1	Concepts	and Sy	ynthesis

2 Climate-linked evolution and genetics in a warming Arctic

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38 Abstract

39 The extent to which species might be able to evolutionarily respond to rapid environmental 40 change relies strongly on their genetic diversity. Accurate knowledge of both patterns of 41 evolution and genetic variation across the species range is important for determining appropriate 42 conservation and management strategies. The Arctic is the fastest-warming region on the planet, 43 with the rest of the world expected to reach temperature increases currently experienced in the 44 Arctic by the turn of the century. Here, we review and synthesize research on evolutionary 45 processes in polar bears. Polar bears are perhaps the best-studied species living at the forefront of 46 climate-mediated habitat change, so patterns of evolutionary change in this species should be 47 instructive for understanding the consequences of warming that are expected to occur elsewhere 48 in the near future. Global warming has led to significant sea ice loss that has altered patterns of 49 gene flow across the Arctic and contributed to declines in genetic variation in some, but not all, 50 polar bear populations. Natural selection due to warming may be driving the evolution of smaller 51 body sizes in polar bears. However, evidence of adaptive change remains limited, despite 52 considerable behavioural plasticity in the species in response to changing sea ice conditions. 53 Following our review, we suggest ways that identifying the effects of warming on evolution and 54 genetic variation in polar bears could improve strategies for locally supported conservation and 55 management decisions. Our results point to variable responses to warming that we can expect to 56 occur across different genetically distinct populations in the same species and the general 57 complexity of predicting the consequences of warming for wide-ranging species.

58 **1. Background**

59 Climate change poses a significant threat to global biodiversity. By 2100, as many as 30% of 60 species are predicted to be exposed to temperatures beyond those they have evolved to tolerate 61 (Murali et al. 2023, Pigot et al. 2023). As species surpass their thermal thresholds, they must 62 adapt to new conditions, respond plastically, disperse to more suitable habitats, or face local 63 extinction (Berg et al. 2010, Morris 2014). Changes in connectivity, dispersal, and population 64 sizes affect the strength and direction of evolutionary responses to climate change by altering the 65 amount and distribution of genetic variation in the population. In turn, genetic variation shapes 66 adaptive evolutionary responses to environmental selection pressures. Phenotypic plasticity, 67 where one genotype produces multiple phenotypes, can offer an opportunity to persist in sub-68 optimal habitats without requiring slow evolutionary responses. Ultimately, the ability of 69 populations to cope with rapid environmental change will shape ecosystem structure and 70 resiliency to further changes.

71 The evolutionary consequences of warming should be most advanced, and thus 72 particularly apparent, in areas where the climate is changing rapidly. The Arctic is currently the 73 fastest-warming region on Earth, warming nearly four times faster than the rest of the planet 74 (Rantanen et al., 2022). Historically, much of the Arctic Ocean was covered by ice year-round, 75 however some climate models predict that the Arctic Ocean could experience completely ice-free 76 days within 10 years (Docquier and Koenigk 2021, Shen et al. 2023). The Arctic is at the 77 frontline of climate change making studies on Arctic populations instructive for how populations 78 in other regions may respond to warming in the coming decades.

Questions pertaining to evolutionary change are often best addressed with consistent
 long-term individual-based data collection across decades (Clutton-Brock and Sheldon 2010).

81 Sustaining such long-term research efforts is difficult even under the best of conditions, making 82 such studies disproportionately rare relative to their value in terms of the knowledge gained 83 about ecological and evolutionary processes. Long-term studies of northern species are rarer still 84 given the additional logistical difficulties of working in the region, but they remain critical for 85 understanding how populations respond to environmental change (Clutton-Brock and Sheldon 86 2010). Polar bears (Ursus maritimus) are one of the best-studied Arctic species, with over 50 87 years of long-term monitoring in some populations, and significant shorter-term complementary 88 research and extensive Indigenous knowledge throughout their range (Biddlecombe et al. 2024a). 89 Given the wealth of data available for polar bears, the species is ideal for exploring questions and 90 generating predictions about how populations may respond to warming. Here, we compiled 91 knowledge of evolutionary responses to warming in polar bears and proposed actions for 92 conservation and management (Figure 1).

93 There are an estimated 23,315 (range: 15,972–31,212) polar bears distributed across the 94 circumpolar Arctic (Hamilton and Derocher 2019). For management purposes, these have been 95 grouped into 20 subpopulations primarily based on geographic, ecological, and genetic 96 differences among regions (Figure 2; Obbard et al. 2010, Laidre et al. 2022b). Due to forecasted 97 declines in the global population, polar bears are listed as Vulnerable under the International 98 Union for the Conservation of Nature (IUCN) Red List (Wiig et al. 2015), although regional 99 conservation designations vary. The consensus across oversight bodies is that the species could 100 become endangered if factors contributing to its population decline are not stopped or reversed 101 (Durner et al. 2018). Continued sea ice loss is predicted to lead to a ~30% decline in the global 102 polar bear population by 2050 (Regehr et al. 2016), an estimate that may be conservative. Other 103 models predict that local extirpation may occur as certain regions of the Arctic become unable to support polar bear survival (Stroeve et al. 2024). However, these and other models focus
primarily on habitat change, and may be missing genetic contributions to adaptation and
evolutionary potential in the future. Given the central role that evolution and genetics play in
shaping species' responses to environmental change, both should be considered when forecasting
population viability (Allendorf 2017, Bernatchez et al. 2023).

109 Polar bears depend on sea ice for basic biological needs such as hunting, movement, 110 mating, and some maternal denning sites (Stirling and Archibald 1977). On the sea ice, polar 111 bears feed primarily on ringed (*Pusa hispida*) and bearded (*Erignathus barbatus*) seals but will 112 often supplement their diets with various other marine mammals (Thiemann et al. 2008). 113 Approximately 70% of the Arctic Ocean is covered by seasonal sea ice that melts during 114 summer, leading to an ice-free period lasting 4-6 months (Stroeve and Notz 2018). In seasonal 115 sea ice ecoregions, polar bears fast onshore during open-water periods, relying on their fat stores 116 until the sea ice reforms (Lunn and Stirling 1985, Pagano et al. 2024). Polar bears have been 117 observed to forage onshore; however, the energetic gain is significantly less than consuming 118 lipid-rich prey on the sea ice and bears may lose up to one kilogram of body mass per day while 119 onshore (Derocher and Stirling 1995, Hobson et al. 2009, Pilfold et al. 2016, Pagano et al. 2024). 120 There is strong evidence that climate warming has altered the ecology of polar bears (Box 121 1; Derocher et al. 2004, Wiig et al. 2008, Stirling and Derocher 2012). By 2100, the ice-free 122 period is predicted to lengthen by at least one month in many parts of the Arctic (Crawford et al. 123 2021), which could force fasting times to extend beyond the physiological limits of many polar 124 bears (Molnár et al. 2020, Archer et al. 2025). Fasting times that exceed 117 days increase the 125 likelihood of starvation, particularly for cubs, young adults, and pregnant or lactating females, 126 diminishing recruitment into the population (Boonstra et al. 2020, Molnár et al. 2020). In several

127 areas, reductions in sea ice availability are correlated with declines in population sizes, and 128 continued sea ice loss will likely exacerbate this problem (Regehr et al. 2007, Lunn et al. 2016, 129 Bromaghin et al. 2021). However, some subpopulations appear to be stable or increasing in 130 population size (IUCN/SSC Polar Bear Specialist Group 2024). The newly recognized Southeast 131 Greenland subpopulation (SE; Figure 2) persists with only 100 days of sea ice per year due to 132 access to glacial ice (Laidre et al. 2022b), suggesting the potential for behavioural adaptation to 133 changing sea ice conditions. Similarly, regions with high prey productivity have been shown to 134 offset the impacts of sea ice decline, allowing bears to maintain body size, body condition, and 135 high levels of recruitment (Rode et al. 2014).

136 Shifts in polar bear ecology have raised questions about the evolutionary responses of the 137 species to warming. To date, patterns of evolution in polar bears have not been synthesized, 138 despite the central importance of evolutionary responses to species survival. The rapid pace of 139 habitat loss in the Arctic requires management and conservation practices that are flexible, 140 integrative, and scientifically sound (Huxel and Hastings 1999, Sgrò et al. 2011). The most 141 effective conservation strategies integrate genetic diversity and evolutionary processes to build 142 sustainable and effective management policies (Cook and Sgrò 2017, DeWoody et al. 2021). 143 Subpopulation monitoring programs that collect genetic data allow for evolutionary mechanisms 144 to be incorporated into management decisions on subpopulation designation, harvest 145 sustainability, and conservation status assessments. Additionally, local observations provide a 146 record of long-term change, essential and often unique information on the effects of climate 147 change. Weaving Western science practices with local Indigenous knowledge together can 148 expand existing knowledge bases, improving resource allocation to maximize the effectiveness 149 of conservation efforts (Wong et al. 2017).

150 This synthesis paper emerged from the first international meeting on polar bear genetics 151 in Winnipeg, Canada, in 2023. We developed a series of questions highlighting the knowledge 152 gaps on evolutionary responses of polar bears to warming. We asked:

- 153 (1) Is there evidence that polar bears are undergoing neutral and adaptive evolution in 154 response to warming?
- 155 (2) How can we best use knowledge of evolutionary processes to guide conservation and 156 management decisions?
- 157 (3) How can we apply Indigenous and Western knowledge about polar bear evolution to 158 meet community and research priorities?

159 To address these questions, we first review the evidence for the effects of global warming on 160 four key evolutionary processes that shape genetic diversity in polar bears: mutation and 161 hybridization rates, genetic drift, gene flow, and natural selection. We then explore the role of 162 phenotypic plasticity in facilitating adaptive and non-adaptive responses to warming. We discuss 163 how a better understanding of these processes can inform conservation and management 164 decisions for polar bears and identify opportunities for weaving Indigenous and Western science 165 for community co-management and scientific research. Lastly, we describe the need for a genetic 166 management plan for polar bears to be co-developed by Indigenous and Western scientists to 167 ensure that policies are supported by both local and scientific knowledge, providing ecosystem-168 level benefits across the Arctic.

169 2. Patterns of recent evolutionary processes in polar bears

170 Evolutionary processes shape how species respond to rapid environmental change. Genetic drift, 171 gene flow, and mutation rates determine how much genetic variation is found within populations, 172 and shape how that variation is distributed across the range. These processes can also dampen the efficiency of natural selection, for example when population sizes are small and genetic drift is strong. In turn, adaptive evolutionary responses to environmental selection pressures rely on genetic variation and, less frequently, *de novo* mutations. In this section, we review research on and identify unanswered questions about how warming has shaped neutral and adaptive evolutionary processes in polar bears.

178 We conducted a literature search to estimate the number of studies that examined recent 179 and historical evolutionary trends in polar bears. Rather than a comprehensive review of the 180 literature, our goal was to summarize general trends in publishing genetic research in polar bears 181 over the last 40 years, We searched Google Scholar using the search string: "("Polar bear*" OR 182 "Ursus maritimus") AND (("Microsat*" OR "SNP" OR "AFLP" OR "ISSR" OR "Genetic*" OR 183 "Genom*" OR "Transcriptome" OR "Methylome*" OR "Epigenetic") AND ("Gene flow" OR 184 "Genetic drift" OR "Natural selection" OR "Plasticity" OR "Adaptation" OR "Mutation"))". We 185 identified 11,000 results and searched through the first 30 pages of output until the remaining 186 studies were no longer relevant to polar bears. We identified 53 published studies that estimated 187 genetic or evolutionary trends in polar bears, with several examining multiple processes at a time 188 (Figure 3; Table S1). Publications increased through time and were primarily focused on gene 189 flow (42%, N = 28). Of the remaining studies, 24% (N = 16) were focused on divergence from 190 brown bears (U. arctos), 18% (N = 12) on natural selection, and 16% (N = 11) on genetic drift. 191 We did not find any published studies that estimated contemporary mutation rates in polar bears. 192 A third of studies (N = 26) attempted to link, directly or indirectly, the genetic or evolutionary 193 patterns they observed to the current climate change event.

194 **2.1 Mutation and hybridization**

Mutations are the ultimate source of genetic variation in all species and thus provide the raw material for evolutionary change. Given that mutations are slow to accumulate in populations and occur at random with respect to function, it is most likely that rapid evolutionary responses in polar bears are driven by standing genetic variation or through structural genomic variation underlying phenotypic divergence (Lin et al. 2024).

200 However, hybridization presents an alternative scenario where the species could gain 201 novel neutral and adaptive variants (Barton 2001, Bashir et al. 2014). New alleles introduced by 202 hybridization may be exposed to selection in different environments and are thus potentially 203 valuable for local adaption to changing environments (Seehausen 2004, Mallet 2007). Since the 204 divergence of polar bears from brown bears approximately 500,000 years ago, there has been 205 extensive historical gene flow between the species, but only eight cases of contemporary 206 hybridization (Cahill et al. 2013, 2015; Pongracz et al. 2017). A genetic survey of 819 polar 207 bears and brown bears sampled between 1975 and 2016 did not identify any new hybrids beyond 208 the eight already identified, suggesting that the frequency of contemporary hybridization is 209 limited by reduced hybrid survival (Miller et al. 2024). As warming temperatures allow for 210 brown bears to expand their range northward (Rockwell et al. 2008, Rode et al. 2021b), there 211 may be more opportunities for gene flow of new, fitness-relevant alleles into the polar bear 212 population. With climate-facilitated hybridization expected to be a major force in both 213 adaptations and extinctions in the future, using genetic markers to identify and monitor hybrid 214 zones will be an important consideration for genetic management of species (Chunco et al. 2014)

215 **2.2. Genetic Drift**

Standing genetic variation is shaped by genetic drift, the strength of which is measured by effective population size (N_e). N_e is the size of an idealized population (e.g., randomly mating

218 with no gene flow or natural selection) that has the same level of genetic drift as the observed 219 population (Wright 1931). N_e and census population size (N_c) are frequently very different, 220 although both are critically important for conservation (Frankham et al. 2019). Whereas 221 ecological processes within populations are governed by N_c , N_e shapes many important 222 evolutionary processes (Waples 2022). Populations lose genetic diversity at higher rates as N_e 223 declines. This is of conservation concern because genetic diversity contributes to a population's 224 capacity to adapt to environmental change (Kardos et al. 2021). Additionally, the efficiency with 225 which natural selection can act is inversely proportional to the strength of genetic drift. As N_e 226 decreases, the random process of genetic drift can overpower the deterministic process of 227 selection, deleterious alleles can accumulate, and adaptive alleles can be lost to chance, limiting 228 adaptive responses to environmental change.

229 In polar bears, genetic diversity has been strongly influenced by multiple population 230 bottlenecks, population size fluctuations, and periods of introgression (i.e., hybridization), 231 beginning with their divergence from brown bears (Miller et al. 2012; Liu et al. 2014; Lan et al. 232 2022). Slightly lower levels of genetic diversity in modern polar bear genomes relative to the 233 genome of an ancient polar bear (110,000–130,000 years old) suggest that genetic diversity in 234 polar bear genomes has eroded since their divergence from brown bears (Lan et al. 2022). The 235 long-term N_e for polar bears is 5,500 (Wilder et al. 2023), significantly lower than the global N_c 236 of 26,000 (Wiig et al. 2015). Within-population estimates of N_e vary widely, ranging from the 237 100's to 1000's (Cronin et al. 2009, Peacock et al. 2015). Historical reductions in sea ice were 238 correlated with declines in N_e in Greenland, likely contributing to evolved genetic and 239 morphological differences in polar bears on the west and east coasts of the country (Westbury et

al. 2023). However, recent fluctuations in N_e associated with global warming have not yet been investigated.

Most polar bear subpopulations are connected by gene flow, which can bolster their genetic diversity. However, small subpopulations may lose genetic diversity if they are isolated. For instance, the southeast Greenland subpopulation has been isolated for more than 200 years and has some of the lowest genetic variation and highest inbreeding of all subpopulations (Laidre et al. 2022b). Reductions in genetic diversity have also been documented in polar bears on the Svalbard Archipelago (Maduna et al. 2021) and in Norwegian Bay (Paetkau et al. 1999, Rivkin et al. 2024).

249 Across taxa, levels of genetic diversity have been linked to organismal fitness and 250 extinction risk (Kardos et al. 2021, Wilder et al. 2023). Genetic diversity at functional loci may 251 be especially critical for resilience. Polar bears have low levels of diversity at major 252 histocompatibility complex (MHC) genes, a group of genes critically involved in immune 253 function, which may make polar bears more susceptible to disease, putting them at risk as 254 warming increases their exposure to novel pathogens (Weber et al. 2013). Low MHC diversity is 255 linked to susceptibility to emerging pathogens across species and may be a conservation priority 256 when developing genetic management plans for some species (Acevedo-Whitehouse and 257 Cunningham 2006, Siddle et al. 2007). However, genetic diversity still needs to be quantified at 258 other functional loci fully investigate the adaptive potential and extinction risk of polar bears. 259 2.3 Gene flow

Gene flow among genetically distinct populations increases standing genetic variation by
introducing novel alleles. High dispersal capacity and relatively few geographic barriers in the
Arctic have allowed for extensive long-distance gene flow among polar bears. Genetic structure

263 is weak over large distances in regions where bears can travel unhindered on the sea ice, such as 264 between northeast Greenland and eastward through the Norwegian and Russian Arctic Seas, and 265 further east to the Beaufort Sea (Paetkau et al. 1999, Cronin et al. 2006, Peacock et al. 2015, 266 Sorokin et al. 2023). In contrast, areas with geographic land barriers such as the Canadian Arctic 267 Archipelago, show more population structure (Paetkau et al. 1999, Campagna et al. 2013, 268 Peacock et al. 2015, Jensen et al. 2020, Rivkin et al. 2024). Additionally, smaller regions of the 269 Arctic, such as James Bay in the southern Hudson Bay and the Norwegian Bay subpopulation are 270 genetically unique, suggesting restricted gene flow in these areas (Crompton et al. 2008, 271 Malenfant et al. 2016b, Rivkin et al. 2024). 272 Even with long-distance gene flow, significant genetic structuring exists at a local scale, 273 likely due to behavioural differences among bears. Female polar bears within the Svalbard 274 archipelago exhibited limited dispersal and strong philopatry to denning location, resulting in 275 local scale genetic structuring and a unique behavioural ecotype where ~300 bears stayed near 276 shore year-round (Zeyl et al. 2009, 2010, Aars et al. 2017). A second "pelagic" ecotype migrates 277 between Svalbard and the western Russian Arctic, exhibiting behavioural differences that have 278 been maintained despite gene flow between the ecotypes (Paetkau et al. 1999, Mauritzen et al. 279 2002). Lastly, the Southeast Greenland subpopulation consists of a few hundred bears living on 280 glacial ice in several fjord systems that are genetically isolated from other bears in the region due 281 to this habitat choice. 282 Several studies have detected recent shifts in gene flow through time. Directional gene 283 flow northward into the high Canadian Arctic and American Arctic was reported over the recent

284 generations (Peacock et al. 2015), although this observation was disputed by Malenfant et al.

285 (2016b) based on the same dataset. Genetic structure increased, and genetic diversity declined

over a period of two decades as sea ice availability decreased in Svalbard (Maduna et al. 2021).

287 As sea ice loss continues to restrict opportunities for dispersal, gene flow and genetic variability

are predicted to continue to decline in the area in future decades, potentially reducing the

289 capacity of more isolated subpopulations to adapt (Maduna et al. 2021, Rivkin et al. 2024).

290 2.4 Natural Selection

291 Differential survival and reproduction drive evolution by natural selection, but for species to 292 evolve, there must be heritable variation underlying traits and genes (Linnen and Hoekstra 2009). 293 Warming temperatures place considerable selection pressure on polar bear survival and 294 reproduction rates (Box 1), however, we know little about the role of natural selection on recent 295 adaptations in polar bears. The divergence from brown bears was marked by rapid adaptation of 296 genes involved in coat colour, cardiac function, and lipid metabolism (Welch et al. 2014, 297 Samaniego Castruita et al. 2020, Sun et al. 2024). In a more contemporary timeframe, increased 298 exposure to environmental contaminants in Svalbard has altered gene regulation in metabolic 299 pathways in mothers and cubs, possibly leading to downstream energetic costs in highly exposed 300 bears (Herst et al. 2020). Polar bears across the Canadian Arctic were adapted to their local sea 301 ice ecoregion (multiyear versus seasonal sea ice; Amstrup et al. 2007), providing a foundation 302 for continued adaptation to changing sea ice (Rivkin et al. 2024). However, polar bears in 303 Western Hudson Bay lack additive genetic variation for lifetime reproductive success—a direct 304 estimate of adaptive potential—suggesting a limited capacity for adaptation to the changing 305 environment in this subpopulation (Newediuk et al. 2025).

There are other possible targets for selection and opportunities for adaptation in polar bears. For instance, there is the potential for pathogen resistance or tolerance to evolve as warmer temperatures facilitate the rapid transmission of disease in the Arctic (Bradley et al.

309 2005). Zoonotic pathogens have been detected at higher frequencies than historical levels in the 310 high Canadian Arctic, driven primarily by the lengthening summer season (Pilfold et al. 2021, 311 Tschritter et al. 2024). Polar bears in the southern Beaufort Sea who summer on land and thus 312 have greater pathogen exposure risk, exhibit heightened immune function relative to bears who 313 summer on sea ice (Whiteman et al. 2019). Bears in this region also exhibit transcription 314 differences in genes involved in immune function (Bowen et al. 2015b, 2015a), offering potential 315 targets for selection. Further investigation into patterns of genomic and transcriptomic 316 upregulation of immunity genes across generations is necessary to determine if and how immune 317 function may be evolving in polar bears.

318 Lengthening fasting seasons could also contribute to the evolution of metabolic rates in 319 polar bears to allow for greater fasting periods. Unlike other bear species that hibernate, polar 320 bears gradually reduce their metabolic rate throughout the summer to cope with the summer 321 fasting period (Whiteman et al. 2015). However, denning females will fast for almost double the 322 length of the typical fasting period of males and non-denning females, demonstrating 323 considerable plasticity in fasting duration (Atkinson and Ramsay 1995, Molnár et al. 2020). 324 Hypothetically, polar bears that can reduce their metabolic rate can survive longer periods of 325 fasting. The lengthening fasting season may select for genes that enable bears to fast for 326 extended periods by lowering metabolic processes or promoting energy conservation, as has 327 been observed in other systems (reviewed in McGaughran et al. 2021). These genes could 328 already be under strong selection in southern subpopulations that are already experiencing >4-329 month fasting seasons. Comparative whole genome sequencing across a spatial gradient in the 330 ice-free season or through time would help establish if metabolic rates are indeed under selection 331 from sea ice loss.

332 Body size is another trait that appears to have sufficient heritable variation in polar bears 333 and may be an important factor in adapting to a changing environment (Malenfant et al. 2018). 334 Some evidence suggests that natural selection against large body sizes may be leading to the 335 evolution of smaller polar bears. In general, bigger bears can survive longer fasting periods, and 336 bigger females may be accompanied by cubs and yearlings with larger masses and higher 337 survival weights (Ramsay and Stirling 1988, Rode et al., 2020). However, persistent declines in 338 body size were observed between 1958 and 1989 in female polar bears in western Hudson Bay 339 (Derocher and Stirling 1995, Atkinson et al. 1996) and between 1982 and 2006 in polar bears in 340 the southern Beaufort Sea (Rode et al. 2010). Smaller skull sizes were also documented in 341 Svalbard and Greenland after 1960 (Bechshøft et al. 2008, Pertoldi et al. 2009). Larger body 342 sizes may be selected against due to greater energy requirements in poor ice years and the 343 preferential harvest of larger bears. The decline in body size may also reflect phenotypic 344 plasticity as environmental conditions become poorer or may be a signal of inbreeding 345 depression associated with declining population sizes (Pertoldi et al. 2009), suggesting that the 346 effects of natural selection act in concert with other evolutionary processes to affect trait 347 evolution. There is little evidence for adaptive body size reductions in response to warming in 348 other systems (Teplitsky and Millien 2013); thus, identifying whether size changes in polar bears 349 are adaptive can be of broader use for establishing general trends of climate change on species 350 evolution.

2.5 Plasticity

Phenotypic plasticity, where multiple phenotypes can be produced by one genotype, is a
mechanism that allows individuals to respond to very rapid environmental change by altering
their physiological or behavioral traits (Whitman and Agrawal 2009). In contrast to evolutionary

355 change, plasticity provides an avenue for acclimation to changing environments within the 356 lifetime of an organism (Boutin and Lane 2014). Behavioural and reproductive plasticity is 357 common in polar bears. The Southeast Greenland subpopulation has circumvented reduced sea 358 ice coverage by switching to hunting seals on glacial ice (Laidre et al. 2022b), and females in the 359 Beaufort and Chukchi Seas exhibit annual differences in den site fidelity depending on their 360 ability to access preferred denning areas on sea ice (Zeyl et al. 2010). Similarly, in years with 361 longer ice-free periods, females in Baffin Bay in poorer body condition produced smaller litters 362 (Laidre et al. 2020b). Plasticity in litter sizes serves as a bet-hedging strategy to allow females to 363 survive lean periods when caring for too many cubs would reduce their body condition below 364 critical levels (Burggren and Mendez-Sanchez 2023). However, while polar bears in Western 365 Hudson Bay can modify their foraging strategies and energy expenditure onshore (Pagano et al. 366 2024), they do not demonstrate physiological mechanisms to cope with starvation (Whiteman et 367 al. 2018). These studies suggest that while polar bears exhibit considerable behavioural plasticity 368 when faced with poor conditions, physiological plasticity may be limited.

369 **3.** Applying evolutionary and genetic data to polar bear conservation and management

Identifying the effects of environmental change on contemporary evolutionary processes and genetic variation can improve the effectiveness of conservation and management strategies. The increasing availability of genetic data for polar bears should facilitate the inclusion of evolutionary processes into conservation and management policies. Below, we outline how this data can be incorporated into management strategies to guide emerging priorities in polar bear conservation and management. We also identify opportunities for weaving Indigenous and Western science to build an integrated understanding to facilitate locally supported research and

377 management. Bridging these fields in polar bears can serve as a case study for other species378 experiencing environmental changes caused by continued warming.

379 **3.1 Subpopulation monitoring**

380 Capture-handling programs provide some of the best data for estimating evolution in the field. 381 During capture-handling programs, free-ranging polar bears are chemically immobilized and 382 tagged, and standardized morphometric measurements and biological samples are taken (e.g. 383 skin, blood, hair, fat, claw; Laidre et al. 2022a). Several long-term capture-handling programs 384 exist for polar bears in the Western Hudson Bay, Southern Beaufort Sea, and Barents Sea 385 subpopulations. The monitoring program in the Western Hudson Bay has generated a robust 386 pedigree with tissue samples collected each year dating back to the 1980s (Malenfant et al. 387 2016a). This level of data collection makes it possible to estimate phenotypic and genetic change 388 between generations, providing a unique opportunity to measure the effects of climate warming 389 in real-time. For instance, this pedigree was leveraged to assess the heritability of size-related 390 morphological traits (Malenfant et al. 2018), aspects of the polar bear mating system that are 391 likely to influence selection and gene flow (Richardson et al. 2020), and quantify the adaptive 392 potential of the subpopulation (Newediuk et al. 2025). Continuation of long-term monitoring 393 programs can directly address outstanding questions and assess the evolutionary potential of the 394 species, providing significant benefit to conservation programs aimed at preserving polar bears. 395 Genetic surveying through remote biopsy darting is becoming increasingly common as a 396 tool for monitoring subpopulations. Remote biopsy darting collects a small amount of skin, hair 397 and adipose tissue from the bear (Pagano et al. 2014), which can then be used to identify 398 individuals to assess survival and movement, estimate population sex ratios and abundance, and

quantify contaminant exposure (McKinney et al. 2017, Laidre et al. 2018, Bromaghin et al. 2021,

400 Dunham et al. 2024). Epigenetic aging from biopsy samples has emerged as a potential tool for 401 estimating age structure and collecting health data on populations with minimal animal handling. 402 A recently developed polar bear epigenetic clock uses the DNA methylation patterns from 403 known-age tissue samples to estimate age in unknown-age samples within ± 2 years of the 404 chronological age (Newediuk et al. 2025). When used to estimate age in other known-age 405 samples, the epigenetic clock can also detect epigenetic age acceleration, the presence of DNA 406 methylation patterns typical of older bears. Epigenetic age acceleration can be influenced by 407 factors such as stress and diet (Oblak et al. 2021), individual health, body condition, or 408 contaminants (Beissinger and Westphal 1998, Larison et al. 2021), and is associated with all-409 cause mortality (Marioni et al. 2015). The development of these epigenetic markers for polar will 410 assist with population age structure estimations, improve population growth models for harvest 411 sustainability, and strengthen estimates of population viability under continued habitat loss. 412 Collaboration with local communities opens additional opportunities to fill data gaps. 413 Specimen samples are regularly collected from hunter-harvest or polar bears killed in defence of 414 life or property across many jurisdictions and have been used in many existing genetic studies 415 (e.g., Paetkau et al. 1999; Malenfant et al. 2018; Rivkin et al. 2024, and many others). These 416 samples provide high-quality DNA from bears over continuous time periods, particularly in 417 remote areas where research may be conducted infrequently or not at all. Communities that 418 harvest from traditional hunting territories can also generate data for closely related bears, 419 providing a potential genomic approach to monitoring population abundance and inbreeding 420 rates from community collaborations. 421 Genetic data may also be obtained non-invasively, for example from hair snags

422 (Langwieder et al. 2023), tracks left in the snow (Hellström et al. 2023), or fecal samples

(Hayward et al. 2022). Despite recent technological advances, the quality of DNA obtained from
these methods may be too low to allow for more in-depth sequencing efforts (Andrews et al.
2021), making it challenging to implement genomic or transcriptomic approaches to samples
collected from remote locations. Thus, careful consideration of the potential biases and return on
capital invested is required to assess the efficacy of these approaches.

428 **3.2 Designation of management units**

429 Management unit designations for polar bears are determined using ecological, political, and 430 genetic information. In 2005, low genetic differentiation across large geographic areas prompted 431 the IUCN Species Survival Commission Polar Bear Specialist Group to adopt the term 432 "population" to encompass all polar bears in the Arctic and the term "subpopulation" to identify 433 management units (Aars et al. 2006, Laidre et al. 2022a). Although many subpopulations are 434 admixed, others are genetically isolated and contain unique genetic variants (Malenfant et al. 435 2020, Rivkin et al. 2024). Changing sea ice conditions may require that subpopulation 436 boundaries be reevaluated if certain habitats become unsuitable for polar bear occupation or if 437 movement across current subpopulation boundaries increases. If range contractions due to sea ice 438 loss become more common (Laidre et al. 2018), polar bears will disperse across subpopulation 439 boundaries or become isolated. Additionally, unique genetic variation may be found outside of 440 traditional subpopulation boundaries, thus the management unit assessments would benefit from 441 range-wide genome scans to ensure that boundaries accurately capture genetic variation among 442 polar bears.

443 **3.3 Harvest sustainability**

444 Polar bears experienced a period of prolonged overharvesting in the early-mid 1900s. In 1973,

the Agreement on the Conservation of Polar Bears banned commercial hunting, limiting hunting

446 primarily to subsistence-based harvests based on traditional rights (Vongraven et al. 2022). Since 447 the signing of the Agreement, an annual average of 800 bears are harvested globally, accounting 448 for 4.6% of bears from each subpopulation (Vongraven et al. 2022). Many jurisdictions require 449 that hunters document their harvests, which is a valuable source of genetic data and can provide 450 an early indication of immigration and emigration that inform harvest management 451 interpretations of trends in abundance and shifts in distribution. Harvest management groups 452 frequently involve Indigenous co-management (i.e., cooperative management by the regional and 453 local governments, wildlife boards, and Indigenous authorities), and quotas differ between 454 jurisdictions depending on the number of bears found in each region (Polar Bear Range States 455 2015).

456 Maintaining sustainable harvest relies on accurate estimates of subpopulation abundance 457 and distribution. To promote stable population growth, breeding females and cubs have 458 historically been protected from harvesting, while a larger proportion of males are harvested (Lee 459 and Taylor 1994, Derocher et al. 1997). A sex-selective harvest may have downstream 460 evolutionary consequences for the evolution of polar bears (e.g., body size evolution) and 461 population viability. A recent shift to a 1:1 male-female harvest system in Nunavut, whose 462 jurisdiction overlaps with 12 subpopulations (Government of Nunavut 2019), will also have 463 implications for population dynamics. Incorporating genetics-based assessments of current N_e 464 and temporal changes in inbreeding coefficients across jurisdictions into harvest measurements 465 would provide robust estimates of population trajectories in each region, ensuring harvests 466 continue to operate at sustainable levels.

467 **3.4 Conservation status assessments**

468 Management strategies that promote large, well-connected populations provide the best chance 469 for species persistence in a changing environment (Frankham et al. 2019). Accurate estimations 470 of population sizes and trends are foundational for monitoring and developing appropriate 471 conservation interventions. The conservation designation of polar bears differs across regions, 472 although most agree that polar bears are threatened by habitat loss and anthropogenic 473 development. The global census population size of polar bears is uncertain due to their wide 474 distribution and challenging field conditions that make it difficult to accurately estimate 475 population trends (Wiig et al. 2015). Combined with comprehensive population sampling, 476 genomic data can provide accurate estimates of recent population trajectories and bolster 477 inferences from census population estimates. Contemporary $N_{\rm e}$ estimators may capture very 478 recent population fluctuations well before changes in genetic variation are detected and can 479 provide critical information when census estimates are unavailable. Additionally, genomics-480 informed simulations of population trajectories under future climate change scenarios can help 481 predict the potential impacts of changes in gene flow and inbreeding in declining populations 482 (Rivkin et al. 2024). Lastly, continued monitoring of more well-studied subpopulations will 483 provide insights into the effects of inbreeding on population viability if population declines 484 continue in response to degrading environmental conditions.

485 **3.5 Weaving Indigenous and Western knowledge for co-management**

Sharing and respecting the priorities, knowledge, and interpretations from Indigenous and
Western science perspectives should be considered throughout the research and management
processes. Polar bears hold significant cultural and economic value for Indigenous communities
across the Arctic. Polar bears are spiritually and symbolically important to many northern
communities and are fundamentally tied to Inuit identity and well-being (Voorhees et al. 2014,

Miller et al. 2025). Harvests support local economies and traditional practices by providing food,
tools, clothes, and art (Dowsley 2010). Through generations of sharing the land, depending on
polar bears as a food source, and encountering and observing bears throughout the year, northern
Indigenous communities have cultivated a deep knowledge about polar bears and the Arctic

495 environment (Born 2011, Voorhees et al. 2014, Wong and Murphy 2016, Rode et al. 2021b).

496 Community observations provide important records of behavioral plasticity, such as polar 497 bears switching prey sources or maternity denning locations, and document long-term changes in 498 polar bear health and habitat use. Such long-term monitoring data is essential for placing 499 observed evolutionary responses into the context of ecological and environmental data. Co-500 development of research projects, collecting tissues through harvest sampling (Peacock et al. 501 2012), and community-based field projects (De Groot et al. 2013, Langwieder et al. 2023) are 502 potential avenues for sharing knowledge. Interpreting genetic patterns within the context of 503 community knowledge of historical and current patterns of polar bear biology, as well as 504 environmental change in the Arctic, can facilitate the development of regionally appropriate 505 management plans that are locally supported within communities.

As part of co-management efforts, it is important to recognize that Indigenous and Western science findings may differ, for example, in subpopulation management approaches, appropriate research methods, and the resiliency of polar bears to warming (Dowsley and Wenzel 2008, Dowsley 2009, York et al. 2016, Wong et al. 2017, Tomaselli et al. 2022). Topics where perspectives differ can serve as valuable indicators to parts of the system where change is occurring or where additional investigation is needed (Frid et al. 2023), as well as identify important distinctions in ways of knowing and worldview. Historical and relational impediments

should be acknowledged and addressed to advance a mutually beneficial understanding of polarbear ecology and evolution.

515 **4. Development of a genetic management plan for polar bears**

516 We recommend developing a genetic management plan for polar bears as a crucial component of 517 future conservation and management decisions. Genetic management plans incorporate explicit 518 goals for maintaining viable levels of genetic diversity and limiting inbreeding depression to 519 minimize the extinction risk of vulnerable populations (Frankham et al. 2019). Implementing a 520 genetic management plan for polar bears would align the field with the Kunming–Montreal 521 Global Biodiversity Framework (GBF). This framework commits signing parties to protect 522 genetic diversity and adaptive potential of vulnerable species using three key indicators: the 523 proportion of meta-populations with $N_e > 500$; the proportion of genetically unique populations; 524 and the number of species that are being monitored using DNA-based methods

525 (CBD/COP/DEC/15/4 2022).

526 Genetic management plans exist for a small number of northern mammal species, 527 including wood Bison (Bison bison athabascae; McFarlane et al. 2005) and Boreal Caribou 528 (Rangifer tarandus caribou; Environment Canada 2012). While each plan prioritizes conserving 529 genetic diversity across populations, the specific goals included in each plan differ. A genetic 530 management plan for polar bears could focus on several core criteria, including the 1) 531 establishment of guidelines for incorporating genetic markers and monitoring tools into existing 532 conservation and management policies, 2) protection of existing global genetic variation and 533 adaptive potential by promoting connectivity and preventing overharvest of genetically unique 534 subpopulations, and 3) integration of evolutionary, ecological, and climate data into population 535 viability projections to measure the vulnerability of subpopulations to continued warming

536	(Figure 1). Regardless of which criteria are included, preserving the genetic integrity of polar	
537	bears will help achieve management and conservation goals across the Arctic.	
538	There are several outstanding questions in the field that, if addressed, will aid in the	
539	implementation of a genetic management plan for polar bears. These include, but are not limited	
540	to:	
541	(1) How are current levels of standing genetic variation, inbreeding, and gene flow	
542	between subpopulations predicted to change with continued sea ice loss?	
543	(2) Are there traits and genes under selection from warming that may facilitate	
544	adaptations to a warmer Arctic?	
545	(3) What is the contribution of evolutionary change versus plasticity to polar bear	
546	survival?	
547	(4) How well does individual-level genetic variation predict population-level health and	
548	fitness?	
549	(5) Can genomics-informed population viability models be integrated with habitat	
550	distribution and energetics models to build holistic predictions of subpopulation	
551	viabilities?	
552	(6) Do genetic estimates of demographic history align with community observations of	
553	historical and contemporary demographic patterns?	
554	Addressing these outstanding questions will reveal avenues for conservation and management	
555	policies that facilitate adaptation and promote survival in the changing Arctic environment. The	
556	long-term monitoring programs and extensive local ecological knowledge of many	
557	subpopulations have set the stage for the development of a comprehensive conservation genetics	
558	program for polar bears. Bridging these fields with genetic data will allow conservation and	

management programs to be guided by leading-edge scientific and community knowledge,
advancing polar bear conservation to provide ecosystem-level benefits throughout the Arctic
(Figure 1).

562 **5. Broader implications**

563 The Arctic is a sentinel ecosystem for climate change. By the end of the century, most of the 564 planet will have warmed to the same degree that the Arctic has already warmed (i.e., a 2-4 °C 565 increase above the historical average; Fan et al. 2020, Rantanen et al. 2022). Advancing 566 evolutionary knowledge about polar bears can provide an early warning system to predict how 567 other species may respond to future warming. Polar bears, and other Arctic species, will be 568 among the first to face the 'adapt or die' paradigm, where extreme habitat loss threatens the 569 persistence of the entire species unless they can behaviourally or genetically adapt in time to 570 survive. As expected, given their large range and ecological variability, evolutionary responses 571 to warming varied, and the likely consequences of climate change will clearly be complex. Some 572 populations appear threatened with respect to their capacity to evolve, whereas others seem to be 573 doing well. However, while genetic diversity varies significantly among populations there is 574 currently little evidence for adaptive change in response to warming. The hope of the Kunming-575 Montreal GBF is that by conserving genetic diversity, we can maintain the capacity for 576 populations to adapt to future environmental change. Our synthesis calls for more work 577 exploring adaptive change to warming, but currently available data points to the possibility that 578 adaptive responses to warming are difficult. Ultimately, the most effective conservation 579 strategies must include reducing carbon emissions to mitigate the level of warming experienced 580 by the planet.

581

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587 Author Contributions

- 588 LRR conceived the study, led the road-mapping discussions, and wrote and revised the original
- 589 draft. APW, LN, KK, JA, and AL wrote the original draft, and all authors contributed to
- 590 revisions.

591 **Conflict of Interest**

592 The authors declare no conflict of interest.

593 **Boxes**

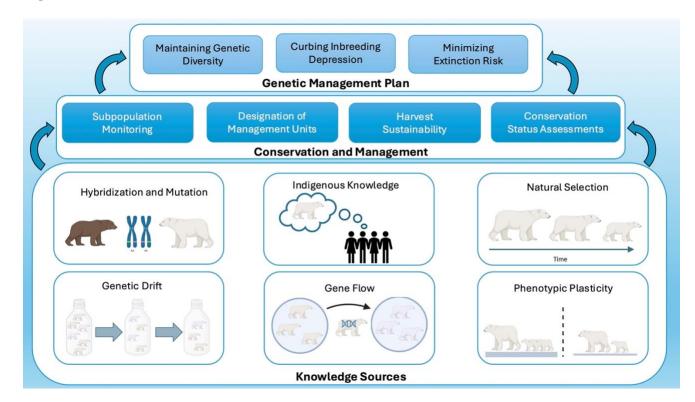
594 Box 1. The effects of global warming on polar bear ecology

595 Polar bears depend on the sea ice to meet many of their basic biological needs (Stirling and 596 Archibald 1977). Fifty years of monitoring in the Western Hudson Bay subpopulation by 597 Environment and Climate Change Canada has identified clear effects of sea ice availability on 598 survival (Regehr et al. 2007, McGeachy et al. 2024, Biddlecombe et al. 2024a) that has led to 599 declines in abundance in the subpopulation (Lunn et al. 2016). Reductions in body condition, 600 increased stress responses, and altered reproductive timing have also been associated with sea ice 601 loss in the subpopulation (Sciullo et al. 2016, Mislan et al. 2016, Newediuk et al. 2025). In other 602 regions of the Arctic, sea ice availability has been correlated with reduced cub recruitment, 603 decreasing body condition, and smaller body sizes (Rode et al. 2010, Obbard et al. 2016, Tartu et 604 al. 2017, Florko et al. 2021). However, these trends are not universal. The Kane Basin and 605 Chukchi Sea subpopulations, whose ranges overlap regions of the Arctic Ocean that are covered 606 by persistent, multiyear sea ice, have exhibited increased population sizes and stable or 607 improving body condition (Laidre et al. 2020a, Rode et al. 2021a). These trends may be 608 temporary as multiyear sea ice is rapidly being converted into seasonal sea ice, and further sea 609 ice declines are expected in the region (Stroeve and Notz 2018, Kwok 2018).

Diminishing sea ice has also altered patterns of movement, habitat use, and health of polar bears. Satellite telemetry data demonstrate that the frequency of long- and short-distance swims has increased due to longer open-water periods (Pagano et al. 2012, 2021, Pilfold et al. 2017, Lone et al. 2018). Because swimming has a higher energetic cost than walking for polar bears, increased swimming frequency may shorten the maximum fasting time that bears can endure (Griffen 2018). Unstable ice conditions have led females to den on land more frequently

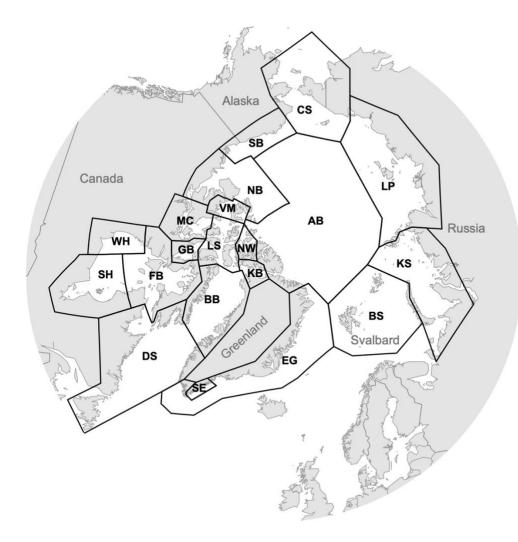
616 than on ice, which could reduce reproductive success and cub survival (Laidre et al. 2022a). Sea 617 ice loss also contributes to disease and contaminant exposure in polar bears (Atwood et al. 2017, 618 Routti et al. 2019). Range expansions of host species have increased the prevalence and 619 transmission rates of infectious diseases and parasites in the Arctic (Fagre et al. 2015, Pilfold et 620 al. 2021, Biddlecombe et al. 2024b). Increased pathogen exposure has led to heightened immune 621 function in polar bears (Whiteman et al. 2019), which is energetically costly and may inhibit the 622 fasting ability of smaller or sickly bears. Lastly, the frequency of polar bear-human conflicts is 623 escalating with the magnitude of warming (Towns et al. 2009, Heemskerk et al. 2020). Attacks 624 on humans are more likely to occur when bears are nutritionally stressed from extended periods 625 on land (Wilder et al. 2017). These encounters pose threats to both bears and humans, and harm 626 public perception of polar bears, resulting in reduced support for conservation programs in the 627 north (Schmidt and Clark 2018, Schmidt et al. 2022).

628



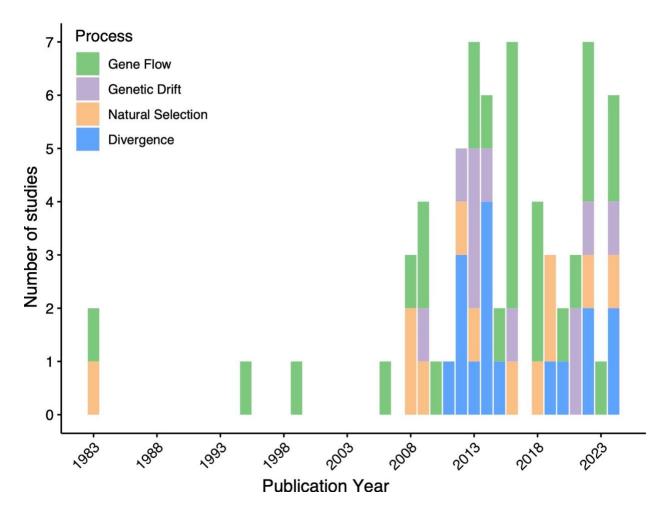
631

632 Figure 1/Graphical Abstract: Pathway toward integrating evolutionary genetics research into 633 polar bear conservation and management. Bridging knowledge sources by assessing patterns of 634 recent evolution in polar bears and weaving Indigenous and Western knowledge can inform 635 conservation and management decisions on subpopulation monitoring, management unit 636 designations, harvest sustainability, and conservation assessments. These decisions would benefit 637 from the development of a genetic management plan to bridge these fields and bring polar bear 638 conservation into line with global biodiversity frameworks. Such a framework can be extended 639 beyond polar bears to preserve ecosystem-level biodiversity in the Arctic.



Subpopulation Arctic Basin (AB) Baffin Bay (BB) Barents Sea (BS) Chukchi Sea (CS) Davis Strait (DS) East Greenland (EG) Foxe Basin (FB) Gulf of Boothia (GB) Kane Basin (KB) Kara Sea (KS) Laptev Sea (LP) Lancaster Sound (LS) M'Clintock Channel (MC) Northern Beaufort Sea (NB) Norwegian Bay (NW) Southern Beaufort Sea (SB) Southeast Greenland (SE) Southern Hudson Bay (SH) Viscount Melville Sound (VM) Western Hudson Bay (WH)

- 641 Figure 2. 2024 subpopulation boundaries for polar bears designated by the IUCN Species
- 642 Survival Commission Polar Bear Specialist Group (https://www.iucn-pbsg.org/population-
- 643 status/).
- 644
- 645



647 Figure 3. Summary of evolutionary genetics research studies published for polar bears. Bars have

648 been color coded based on the type of process they represent.

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