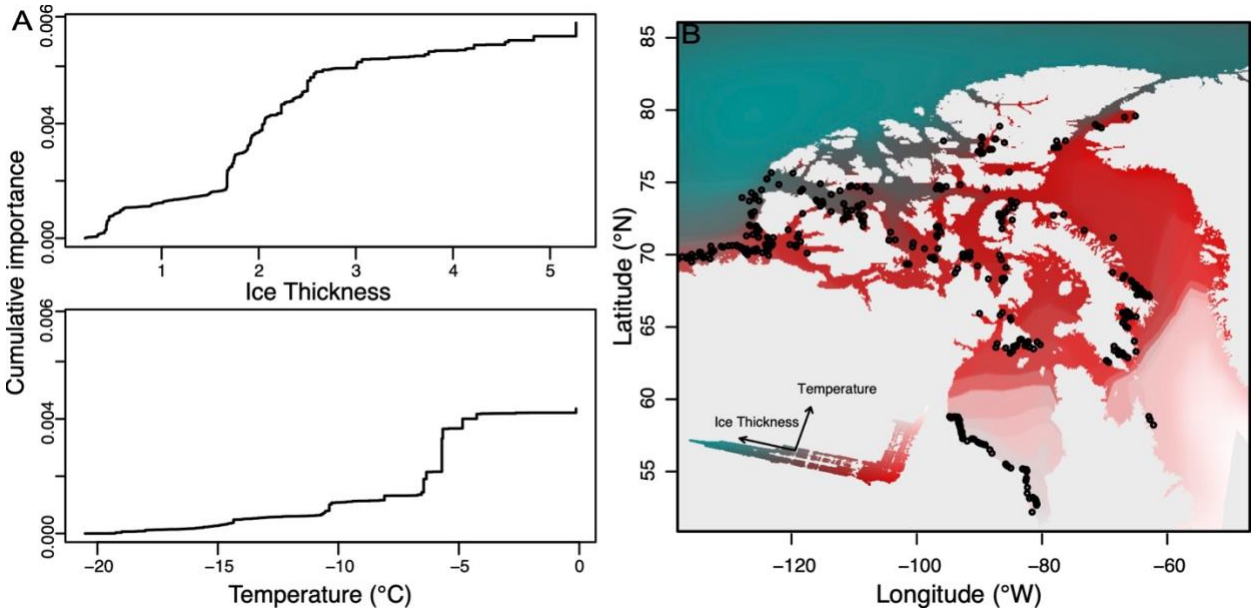

Figure 2. Allele turnover associated with ice thickness and air temperature in geographic and genetic space (N = 411 polar bears, 3,830 SNPs). A) Cumulative importance of allele turnover across all bears associated with the gradient in ice thickness and temperature, where steeper slopes indicate greater turnover in allele frequencies. B) Gradient in genetic turnover derived from transformed ice thickness and temperature predictors. Locations with similar colours are predicted to harbour populations with similar genetic composition. Inset depicts the PCA biplot with arrows showing the direction and magnitude of the contributions from each predictor. Points depict sampled bears.

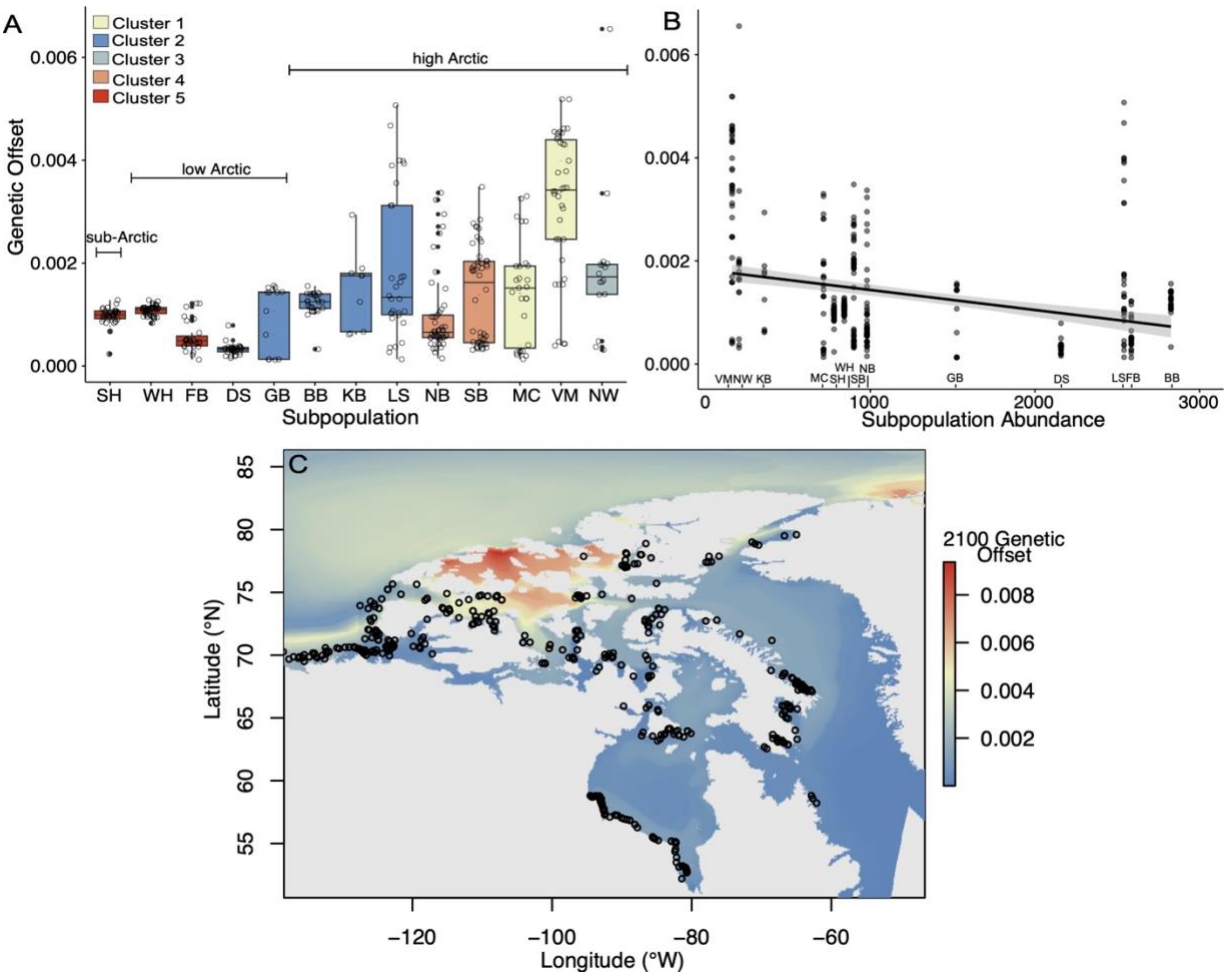

Figure 3. Genetic offset values predicted under RCP8.5 by 2100. A) Boxplot of genetic offset scores for each subpopulation, color coded by ancestry assignment (Clusters 1-5). Subpopulations are grouped into sub, low, and high Arctic categories and were significantly different from one another ($p < 0.001$). B) Genetic offsets scores as a function of subpopulation abundance. Genetic offset declined with increasing abundance ($p < 0.001$). Subpopulations are labeled on the x-axis to provide an indication of where each fall along the axis, see Table 1 for exact values. C) Individual genetic offsets ($N = 411$ polar bears, 3,830 SNPs) plotted in geographical space. Warmer colors represent higher offset, and each black point represents a polar bear individual.

Supplementary Results

Gradient Forest model of allele turnover (ice cover model)

We found a similar trend for the GF model with ice cover and temperature. Mean weighted R^2 was 0.0023. PCNM-2 was the top ranked variable ($R^2 = 0.018$). Ice cover was the second ranked variable ($R^2 = 0.015$), with the largest turnover in alleles occurring at 60% ice cover (Fig. S4a). Temperature was the fourth ranked variable ($R^2 = 0.0050$), with the largest turnover in alleles at -5 °C (Figure. S4a). Visualization of the PCA scores highlights a longitudinal split in genetic composition between bears that was best explained by changes in ice cover (Figure S4b). Temperature contributed to latitudinal variation in genetic composition, with Hudson Bay polar bears exhibiting stronger turnover in response to temperature than the rest of the Arctic (Figure S4b).

Supplemental Tables and Figures

Table S1. Mean genetic diversity for each subpopulation estimated for the complete HWE-filtered dataset (*N* = 3,685 SNPs), the RAD-derived dataset (*N* = 2,304 SNPs), and the transcriptomic-derived dataset (*N* = 1,381 SNPs).

Subpopulation	Complete		RAD-derived		Transcriptomic	
	H_O	π	H_O	π	H_O	π
Baffin Bay (BB)	0.268	0.131	0.223	0.11	0.343	0.166
Davis Strait (DS)	0.267	0.133	0.222	0.11	0.343	0.171
Foxe Basin (FB)	0.269	0.133	0.214	0.106	0.361	0.178
Gulf of Boothia (GB)	0.270	0.129	0.230	0.109	0.337	0.163
Kane Basin (KB)	0.271	0.128	0.229	0.109	0.341	0.16
Lancaster Sound (LS)	0.265	0.131	0.224	0.111	0.333	0.164
M'Clintock Channel (MC)	0.259	0.128	0.221	0.109	0.323	0.161
Northern Beaufort Sea (NB)	0.263	0.130	0.227	0.113	0.322	0.159
Norwegian Bay (NW)	0.240	0.118	0.204	0.100	0.300	0.148
Southern Beaufort Sea (SB)	0.259	0.130	0.225	0.113	0.315	0.159
Southern Hudson Bay (SH)	0.264	0.131	0.210	0.105	0.352	0.175
Viscount Melville Sound (VM)	0.259	0.131	0.223	0.112	0.320	0.161
Western Hudson Bay (WH)	0.269	0.133	0.214	0.105	0.360	0.178

Table S2. Pairwise F_{ST} values between each subpopulation. Each pairwise comparison is significant at $p < 0.05$ except for Kane Basin-Baffin Bay ($p = 0.29$).

	BB	DS	FB	GB	KB	LS	MC	NB	NW	SB	SH	VM
Davis Strait (DS)	0.010											
Foxe Basin (FB)	0.029	0.014										
Gulf of Boothia (GB)	0.009	0.012	0.027									
Kane Basin (KB)	0.001	0.011	0.032	0.008								
Lancaster Sound (LS)	0.006	0.016	0.035	0.007	0.002							
M'Clintock Channel (MC)	0.022	0.032	0.050	0.015	0.018	0.014						
Northern Beaufort Sea (NB)	0.033	0.037	0.055	0.031	0.030	0.030	0.037					
Norwegian Bay (NW)	0.050	0.055	0.076	0.051	0.044	0.036	0.056	0.068				
Southern Beaufort Sea (SB)	0.036	0.039	0.058	0.033	0.033	0.033	0.043	0.002	0.071			
Southern Hudson Bay (SH)	0.042	0.025	0.007	0.039	0.044	0.048	0.062	0.066	0.089	0.069		
Viscount Melville Sound (VM)	0.022	0.028	0.047	0.016	0.017	0.014	0.015	0.018	0.055	0.022	0.059	
Western Hudson Bay (WH)	0.040	0.024	0.004	0.039	0.043	0.047	0.061	0.065	0.088	0.068	0.009	0.058

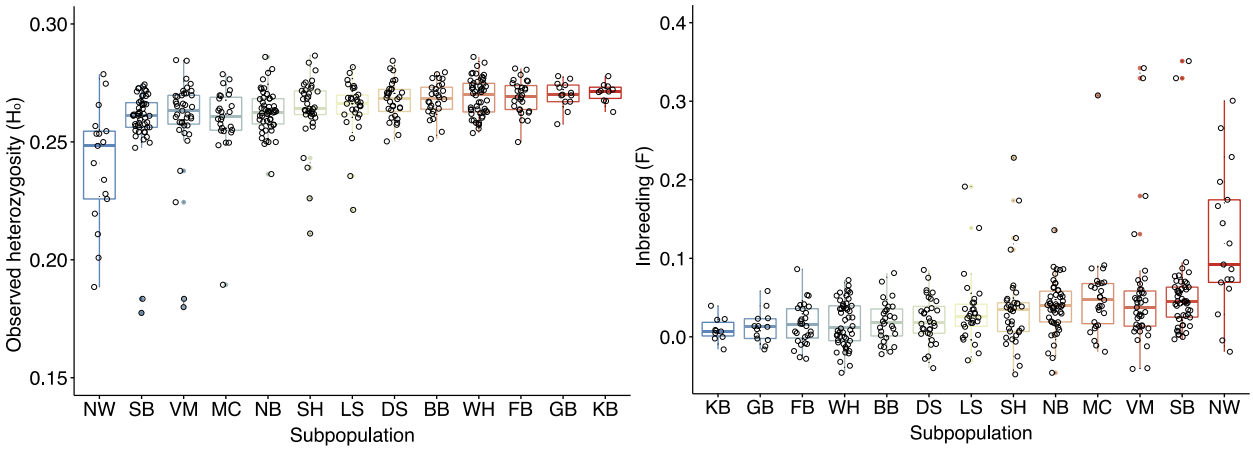

Figure S1: Individual heterozygosity (H_O) and inbreeding (F) averaged per subpopulation. Estimated on SNPs filtered for Hardy-Weinberg Equilibrium (N = 3,685 SNPs).

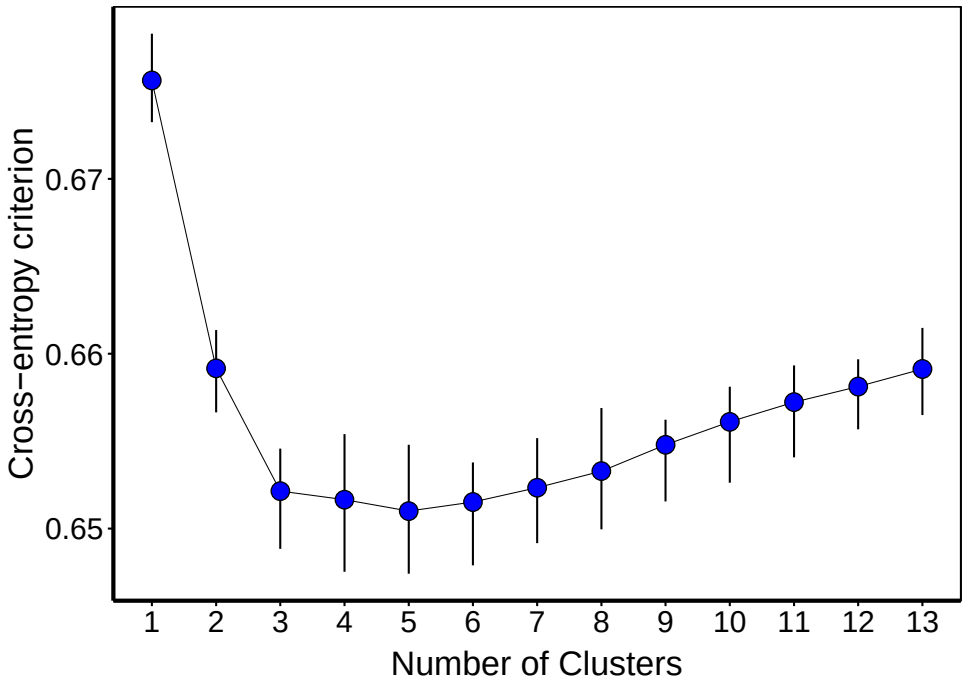

Figure S2. Cross-entropy score comparison of clustering assignment for 411 polar bears. The model with the lowest score (K=5) is considered to be the best fitting model.

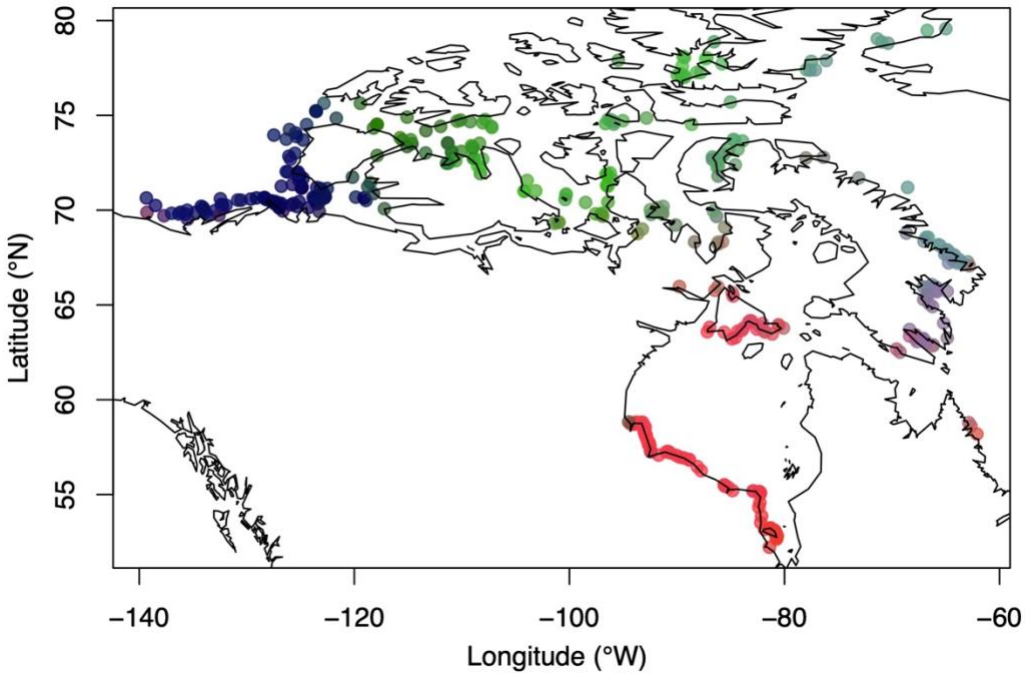

Figure S3. Translated principal component scores from the sPCA. Each point represents an individual (N = 411, N = 3,685 SNPs). Similar colors indicate shared genetic variation among individuals.

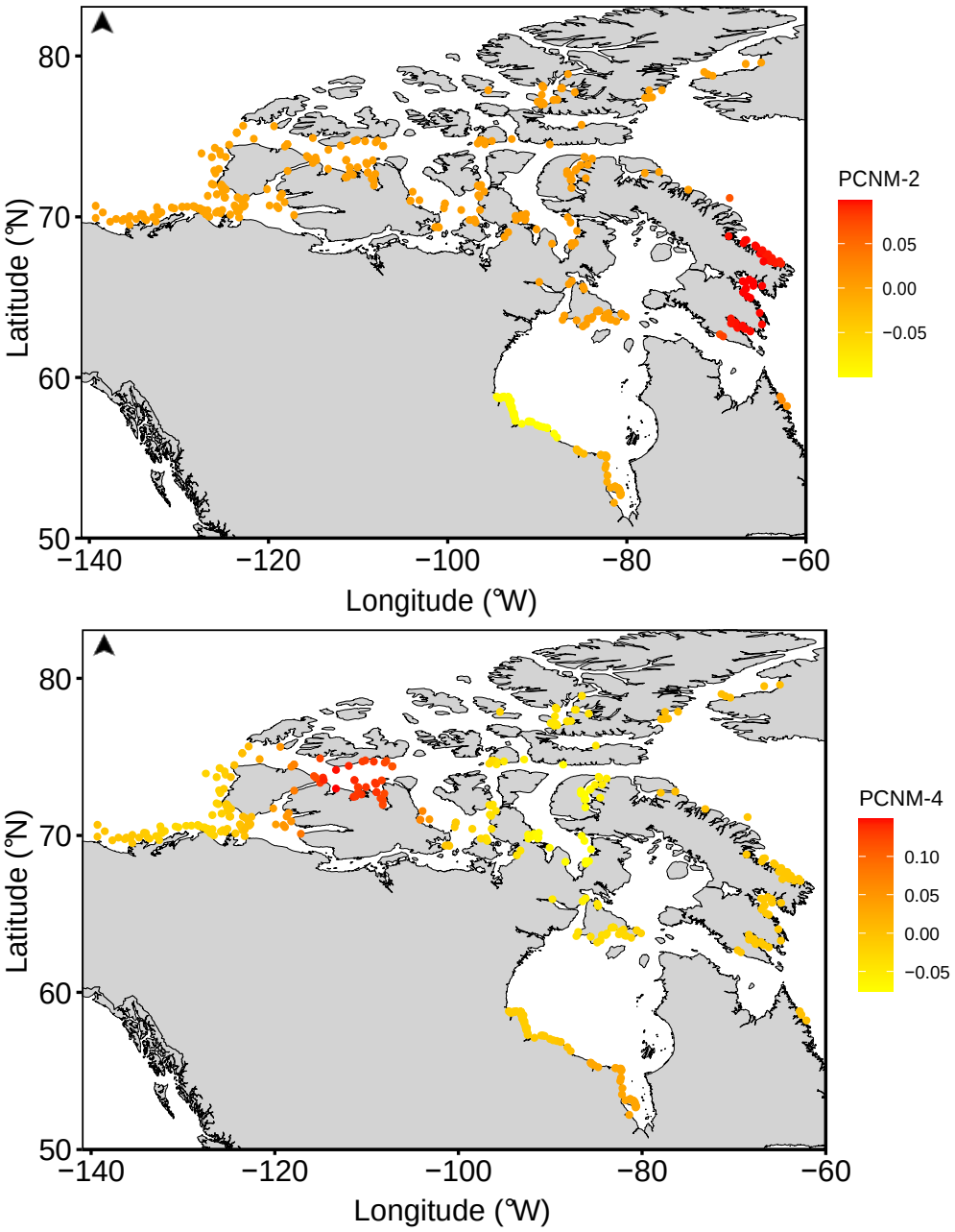

Figure S4. Map of spatial the top-ranked predictor variables from the Gradient Forest model with ice thickness and temperature. Individual sampling points are color coded by their PCNM value for each predictor. Top: Spatial scores (PCNM-2) that corresponded to variation in latitude and population abundance. Bottom: Variation in spatial scores (PCNM-4) that corresponded to maps of genetic structure among individuals.

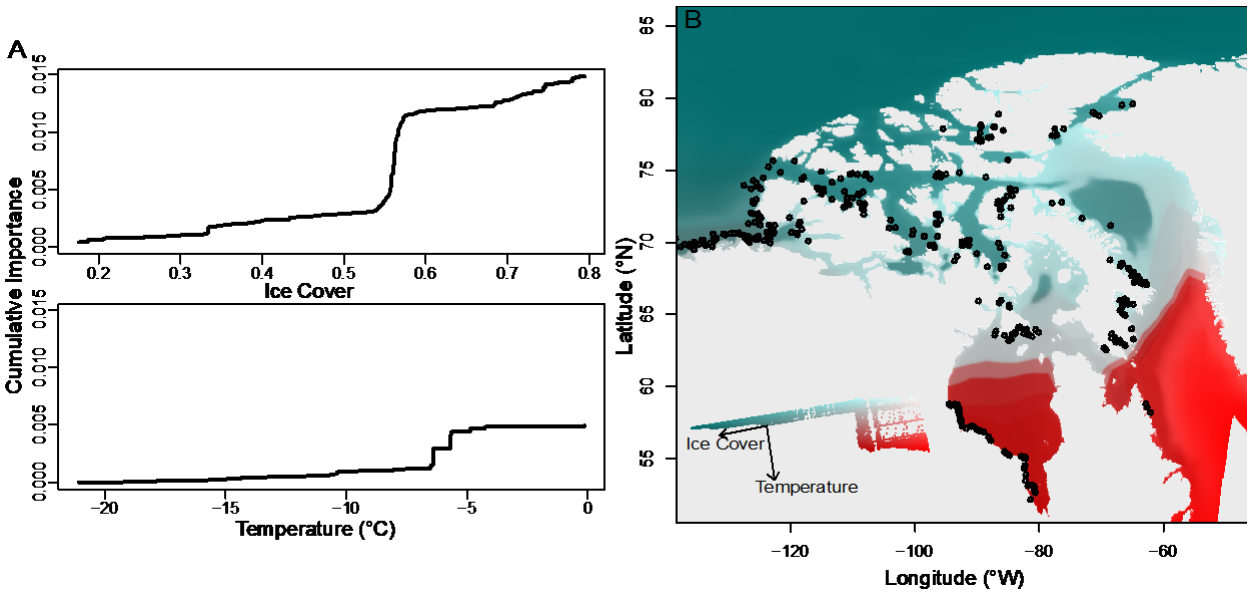

Figure S5. Allele turnover associated with ice cover and temperature in geographic and genetic space ($N = 411$ polar bears, 3,830 SNPs). A) Cumulative importance of allele turnover across all bears associated with the gradient in ice cover and temperature, where steeper slopes indicate greater turnover in allele frequencies. B) Gradient in genetic turnover derived from transformed ice thickness and temperature predictors. Locations with similar colours are predicted to harbour populations with similar genetic composition. Inset depicts the PCA biplot with arrows showing the direction and magnitude of the contributions from each predictor. Points depict sampled bears.

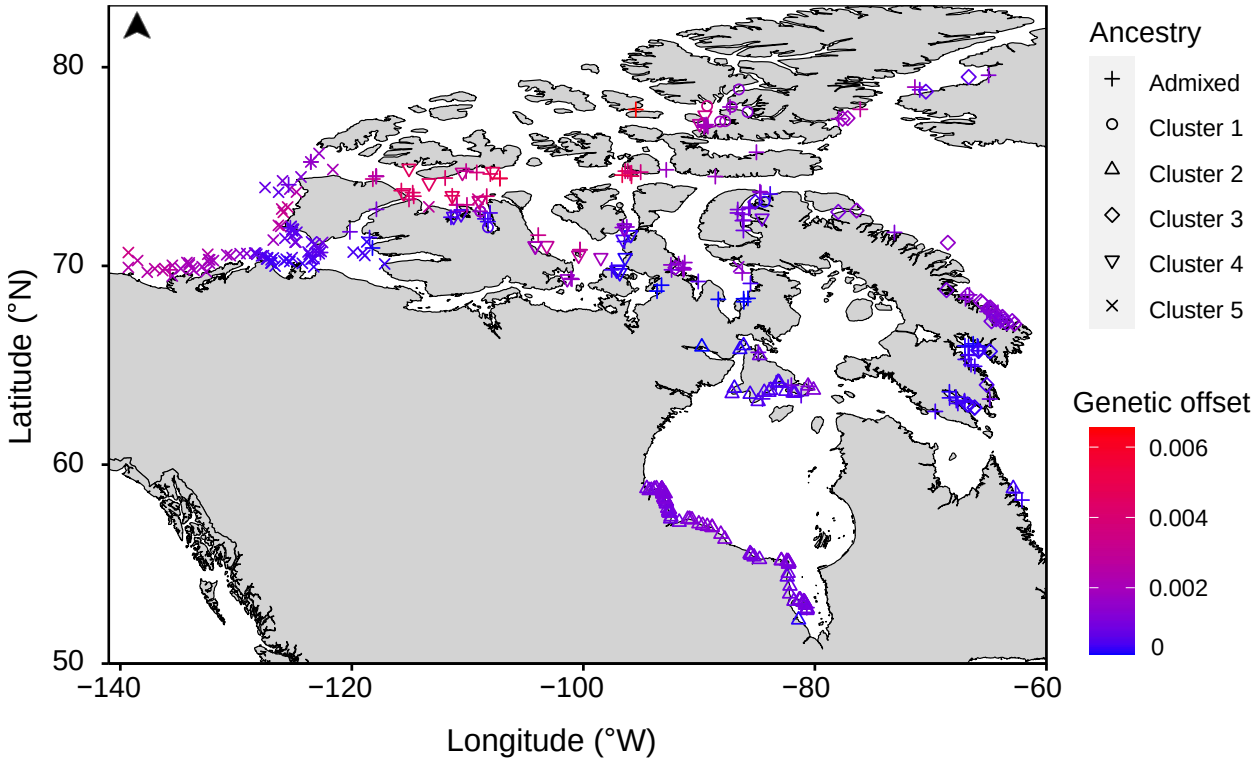

Figure S6. Map of individual genetic offset scores estimated from projected environments in 2100. Color gradient denotes offset values, with blue representing low values and red representing high values. Shapes denote ancestry assignments.

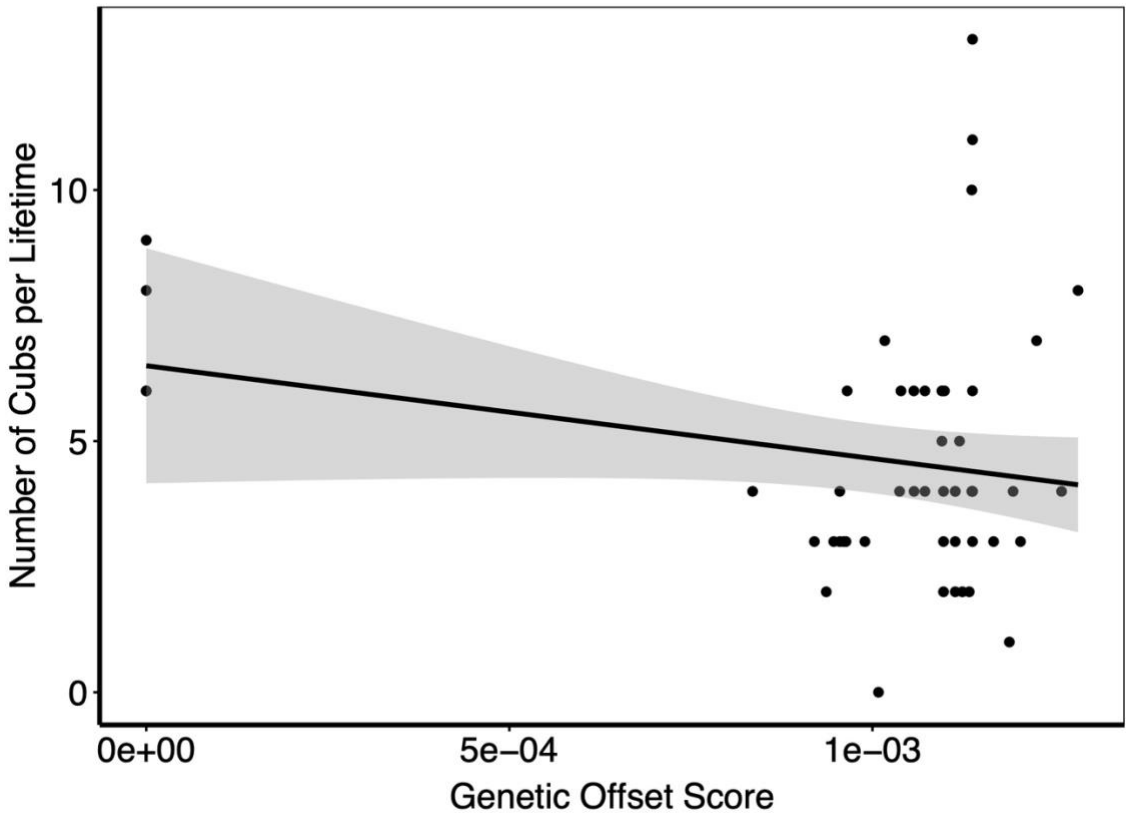

Figure S7. Genetic offset scores correlated negatively (p = 0.113) with lifetime reproductive success in 50 bears from the Western Hudson Bay subpopulation.