

Genetic diversity in caribou linked to past and future climate change

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Climate-driven range fluctuations during the Pleistocene have continuously reshaped species distribution leading to populations of contrasting genetic diversity. Contemporary climate change is similarly influencing species distribution and population structure, with important consequences for patterns of genetic diversity and species' evolutionary potential¹. Yet few studies assess the impacts of global climatic changes on intraspecific genetic variation^{2–5}. Here, combining analyses of molecular data with time series of predicted species distributions and a model of diffusion through time over the past 21 kyr, we unravel caribou response to past and future climate changes across its entire Holarctic distribution. We found that genetic diversity is geographically structured with two main caribou lineages, one originating from and confined to Northeastern America, the other originating from Euro-Beringia but also currently distributed in western North America. Regions that remained climatically stable over the past 21 kyr maintained a high genetic diversity and are also predicted to experience higher climatic stability under future climate change scenarios. Our interdisciplinary approach, combining genetic data and spatial analyses of climatic stability (applicable to virtually any taxon), represents a significant advance in inferring how climate shapes genetic diversity and impacts genetic structure.

When looking at impacts of climate change on biodiversity, numerous studies treat ecosystem and species as a unit and thus ignore intraspecific genetic diversity^{2,5}. Intraspecific genetic variation is the most fundamental level of biodiversity, provides the basis for any evolutionary change and is crucial for maintaining the ability of species to adapt to new environmental conditions⁶. Species may respond to climate change by local adaptation, shifting or reducing range or a combination of these¹. In many cases, these changes will reduce genetic diversity in populations and species, in extreme situations to the point where genetic impoverishment will contribute to reduce population viability⁶. In the light of present global climate change, it is necessary to study the effects of past climatic changes on intraspecific genetic diversity to decipher the evolutionary consequences of climate change and its effects on biodiversity. Phylogeographic studies that disentangle population history during the Pleistocene and through the Holocene warming implicitly reconstruct the fate of genetic diversity during a major climate change and then can provide important insights into species' reactions to present and future climate change⁵.

Here we applied a multidisciplinary approach to quantitatively estimate climate-related past and future changes of genetic diversity in the iconic northern species *Rangifer tarandus*, commonly named reindeer in Eurasia and caribou in North America (hereafter termed caribou for simplicity). This is particularly relevant because climate

change is taking place more rapidly and severely in higher latitudes than anywhere else on the globe⁷, exposing northern organisms to a suite of potential impacts. In this context, the caribou—as most species adapted to cold environments—is expected to experience direct and indirect effects of climate warming^{8,9}, including range reduction. Caribou is one of the last remnants of the Beringian megafauna¹⁰, a keystone species structuring northern ecosystems, with high cultural and food value for Aboriginal peoples¹¹. Alterations in the distribution and health of its populations could locally have major biological, societal and economical implications. Yet, the persistence of caribou throughout its present range is under threat^{12,13} and a worldwide decline of many major populations has been reported¹⁴. Examining caribou across its entire range provides a unique opportunity to assess the effects of historical processes on population genetic structure and the impact of climatic suitability on gene flow and genetic diversity. Its circumpolar distribution makes this species a good case study to show on a global scale how the integration of genetic data and new spatial analyses can help to anticipate the consequences of ongoing climate change on intraspecific genetic diversity.

We combined information from species distribution modelling (SDM) with new genetic data on caribou populations (1,297 caribou genotyped at 16 nuclear microsatellite loci and 347 mitochondrial deoxyribonucleic acid (mtDNA) cytochrome *b* sequences) sampled throughout the species' Holarctic distribution (Fig. 1). We used climatic reconstructions from the Last Glacial Maximum (LGM; 21 ± 2 ka) to the present at intervals of 1,000 years¹⁵ to model the range dynamics and stability of caribou through the past and project the future range of the species under a business-as-usual scenario of the Intergovernmental Panel on Climate Change (scenario 2080 A1b; ref. 7). We expect the combined use of phylogeography and spatial modelling to provide detailed information on how the present lineages moved in space and time to reach their present range, how climatic stability maintained genetic diversity within lineages and how they could evolve in a warming future.

Bayesian multilocus genotype clustering analysis and phylogenetic reconstruction of mtDNA samples divided caribou populations into two phylogeographic lineages (Fig. 1). The first lineage covers a vast portion of the species range, from Eurasia to Northwestern America (hereafter termed the Euro-Beringia, according to its distribution 21 ka; see below), including Greenland, Svalbard and the Canadian archipelagos (Fig. 1). The second lineage has a more restricted distribution and includes herds distributed from the island of Newfoundland to the interior plains of Canada (hereafter termed North America, according to its distribution 21 ka; see below). The timing of the coalescence between the two clades was estimated to be 300 ka (95% highest posterior densities: 184–430), that

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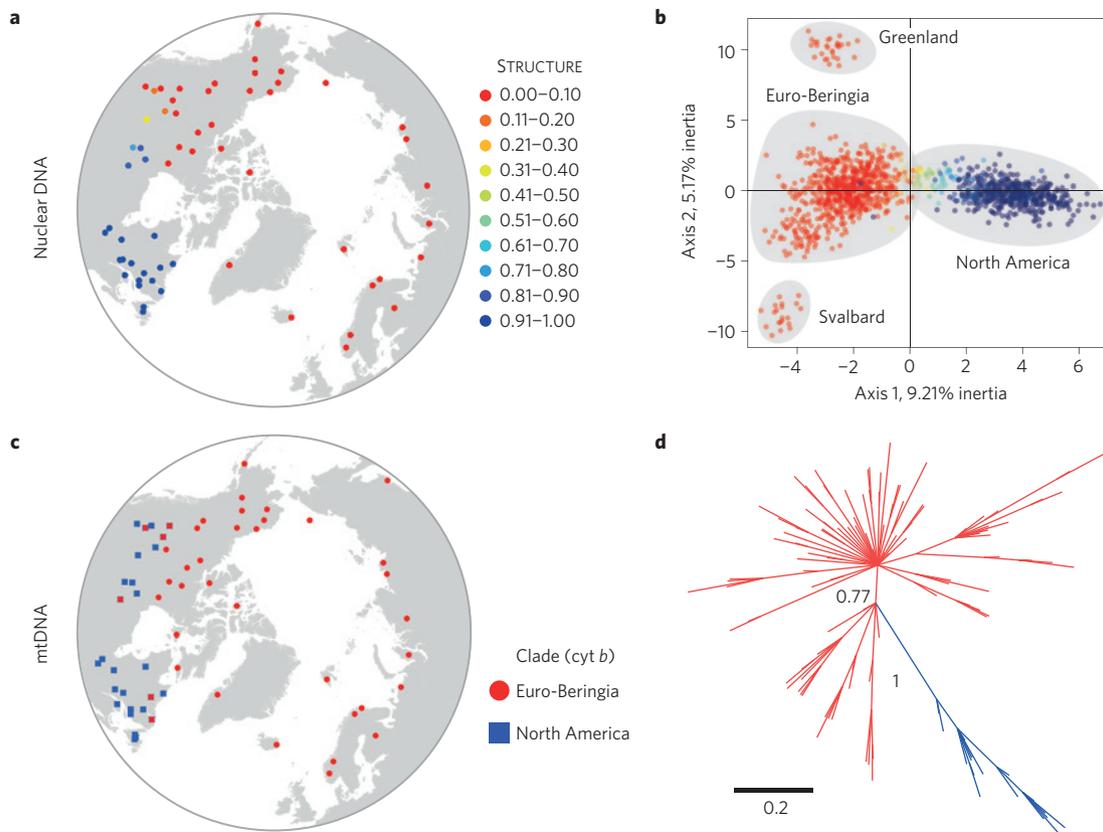


Figure 1 | Population genetic structure of caribou. **a**, The proportion of population membership for each herd to the North American clade, considering two genetic clusters ($K = 2$; blue for North American clade and red for Euro-Beringian clade, respectively). **b**, Plot of the first two coordinates from a principal component analysis on microsatellite loci. **c, d**, The geographic distribution (**c**) and unrooted Bayesian phylogenetic tree (**d**) of mtDNA haplotype lineages is represented in red for Euro-Beringia and blue for North America.

is, during the middle Pleistocene, a time of widespread continental glaciations in North America, which pre-dates the onset of the LGM (21 ± 2 ka). These two lineages have remained genetically homogenous since they diverged two interglacial–glacial cycles ago.

SDM identified two main climatically suitable areas of distribution for caribou at the LGM, that is, 21 ka (Fig. 2). The model suggests that the species was more widespread in Eurasia than today, whereas the species range was reduced in North America during the same time period (Fig. 2 and Supplementary Fig. 5). In North America, the glacial advances were the most extensive worldwide and ice sheets reached their largest extent some 20 ka when they covered much of the continent¹⁶. The high rate of climatic changes in North America may have forced populations to continuously shift their distribution to track suitable climatic conditions or to persist throughout the LGM in climatically stable refugia. Models of range shift through time showed a high congruence with the present spatial distribution of genetic lineages (correspondence of the final 1 ka modelled climatic distribution with the nuclear genetic structure: 85% of congruence, and with the mtDNA haplotype distribution: 87% of congruence; Fig. 2), therefore accurately unravelling the paths followed by caribou lineages across the past millennia. Past projections further show that hindcasted regions include the known fossil records (Boyce index: 0.58; Supplementary Fig. 1). Secondary contact between the two lineages occurred in central Canada about 8 ka (Fig. 2 and Supplementary Fig. 5), which corresponds to the final deglaciation of North America¹⁶. This allowed a progressive colonization of regions previously covered by ice.

Demographic reconstructions based on microsatellites indicated population expansion for both lineages. Demographic expansion is

dated at about 10 ka for the North America lineage (Supplementary Table 7 and Fig. 4), which is congruent with the spatial expansion seen in SDMs (Fig. 2 and Supplementary Fig. 5). For the Euro-Beringian lineage, the expansion is more recent and dated about 2.2 ka, with large 95% highest posterior densities (1.45–5.31; see Supplementary Information). We observed lower mtDNA haplotype ($h \pm$ s.d.) and nucleotide ($\pi \pm$ s.d.) diversity in North America ($h = 0.774 \pm 0.031$, $\pi = 1.84 \times 10^{-03} \pm 0.2 \times 10^{-03}$) than in Euro-Beringia ($h = 0.981 \pm 0.003$, $\pi = 6.30 \times 10^{-03} \pm 0.16 \times 10^{-03}$; permutation tests: all $P < 0.01$; Supplementary Table 8). At the microsatellite level, present genetic diversity was also significantly higher in Euro-Beringia (expected heterozygosity, $H_E \pm$ s.d. = 0.76 ± 0.13) than in North American populations ($H_E \pm$ s.d. = 0.69 ± 0.04 ; Wilcoxon rank sum test, $W = 54.5$, $P < 0.001$; Supplementary Table 1).

On a local population scale, we found a positive correlation between nuclear genetic diversity (H_E and allelic richness, A_r) and climatic stability (Fig. 4b and Supplementary Fig. 7b), defined as regions having a high climatic suitability for caribou during the longest time period since the LGM (Fig. 3a and Supplementary Tables 9–12). Climatic stability also best explained both the present mtDNA haplotype (h :corrected Akaike information criterion (AICc) weight, $w_i = 0.52$, $R^2 = 0.57$; Fig. 4C) and nucleotide diversity (π : $w_i = 0.36$, $R^2 = 0.54$; Supplementary Fig. 7c and Tables 13–14). This lends support to the expectation of higher levels of genetic diversity in populations located in stable areas in comparison with those from regions experiencing greater climatic fluctuations¹⁷. Across the range of caribou, our results revealed that a decrease in nuclear genetic diversity occurred in populations

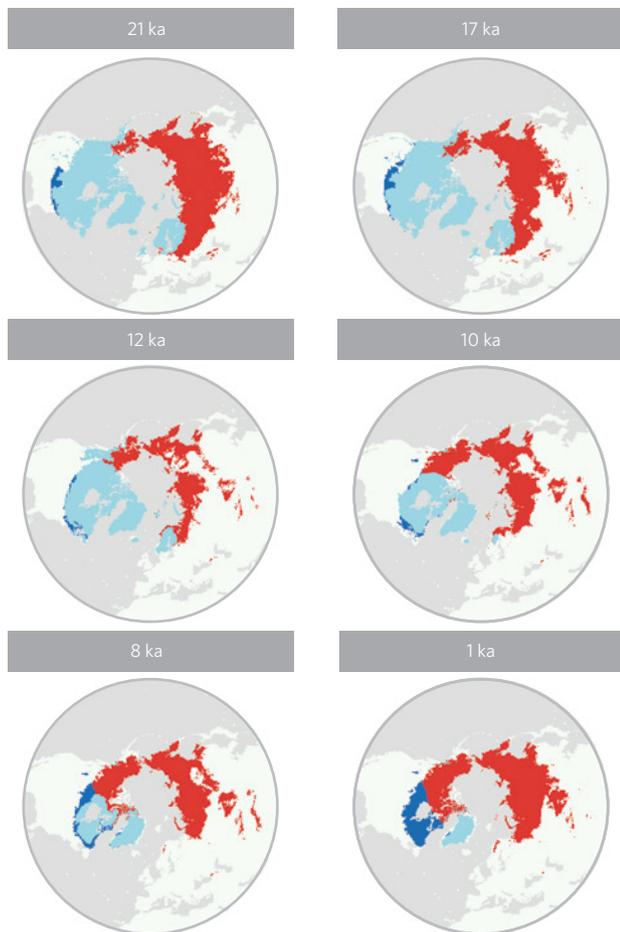


Figure 2 | Hindcasted distribution of caribou genetic lineages, as defined by SDMs from 21 ka to present. Six time points are shown (see Supplementary Fig. 5 for the complete time lapse). Colours correspond to the location and range shift of the two genetic lineages over time: North American clade in blue and Euro-Beringian clade in red. Light grey regions represent unsuitable areas, that is, areas falling below the relative operating characteristic threshold. Light blue regions correspond to areas covered by ice.

located at the lowest and highest latitudinal extremes of the species range (Fig. 4a, Supplementary Fig. 7a and Tables 9–12). Greenland and Svalbard exhibited extremely low gene diversity ($H_E = 0.27$ and $H_E = 0.29$, respectively) as well as low mean numbers of alleles per locus (with 3 and 4 monomorphic loci, respectively; Supplementary Table 1), probably resulting from severe genetic drift and loss of genetic variability owing to their isolated geographic position.

We observed a quadratic relationship between mean pairwise F_{ST} and latitude (linear term: $F_{1,55} = 9.94$, $P < 0.01$; quadratic term: $F_{1,55} = 32.39$, $P < 0.001$; Fig. 4d), indicating a higher genetic differentiation among herds both at the southern and northern margins of the species range. Caribou are very mobile, capable of long-distance migrations of hundreds of kilometres. At its southern limit, however, the species mainly occupies mountain and boreal forest habitat, where herds generally have smaller population sizes, occupy smaller landscape patches and exhibit higher site fidelity¹⁸. At the northern extreme of the range, caribou occur primarily on islands throughout the Canadian Arctic Archipelago, Greenland or Svalbard, where natural barriers such as glaciers, islands and wide fjords probably limit gene flow and contribute to isolate populations. These phenomena have probably resulted in decreased genetic diversity coupled with increased population differentiation

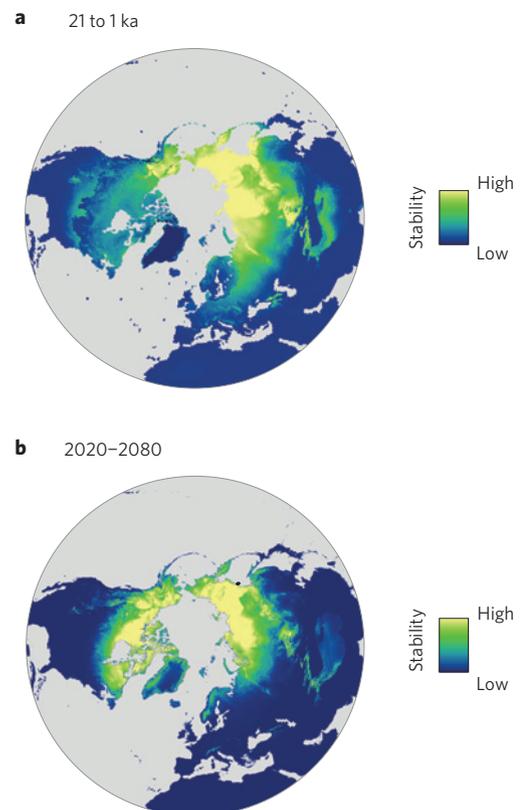


Figure 3 | Stability of climatic suitability for caribou. **a**, In the past since the LGM and **b**, in the future projected for the next 70 years. The maps were obtained by stacking projections of species distribution models at intervals of 1 kyr (for the past—Supplementary Fig. 5) and ten years (for the future—Supplementary Fig. 6).

at the latitudinal extremes, in accordance with the theoretical central-marginal model¹⁹. These populations at the range edges can, however, be of particular importance from a biodiversity conservation standpoint, as they may have unique adaptive traits (for example, tolerance to extreme climates) or be locally adapted (for example, to mountain, forest or high-Arctic environments).

Forecasting the range of the species for the next 70 years predicts strong modification of the distribution of caribou (Fig. 3b and Supplementary Fig. 6). Under the severe climatic warming scenario, our model predicts the distribution of caribou to become more restricted to high latitudes than today, with possible extirpations in the southernmost regions. Climate change, however, is predicted to influence the two clades differently. The North America genetic cluster is likely to become increasingly fragmented, possibly disappearing from most of its present range (89% of the suitable area lost) in 60 years. Most of the herds that belong to this lineage are already considered as endangered or threatened¹³. The Euro-Beringia region is predicted to be less dramatically affected by climate change (60% of suitable area lost), probably supporting in the future large populations with higher genetic diversity and therefore higher evolutionary potential to adapt to a changing environment.

Despite the usefulness of combining phylogeographic data sets based on microsatellite loci, mtDNA sequences and SDM, our conclusions rest on several assumptions. We used putative neutral genetic variation as a surrogate for intraspecific genetic diversity. The natural next step would be to quantify genetic variation for potential adaptive loci. An important issue for SDM-based predictions is the difficulty of implementing interspecific interaction, dispersal and migration scenarios into projections of past and future distribution,

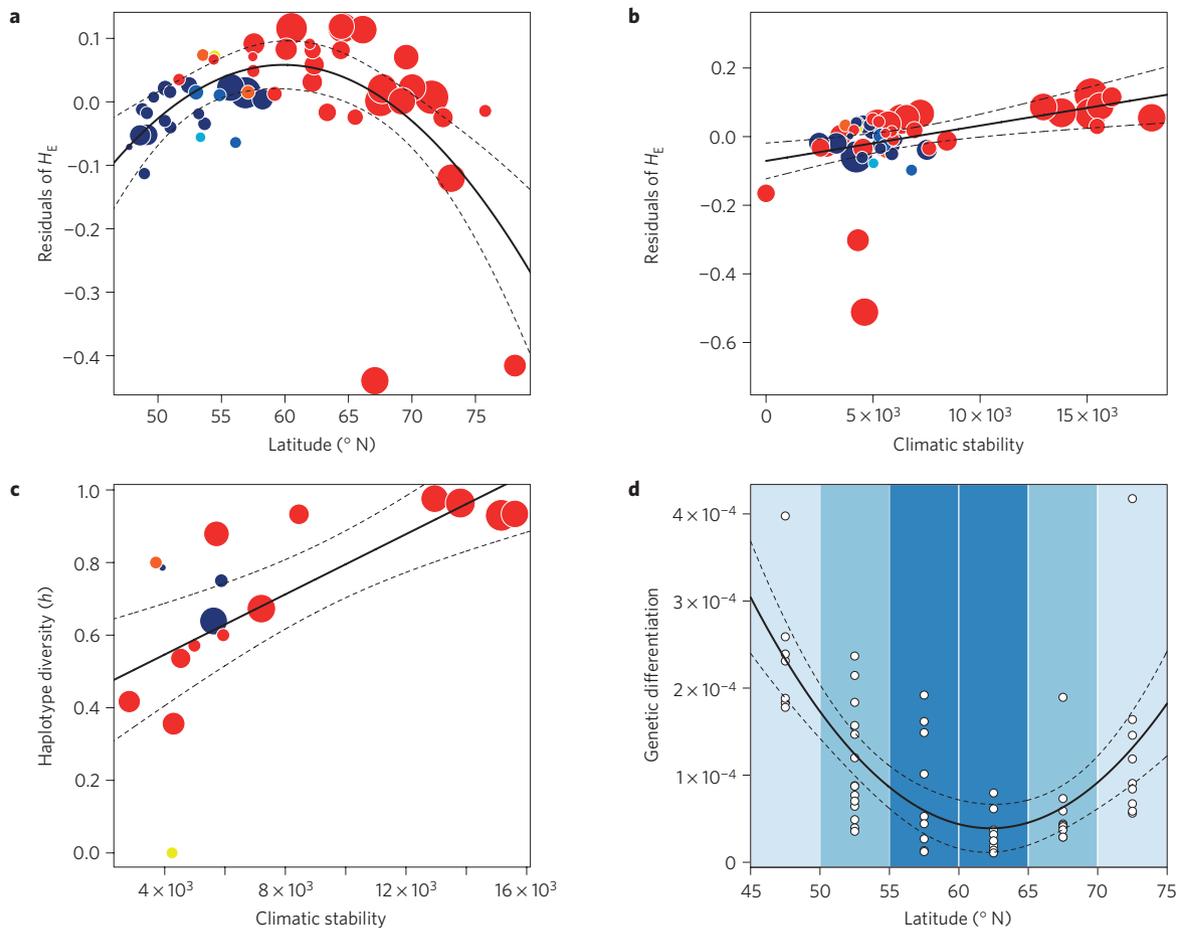


Figure 4 | Models of genetic diversity. **a,b**, Relationships between expected heterozygosity (H_E) and latitude (**a**) and climatic suitability for the microsatellite data set (**b**), respectively. H_E is expressed as statistical residuals (the two covariates are included in the best selected models, $\Delta AIC \leq 2$; Supplementary Table 9). **c**, Relationship between mtDNA haplotype diversity (h) and habitat stability for the mitochondrial data set (for $n \geq 5$ sequenced samples per herd). Dot size is proportional to the (\log_{10}) census size of the analysed populations. Dot colours correspond to Bayesian membership of each population to the North American clade, considering two genetic clusters ($K = 2$; blue for North American clade and red for Euro-Beringian clade, respectively) obtained with STRUCTURE (Fig. 1). **d**, Relationship between pairwise genetic distance among herds and latitude. Herds are clustered according to their latitudinal range in 5° -latitude-wide strips. For each focal herd, we estimated the mean pairwise genetic distance with all the other herds within the same latitudinal strip, excluding between genetic lineage (Euro-Beringia versus North America) and between continent (Eurasia versus America) herd pairs. Genetic distance was estimated as mean pairwise $F_{ST}/(1 - F_{ST})$ divided by the geographic distance between each herd. Regression lines and 95% confidence intervals of the predicted models are represented with solid and dashed lines, respectively.

which also rely on the assumption that the species' fundamental niche has not changed over time. Although the simulation of the caribou range shift through time recovered most of the population's genetic structure, few populations were incorrectly assigned (see Supplementary Information). Inconsistencies may stem from uncertainty related to ice sheet or climatic reconstructions. During deglaciation of the Northern Hemisphere (20–8 ka; ref. 16), giant proglacial lakes formed at the edges of ice sheets in North America and Eurasia²⁰. Such features, which were not taken into account in SDMs, may lead to an overestimation of the past caribou distribution and to incongruence between the empirical and modelled spatial genetic structures.

Nevertheless, the overall congruence observed here between model-based predictions of intraspecific range changes in space and time and multilocus analyses of genetic diversity shows that SDMs and molecular genetic analyses can be successfully combined to forecast spatial patterns of genetic diversity. By being virtually applicable to any threatened and endangered species with more limited distributions, and assuming that enough occurrences are available for calibrating SDMs in species with restricted range²¹, this predictive approach opens exciting new

research avenues and applied perspectives in inferring how climate change impacts intraspecific genetic diversity and distribution in tandem. From this perspective, our study is a breakthrough in interdisciplinary approaches and opens new doors in the understanding of the evolutionary trajectories of species under changing environmental conditions.

Methods

Sample collection. We assessed neutral genetic variation from 1,297 caribou and reindeer, obtained from 59 locations throughout the entire circumpolar native species range, including Alaska, Canada, Greenland, Svalbard, Norway, Finland and the Russian Federation (Fig. 1 and Supplementary Information).

Microsatellite genotyping and analysis. All samples were genotyped at 16 microsatellite loci (Supplementary Table 2). Population genetic structure was investigated by using the clustering programme STRUCTURE²²; carrying out principal component analysis using adegenet in R (ref. 23); and estimating population differentiation using FSTAT (ref. 24; Supplementary Information). We used the coalescent-based approach implemented in msVAR (ref. 25) to test whether microsatellite data were consistent with the climatic reconstructions of past population demographic change. The parameters of interest were: present effective population size (N_0), ancestral population size at the time of demographic change (N_1) and time since this change (T).

Mitochondrial DNA and phylogeographic reconstruction. A 1,147-base-pair mtDNA fragment encompassing the entire *cyt b* was sequenced for a subset of caribou samples ($n = 167$ sequences). Additional sequences ($n = 178$) were retrieved from GenBank (Supplementary Table 4). Using these pooled *cyt b* data sets ($n = 345$), phylogenetic reconstruction was undertaken using MRBAYES (ref. 26; Supplementary Information). Time to the most recent common ancestor between lineages was estimated using a fossil-based clock calibration in BEAST (ref. 27). Ancient DNA samples are available for caribou and reindeer¹⁰. However, because of a biased record towards the Euro-Beringian lineage¹⁰, we did not include ancient DNA samples in our analyses.

SDM. To assess changes in range size overtime, we first modelled the potential present climate-based distribution of caribou within an ensemble framework of five modelling techniques²⁸. Based on the Hadley Centre climate model²⁹, the contemporary species–climate relationships (averaged from 1950 to 2000) were then projected into the past in different time frames (from the present to 21 ka, every 1 kyr) and into the future at ten-year intervals from 2020 to 2080. Species distribution data were obtained from the International Union for Conservation of Nature range map (available from <http://www.iucnredlist.org/>) from which 10,000 occurrence points were randomly sampled across the species range. Regions covered by ice were considered unsuitable.

We defined potential refugia occupied by the genetic lineages at the LGM (21 ka), as areas distinguished by discontinuous suitability for the species, that is, suitable areas located south and northwest of the Laurentide Ice Sheet in North America (panel '21 ka' in Fig. 2). This approach corresponds to the user-defined scenario proposed in ref. 30. For each following time step (every 1 kyr) up to the present, we let any suitable pixel from a given time frame t be colonized by the genetic group from the closest suitable pixel from time frame $t-1$; a procedure that we refer to as diffusion (or migration). This model is fully deterministic without any variability or stochasticity.

We then used two validation techniques. First, we showed that the SDMs were able to predict the presence of dated fossils through time (Supplementary Fig. 1). Second, we compared the spatial correspondence of the present genetic structure predicted by the simulated scenarios with the empirical population genetic data following a procedure described in ref. 30. For this, we assigned each genetically analysed population to a lineage by considering the highest assignment probability obtained when applying clustering approaches (with STRUCTURE) or mtDNA haplotypes frequency. A population was assumed to be properly recovered by the model if it was assigned to the same genetic cluster both at the end of the spatial simulation process and with the empirical molecular approach, for example, STRUCTURE results. We then estimated the match of the two approaches, that is, the percentage of populations assigned to the same lineage using spatial simulation and molecular approaches. Finally, from the continuous suitability maps obtained by SDMs, we summed the values of the pixels of all time frames to generate maps of climatic stability, for the past since the LGM and for the next 70 years.

Factors influencing genetic diversity. We tested which factors best explained the population genetic diversity at both nuclear and mitochondrial levels using Generalized Linear Models and a model selection procedure, considering four explanatory covariates: latitude; climatic stability since the LGM (we hypothesized that populations located in an area climatically stable would present higher genetic diversity than populations located in continuously changing environments); log-transformed census population size; and genetic cluster, estimated as the probability of population membership (q) according to STRUCTURE. Models included quadratic effects for latitude to test for the potential higher levels of genetic diversity in populations located at mid-latitudes in comparison with those located in the extreme margins of the species range. We ranked candidate models using the AICc corrected for small sample sizes in R (ref. 23).

Accession codes. Mitochondrial DNA sequences generated here are deposited in GenBank under accession numbers JX846827 to JX846902.

Received 5 December 2012; accepted 8 November 2013; published online 15 December 2013; corrected online 9 January 2014

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Acknowledgements

We thank J. Adamczewski, T. Baker, A. Beauchemin, K. Beckmen, V. Brodeur, M. Campbell, D. Cooley, S. Crowley, M. Dumond, D. Elliott, D. Ehrich, D. Fortin, M. Gamberg, R.A. Ims, L. Jourdain, M. Kholodova, I. Menyshena, J. Neville, M. Paré, D. Paetkau, K. I. Prokovsky, K. Poole, D. Riach, S. Rivard, G. H. Roffler, D. Russel, M.-H. St-Laurent, R. Serrouya, A. Sokolov, V. Sokolov, A. Stien, J. Taillon, J. Williams, N. G. Yoccoz, the Government of Yukon, the Government of Northwest Territories, the Government of Nunavut, the Government of Labrador and Newfoundland, le Gouvernement du Québec, the Alaska Department of Fish and Game, Hydro-Québec and Manitoba Hydro for providing help to collect samples. Financial support was provided by partners of Caribou Ungava, that is, ArcticNet, Natural Sciences and Engineering Research Council of Canada (NSERC), Hydro-Québec, Xstrata Nickel-Mine Raglan, Fédération des Pourvoires du Québec, CircumArctic Rangifer Monitoring and Assessment Network, Ministère des Ressources Naturelles et de la Faune du Québec, Labrador and Newfoundland Wildlife Division, First Air, Makivik Corporation, Fédération Québécoise des Chasseurs et Pêcheurs, Fondation de la Faune du Québec, Institute for Environmental Monitoring and Research, Canada Foundation for

Innovation, Petroleum Technology Alliance of Canada, Canadian Association of Petroleum Producers and Norwegian Research Council. K.M. acknowledges support from the National Science Foundation IGERT program, the National Fish and Wildlife Foundation, and Alaska EPSCoR NSF award #EPS-0701898 and the state of Alaska. We are grateful to C. Hins, S. de Bellefeuille and G. Côté for logistic support and T. Broquet and P. Legagneux for discussions.

Author contributions

S.D.C. had the original idea for the study. L.B. was responsible for supervising the genetic analyses. G.Y., L.P., S.D.C. and L.B. designed the research. S.C., C.C., C.D., K.J.H., R.J.L., D.A.J., L.K., N.L., K.M., M.M., K.L.P., K.H.R., T.S., S.G.P., B.V.W. and S.D.C. collected the samples. G.Y., L.P. and J.O. carried out the

analyses, wrote the manuscript and the Supplementary Information, with input from N.L., A.G., S.D.C. and L.B. All authors discussed the results, implications and edited the manuscript.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to G.Y.

Competing financial interests

The authors declare no competing financial interests.

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