Population genomics reveals historical divergence and local adaptation in polar bears

René Malenfant[1], Catherine Cullingham[2], David Coltman[2], Evan Richardson[3], Markus Dyck[4], Nicholas Lunn[5], Martyn Obbard[6], Jodie Pongracz[7], Stephen Atkinson[8], Vicki Sahanatien[2], Kristin Laidre[9], Erik Born[10], Øystein Wiig[11], and Corey Davis[2]

[1]University of New Brunswick
[2]University of Alberta
[3]Environment and Climate Change Canada
[4]Government of Nunavut
[5]Environment and Climate Change Canada Prairie and Northern Region
[6]Ontario Ministry of Natural Resources and Forestry
[7]Government of the Northwest Territories
[8]Affiliation not available
[9]University of Washington Applied Physics Laboratory
[10]Gronlands Naturinstitut
[11]University of Oslo

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Abstract

Single-nucleotide polymorphisms (SNPs) have numerous advantages over microsatellites, including greater power to infer population structure and history and to detect loci undergoing selection. Here, we conduct the first continental-level SNP study of polar bears (Ursus maritimus) using genotypes from an array of 5441 SNP loci genotyped in 16–30 polar bears sampled in each of 16 geographic regions in Canada and West Greenland. Our study aimed to assess population history and genetic structure and to identify evidence of adaptive loci. Using these data, we confirmed the existence of four broad-scale genetic clusters in North America (FCT = 0.035) and identified nine fine-scale subclusters using more powerful spatial methods. An assessment of historical patterns of migration suggests that polar bears migrated into North America from the Beaufort Sea after the last glacial maximum. Using a conservative approach, we identified 17 loci that may represent adaptive variation, including one SNP in the 3' untranslated region of PDLIM5 (PDZ And LIM Domain 5), a gene involved in cardiovascular function, which has undergone substantial selection in polar bears since their divergence from brown bears. Outlier loci differentiated the Norwegian Bay genetic cluster more strongly from remaining clusters than did our complete dataset, suggesting possible adaptive differences in the High Arctic. Through careful consideration of SNP loci, sample inclusion, and analytical approaches, we provide a comprehensive picture of polar bear population structure at a continental level. This study provides a model for the analysis of wide-ranging species that can contribute to their conservation and management.

Introduction

With the development and increased accessibility to large-scale genotyping approaches for non-model organisms (e.g. RAD-Seq, exome capture, SNP arrays), new opportunities exist for the application of genomic data for conservation (Allendorf, Hohenlohe, & Luikart, 2010; Ouborg, Pertoldi, Loeschcke, Bijlsma, & Hedrick,

2010). While there is discussion in the field as to whether there is effective uptake among conservation practitioners (Shafer et al., 2015), there appears to be a consensus that genomic approaches will provide additional benefits to the field beyond traditional population genetics (Allendorf, Hohenlohe, & Luikart, 2010; Bradbury et al., 2015; Flanagan, Forester, Latch, Aitken, & Hoban, 2018; Funk, McKay, Hohenlohe, & Allendorf, 2012; Garner et al., 2016; McMahon, Teeling, & Höglund, 2014; Shafer et al., 2015). This includes improving parameter estimates (Allendorf, Hohenlohe, & Luikart, 2010; Ouborg, Pertoldi, Loeschcke, Bijlsma, & Hedrick, 2010; Primmer, 2009), fine-scale resolution of population clusters (Bradbury et al., 2015), and identifying locally adapted populations to highlight important units for conservation (Flanagan, Forester, Latch, Aitken, & Hoban, 2018; Funk, McKay, Hohenlohe, & Allendorf, 2012; McMahon, Teeling, & Höglund, 2014). Through the accurate estimation of important parameters, and identifying locally adapted units, we can use genomics to ensure resources are appropriately allocated. This is important because practitioners are under pressure to do more with less as threats to biodiversity increase (Naidoo et al., 2006).

One of the major threats to biodiversity is climate change, the effects of which are significantly impacting species in the Arctic (Turner & Overland, 2009). For example, polar bears (*Ursus maritimus*) have been listed as Vulnerable by the IUCN Polar Bear Specialist Group as a result of significant declines because of dwindling sea-ice habitat (Armstrup, 2003, Wiig et al., 2015). Polar bears are Holarctic marine mammals that are highly dependent on the sea ice as a platform for movement, hunting, and mating. Currently, 23,000 individuals are thought to exist in 19 subpopulations worldwide (Regehr et al., 2016); approximately 50–65% live in the 14 subpopulations lying partially or entirely within Canadian jurisdiction (Durner, Laidre, & York, 2018; Wiig et al., 2015).

Genomic approaches have not been used for the analysis of contemporary polar bear population structure at a continental level. To date, large-scale studies of polar bear genetic structure have used only 14–21 microsatellite loci (Malenfant et al., 2016; Paetkau et al., 1999; Peacock et al., 2015). These have shown four broad-scale genetic clusters of polar bears worldwide, which are all represented in North America by: the Beaufort Sea, the Canadian Arctic Archipelago, the Hudson Bay Complex (incl. the Foxe Basin, Hudson Bay and the coasts of Labrador and Newfoundland), and Norwegian Bay (Table 1). A number of previous studies have shown additional differentiation within Hudson Bay (Crompton, Obbard, Petersen, & Wilson, 2008; Crompton, Obbard, Petersen, & Wilson, 2014; Peacock et al., 2015; Viengkone et al., 2016), as well as east–west differentiation in the Canadian Arctic Archipelago (Malenfant et al., 2016), including the differentiation of the Gulf of Boothia subpopulation from the neighbouring M'Clintock Channel subpopulation (Campagna et al., 2013; Malenfant et al., 2016). A genomics approach to assessing neutral variation would provide a consensus of population structure to base conservation decisions (Bradbury et al., 2015; McCartney-Melstad, Vu, & Shaffer, 2018).

While neutral population structure is important information for directing conservation resources, the identification of locally adapted units is also important to ensure their inclusion in conservation efforts (Funk, McKay, Hohenlohe, & Allendorf, 2012). The most divergent cluster of polar bears occurs in Norwegian Bay: an isolated subpopulation of ˜200 individuals in the High Arctic (Taylor, Laake, McLoughlin, Cluff, & Messier, 2009), which Inuit harvesters have suggested are phenotypically distinct (Taylor et al., 2001). However, genome scans for divergent loci among polar bear genetic clusters have never been conducted, and the potential genetic basis for any phenotypic differentiation is unknown despite the development of methods to reliably test for local adaptation (e.g., Gautier, 2015; Luu, Bazin, & Blum, 2017; Whitlock & Lotterhos, 2015). A genomics approach will help determine whether any of the polar bear subpopulations harbour local adaptations.

Movement patterns for polar bears may be changing as a result of sea-ice loss, and understanding these patterns will be important for understanding future demographic changes. Two recent microsatellite studies drew differing conclusions regarding the potential movement response of polar bears to climate-change-induced sea-ice loss. Peacock et al. (2015) suggested that polar bears from the eastern Polar Basin (i.e., the Eastern Greenland, Barents Sea, Kara Sea, and Laptev Sea subpopulations) are migrating into the Canadian Arctic Archipelago to take refuge from climate change-induced habitat loss. A reanalysis of these

data attributed this high apparent immigration rate to non-convergence of the program BayesAss (Malenfant et al., 2016). However, the reanalysis had limited resolving ability because only 14 microsatellite loci were used, making it difficult to completely discount the possibility of high gene flow from the Polar Basin into the Archipelago or to identify other large-scale migrations. The use of high-resolution markers that provide more precise admixture estimates would help to further test for migration events (including into North America), which is important for determining how polar bear population dynamics are being affected by current climate change.

Of course, current patterns of substructure and migration are more informative in light of the population history (He, Edwards, & Knowles, 2013; Epps & Keyghobadi, 2015); however, the history of polar bear migration into North America is unknown. Polar bear–brown bear (*Ursus arctos*) divergence time is disputed (e.g., Hailer et al., 2012; Liu et al., 2014; Miller et al., 2012), but we know that the contemporary distribution of polar bears in North America was established only after the last glacial maximum (LGM) ˜20,000 years ago, which left most of the continent and the Arctic Basin uninhabitable (Bradley & England, 2008). The range of polar bears during the LGM has not been determined; however, the presence of polar bears' primary prey—ringed seals (*Pusa hispida*)—in caves of the Alaska Panhandle (i.e., Southeast Alaska) (Heaton & Grady, 2003), as well as the presence of polar bear mitochondrial haplotypes and X-linked variants among some Panhandle brown bears (Cahill et al., 2013), suggest that polar bears used the Northeast Pacific as a refugium during this period. However, mitochondrial haplotypes from modern polar bears are closer to Irish brown bears than to Panhandle brown bears (Edwards et al., 2011), and an Atlantic refugium is supported by polar bear subfossils from Scandinavia immediately predating and postdating the LGM (Ingólfsson & Wiig, 2009). Likewise, winter sea ice as far south as Spain (de Vernal et al., 2005) may have allowed for colonization across the Atlantic into North America. Recent methodological advances using SNP data allow for the determination of historical population divergences and subsequent migration events (Pickrell & Pritchard, 2012), though these have not yet been applied to polar bears.

In this study, we use a 9K Illumina BeadChip (Malenfant, Coltman, & Davis, 2015) to determine the current population structure and historical divergence of polar bears, and to identify evidence of local adaptation. Our SNP assay interrogates restriction-site associated DNA (RAD) SNPs—most of which are in non-coding DNA and are putatively neutral—and potentially adaptive transcriptomic SNPs developed from fat and blood allowing for the assessment of neutral and adaptive genetic variation. This study provides an estimation of polar bear history, and helps to clarify population structure and identify locally adapted subpopulations. This contribution gives wildlife managers important information for developing a conservation plan for this iconic Arctic species.

Materials and methods

SNP chip development and genotyping

The SNP chip development, sampling, and genotyping process has been described by René M. Malenfant et al. (2015). In brief, we used high-throughput transcriptome and RAD sequencing to develop a 9K Infinium iSelect HD BeadChip. Transcriptomic SNPs were detected in blood and fat samples of 10 bears from Western Hudson Bay (Genomic Resources Development Consortium et al., 2014), whereas RAD SNPs were developed from 38 bears from across their circumpolar range (Malenfant et al., 2015). To reduce effects of the SNP ascertainment process, RAD SNPs were selected without consideration of the frequency or subpopulation in which the SNP was detected in the ascertainment sample. In total, 3411 RAD SNPs and 2030 transcriptomic SNPs were found to be well-clustered and polymorphic. We used 107 SNPs that displayed X-linked inheritance to confirm the sex of all individuals. Genotype scores were highly reliable: no errors were detected among 14 duplicate samples. The full polar bear dataset comprised 1427 individuals genotyped at 5328 unique autosomal SNPs; 860 of these samples came from the Western Hudson Bay subpopulation, primarily for a quantitative genetics study (Malenfant, 2016).

Quality control

We used quality-control procedures similar to those of Jakobsson et al. (2008). First, to select a subset of individuals for this population genomics study, we excluded ten individuals whose genetic sex did not match their reported sex (Malenfant et al., 2015) and four additional individuals who had identical SNP (or microsatellite) genotypes to different bears, suggesting unknown duplicate sampling, sample labelling or laboratory errors. We excluded four samples collected from the Arctic Basin subpopulation from this analysis because sample size was inadequate to make inferences. We also excluded three Foxe Basin bears lacking sampling coordinates because it was unclear if they were sampled in northern or southern Foxe Basin. We excluded 101 individuals sampled prior to 1990, which we selected as a cutoff date for inclusion in our study. Because the presence of relatives can confound genetic clustering analyses (Rodriguez-Ramilo & Wang, 2012), we used KING 1.4 (Manichaikul et al., 2010) to generate a subset of individuals containing no first- or second-degree relatives (cf. Rosenberg, 2006). Finally, we used the*sample()* function in R 3.3.1 (R Core Team, 2016) to reduce the sample from each geographic sampling location to a maximum of 30 individuals, resulting in a total of 391 samples from 16 locations for the analyses (Table 1). These locations included subpopulations with partial or full Canadian jurisdiction ($N = 13$). For three of these subpopulations, two geographic regions were included. To ensure we obtained quality genotypes, samples that we chose were run on agarose gel, and were subject to spectrophotometry and floutometry to ensure they were of high quality molecular weight prior to genotyping.

Previous studies have shown north–south genetic differentiation in the Foxe Basin, Davis Strait and Southern Hudson Bay subpopulations (Crompton et al., 2008; Crompton et al., 2014; Malenfant et al., 2016; Peacock et al., 2015; Viengkone et al., 2016), so we treated Northern Foxe Basin, Southern Foxe Basin, Northern Davis Strait, Southern Davis Strait, Southern Hudson Bay and James Bay (in Southern Hudson Bay) as being distinct. The median collection date for the remaining 391 samples was 2008 (range: 1991–2012; Table 1).

We removed all SNPs that had call rate <0.9 or that had a minor allele frequency of <0.01 (cf. Huckins et al., 2014) among the unrelated individuals. Preliminary analyses suggested non-significant overall F_{IS} in the Baffin Bay, Southern Beaufort Sea, and southern Foxe Basin sampling locations. We used hweStrata 1.0 to perform exact stratified tests (Schaid, Batzler, Jenkins, & Hildebrandt, 2006) across Baffin Bay, Southern Beaufort Sea, and southern Foxe Basin to identify loci that deviated from Hardy–Weinberg equilibrium; however, no locus deviated significantly ($\alpha = 0.05$). Because Bayesian clustering methods assume that linkage disequilibrium (LD) is generated by population structure rather than background LD caused by physical linkage between loci, we generated an "LD-pruned dataset" from the filtered RAD SNPs, using pairwise LD pruning (–indep-pairwise 10 1 0.1) in a customized version of PLINK 1.07 (René M. Malenfant et al., 2015; Purcell et al., 2007). Unless otherwise indicated, all subsequent analyses used this LD-pruned RAD dataset of 2770 SNPs genotyped in 391 unrelated individuals. We used GenoDive 2.0b27 (Meirmans & Van Tienderen, 2004) to calculate genetic diversity statistics (using 1000 permutations to test for significance) and ADZE 1.0 (Szpiech, Jakobsson, & Rosenberg, 2008) to calculate allelic richness with a per-location missing-data tolerance of 1%, which resulted in the maximum possible sample size.

Population structure

To explore population structure using a non-model-based method, we used a principal component analysis (PCA) in adegenet 2.0.1 with default settings (Jombart, 2008; Jombart & Ahmed, 2011). The number of significant principal components (PCs) was determined using Velicer's minimum average partial test (Shriner, 2011; Velicer, 1976). We then performed Bayesian genetic clustering using BAPS 6.0, which also assesses the significance of admixture and is much faster than other Bayesian methods such as structure (Corander & Marttinen, 2006). Population structure was estimated in BAPS in three phases: first, the optimal number of genetic clusters ($K_{max} = 20$) was determined in a mixture analysis using stochastic partitioning (Corander, Marttinen, & Mäntyniemi, 2006); then, admixture coefficients for each individual were estimated by averaging their maximum *a posteriori* estimates obtained from each of 100 realizations of

allele frequencies simulated from the posterior distribution from mixture analysis (Corander & Marttinen, 2006); finally, a p -value for the significance of admixture for each individual was obtained by comparison to an empirical distribution of admixture coefficients for 200 simulated reference individuals from each cluster (generated by averaging over 20 realizations of simulated allele frequencies). Admixture plots were created using distruct 1.1 (Rosenberg, 2004). Mixture analysis determined four clusters as being optimal, which roughly corresponded to the Canadian Arctic Archipelago, the Beaufort Sea, the Hudson Bay Complex, and Norwegian Bay. The 323 individuals that were not significantly admixed (p [?] 0.05) were assigned to four cluster-specific datasets (n $_{\text{Archipelago}}$ = 121,n $_{\text{Beaufort}}$ = 53, n $_{\text{Hudson}}$ = 137, n $_{\text{Norwegian Bay}}$ = 12). We then estimated allelic richness and the private allelic richness for each of these cluster-specific datasets using the rarefaction method implemented in ADZE, using a per-cluster missing-data tolerance of 0.1%, which guaranteed the maximum possible sample size. Our cluster-specific datasets were used as the pre-defined populations for outlier analyses. (See below.)

To test for more subtle population structure, we used tess3r 1.10, which is more powerful than non-spatial methods because it incorporates geographical sampling information to produce accurate least-squares estimates of admixture coefficients (Caye, Jay, Michel, & Francois, 2016). We ran tess3r from K =1–20 for ten repetitions for each K -value and a tolerance threshold of 1x10^{-7}. The optimal K -value was determined with the cross-entropy criterion using cross-validation with 5% of genotypes masked.

We characterized the genetic diversity of polar bears across their range using an analysis of molecular variance (AMOVA; Excoffier, Smouse, & Quattro, 1992) in GenoDive, which, as a first step, uses$K$ -means clustering to generate hierarchical structure (Meirmans, 2012). To force all 16 sampling locations into the four major clusters identified by clustering of individuals in BAPS, we used $K = 4$ for K -means clustering. To determine pairwise genetic differentiation between locations for comparison with previous studies (R. M. Malenfant et al., 2016; Paetkau et al., 1999; Peacock et al., 2015), we then used a custom R script to calculate Reynolds' distance (Reynolds, Weir, & Cockerham, 1983), a coancestry estimator that assumes that populations diverge by drift without mutation, and Hudson'sF $_{\text{ST}}$ (Hudson, Slatkin, & Maddison, 1992), an unbiased measure of differentiation for SNPs that is robust to unequal sample sizes (Bhatia, Patterson, Sankararaman, & Price, 2013). Significance was assessed using 10,000 permutations. Finally we performed an assignment test in GenoDive (default settings, 1000 permutations) to identify recent migrants and the extent of admixture among the subpopulations.

Outlier detection

To identify RAD or transcriptomic loci that may have undergone selection, we used three recent approaches: BayPass 2.1 (Gautier, 2015), pcadapt 3.0.3 (Luu et al., 2017), and OutFLANK 0.1 (Whitlock & Lotterhos, 2015). Each of these methods takes a very different approach to outlier identification, and by looking for concordance between results, we hoped to reduce the number of false positives. In total, 4912 non-LD pruned loci were tested.

BayPass calculates the X^TX statistic (Gunther & Coop, 2013), which is analogous to$F$ $_{\text{ST}}$, but which accounts for genetic variance–covariance of the populations and differences in sample size because it is based on standardized allele frequencies. After calculating X^TX values for the original dataset, a pseudo-observed dataset (POD) of 1000 loci is created using the variance–covariance matrix estimated from the real data, andX^TX values are calculated for the POD. Empirical X^TX values from the POD are used as a null distribution; its 99$^{\text{th}}$ percentile is a suggested cutoff for identifying loci in the real dataset that may be undergoing selection. We used default settings for all steps.

pcadapt generates a vector for each SNP which contains az -score for each of the K PCs retained. The Mahalanobis distance for each SNP is calculated, and p -values are obtained assuming that distances are ?^{2}-distributed with$K$ degrees of freedom. We used default settings and retained five PCs (based on the results of Velicer's minimum average partial test described above).

OutFLANK assumes that F $_{\text{ST}}$ is ?^{2}-distributed with unknown degrees of freedom. Loci in the 5% tails of

the distribution of F_{ST}, which is calculated without a sample-size correction, are removed, then the degrees of freedom are estimated using maximum likelihood, and ap -value is obtained for each locus. We used the method of Francois, Martins, Caye, and Schoville (2016), which takes into consideration genomic inflation, to combine p -values from pcadapt and OutFLANK. Significance was assessed using a false-discovery rate (FDR) cut-off of $q < 0.1$.

We identified 19 loci as significant outliers (see Results). To test whether outlier loci were over-represented in any biological pathways, we assessed gene ontology (GO) enrichment using SNP2GO 1.0.5 (FDR = 0.1; Szkiba, Kapun, von Haeseler, & Gallach, 2014). GO information was obtained from BioMart's (Kasprzyk, 2011) ailMel1 gene set for panda (last accessed Sept. 4, 2014), and mapped onto NCBI *Ursus maritimus* Annotation Release 100.

Historical divergence

To examine historical divergence of polar bears from each sampling area and subsequent migration among them, we used TreeMix 1.12 (Pickrell & Pritchard, 2012), exploring 0–5 migration events. We rooted the tree using SNP chip genotypes obtained from a single grizzly bear (*Ursus arctos horribilis*) sampled from Kootenay National Park (British Columbia, Canada). Of the 2770 LD-pruned RAD SNPs, 2740 loci were genotyped in the grizzly bear sample, of which 94 loci were heterozygous. Because the TreeMix algorithm is sensitive to recent admixture and migration, we excluded admixed individuals based on the assignment test using GenoDive. After excluding all significantly admixed individuals and significantly cross-assigned individuals, 317 individuals remained for TreeMix analysis. We also attempted to determine current migration rates using BayesAss; however, the program did not converge (cf. Meirmans, 2014).

Results

SNP genotyping

After MAF-filtering and LD-pruning, 2770 RAD SNPs remained on 247 scaffolds representing 92.4% of the draft polar bear genome (Liu et al., 2014). Sample size per location ranged from 16 to 30 (Table 1). The inbreeding coefficient (G_{IS}) was significant in samples from 10 out of 16 locations (9 out of 16 after Holm correction (Holm, 1979)); however, in all cases but one, G_{IS}values were low ([?]0.02). Norwegian Bay displayed moderateG_{IS} (=0.05) consistent with the presence of immigrants near its southern border. (See below.) Allelic richness was slightly lower in among sampling sites in Norwegian Bay and the Hudson Bay Complex than in Canadian Arctic Archipelago or the Beaufort Sea (Table 1).

Population structure

We retained the first five PCs when examining population structure based on Velicer's minimum average partial test. Collectively, these PCs accounted for 8.2% of the observed genetic variation. Plots of PC 1 vs. PCs 2–5 are shown in Figure 1. PCs 1–3 distinguish the four primary clusters of polar bears identified by Paetkau et al. (1999); PCs 4 and 5 highlight east–west differentiation in the Archipelago (e.g., Malenfant et al., 2016) and north–south differentiation in the Hudson Bay Complex, including the divergence of James Bay from Southern Hudson Bay (Crompton et al., 2008).

BAPS identified four genetic clusters as being optimal, which correspond roughly to the Hudson Bay Complex, the Canadian Archipelago, the Beaufort Sea, and Norwegian Bay (Table 1 lists the sampling sites belonging to each cluster). Substantial admixture was observed in Davis Strait (particularly in northern Davis Strait), southern and western Norwegian Bay and in Viscount Melville Sound, with lower rates of admixture also observed in Gulf of Boothia (Figure 2). K -means clustering in GenoDive (using $K = 4$) generated clusters of geographic sampling areas concordant with those identified by BAPS. In an AMOVA,

genetic clusters accounted for 3.5% of total genetic variation ($F_{CT} = 0.035$) and subpopulations/sampling areas within clusters accounted for 1.0% of total genetic variation ($F_{SC} = 0.011$).

tess3r's cross-validation procedure suggested 5–8 genetic clusters were optimal (Figure 3; top-left panel); however, results for$K$ = 5–9 were plotted, because nine clusters captured all previously reported genetic differentiation amongst polar bears. The nine clusters correspond roughly to: 1) the Beaufort Sea (northern and southern); 2) the western Archipelago (Viscount Mellville Sound, M'Clintock Channel); 3) Gulf of Boothia; 4) the Eastern Archipelago (Lancaster Sound, Kane Basin, Baffin Bay); 5) Norwegian Bay; 6) southern Davis Strait (incl. Hudson Strait); 7) northern Foxe Basin; 8) Hudson Bay (southern Foxe Basin, Southern Hudson Bay, Western Hudson Bay); 9) James Bay. At $K = 10$, a discontiguous cluster containing parts of Lancaster Sound and part of Viscount Melville Sound appeared, and therefore K -values greater than 9 were not considered.

Diversity and differentiation

Patterns of allelic richness for SNPs revealed that overall richness was greatest in the Archipelago; however, few alleles were private to this cluster (Figure S1). Private allelic diversity was highest in the Beaufort Sea. Norwegian Bay had significantly lower levels of both allelic richness and private allelic richness than any other cluster. These observed patterns across clusters were not caused by our SNP ascertainment scheme, as rarefaction analyses using microsatellites revealed a similar pattern.

Pairwise Hudson's F_{ST} values and Reynolds' distances (ϑ_W) suggest low differentiation between sampling locations within a cluster (F_{ST}[?] 0.03, ϑ_W [?] 0.05) and low–moderate differentiation between clusters (F_{ST} [?] 0.10,ϑ_W [?] 0.12). The most divergent pair of locations was Norwegian Bay in the High Arctic vs. James Bay at the southernmost limit of the polar bear range. F_{ST} values did not seem to be affected by ascertainment scheme: corresponding values calculated using microsatellites were highly correlated and did not differ significantly in a paired t -test (Malenfant, 2016). Except for the Northern and Southern Beaufort Sea ($p = 0.26$), all other pairs were significantly differentiated (with or without a Holm correction); however, sampling across the border of these two subpopulations was also much more continuous than was the sampling across any of the other borders (Figure 2).

Migration rates

In an assignment test, 221/391 (=56.5%) of individuals were assigned to their home sampling location, and 359/391 (=91.8%) were assigned to a location within their broad genetic cluster. Rather than suggesting large-scale migration of bears amongst locations within a cluster, the low home-location assignment results likely reflect the inability of our genetic data to discriminate individuals from neighbouring locations. However, only 7/391 individuals (=1.8%) were significantly cross-assigned (i.e., significantly identified as migrants). These results were consistent with migrants that are apparent in the BAPS results (Figure 2). We found no substantial Polar Basin ancestry (represented by the Beaufort cluster in our sample) in the eastern Canadian Arctic Archipelago.

Outlier analysis

We identified 17 SNPs (three transcriptomic and 14 RAD) as significant outliers ($q < 0.1$) using the combined OutFLANK and pcadapt p -values (Figure 5; Table 4). Eight of the 17 SNPs were in a gene: The two top-ranked SNPs were both located in a 3' untranslated region (UTR); five SNPs were in an intron, and one SNP was in a long non-coding RNA. Another four SNPs were located within 10 kb of a gene, corresponding to LD of $r^2 = 0.25$–0.35 in polar bears (Malenfant et al., 2015).X^TX values for 16 of the 17 significant outlier loci also fell into the upper 1% tail of simulated neutral values calculated using BayPass; the remaining locus (88377_240) had the third highest p -value of all the putative outliers and was also the SNP most distant from any gene (147,780 bp downstream of the closest gene). Outlier SNPs better distinguished Norwegian Bay from the remaining genetic clusters than did the pruned RAD SNP dataset (Figure 6; cf. Figure 1). One transcriptomic SNP, scaffold62_6020088, located in the 3' UTR of the gene PDLIM5 (PDZ and LIM

domain 5) had a substantially lower p -value than any other locus ($p = 1.5\times10^{-9}$). The globally minor allele of this SNP reached a frequency of 0.91 in the Norwegian Bay cluster but did not exceed 0.10 elsewhere. Likewise, for the second-most significant SNP (RAD SNP 85370_147; $p = 3.9\times10^{-7}$) in the 3' UTR of the gene SPECC1 (sperm antigen with calponin homology and coiled-coil domains 1), the globally minor allele had a frequency of >0.70 in Norwegian Bay, but <0.1 elsewhere (incl. a frequency of 0.0 in Hudson Bay). In both cases, the Kootenay grizzly was homozygous for the allele that was most common in Norwegian Bay. SNP2GO did not detect any significant GO enrichment using all 17 outlier loci as candidates or using the 16 loci recognized consistently across methods (i.e., excluding 88377_240).

Historical migration

After removing significantly cross-assigned and admixed individuals, TreeMix generated a tree showing dispersal from the Beaufort Sea through the Archipelago into the Hudson Bay Complex (Figure 4). The tree also suggests that Norwegian Bay has undergone substantial drift since its divergence from its neighbouring Archipelago sampling locations. The single migration event in the tree was from the Southern Beaufort Sea into Viscount Melville Sound (weight = 0.40, $p< 1\times10^{-10}$), which is consistent with observed admixture in Viscount Melville Sound, and which may have resulted from residual admixture in individuals that were retained because their admixtures coefficients failed to reach statistical significance. We chose to display only one migration event, because allowing for additional migration suggested gene flow from James Bay into grizzly bears (Reich, Thangaraj, Patterson, Price, & Singh, 2009), and which may represent an artefact caused by cross-species application of the grizzly bear on the SNP array. TreeMix results including a single-migration event explained 98.8% of the variance in the data.

Discussion

Our genomic analysis of polar bears has increased our understanding of this iconic Arctic species. We have been able to provide an understanding of population history, assess both large-scale and fine-scale population structure, estimate current levels of migration, and identify locally adapated populations. This information will be important for the future management and conservation of the polar bear, a species that is particularly vulnerable to loss of critical sea ice habitat as a result of rapid climate change (Hunter et al., 2010; Wiig et al., 2015).

Neutral population structure

Our study supports the primary findings of previous population genetics studies of polar bears that have used low-resolution microsatellite marker sets (Malenfant et al., 2016; Paetkau et al., 1999), as well as our own preliminary population genetics study using these SNPs on a subset of six individuals per subpopulation (Malenfant et al., 2015). All of the clustering methods (BAPS, PCA, and tess3r) detected the four major genetic clusters of polar bears in North America, corresponding to the Hudson Bay Complex, the Canadian Arctic Archipelago, the Beaufort Sea, and Norwegian Bay. Additonal fine-scale clusters were identified using the more powerful spatial method of tess3r, which simultaneously detected all genetic clusters among North American polar bears that have previously been reported (Campagna et al., 2013; Crompton et al., 2008; Crompton et al., 2014; Malenfant et al., 2016; Viengkone et al., 2016). All subpopulations (including those subdivided into two sampling locations constructed for this study: northern and southern Davis Strait, northern and southern Foxe Basin, and James Bay and southern Hudson Bay) were significantly differentiated from each other, except for the Northern and Southern Beaufort Sea. The lack of distinction between these subpopulations may be caused by our continuous sampling distribution across their management boundary.

Overall, the four major regions were slightly–moderately differentiated ($F_{\mathrm{CT}} = 0.035$), and demarcations between clusters align with geographical features—such as the presence of land or thick multiyear ice. Norwegian Bay is surrounded by islands to the north, south, and east, and by polynyas in the south and thick ice to

the west, which limit exchange with neighbouring subpopulations (Taylor et al., 2001). The Beaufort Sea and the Archipelago are separated by dense multiyear ice, which forms a barrier to movement (Bethke, Taylor, Amstrup, & Messier, 1996). However, there is some overlap of bears from the Northern Beaufort Sea and Viscount Melville Sound when individuals mix on the pack ice together (Taylor et al., 2001), thus resulting in the admixture in Viscount Melville Sound observed in our study. The Hudson Bay Complex is separated from the Archipelago by land to the north and east. Substantial Hudson Bay–Archipelago admixture was observed in northern Davis Strait, corresponding to observed movements between southern and northern Davis Strait and between northern Davis Strait and Baffin Bay (Peacock, Taylor, Laake, & Stirling, 2013).

Adaptive population structure

Using a conservative approach, we detected 17 putative outlier loci, indicating that divergent selection may have occurred between polar bear genetic clusters across the North American Arctic, although it is difficult to rule out past demographic events such as bottlenecks and range expansions (e.g., Hofer, Ray, Wegmann, & Excoffier, 2009; Lotterhos & Whitlock, 2014). Outlier loci distinguished Norwegian Bay more strongly from remaining clusters than did our RAD SNP dataset, and lower allelic richness and private allelic richness (as seen in rarefaction analyses) suggest the loss of genetic diversity owing to inbreeding and drift. Lack of significant GO enrichment for outlier SNPs suggests that if selection is occurring, it is not targeting genes in a subset of pathways, or that the gene coverage of our SNP panel is inadequate to detect this. However, the top two outlier loci are of particular interest: both are in 3' UTRs, which contain regions that regulate gene expression (Matoulkova, Michalova, Vejtesek, & Hrstka, 2012).

The top-ranked SNP (scaffold62_6020088) is in the gene PDLIM5, which is expressed in striated muscle, is believed to play a role in heart development by modulating cardiomyocyte expansion (Bang et al., 2014), and which has been associated with dilated cardiomyopathy in mice (Cheng et al., 2010). Since their divergence with brown bears, cardiomyopathy-related genes have experienced the strongest selection in polar bears, possibly causing a reorganization of the circulatory system related to selective pressure for long-distance swimming (Liu et al., 2014). The brown bear allele is found at high frequency in Norwegian Bay, we suggest it is because of the lack of long-distance swimming or migration in this subpopulation: as an isolated region characterized by thick multiyear ice, long-range swimming is generally unnecessary as most individuals restrict themselves to small bays, fiords, and coastal tide cracks in the east (Taylor et al., 2001; Taylor et al., 2009). Therefore—as opposed to elsewhere in their range—there may have been little selection in Norwegian Bay for genes related to the cardiovascular system. The second-highest-ranked SNP (85370_147) is in the gene SPECC1, which is highly expressed in the testes and likely produces a sperm antigen (Sang, Fath, & Giordano, 2004). The grizzly bear allele is frequent among Norwegian Bay bears, and it is possible that the isolation and persistence of the Norwegian Bay cluster (in the face of some observed migration and admixture) is partially attributable to immunological subfertility related to anti-sperm antibodies, which has been posited as a cause of postmating, prezygotic isolation (Howard, Palumbi, Birge, & Manier, 2009).

Norwegian Bay is expected to be one of the last Arctic sea-ice areas and may become a refugium for polar bears if climate change continues (Derocher, 2012); however, it has not been surveyed since 1997 (when our samples were collected), and the current status of this unique genetic cluster is unknown. Because of rapid LD decay in polar bears (Malenfant et al., 2015), our limited scan for differentiated loci is also unlikely to have captured the full array of potentially adaptive differences among subpopulations. Because local adaptation is considered when defining evolutionarily significant units (e.g., Crandall, Bininda-Emonds, Mace, & Wayne, 2000; Waples, 1991) and designatable units for conservation under Canadian law (COSEWIC, 2015), the potential adaptive divergence between Norwegian Bay and the other subpopulations needs to be considered. Further tests using more recent samples should be conducted to determine the degree to which Norwegian Bay may be locally adapted and reproductively isolated or has merely been subject to loss of adaptive diversity.

Polar bear migration

Although polar bears are capable of dispersing long distances (e.g., Durner & Amstrup, 1995), evidence of long-distance migration between the four major genetic clusters was limited in our data. We detected a single (male) migrant from the Beaufort Sea (or possible from elsewhere in the Polar Basin genetic cluster) in the Gulf of Boothia, and a small number of individuals of Norwegian Bay ancestry who had apparently migrated to the neighbouring Lancaster Sound and Kane Basin subpopulations. Amongst our samples from northern Davis Strait, Baffin Bay, and Kane Basin, which are the most likely subpopulations to receive immigrants from the eastern Polar Basin, and which were very recently sampled (median years of collection: 2010–2012), we did not detect any Polar Basin immigrants or any significant ancestry from the global Polar Basin cluster (which is reflected in our sample by the Beaufort Sea subpopulations). Although our conclusion would be bolstered by further sampling from the Eastern Polar Basin (e.g., Barents Sea, Eastern Greenland), there is no evidence in this study to suggest that the Canadian Arctic Archipelago is genetically or demographically linked with the Eastern Polar Basin. Limited migration among the four clusters suggests they should currently be managed as independent units.

Historical migration of polar bears into North America

Our TreeMix results suggest that polar bears populated North America from the northwest, migrating from the Beaufort Sea through the Canadian Archipelago into the High Arctic and Baffin Bay, then south through Davis Strait and into the Hudson Bay Complex. Based on the oldest known Canadian subfossil—undated Pleistocene remains from Baillie Island, Northwest Territories (Vincent, 1989)—polar bears were present in the Beaufort Sea by the late Pleistocene (i.e., [?]11,700 years ago), and their subsequent migration into North America would be consistent with the breakup sequences of the Laurentide and Innuitian ice sheets (Dyke, 2004). Ice sheets had receded in most of the Archipelago and Norwegian Bay 9500 years ago and in most of Hudson Bay by 8400 years ago (Dyke, 2004), making the regions habitable for polar bears and their prey. However, our sampling did not include bears from northern Europe or Asia, and this question should be re-examined using global sampling.

Conclusion

Genomic data are increasingly being used to study wildlife populations, but the uptake to conservation research has been slow (or unrecognized Garner *et al.* 2016). Here we have developed a SNP dataset that is capable of examining a range of important questions for the conservation and management of polar bears. While our current study has been limited to the Canadian population, this encompasses well over half of the global population. Through careful consideration of SNP ascertainment, sample inclusion, and analytical approaches, we have provided a comprehensive overview of the status of polar bear subpopulations at a continental scale. The resources we have developed can be applied to a global analysis of polar bear subpopulations to develop a comprehensive management strategy that transcends geo-political boundaries.

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Data Accessibility

The data that support the findings of this study (e.g., SNP genotypes for all 391 polar bears plus the Kootenay grizzly and lat/lon coordinates of individuals where known) are openly available in Dryad at https://doi.org/10.5061/dryad.rbnzs7h7m

Author Contributions

RMM conducted all analyses. CSD conceived the initial study design and prepared samples for genotyping. RMM, CSD, and DWC collaborated in determining the nature of the analyses. ESR, MGD, NJL, MO, JP, SNA, VS, KLL, ØW, and EWB provided samples and support, and they assisted in interpretation of results. RMM and CIC drafted the manuscript. All authors read and approved the final manuscript.

Table 1. Summary statistics for LD-pruned SNPs in each of 16 sampling locations; the officially recognized Davis Strait, Foxe Basin, and Southern Hudson Bay subpopulations have been further subdivided into northern and southern areas based on previous genetic studies. The broad-scale genetic clusters ("Clusters") have been included for reference. n = sample size; YOC = median year of collection; R (32) = allelic richness calculated in ADZE using a standardized sample size of 32 gene copies; H_O = observed heterozygosity; H_E = expected heterozygosity; G_{IS} = inbreeding coefficient. Significant G_{IS} values ($p < 0.05$, determined using 1000 permutations) are bolded.

Sampling location	**Clusters**	n	YOC	R**(32)**	$H_{\mathbf{O}}$	$H_{\mathbf{E}}$	$G_{\mathbf{IS}}$
Baffin Bay (BB)	Archipelago	25	2010	1.82	0.231	0.232	0.002
Davis Strait – northern (nDS)	Archipelago	27	2010	1.82	0.230	0.232	**0.008**
Davis Strait – southern (sDS)	Hudson Bay	21	1993	1.79	0.223	0.227	**0.017**
Foxe Basin – northern (nFB)	Hudson Bay	30	2008	1.78	0.219	0.224	**0.020**
Foxe Basin – southern (sFB)	Hudson Bay	30	2010	1.76	0.222	0.222	0.001
Gulf of Boothia (GB)	Archipelago	24	2010	1.83	0.232	0.233	**0.006**
Kane Basin (KB)	Archipelago	22	2012	1.82	0.233	0.235	0.006
Lancaster Sound (LS)	Archipelago	28	2010	1.82	0.229	0.232	**0.013**
M'Clintock Channel (MC)	Archipelago	22	2000	1.79	0.226	0.230	**0.018**
Northern Beaufort Sea (NB)	Beaufort Sea	25	2005	1.81	0.231	0.232	0.002
Norwegian Bay (NW)	Norwegian Bay	17	1997	1.74	0.201	0.212	**0.052**
Southern Beaufort Sea (SB)	Beaufort Sea	27	2005	1.80	0.229	0.230	0.004
Southern Hudson Bay – proper (SH)	Hudson Bay	30	2007	1.73	0.218	0.220	0.007
Southern Hudson Bay – James Bay (JB)	Hudson Bay	16	2008	1.72	0.213	0.218	**0.024**
Viscount Melville Sound (VM)	Archipelago	17	2010	1.82	0.230	0.233	**0.013**
Western Hudson Bay (WH)	Hudson Bay	30	2000	1.73	0.215	0.220	**0.020**

Table 2. Hierarchical AMOVA for 391 polar bears from 16 sampling locations grouped into four regions identified by K -means clustering of locations in GenoDive.

Source of variation	**% variance**	F**-statistic**	F**-value (95% C.I.)**
Within individuals	94.4%	F_{IT}	0.056 (0.054–0.059)
Among individuals	1.1%	F_{IS}	0.012 (0.009–0.014)
Among locations	1.0%	F_{SC}	0.011 (0.011–0.011)
Among clusters	3.5%	F_{CT}	0.035 (0.033–0.037)

Table 3. Pairwise Hudson's F_{ST} values (below diagonal) and Reynolds' distances (above diagonal). Location abbreviations are as in Table 1. Significance was assessed using 10,000 permutations, and *non-significant* values are indicated with asterisks. Colouring indicates each of the four clusters identified by$K$ -means clustering in GenoDive; Beaufort sea – red, Norwegian Bay – orange, Archipelago – green, Hudson Bay – blue.

	SB	**NB**	**NW**	**VM**	**MC**	**GB**	**LS**	**KB**	**BB**	**nDS**	**sDS**	**nFB**	**sFB**	**WH**	**SH**	**JB**
SB	–	0.02*	0.09	0.05	0.06	0.06	0.05	0.05	0.06	0.06	0.07	0.07	0.08	0.09	0.09	0.10
NB	0.00*	–	0.09	0.04	0.06	0.05	0.05	0.05	0.05	0.05	0.07	0.07	0.08	0.08	0.09	0.10
NW	0.07	0.07	–	0.08	0.08	0.07	0.06	0.06	0.08	0.08	0.09	0.10	0.11	0.11	0.11	0.12
VM	0.02	0.02	0.05	–	0.04	0.04	0.04	0.04	0.05	0.05	0.07	0.07	0.08	0.08	0.09	0.10
MC	0.04	0.04	0.05	0.01	–	0.04	0.03	0.04	0.04	0.05	0.06	0.06	0.07	0.08	0.08	0.09
GB	0.04	0.03	0.05	0.02	0.01	–	0.03	0.03	0.03	0.03	0.04	0.04	0.05	0.05	0.06	0.07
LS	0.03	0.03	0.04	0.01	0.01	0.01	–	0.02	0.02	0.03	0.05	0.05	0.06	0.06	0.07	0.08
KB	0.03	0.03	0.04	0.02	0.02	0.01	0.00	–	0.02	0.03	0.05	0.05	0.06	0.07	0.07	0.08
BB	0.04	0.03	0.05	0.02	0.02	0.01	0.01	0.00	–	0.03	0.04	0.05	0.05	0.06	0.06	0.07
nDS	0.04	0.04	0.06	0.03	0.03	0.01	0.01	0.01	0.01	–	0.03	0.03	0.04	0.04	0.04	0.06
sDS	0.05	0.05	0.07	0.04	0.04	0.02	0.03	0.03	0.02	0.01	–	0.03	0.03	0.04	0.04	0.05
nFB	0.06	0.05	0.08	0.05	0.04	0.02	0.03	0.03	0.03	0.01	0.01	–	0.03	0.03	0.03	0.05
sFB	0.06	0.06	0.09	0.05	0.05	0.03	0.04	0.04	0.04	0.02	0.01	0.01	–	0.02	0.02	0.04
WH	0.07	0.07	0.09	0.06	0.06	0.03	0.05	0.05	0.04	0.03	0.02	0.01	0.00	–	0.02	0.04

	SB	NB	NW	VM	MC	GB	LS	KB	BB	nDS	sDS	nFB	sFB	WH	SH	JB
SH	0.07	0.07	0.09	0.06	0.06	0.04	0.05	0.05	0.04	0.03	0.02	0.02	0.00	0.00	–	0.03
JB	0.08	0.07	0.10	0.07	0.07	0.04	0.06	0.05	0.05	0.03	0.03	0.03	0.02	0.02	0.01	–

Table 4. Seventeen SNPs identified as significant outliers ($q < 0.1$) using combined p -values from OutFLANK and pcadapt. A checkmark in the rightmost column indicates whether a SNP also fell into the upper 1% tail of simulated X^TX values in BayPass. Protein roles and mutation effects were taken from GeneCards (www.genecards.org; last accessed: Nov. 22, 2016).

SNP	**Type**	**Position (scaffold: bp)**	**Nearest gene**	**Protein role (*or mutation effect)**	**Gene feature located in (or distance from gene)**	p**-value**	**In 1% tail of X^TX**
scaffold62_-6020088	Transcriptomic	62: 6020088	PDLIM5	Heart development	3' UTR	1.5×10^{-9}	
85370_147	RAD	174: 2025836	SPECC1	Sperm antigen	3' UTR	3.9×10^{-7}	
87557_138	RAD	160: 836356	MCPH1	*Microcephaly	86,891 bp upstream	2.7×10^{-6}	
16421_111	RAD	80: 3930568	CD82	*Cancer (esp. prostate)	Intron	7.1×10^{-6}	
scaffold29_-8739023	Transcriptomic	29: 8739023	TMED4	TNF signaling	272 bp downstream	1.1×10^{-5}	
75533_92	RAD	85: 4212523	SLC15A5	Symporter	34,296 bp downstream	2.6×10^{-5}	
97766_277	RAD	130: 1438494	LOC103661688	N/A (lncRNA)	31,658 bp upstream	2.9×10^{-5}	
25548_115	RAD	17: 5826726	ATP8A1	Phospholipid translocation	Intron	4.4×10^{-5}	
scaffold94_-1529937	Transcriptomic	94: 1529937	ACER2	Sphingolipid metabolism	1525 bp downstream	2.2×10^{-4}	
129937_-226	RAD	98: 6537390	LOC103675794	N/A (lncRNA)	N/A	3.5×10^{-4}	
124135_-183	RAD	35: 562475	NABP2	DNA repair	194 bp downstream	4.6×10^{-4}	
124534_-129	RAD	67: 3540470	ISX	Vitamin A metabolism	23,238 bp upstream	5.6×10^{-4}	
88689_94	RAD	65: 10384665	TMEM150C	Transmembrane protein	4933 bp downstream	6.4×10^{-4}	
64159_205	RAD	168: 168381	MRVI1	Platelet activation	Intron	7.5×10^{-4}	
88377_240	RAD	30: 11311226	ZNF804B	Gene expression	147,780 bp downstream	7.8×10^{-4}	
133814_91	RAD	29: 8805815	NUDCD3	Dynein chain stabilization	Intron	1.0×10^{-3}	

SNP	Type	Position (scaffold: bp)	Nearest gene	Protein role (*or mutation effect)	Gene feature located in (or distance from gene)	p-value	In 1% tail of X^TX
12566_120	RAD	25: 8999569	PCDH7	Platelet degranulation	Intron	1.3×10^{-3}	

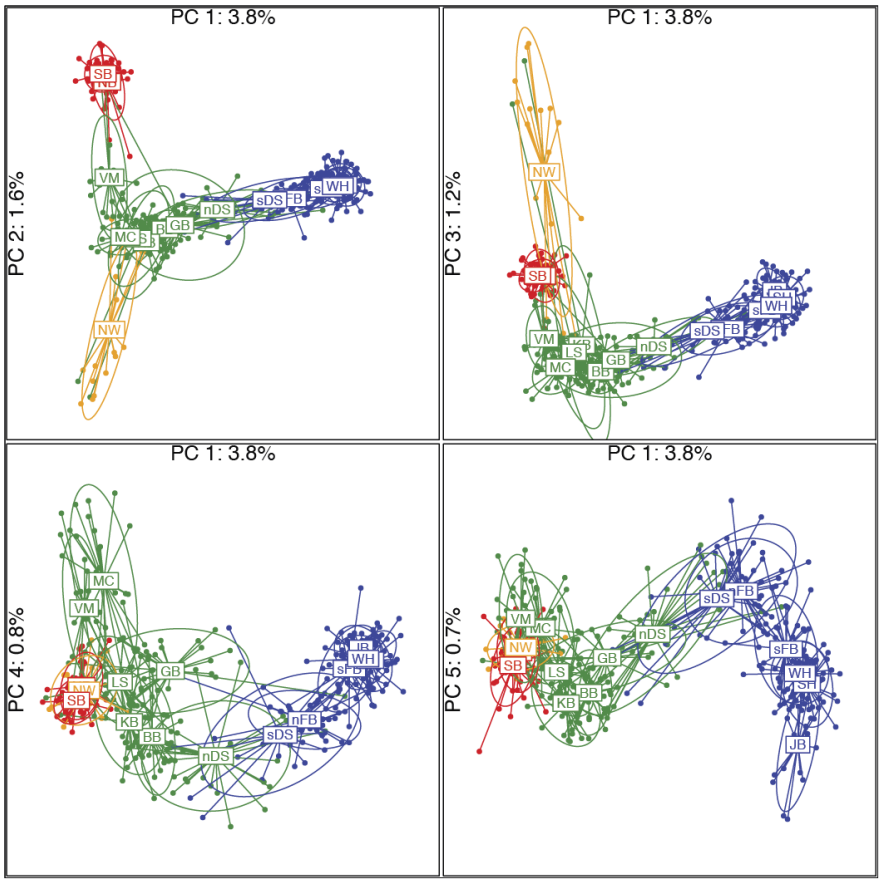

Figure 1. Principal component analysis of 391 polar bears; principal components 1–5. Sampling location abbreviations are as in Table 1, and locations are colour-coded according to the four major genetic clusters identified by K -means clustering in GenoDive (Beaufort Sea – red, Norwegian Bay – orange, Archipelago – green, Hudson Bay – blue). Inertia ellipses are drawn using default settings, such that approximately 67% of all individuals sampled in each location are contained in the ellipse.

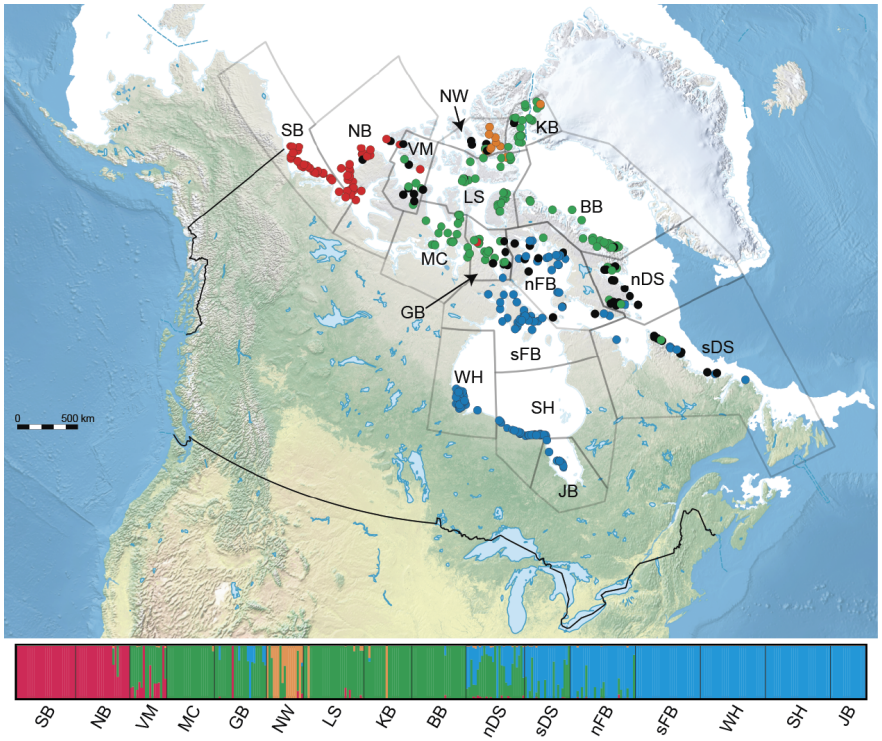

Figure 2. Sampling locations and cluster membership for 388 of the 391 polar bears used in this analysis (top); for the remaining three individuals, sampling coordinates were unavailable. Individuals are colour-coded by genetic cluster according to the BAPS clustering results for $K = 4$ (bottom; Beaufort Sea – red, Norwegian Bay – orange, Archipelago – green, Hudson Bay – blue). Samples coloured black in the map were significantly admixed according to BAPS ($p< 0.05$). Sea-ice extent during the breeding season is shown using measurements for April 15, 2008 (Fetterer, Savoie, Helfrich, & Clemente-Colón, 2010, updated daily). Sampling location name abbreviations are as in Table 1.

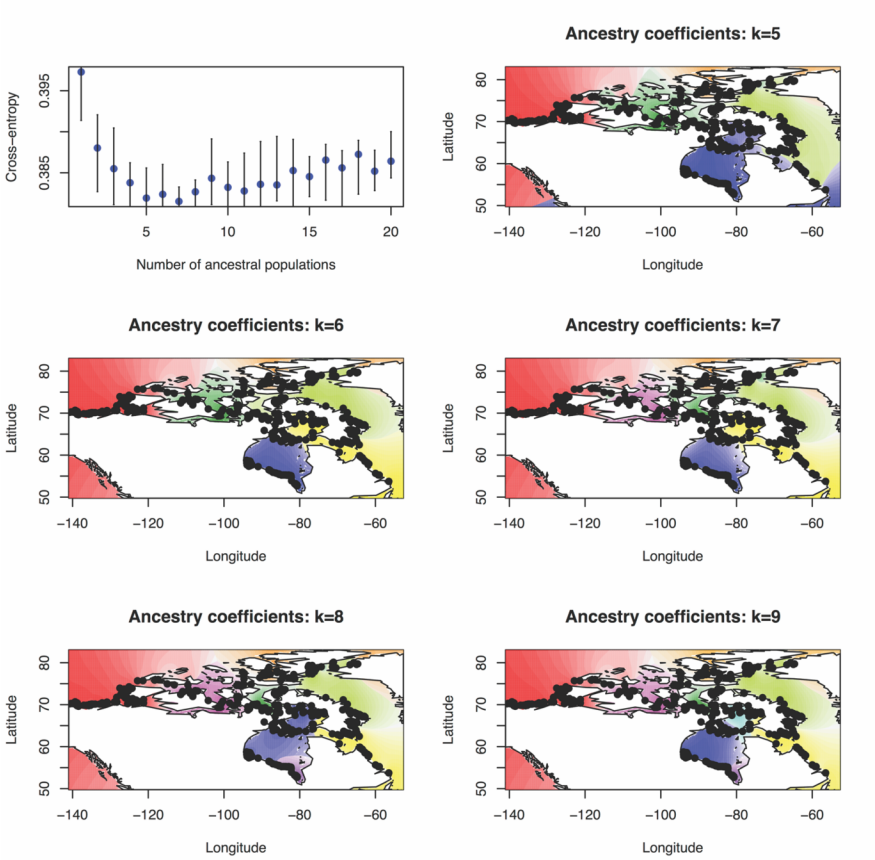

Figure 3. tess3r results. The top-left panel shows the cross-entropy for ten repetitions of each K -value for K = 1–20. The remaining panels show the genetic clusters generated by tess3r assuming K = 5–9. Each of the 388 black points represents a polar bear; the remaining three individuals that lacked sampling coordinates were omitted from this analysis.

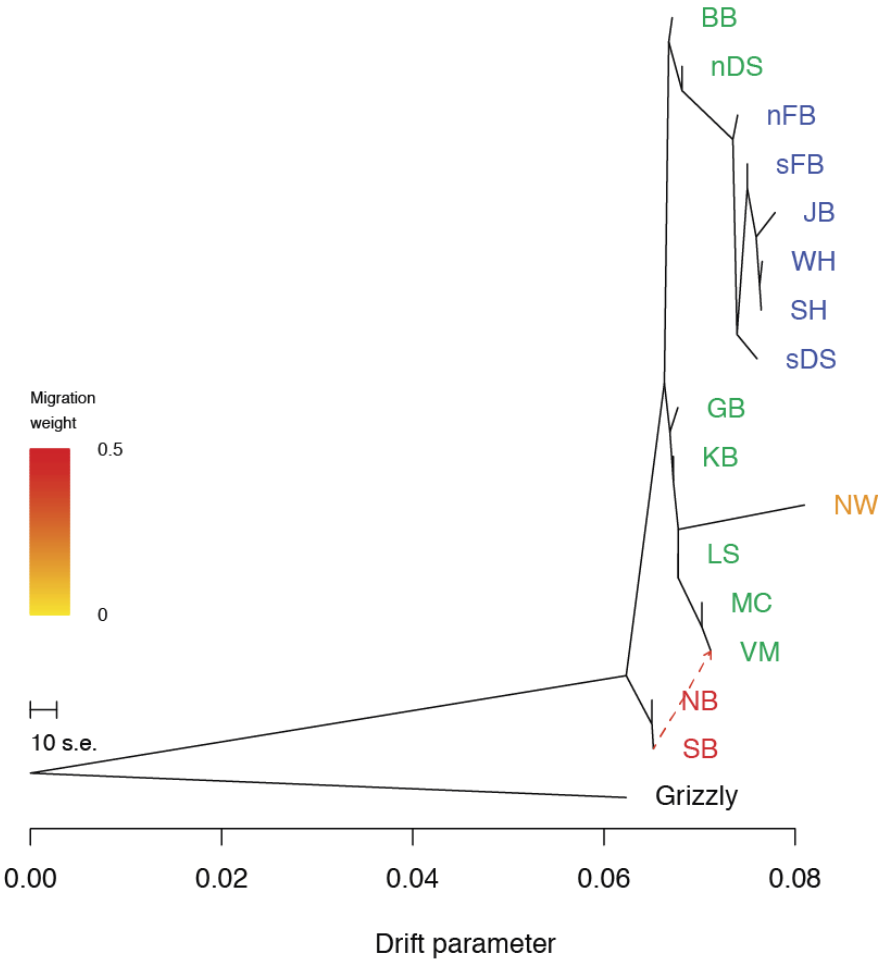

Figure 4. Maximum-likelihood tree of historical splits (solid lines), allowing for one subsequent migration event (dashed line) in TreeMix. Names of sampling locations are color-coded to match each of the four clusters identified by K -means clustering in GenoDive: Beaufort Sea – red, Norwegian Bay – orange, Archipelago – green, Hudson Bay – blue

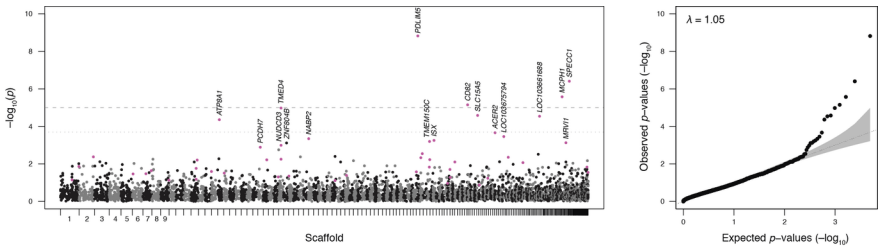

Figure 5. Results of a genome scan ($n_{\text{loci}} = 4912$) for outlier loci using combined p -values from pcadapt and OutFLANK. The dashed line in the left panel indicates genome-wide significance based on a strict Bonferroni correction (i.e.,$p < 0.05 \div$ no. of loci); the dotted line indicates genome-wide suggestiveness (i.e., $p < 1 \div$ no. of loci). However, these cutoffs are overly conservative because of non-independence among loci. SNPs deemed significant using aq -value < 0.1 are annotated with the name of the nearest gene. (See Table 4.) Colored points represent SNPs withX^TX values that fall into the upper 1% tail of values calculated on

simulated neutral loci in BayPass. The right panel shows a quantile–quantile plot for p -values. The dotted line indicates the 1:1 line of expectation; the shaded area represents its 95% confidence interval. The genomic inflation factor (λ) was calculated using the regression method.

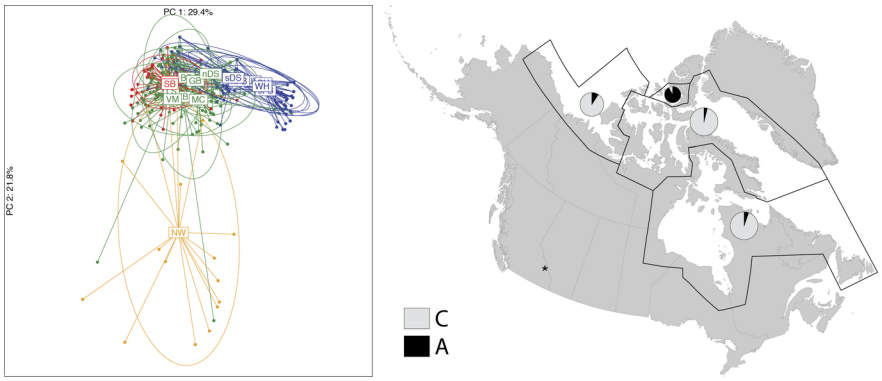

Figure 6. Left panel: Principal component analysis of 16 polar bear sampling locations using 17 outlier SNPs. Right panel: Allele frequencies for the transcriptomic SNP scaffold62_6020088, located in the 3' UTR of the gene PDLIM5 (PDZ and LIM domain 5). Frequencies were calculated using non-admixed individuals from each of the four major genetic clusters of polar bears, which correspond roughly to the four regions delimited on the map. A single grizzly sampled from Kootenay National Park (British Columbia, Canada; indicated as "*") was homozygous for A.

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