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SPECIAL PAPER

Quantifying the similarity between genes and geography across Alaska's alpine small mammals

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ABSTRACT

Aim Quantitatively evaluate the similarity of genomic variation and geography in five different alpine small mammals in Alaska, and use this quantitative assessment of concordance as a framework for refining hypotheses about the processes structuring population genetic variation in either a species-specific or shared manner.

Location Alaska and adjacent north-western Canada.

Methods For each taxon we generated 3500–7500 single-nucleotide polymorphisms and applied a Procrustes analysis to find an optimal transformation that maximizes the similarity between principal components analysis maps of genetic variation and geographical maps of sample locations. We generate stability maps using projected distributions from ecological niche models of the Last Glacial Maximum and the present.

Results Significant similarity between genes and geography exists across taxa. However, the extent to which geography is predictive of patterns of genetic variation not only differs among taxa, but the correspondence between genes and geography varies over space. Geographical areas where genetic structure aligns poorly with the geographical coordinates are of particular interest because they indicate regions where processes other than isolation by distance (IBD) have influenced genetic variation. The clustering of individuals according to their sample location does not support suppositions of admixture, despite the presumed high vagility of some species (e.g. arctic ground squirrels).

Main conclusions Genomic data indicate a more nuanced biogeographical history for the taxa than suggested by previous studies based on mtDNA alone. These include departures from IBD that are shared among taxa, which suggest some shared processes structuring genetic variation, including new potential ancestral source populations. In addition, some regions fit expectations of IBD where incremental migration and gene flow play a strong role in population structure, despite any ecological difference among taxa. Differences in dispersal capabilities do not result in different species-specific local patterns of population structure, at least at the sampling scale examined here. We highlight how the general fit to, as well as departures from, expectations for patterns of genetic variation based on the Procrustes analyses can be used to generate hypotheses about the underlying processes.

Keywords

Alaska, climate change, isolation by distance, mammal, next generation sequencing, phylogeography, Procrustes analyses, RADseq

INTRODUCTION

The geographical structure of population genetic variation is the foundation of phylogeography. Such spatial structure provides a basis for investigating the history of migration and/or colonization routes. The most common method applied for assessing the correspondence between genes and geography is a test of isolation by distance (IBD), where a pairwise measure of population similarity/dissimilarity is compared to a pairwise measure of geographical distance separating populations. Although the exact metric used in such tests might vary (e.g. the pairwise genetic distance or a measure of F_{ST} might be used to characterize the axis of genetic divergence, and the Euclidean distance or some rescaled distance based on the habitat suitability separating populations might be used to characterize the axis of geographical distance; see Wang & Bradburd, 2014), the utility of such tests is a statistical evaluation of the extent to which geography predicts patterns of genetic variation. However, a drawback to these broadly applied tests is that, because they do not retain information about the relative positions of populations across space, they do not contain information for interpreting the relative deviations from an IBD of specific sampled populations (Papadopoulou & Knowles, 2015a).

Principal components analysis (PCA) and non-metric multidimensional scaling provide a means for visualizing summaries of genetic data, decomposing the high dimensionality of genomic data into a reduced number of axes to qualitatively investigate the clustering patterns of genetic variation. When single-nucleotide polymorphisms (SNPs) are adequately sampled across populations, distances between population clusters on a two-dimensional (2D) principal components (PC) space are proportional to their pairwise F_{ST} measures (McVean, 2009). Therefore, the positioning of population clusters in PC space matches exactly with their geographical distributions under a strict IBD model. A recently developed Procrustes analysis approach to studying genetic variation makes use of this important feature of PCA analysis by statistically quantifying the association between genetic PCA and geographical maps (Wang *et al.*, 2012). Specifically, this approach finds an optimal transformation that maximizes the similarity between genes and geography by minimizing the sum of squared Euclidean distances between a PCA map of genetic variation and geographical coordinates while preserving relative pairwise distances among points within the genetic and geographical maps. When coupled with permutations, the statistical significance of the similarity between genes and geography can be evaluated. In addition, the relative deviations of sampled individuals from expectations based on their geographical location can be visualized, identifying both the magnitude of deviations and also the general direction of such deviations (e.g. individuals that are more closely related to those at different latitudes or longitudes than expected based on where they were sampled; see Papadopoulou & Knowles, 2015a).

We apply a Procrustes analysis approach to not only systematically test for an association between genes and geography among sampled populations in different species of alpine small mammals across Alaska and adjacent regions of north-western Canada, but also to systematically assess how this association differs across taxa. Moreover, by using this approach, we can visualize the role of geography in explaining the genetic similarity of populations from different locations, and identify regions that correspond more (or less) to expectations based on the geographical locality of sampled individuals. The five mammal taxa – collared pika [*Ochotona collaris* (Nelson, 1893)], hoary marmot [*Marmota caligata* (Eschscholtz, 1829)], singing vole [*Microtus miurus* (Osgood, 1901)], brown lemming [*Lemmus trimucronatus* (Richardson, 1825)] and arctic ground squirrel [*Spermophilus parryii* (Richardson, 1825)] – are broadly distributed across much of Alaska, but differ in the latitudinal extent of their ranges (e.g. the ranges of the arctic ground squirrel, brown lemming and singing vole extend to higher latitudes compared to the hoary marmot and collared pika). A comparative phylogeographical study based on mtDNA has identified seemingly concordant east-west splits in all five species, which may be indicative of a shared refugial history (Lanier *et al.*, 2015a). Given their overlapping ranges in the region and reliance on alpine or tundra habitat, they provide an ideal context for testing the extent to which taxa from similar geographical areas, some of which have a dynamic history that includes extensive glacial impacts, show common versus species-specific spatial patterns of genetic variation, especially given differences in the dispersal capabilities and habitat affinities of the taxa (Lanier *et al.*, 2015a). We discuss how deviations of individuals in the PC maps from predictions based on geography can be used to generate hypotheses about underlying processes and consider the challenges with interpreting spatial patterns in PCA maps (see Novembre *et al.*, 2008; Francois *et al.*, 2010). In addition, we consider a set of refined hypotheses based on comparing the patterns from the Procrustes analyses with projections of distributional stability inferred from ecological niche models (ENMs) for the present and the past (specifically, the Last Glacial Maximum, LGM) (Alvarado-Serrano & Knowles, 2014). Lastly, through a series of sequential exclusion of sampled populations, the robustness of the similarity between geography and genes, as well as between the genetic PCAs with and without particular populations, is assessed in each species.

MATERIALS AND METHODS

Species sampling and genomic library preparation

Genomic data were collected from individuals in populations sampled across the Alaskan and north-western Canadian ranges of each of five species: collared pikas (59 individuals from 9 populations), hoary marmots (55 individuals from 9

populations), singing voles (62 individuals from 9 populations), brown lemmings (60 individuals from 8 populations) and arctic ground squirrels (63 individuals from 9 populations; see Fig. 1 and Tables S1.1 & S1.2 in Appendix S1 in Supporting Information). See Appendix S1 for details about DNA extraction and library construction.

Processing of illumina data

Sequences for each species were demultiplexed and reads with an average Phred score > 30 and an unambiguous barcode and restriction cut site were retained (scripts are available on Dryad under doi: 10.5061/dryad.8jm51). The STACKS 1.07 pipeline (Catchen *et al.*, 2013) was used to identify SNPs in the processed genomic data from the species-specific genomic libraries constructed for each species (see Appendix S1 for details about the processing of genomic data).

Genetic diversity statistics

After genomic variation was identified within individuals, the STACKS output files were loaded into species-specific MySQL databases. Loci were exported from each species' MySQL database using the *export_sql.pl* script, allowing one to four SNPs per RADseq locus; only biallelic RADseq loci were considered in order to comply with the assumptions of the current methods for analysing SNP data. The POPULATIONS program in STACKS was used to calculate population genetic statistics on the exported RADseq loci, including nucleotide diversity (π), major allele frequency, observed heterozygosity and Wright's inbreeding coefficient (F_{IS}). Only loci present in at least two populations ($P = 2$) and genotyped in at least 50% of the individuals of each population ($r = 0.50$) were used to create molecular summary statistics for each species; in instances where 50% did not result in a round number of individuals in a population, the number of individuals

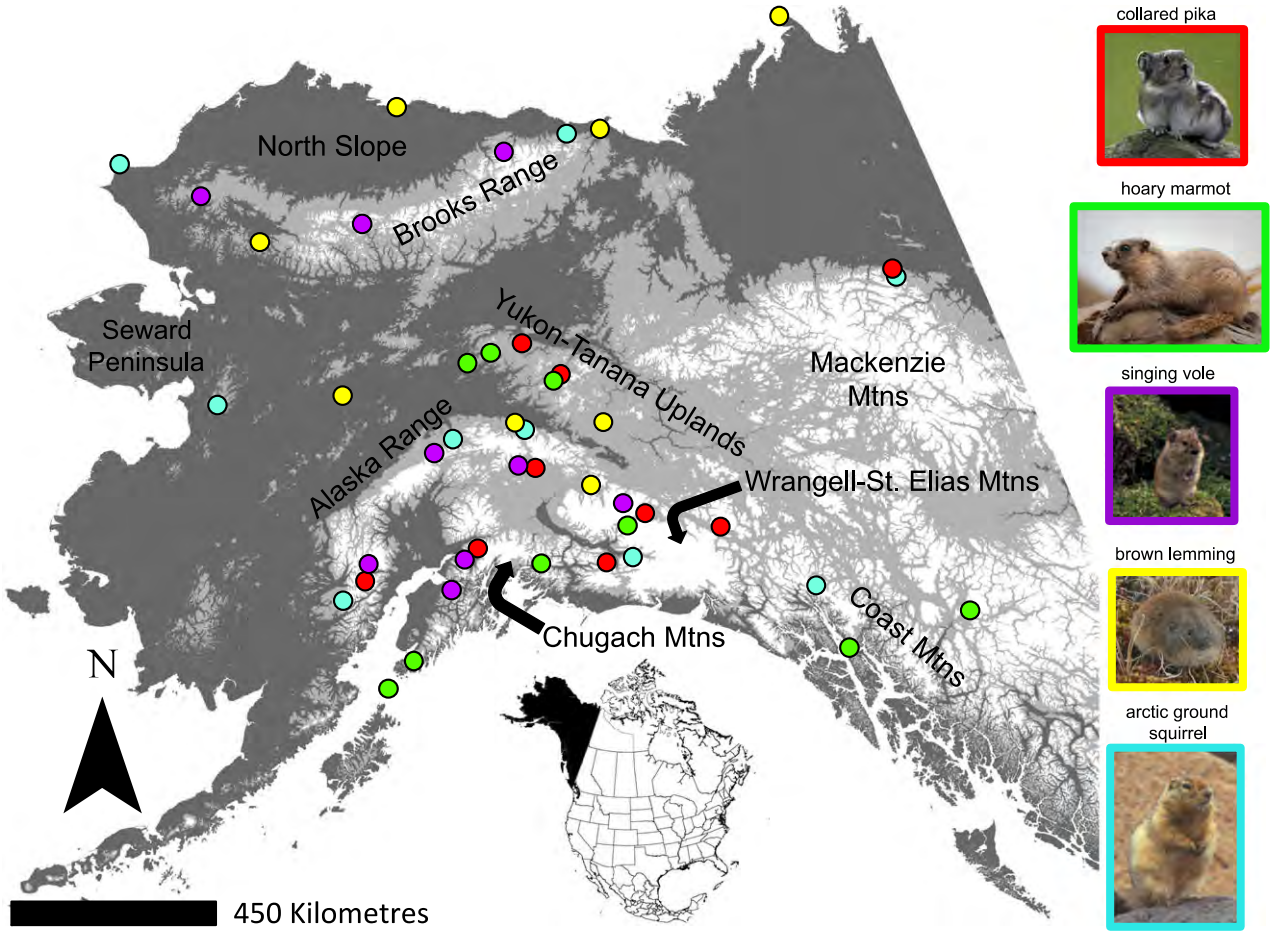

Figure 1 Sampled populations for the five mammal taxa in Alaska: collared pika (*Ochotona collaris*), hoary marmot (*Marmota caligata*), singing vole (*Microtus miurus*), brown lemming (*Lemmus trimucronatus*) and arctic ground squirrel (*Spermophilus parryii*). Also marked are the primary mountain ranges and uplands against a grey scale background. The sampling locations are representative of each species' range within the study area. The extent of overlap of their respective ranges differs; for example, collared pikas and hoary marmots do not occur in northern Alaska (e.g. the Brooks Range). Overlapping sampling points indicate species were collected from the same site. Photos credits: Moose Peterson (collared pika), Ivan Andrijevic (brown lemming), Link Olson (arctic ground squirrel), Jonathan L. Fiely (hoary marmot) and Creative Commons (singing vole).

required before the locus was processed was rounded up (e.g. a locus would need to be genotyped in three out of five individuals with $r = 0.50$).

Quantitative comparison of the similarity between genes and geography

Principal components analyses were performed on customized STRUCTURE files. To create these files, the loci names exported from the MySQL databases (see above) were used as a 'whitelist' by the POPULATIONS program in STACKS; in order to stop POPULATIONS from filtering out loci from our data set (we wanted all of the data irrespective of the number of populations a locus occurred in or the number of individuals a locus was present in within a population), we set all parameters to 0. POPULATIONS wrote the genomic data in a Variant Call Format (vcf) file, which we converted to a STRUCTURE file format using PGDSPIDER 2.0.7.2 (Lischer & Excoffier, 2012). The STRUCTURE file for each species was edited to exclude linked SNPs, as well as SNPs and individuals that contained a high proportion of missing data, which can disproportionately affect patterns in a PCA (Wang *et al.*, 2012). First, all SNPs with > 70% missing data were deleted. Next, the amount of missing data per individual was calculated, and individuals with prohibitively high amounts of missing data (such that the final data set would contain too few SNPs) were excluded (these individuals were obvious because they generally contained > 90% missing data). The final step was to maximize the number of SNPs and individuals such that each individual had < 15% missing data (Lischer & Excoffier, 2012); the final number of individuals used in subsequent analyses is presented in Table S1.1 in Appendix S1.

Principal components analysis were performed on species-specific matrices in R (R Core Team, 2014) using the ADEGENET R package (Jombart *et al.*, 2008). Missing data were replaced by the mean frequency of the corresponding allele, which is recommended for centred PCAs (Jombart et al., 2008). Major axes for genome-wide SNP data were identified using the R DUDI.PCA function (centre = T, scale = T). An association between genetic differentiation and geography was assessed considering divergence along both latitudinal and longitudinal axes across populations using a Procrustes transformation approach. Specifically, species-specific PC1 and PC2 scores and the projected latitude and longitude of sampling localities were inputs in a Procrustes analysis, which maximizes the similarity between PCA maps of genetic variation and geographical locations of sampled populations (see Wang *et al.*, 2010, 2012). Geographical coordinates were transformed to an Albers Equal Area Conic projection using the SPTRANSFORM function in the RGDAL R package (Bivand *et al.*, 2014). Analyses were performed using the PROTEST function in the VEGAN R package (Oksanen *et al.*, 2013). Because Procrustes analysis superimposes a PCA plot of genetic variation onto a geographical map by rotating the PC axes to achieve maximum similarity to the geographical distribution of sampled locations (i.e. the sum of squared differences between the two data sets are minimized), it is ideal for quantitative comparison of the similarity between genes and geography across taxa (as it is for comparing the association between regions; see Wang *et al.*, 2010). We report the angle of the PCA map (i.e. θ, the rotation measured in degrees) that optimally minimizes the sum of squared Euclidean distance between the PCA map from the SNP data and the geographical map. The significance of the association statistic between the first two PCs of genetic variation and the geographical coordinates of the populations (denoted as t_0) for each species was evaluated based on 10,000 permutations, where geographical locations were randomly permuted across the different sample localities (note that all individuals from the same locality were assigned to a single geographical location in the permuted data set, such that observed levels of population structure were maintained).

As the aim of the work was to evaluate the overall similarity (or lack thereof) in the association between genes and geography across taxa, we assessed the robustness of our results by excluding one population at a time and repeating the PCA and Procrustes analyses on the new data sets. Comparison of the PCA coordinates from the new data sets and the original geographical data sets were applied systematically to identify the maximum extent to which the association between genes and geography might increase or decrease as different populations were excluded, denoted by the similarity score t'' (following the notation of Wang *et al.*, 2012). In addition, a similarity score denoted by t' (following the notation of Wang *et al.*, 2012) was computed between the new PCA coordinates for the SNP data and the original PCA coordinates for the SNP data (i.e. before removing any population) to assess how robust the patterns among populations in PCA space are to individual populations.

Environmental niche modelling

Environmental niche models (ENMs) were generated from bioclimatic variables for the present and the LGM with MAXENT 3.3.3e (Phillips *et al.*, 2006). We performed *a priori* model testing to determine optimal combinations of the regularization and feature parameters for the construction of each species' present-day ENM (Warren & Seifert, 2011). Specifically, we used SDMTOOLBOX (Brown, 2014) to test models over combinations of regularization parameters from 0.25 to 3 in intervals of 0.25 and the Linear, Quadratic, Hinge, Product and Threshold features. Each model parameter class was replicated 25 times using cross-validation. Georeferenced distribution points from vetted occurrence data used in the modelling were representative of the entire ranges of the five species, respectively, throughout northwestern North America (Dryad doi:10.5061/dryad.8jm51). For each species, occurrence data were spatially rarefied using SDMTOOLBOX at a resolution of 10 km to reduce spatial autocorrelation.

We used 19 bioclimatically informative variables to model present-day distributions (WorldClim 1.4; Hijmans *et al.*, 2005) and LGM distributions (PMIP2-CCSM; Braconnot *et al.*, 2007) for each species. To avoid overfitting of the distribution models, the geographical extent of the environmental layers was reduced to an area *c.* 20% larger than the known distribution of each species (Anderson & Raza, 2010) and coupled with background sampling bias files (Phillips *et al.*, 2009; Merow *et al.*, 2013). Sampling bias files were constructed in SDMToolBox using a buffer distance of 100 km, which was reasonable given the geographical extent of Alaska and the distance among species' occurrence points. Subsequently, the following procedure was carried out for each species to guard against the inherent difficulties in extrapolating distributions into novel climates (reviewed in Alvarado-Serrano & Knowles, 2014). Specifically, an iterative approach was used to generate ENMs for the LGM in which multivariate environmental similarity surfaces (MESS maps) were used to identify bioclimatic variables that result in areas of low reliability because of predicted values that are outside of the range of present-day environmental values for any given taxon (Elith *et al.*, 2010). Maxent was rerun excluding these out-of-range variables, and this process of analysis with MESS maps was repeated until no LGM variables were out-of-range compared to present-day bioclimatic variables. Because MESS maps do not indicate changes in correlations among the environmental variables used for LGM reconstructions (Elith *et al.*, 2010), we checked our ENM for the LGM using only the most informative variable for each species to ensure that we were not reporting errant distributional patterns. In addition, a present-day ENM was generated using the subset of variables that were not out-of-range during the LGM and compared to an ENM constructed using the most important variable (as determined by Maxent) and the remaining variables that had Pearson's r correlations to this variable of $< 90\%$, as determined by ENMTools (Warren *et al.*, 2010); while these models were not expected to be identical, we checked that both models reported similar distributional patterns. Details about species-specific environmental variables and parameters for the different models are reported in Table S2.1 in Appendix S2.

RESULTS

Sequence data and genetic diversity

More than 500-million reads were produced across the four lanes of Illumina sequencing (average of 1,821,116 ± 825,584 reads per analysed individual across species; for details see Table S1.2 in Appendix S1). After excluding SNPs that were linked and/or that had greater than 15% missing data, the number of independent SNPs per species was: collared pika, 7463; hoary marmot, 5524; singing vole, 3666; brown lemming, 4718; arctic ground squirrel, 3502 (note that variation in the number of SNPs primarily reflects differences in genome size and effective population size across taxa, given the similar quality of reads, and the number and distribution of reads across specimens, in each library). Summaries of genetic diversity per population are given for each of the five taxa in Table S3.1 in Appendix S3. Heterozygosity was generally consistent across populations (with the exception of the Sud Island population of the hoary marmot, which had a considerably lower observed heterozygosity compared to other populations), but differed among taxa.

Procrustes analyses and ENMs

We find significant similarity between genes and geography across taxa (see Table S3.2 in Appendix S3). However, the strength of similarity differs among taxa and across geographical regions (see Fig. S3.2 in Appendix S3). Below we describe these associations between genes and geography on a per-species basis, including the robustness of the association with the exclusion of populations, as well as how the results from the Procrustes analyses conform to the projections of the species' distributions in the past based on the ENMs.

Collared pika

Although the similarity score between the pika populations in PC space and their actual geographical locations is significant ($t_0 = 0.71$; $P < 1.0^{-5}$), t_0 is generally low compared to other taxa (only the brown lemming has a lower t_0). This is in part due to departures associated with Jawbone Lake and the Pika Camp populations. For example, given the distance from Jawbone Lake in the east to Lake Kenibuna in the west, we would expect a large distribution of genetic variation along the longitudinal axis. Instead, individuals from these populations cluster with individuals from more centrally located populations (Fig. 2 and Fig. S3.1 in Appendix S3). In contrast, the Pika Camp population is more divergent genetically than would be predicted by geography alone (i.e. the population occupies a more distant area of PC space relative to the other populations).

Although reconstructions of glacial margins during the LGM suggest a north-western refuge (as previously suggested; Lanier *et al.*, 2015b), this was not supported by the Procrustes analyses (Fig. 4 and see Fig. S2.1 in Appendix S2). Collared pikas (like hoary marmots) are not known from the Brooks Range or anywhere north of the Yukon River in Alaska (Gunderson *et al.*, 2009; Lanier & Olson, 2013). If there was a more northerly population in the past, as predicted by the LGM ENM (see Fig. S2.1 in Appendix S2), it did not contribute to the current standing genetic diversity (i.e. we would expect strong deviations of populations from the central and southern areas if these areas were indeed colonized from a distant geographical source, which are not observed; Fig. 2). Likewise, despite the proximity of other sampled populations (e.g. Rock Lake) and suitable habitat during the past and present (Fig. 4), individuals from Pika Camp have a distinct ancestry that may

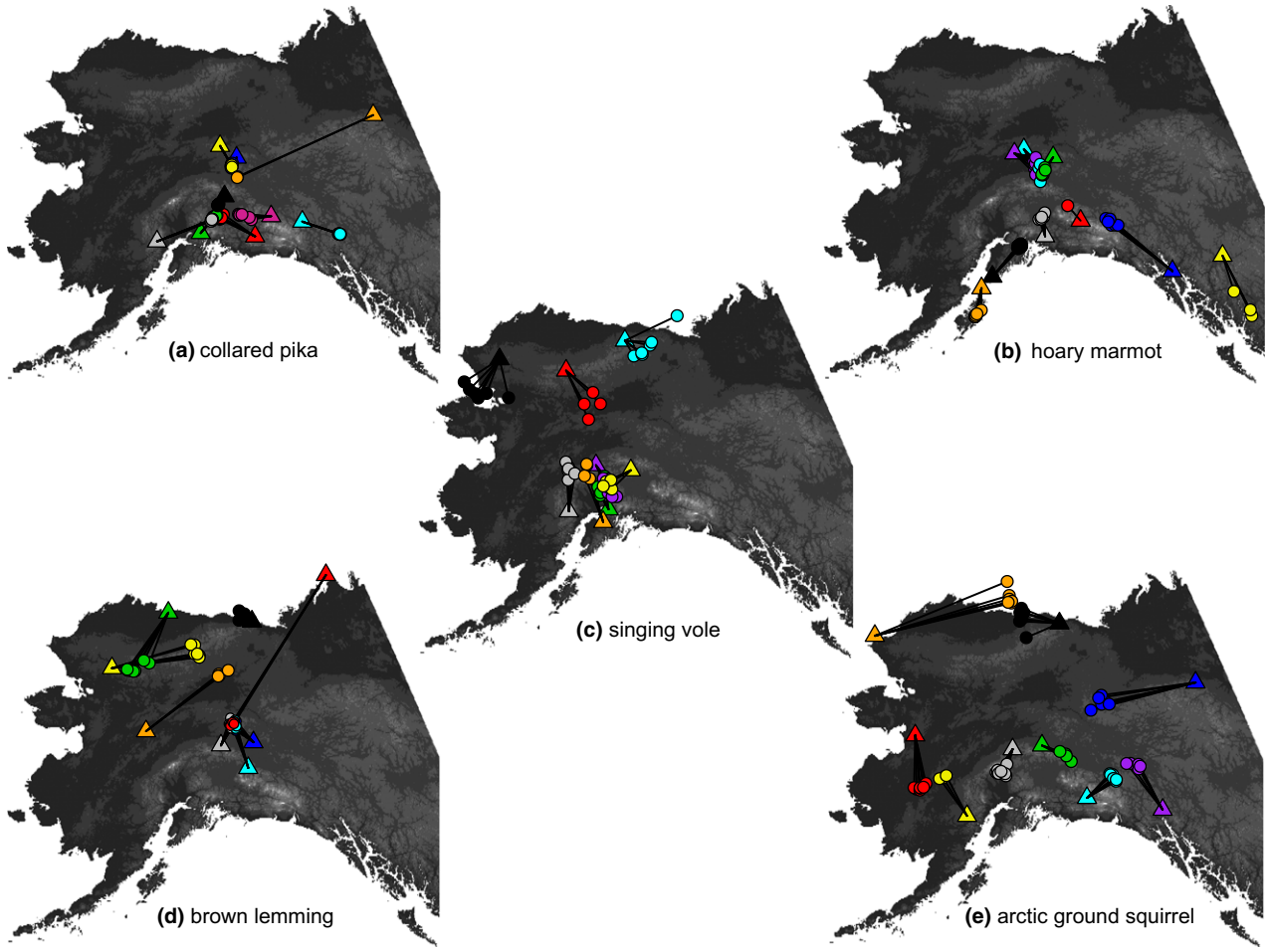

Figure 2 Procrustes-transformed PCA plot of genetic variation with each individual mapped in principal components (PC) space (small open circles) relative to the geographical location of populations (triangles) for each of the taxa (i.e., the plots for each taxa, a through e, as projected upon the map of Alaska). The length of the line connecting individuals in PC space to their geographical location represents the extent of the deviation from the expected pattern of genetic variation based on geography.

indicate that it was colonized from a different refugial source population (see below).

Hoary marmot

This species showed the highest similarity between genes and geography ($t_0 = 0.90$, $P < 1.0^{-5}$) and it became very high with either the exclusion of the south-eastern Juneau ($t'' = 0.95$) or Northwestern British Columbia (NWBC) population ($t'' = 0.96$) (Fig. 3; see Table S3.2 in Appendix S3). The position in PC space of marmots from the Juneau population (Fig. 2) shows that they are genetically consistent with a population located much further to the west, whereas the NWBC population sampled at the same latitude, but just to the east (Fig. 2), is genetically consistent with populations farther south.

Geographical structuring of genetic patterns in hoary marmots in some ways mirrors that in collared pikas. The south-eastern-most marmot population is projected to a more southern location in the Procrustes analysis (Fig. 2), like the pikas. However, the inferred boundary between these putative refugia is discordant between the two species. Specifically, this west-versus-southern deviation occurs in the more eastern extent of the hoary marmot's sampled range compared to that for the collared pika. In both species, the central Alaskan populations show a strong correspondence between genes and geography (Fig. 2), suggesting historical stability (Fig. 4).

Singing vole

This species shows the second-highest similarity score between genes and geography ($t_0 = 0.89$; $P < 1.0^{-5}$) of all the taxa (see Table S3.2 in Appendix S3) as evidenced by the consistently small distortions of individuals from their expected genetic patterns based on the geographical location of sampled populations (Fig. 2). This pattern was generally robust to sequential population exclusion (Fig. 3).

The ENMs project suitable, stable habitat in both the northern and southern parts of the singing vole's current

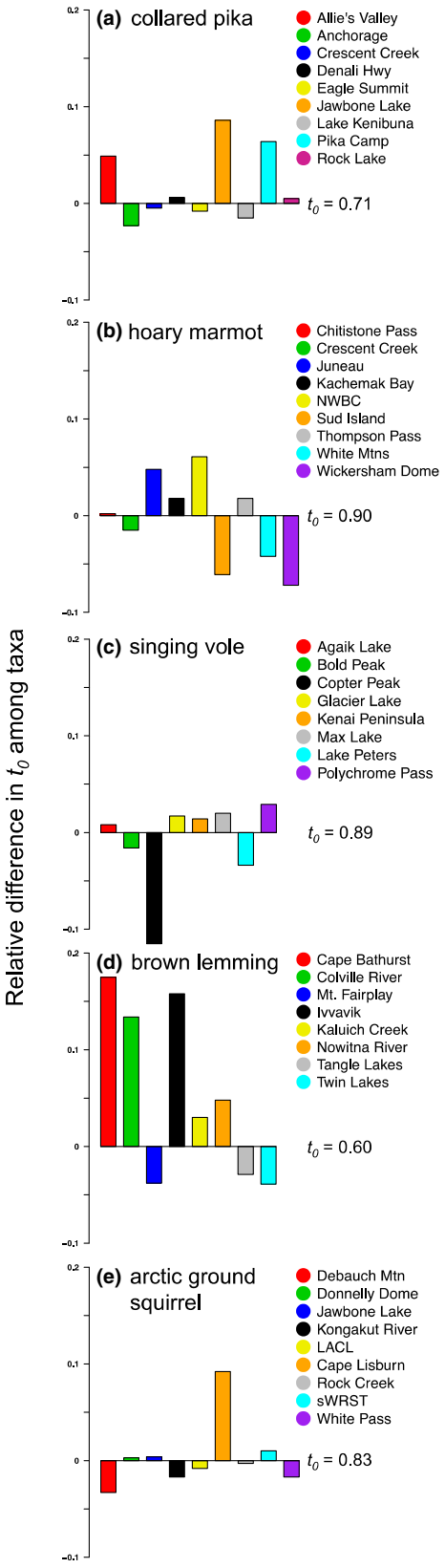

Figure 3 Comparison of the changes in the association between genes and geography with the exclusion of individual populations (i.e. t'') relative to when all populations are analysed (i.e. t_0) for: (a) collared pikas; (b) hoary marmots; (c) singing voles; (d) brown lemmings; and (e) arctic ground squirrels. Values for each species are standardized by t_0 (i.e. 0 on y-axis corresponds to t_0) such that positive values indicate a stronger association between genes and geography when a population is excluded, whereas negative values indicate a weaker association. Bar colours represent sampling populations; the same colours for each species' populations are used throughout all figures (Fig. 2 and Appendix SI).

range, but not in the central part of the range (Fig. 4). The northern populations remain genetically differentiated (see Fig. S3.2 in Appendix S3), and these differences generally correspond to the geographical distances separating the populations (Fig. 2), in contrast with patterns seen in the northern populations of the arctic ground squirrel and brown lemming (below), which tend to show less genetic distinctiveness. For example, northern arctic ground squirrel populations tend to be much more genetically similar to one another than similarly distributed singing vole populations (Fig. 2).

There is also no indication that singing voles were displaced to central Alaska based on the Procrustes analysis (Fig. 2), corresponding to the lack of suitable stable habitat in that region (Fig. 4). This is consistent with the rarity of reports of singing voles from central Alaska, despite intensive and repeated sampling efforts (Weksler *et al.*, 2010; Baltensperger & Huettmann, 2015).

Brown lemming

This species exhibits the lowest similarity between genes and geography of all five species (t_0 = 0.60, $P < 1.0\times10^{-5}$). Of the five focal species, the brown lemming is inferred to have the largest geographical extent of stable habitat (Fig. 4), based on projections of the species' present and past distributions (see Fig. S2.1 in Appendix S2). However, there is no obvious corridor of suitable habitat identified from the ENMs (Fig. 4) between the Cape Bathurst population in the north-east and the south-central Alaskan region that might explain the high genetic identity of individuals from this area with the central populations (Figs 1 & 2, and Fig. S2.1 in Appendix S2).

Arctic ground squirrel

This species exhibits several patterns unique among the sampled taxa. Individuals from the two northernmost populations (Figs 2 & 3) overlap genetically despite their geographical separation, unlike the patterns in singing voles and brown lemmings. In contrast to all other species with populations sampled in or near the northern Alaska Range (Fig. 1), arctic ground squirrels from this area do not overlap in PC space, instead remaining distinct (and even diverging from each other in opposite directions; Fig. 2). Furthermore, individuals from all of the remaining populations generally form distinct, non-overlapping clusters in the

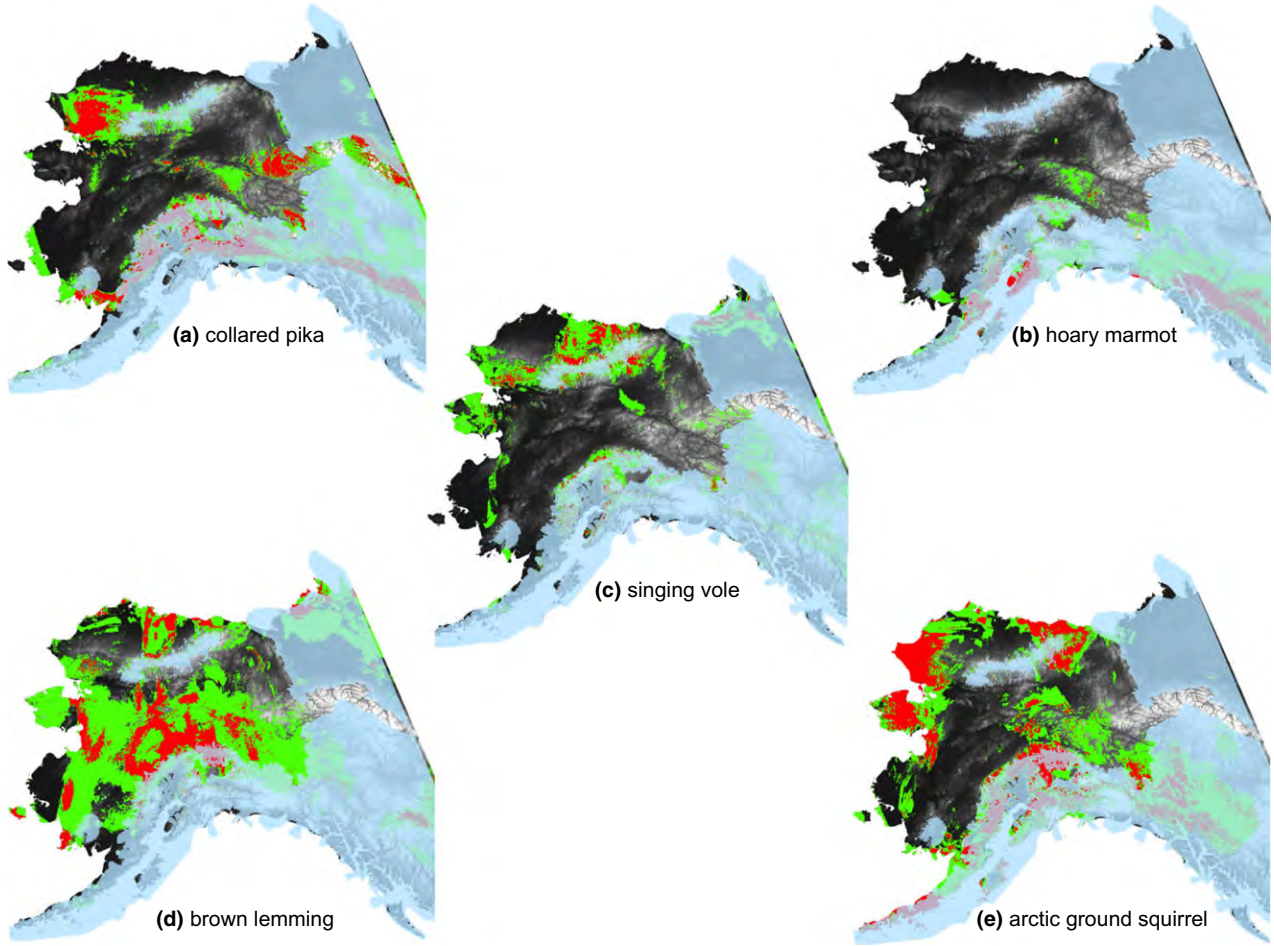

Figure 4 Maps of habitat predicted to be stable throughout Pleistocene glacial cycles. For each species (i.e., a through e), stable habitat (shown in red) is defined by the overlap of ENMs for the present and the Last Glacial Maximum (LGM), whereas unstable habitat (shown in green) is habitat predicted to be suitable in either the present or the LGM. The extent of glacial coverage at the LGM is shown in light blue. Note that the glacial reconstruction is based on independent geologic information from glacial moraines. Separate projections of current and past distributions are available in the supplement (see Fig. S2.1 in Appendix S2).

vicinity of their sampling localities (similar to the southern populations of hoary marmots). Despite these differences, individuals from Jawbone Lake still deviate longitudinally towards central Alaska, similar to the patterns seen in collared pikas and brown lemmings (from the more northern Cape Bathurst population).

While these patterns are unusual, the association between genes and geography in the arctic ground squirrel is significant and within the range of variation seen in the other taxa ($t_0 = 0.83$; $P < 1.0^{-5}$). Examination of stable habitat indicates that all of the individuals projected onto geographical space are near habitat expected to be stable in both the LGM and present (Fig. 4), except for the western and south-western populations of Debauch Mountain and LACL, respectively.

DISCUSSION

Species-specific analyses are useful for identifying a correspondence between genes and geography, but a comparison across taxa can also be used to generate hypotheses about shared versus taxon-specific biogeographical histories. In particular, the patterning of spatial variation differs among taxa, and the patterns of genetic variation in some areas more closely fit predictions based on where an individual was sampled compared to others. Below we highlight what our findings suggest about the history of arctic and subarctic alpine mammals, and in particular, specific hypotheses about their biogeographical and demographic histories. We also discuss the limitations of the approach, especially with respect to understanding the cause of deviations of genetic variation from expectations based on geography. Specifically, we focus on the utility of the approach for identifying hypotheses that might be tested with other approaches, rather than inferring process from the results of the Procrustes analyses themselves.

Comparison of Procrustes analyses across taxa

The similarity between geography and genes varied among taxa. For example, with all sampled populations included, t_0

ranged from a high of 0.90 in the hoary marmot to a low of 0.60 in the brown lemming (see Table S3.2 in Appendix S3). However, this variation reflects in part the disproportionate effect of individual populations (or combinations of several outlier populations) on decreasing t_0. Indeed, in none of the species was the highest t_0-value observed when all populations were analysed. The highest similarity between geography and genes was achieved when a population was excluded (e.g. the similarity between geography and genes increased in all taxa, ranging from $t'' = 0.77$ in brown lemmings to $t'' = 0.96$ in hoary marmots). Interestingly, taxa differed with respect to which geographical regions, when excluded, maximized the association between genes and geography. For example, exclusion of the Cape Lisburn population of arctic ground squirrels maximized the similarity between genes and geography, but in the hoary marmot it was the south-eastern NWBC population that maximized t'' (Figs 2 & 3). This suggests there is no single and common cause to the departure from IBD across these taxa, which is relevant to forming comparative phylogenetic hypotheses for additional testing (see below).

Increases in the similarity between geography and genes when a particular population was excluded (i.e. t'') was not due to a disproportionate effect of the excluded population on the relative positions of individuals in PC space (see Table S3.2 in Appendix 3 for t'-values, which remained consistently very high). In all cases, the similarity between the PCA of genes with and without the population that maximized the similarity between genes and geography (i.e. t'') was 1.0 (the maximum value for t'), except for in hoary marmots where $t' = 0.96$. In contrast, for cases in which the exclusion of a population reduced the association between genes and geography (see Table S3.2 in Appendix S3), the large drop in t'' was also accompanied by a shift in the similarity of the PCAs of genes, t'. This suggests that inclusion of such populations is critical to characterizing the spatial structure in each taxon across the sampled region. In fact, in each species, the exclusion of several different populations results in t''-values that are lower than t_0-values, which highlights the importance of representative sampling across the species range when characterizing spatial structure (see DeGiorgio & Rosenberg, 2013). Again, the effect is not due solely to fewer data points when populations are excluded because in all species t_0, with all populations analysed, was lower than the maximum t''-value achieved when one population was excluded from the Procrustes analyses (as described above; see also Fig. 3).

Hypotheses motivated by results of the Procrustes analyses

The statistical association between genetic variation and geography in all species is an important finding. However, it is also noteworthy to consider what populations deviate from IBD expectations (especially when viewed in a comparative context and visualized geographically). In particular, these aspects of the Procrustes analyses can be useful for formulating hypotheses. To be clear, other approaches might be used to test for an association between genetic variation and geography (see Jombart *et al.*, 2008; Frichot *et al.*, 2012). However, with visualizations of distortions in genetic variation in relation to the geographical localities of sampled individuals, Procrustes analyses also provides a useful framework for generating hypotheses (see also Papadopoulou & Knowles, 2015a). As such, the output from Procrustes analyses can address one of the major challenges in statistical phylogeographical study – the identification of hypotheses (Knowles, 2009).

A notable departure (with regard to both the magnitude and geographical orientation of deviations) pertains to sampled populations along the periphery of the Alaskan mammal ranges relative to those from the interior. Specifically, the positioning of individuals in the Procrustes analyses span the entire latitudinal range of sampled populations in all the species. However, the full geographical extent of sampled populations along the longitudinal axis is underrepresented genetically, especially in collared pikas, brown lemmings and arctic ground squirrels (see Fig. S3.2 in Appendix S3). That is, individuals are clustered towards the Alaskan interior more than would be expected based on the longitudinal position of populations (Fig. 2). For example, any population sampled in the north-eastern portion of the ranges (e.g. in the area of the Mackenzie River Delta) shows patterns suggestive of a shared ancestor with other more centrally located populations, rather than an ancestral refugial source population in the north-east.

Other repeated patterns of deviations from IBD across taxa are suggestive of a shared biogeographical history in which populations within a region may have been colonized from multiple refugial source populations. For example, hoary marmots and collared pikas from the south-east are much more distant in genetic space from other geographically proximate populations (Fig. 2). Singing voles show a similar displacement (results not shown), but because of questions surrounding their taxonomic identity (Weksler *et al.*, 2010), these specimens were excluded from this study. However, not all taxa from this region show the same deviation. Arctic ground squirrels sampled in this south-eastern region (Fig. 1) are genetically most similar to populations to the north and west. Hence, although the genetic data in the taxa suggest the north-eastern region has not been consistently inhabited (i.e. these regions do not fit with general expectations under an equilibrium isolation-by-distance model), it seems unlikely that the deviations could be explained by one hypothesis regarding the geographical position of refugial source populations. For example, south-eastern populations of hoary marmots, collared pikas and possibly singing voles, but not arctic ground squirrels, may have been founded from an ancestral population further to the south and east than predicted by the current localities of sampled individuals (Fig. 2).

The results from the sequential exclusion of populations identifying regions (or populations) that have a dispropor-

tionate effect on the association between genes and geography can also be a source of information for developing hypotheses about region-specific processes. For example, a much higher association between genes and geography results when brown lemmings from northern coastal populations (Fig. 2) are excluded in Procrustes analyses (Fig. 3). This suggests that a possible hypothesis to explain the deviations between genes and geography in brown lemmings (Fig. 2) would have to accommodate the entire northern coastal region (not just one or two specific populations). Moreover, latitudinal differences in the genetic similarity of individuals suggest the region might have experienced fairly localized processes. These might include aspects of the demography of colonization and/or different ancestral source populations (i.e. individuals from Cape Bathurst and Colville River show genetic variation consistent with individuals sampled from more southern latitudes, in contrast to the Ivvavik population).

This more nuanced picture with concordance limited to specific taxa and certain geographical regions differs from more generalized hypotheses identified from mtDNA (Galbreath *et al.*, 2011; Lanier *et al.*, 2015a). Perhaps this is not entirely unexpected given that different markers provide differing degrees of resolution (Knowles, 2009). With the additional resolution of genomic markers it is increasingly clear that relying on mtDNA (or any single linkage partition) alone overlooks processes that may actually structure genomic variation. For example, unlike interior Alaska, which was part of ice-free Beringia during the LGM, formerly ice-covered localities within the hoary marmot's current distribution show the greatest discordance between genes and geography (i.e. Figs 2b & 3b). Likewise, a rapid expansion of hoary marmots from one or more south-central refugia (either nunataks or periglacial areas predicted as being suitable marmot habitat during the LGM; Fig. 4b) suggests a more dynamic history than suggested by past studies. Nevertheless, the genomic analyses also provide corroborative support for some species-specific hypotheses suggested by patterns of mtDNA differentiation. For example, a possible inland incursion from a coastal refugium (see Kerhoulas *et al.*, 2015) originating south of our sampling regime is suggested by the seemingly anomalous discordance in the NWBC marmots (Fig. 2).

Testing hypotheses developed from the findings of the Procrustes analyses

Some hypotheses suggested by the Procrustes analyses appear to be corroborated from independent data sources. For example, we have hypothesized that the Yukon-Tanana uplands are a potential refugium for hoary marmots and collared pikas based on deformations in the north-central parts of their range in the Procrustes analyses (Fig. 2). This area is also projected to be highly suitable and stable habitat by the ENMs (see Fig. S2.1 in Appendix S2), and it has been identified as a biodiversity hotspot for Alaskan small mammals (Baltensperger & Huettmann, 2015).

More generally, and as we advocate here, departures from IBD detected in the Procrustes analyses can be used to generate hypotheses for future study (as discussed above). However, the results from the Procrustes analyses, by themselves, are not sufficient for interpreting the processes underlying the lack of a correspondence between genes and geography (see below).

Not only might different processes leave similar signatures that can be difficult to distinguish, but the signal of a specific process may not be easily intuited from the pattern of deviations evident in the Procrustes plots, as with other summaries of genetic variation (see Knowles & Alvarado-Serrano, 2010; Brown & Knowles, 2012; He *et al.*, 2013; Wang & Bradburd, 2014). For example, it is difficult to identify one hypothesis that might have generated the deviations from IBD observed in the arctic ground squirrel (Fig. 2). Only the exclusion of the north-western population lead to an appreciable increase in this association (Fig. 3), leaving a fair amount of genetic variation that is not explained by IBD. A possible hypothesis that might be considered is isolation by colonization in which the populations were founded from a single centrally located ancestral source. However, this model alone wouldn't necessarily explain why the southern populations show latitudinal departures, but little deformation from longitudinal positions of populations (Fig. 2). Perhaps a non-equilibrium model in which the rate, or timing, of latitudinal spread differed from the longitudinal spread in the south could generate the observed deviations from IBD. Without further analysis, it is not possible to evaluate the likelihood of such a hypothesis. Such detailed demographic scenarios might be informed directly from the ENMs (see Fig. S2.1 in Appendix S2), including inferred areas of stability (Fig. 4), as with modelling approaches like the iDDC (He *et al.*, 2013). For example, changes in the suitability of habitats across the landscape, and changes in suitability over time, can be used to inform the colonization process associated with shifting distributions driven by glacial cycles (Brown & Knowles, 2012).

In addition to the multiple processes that might generate a departure from IBD, the magnitude and orientation of deformations in the Procrustes plots (i.e. the length of the arrows; see Fig. 2) may also be impacted by the timing of the events that cause a departure between genes and geography (e.g. Excoffier *et al.*, 2009). For example, for a recent expansion the direction of the deviations might be captured in a Procrustes analysis, but a population near the site of an expansion centre might show higher deviations relative to more geographicalally distant populations if the expansion has been recent (see simulation results in He *et al.*, 2013). Likewise, because PCA can be sensitive to the sampling of individuals over geographical space (e.g. over- or under-representative sampling for some regions; see DeGiorgio & Rosenberg, 2013), it is possible that such effects could influence some of the Procrustes analyses. We note that in general the patterns in the genetic PCs were not significantly impacted when we excluded one population at a time (see t'-values in Table S3.2 in Appendix S3). This suggests that

results from analyses of the full Alaskan mammal data sets considered here are not being biased by geographical unevenness in the sampling of individuals. However, whether the results from Procrustes analyses are robust to different sample sizes across space is not known.

Does this mean that the results from Procrustes analyses have no utility for identifying the processes causing departures from IBD? Not at all – it just means that any interpretation will have to take into to account the uncertainty that would come with a single summary of genetic variation. For example, the statistical summaries from the Procrustes analyses (e.g. the t_0, t', and t''-values, as well as the angle of rotation to maximize the covariance between genes and geographical matrices) could provide valuable summary statistics for incorporation into procedures like Approximate Bayesian Computation (ABC) to test phylogeographical hypotheses. Likewise, integrated models of phylodemographic movements (e.g. iDCC; He *et al.*, 2013) may be useful in teasing apart these alternative hypotheses, especially if the differences among species discovered here are indicative of an interaction of species history and biology (e.g. Massatti & Knowles, 2014; Papadopoulou & Knowles, 2015b). In particular, our results hint at a possible distinction between more mesic species (such as brown lemmings) and more xeric species (such as collared pikas and hoary marmots). Brown lemmings show little geographical concordance in terms of direction of deformation relative to contemporary populations. For example, the projections onto geographical coordinates based on patterns of genetic variation do not overlap (i.e. individuals from populations form discrete clusters), and there is no concerted direction of movement as would be expected when previously glaciated habitat are colonized (Fig. 2). Other work has suggested that this region was a tundra mosaic (Elias *et al.*, 1996; Anderson *et al.*, 2004), which may have contributed to the lack of uniformity in the direction of deformation.

The Procrustes analyses are just the first step towards identifying future studies of genomic variation. With respect to this fascinating group of mammals, the lack of concordant genomic variation suggests there is no single geographical region in Alaska that has remained isolated geologically (i.e. a region that has remained independent of other regions) or ecologically (i.e. a barrier that prohibited historical gene flow among populations). However, some repeated patterns of variation across subsets of taxa in some parts of their ranges suggest a role for shared processes operating at more local geographical scales. Future tests will explore the hypotheses generated here, and evaluate the relative roles of taxon-specific versus regional processes in structuring genomic variation across these alpine small mammal communities.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Summaries of geographical information and genomic sampling.

Appendix S2 Summaries of ENM settings and projections of current and LGM distributions.

Appendix S3 PC maps of genetic variation and summaries of genetic variation.

BIOSKETCH

L. Lacey Knowles and her lab are interested in understanding the processes that structure patterns of genetic variation across geographical landscapes and among taxa. Her lab works on a diversity of empirical systems to discover how species-specific responses to past events, especially those caused by climate change, influence the connections among populations that shape divergence patterns over space and time. This work is also complemented by methodological study and development to identify approaches that are useful for making inferences about the processes that shape genetic patterns within and among taxa.

Author contributions: L.L.K., Q.H. and R.M. conceived the ideas; L.L.K. led the writing with input from all the other co-authors; L.E.O. and H.C.L. collected the specimens; H.C.L. and Q.H. collected the genomic data; Q.H. conducted bioinformatics processing of genomic data; R.M. did the genetic analyses and ENMs.

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Appendix S1. Summaries of geographical information and genomic sampling

Details about locality information (Table S1) and genomic data (Table S2) for sampled individuals are provided in this appendix, Appendix S1, along with details about library construction and processing. Genomic DNA was extracted from either fresh or frozen tissue using either Qiagen DNeasy or Gentra PureGene kits (Gentra Systems Inc., Minneapolis, MN, USA) following the manufacturer's Animal Tissue Protocol. Four reduced-representation libraries were constructed using a restriction-fragment-based procedure (for details see Peterson *et al.*, 2012). Within each library, individuals were doubly digested with the restriction enzymes *Eco*RI and *Mse*I and uniquely tagged with a 10bp barcode. The digested products were then pooled and size-selected for 350-450bp fragments using a Pippin Prep (Sage Science, Beverly, MA, USA). Size-selected fragments were then amplified by PCR with iProof™ High-Fidelity DNA Polymerase (BIO-RAD). DNA quantification and cleaning with Agencourt AMPure XP (Beckman Coulter, Indianapolis, IN, USA) occurred after every step in the library construction procedure. Each genomic library was sequenced on an Illumina HiSeq2000 at the University of Michigan DNA Sequencing Core to generate 100bp paired-end reads; however, only the first read was retained here due to the need for unlinked single nucleotide polymorphisms (SNPs) in our analyses.

The *Stacks* v1.07 pipeline (Catchen *et al*., 2013) was used to identify SNPs in the processed genomic data from the species-specific genomic libraries constructed for each species. Specifically, in each species-specific library, the USTACKS program was used to create a *de novo* assembly of reads with a minimum coverage depth (m = 3) into putative loci (i.e. into a "stack"). 'RADseq locus/loci' is hereafter used interchangeably with 'locus/loci' and refers to groups of 90 base-pair reads that are homologous (both within and among individuals); RADseq loci contain both invariable and variable DNA sites (i.e. SNPs). Reads were filtered using a removal algorithm that eliminated highly repetitive stacks (i.e. stacks that exceed the expected number of reads for a single locus given the average depth of coverage, for example, when loci are members of multi-gene families) and the 'deleveraging algorithm' to resolve over-merged loci (i.e. non-homologous loci misidentified as a single locus). SNPs were identified at each locus and genotypes were called using a multinomial-based likelihood model that accounts for sequencing error (Hohenlohe *et al*., 2010; Catchen *et al*., 2011; Catchen *et al*., 2013), with the upper bound of the error rate (ε) set to 0.1. A conservative upper bound was selected for ε, as these models have been developed primarily for higher-coverage data; a conservative bound was preferred over the unbounded model because the latter has been shown to underestimate heterozygotes *(*Catchen *et al*., 2013). A catalog of consensus loci among individuals was constructed with the CSTACKS program from the USTACKS output files using all of the individuals of each species. Loci were recognized as homologous across individuals if the distance between the consensus sequences (n) was ≤ 2. Each individual was matched against the catalog and alleles were identified in each individual using SSTACKS. A summary of the number of pre- and post-processing reads, as well as

the number utilized by *Stacks*, is given in Table S2 in this appendix. At this stage, 12 individuals with low coverage were excluded from further analyses (collared pika: 2, hoary marmot: 1, singing vole: 4, brown lemming: 3, arctic ground squirrel: 2; see Table S1 in this appendix); this first round of exclusions was based on those specimens with <35% of the reads utilized by *Stacks* (see Methods and Materials in main text for other processing steps).

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Table S1.1. Locality information for each sampled population of the five focal mammal taxa. See Fig. 1 for the locations of the mountain ranges and Figs 2 & 3 for the population locations and names, respectively. Also noted is the number of individuals used in analyses; see the Methods for filtering details.

a) collared pika

Population	Mountain Range	Latitude	Longitude	Individuals used in analyses (Individuals sampled)
Allie's Valley	Chugach Mtns	60.972	-143.141	8 (8)
Anchorage	Chugach Mtns	61.451	-148.465	6 (6)
Crescent Creek	Yukon-Tanana Uplands	64.821	-143.751	7 (7)
Denali Highway	Alaska Range	63.074	-145.636	6 (6)
Eagle Summit	Yukon-Tanana Uplands	65.483	-145.417	6 (6)
Jawbone Lake	Mackenzie Mtns	65.000	-127.617	2 (2)
Lake Kenibuna	Alaska Range	61.156	-152.855	8 (8)
Pika Camp	Wrangell-St. Elias Mtns	61.217	-138.267	6 (8)
Rock Lake	Wrangell-St. Elias Mtns	61.786	-141.209	7 (7)

b) hoary marmot

Population	Mountain Range	Latitude	Longitude	Individuals used in analyses (Individuals sampled)
Chitistone Pass	Wrangell-St. Elias Mtns	61.613	-142.037	1 (2)
Crescent Creek	Yukon-Tanana Uplands	64.811	-143.779	4 (4)
Juneau	Coast Mtns	58.260	-134.639	7 (8)
Kachemak Bay	Kenai Mtns	59.432	-151.162	8 (8)
NWBC		58.188	-129.888	3 (3)
Sud Island		58.897	-152.211	10 (10)
Thompson Pass	Chugach Mtns	61.136	-145.771	6 (6)
White Mountains	Yukon-Tanana Uplands	65.367	-146.938	7 (7)
Wickersham Dome	Yukon-Tanana Uplands	65.211	-148.060	7 (7)

c) singing vole

Population	Mountain Range	Latitude	Longitude	Individuals used in analyses

				(Individuals sampled)
Agaik Lake	Brooks Range	68.078	-152.921	4 (8)
Bold Peak	Chugach Mtns	61.365	-148.908	5 (5)
Chisana	Wrangell-St. Elias Mtns	62.065	-142.046	0* (3)
Copter Peak	Brooks Range	68.471	-161.478	7 (8)
Glacier Lake	Alaska Range	63.111	-146.247	4 (8)
Kenai Penninsula	Kenai Mtns	60.782	-149.531	4 (6)
Lake Peters	Brooks Range	69.303	-145.025	6 (8)
Max Lake	Alaska Range	61.358	-152.869	7 (8)
Polychrome Pass	Alaska Range	63.498	-149.886	6 (8)

*Individuals from the Chisana population likely represent a different species and were not used in PCA analyses because they heavily influenced the relationships among the populations.

d) brown lemming

Population	Mountain Range	Latitude	Longitude	Individuals used in analyses (Individuals sampled)
Cape Bathurst	North coastline	70.500	-127.983	4 (4)
Colville River	North coastline	70.383	-150.800	7 (8)
Ivvavik National Park	North coastline	69.417	-139.600	6 (8)
Kaluich Creek	Brooks Range	67.664	-158.191	6 (8)
Mt. Fairplay	Yukon-Tanana Uplands	63.698	-142.255	8 (8)
Nowitna River	Kuskokwim Mtns	64.685	-153.937	4 (8)
Tangle Lakes	Alaska Range	63.784	-145.785	9 (9)
Twin Lakes	Wrangell-St. Elias Mtns	62.530	-143.258	7 (7)

e) arctic ground squirrel

Population	Mountain Range	Latitude	Longitude	Individuals used in analyses (Individuals sampled)
Cape Lisburn	North coastline	68.871	-166.040	6 (7)
Debauch Mountain	Nulato Hills	64.390	-159.656	8 (8)
Donnelly Dome	Alaska Range	63.788	-145.800	4 (7)
Jawbone Lake	Mackenzie Mtns	64.817	-127.617	6 (8)
Kongakut River	Brooks Range	69.449	-141.461	7 (8)
LACL	Alaska Range	60.654	-153.936	3 (4)

Rock Creek	Alaska Range	63.750	-149.000	8 (8)
sWRST	Chugach Mtns	60.994	-142.029	7 (7)
White Pass	Coast Mtns	59.616	-135.168	5 (6)

Table S1.2. Summary of genomic data collected in each individual. Shown are the raw count of reads from the Illumina run and the number of reads after processing for quality control (i.e., after excluding reads with low quality scores and ambiguous barcodes), as well as the number of reads analyzed with Stacks to identify homologous loci. Individuals excluded from analyses because of too few reads are marked with asterisks. Specimen IDs refer to University of Alaska Museum Mammalogy Collection catalog number (UAM) or sample IDs (Hik = David Hik lab, University of Alberta Edmonton).

a) collared pika

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Allie's Valley	UAM 102431	2200193	2057166	1759078	80.0
Allie's Valley	UAM 102422	1586907	1487171	1321899	83.3
Allie's Valley	UAM 102435	1267564	1138753	1010043	79.7
Allie's Valley	UAM 102438	1089077	1000485	882573	81.0
Allie's Valley	UAM 102432	1195011	1033694	954753	79.9
Allie's Valley	UAM 102423	510333	451607	350175	68.6
Allie's Valley	UAM 102434	1179276	1114169	995286	84.4
Allie's Valley	UAM 102424	1327323	1216267	1053178	79.3
Anchorage	UAM 102564	774418	753014	523482	67.6
Anchorage	UAM 102565	1126031	1065314	962098	85.4
Anchorage	UAM 102566	3080176	2335737	2560219	83.1
Anchorage	UAM 102567	1646939	1553367	1340924	81.4
Anchorage	UAM 102568	1945449	1849269	1657894	85.2
Anchorage	UAM 64363	420780	381384	278705	66.2
Crescent Creek	UAM 58204	844108	786027	697267	82.6
Crescent Creek	UAM 58205	1166926	1081539	982342	84.2
Crescent Creek	UAM 58213	1876591	1755355	1637374	87.3
Crescent Creek	UAM 58206	1984311	1742179	1674900	84.4
Crescent Creek	UAM 58211	1605214	1410616	1277115	79.6
Crescent Creek	UAM 58212	1771977	1520730	1446598	81.6
Crescent Creek	UAM 58208	1627884	1418606	1305664	80.2
Denali Highway	UAM 102482	1621668	1568650	1372480	84.6
Denali Highway	UAM 102502	621042	564908	494274	79.6
Denali Highway	UAM 102507	1157720	1107975	958350	82.8
Denali Highway	UAM 102498	1072082	961926	838466	78.2
Denali Highway	UAM 102497	1056373	1008968	860030	81.4
Denali Highway	UAM 102562	1067428	969240	844903	79.2
Eagle Summit	UAM 67030	2418283	2159229	2135761	88.3
Eagle Summit	UAM 63938	858050	830613	709030	82.6
Eagle Summit	UAM 63931	1147774	1090189	908065	79.1
Eagle Summit	UAM 63935	1367964	1299827	1150204	84.1
Eagle Summit	UAM 63932	1456907	1369052	1229103	84.4

Table S1.2. Continued

a) collared pika (continued)

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Eagle Summit	UAM 63936	923332	867221	769652	83.4
Jawbone Lake	UAM 88534	2267399	1992588	1921927	84.8
Jawbone Lake	UAM 88532	783793	733337	579604	73.9
Lake Kenibuna	UAM 100776	1104630	1027784	935020	84.6
Lake Kenibuna	UAM 100849	1278694	1197040	1078639	84.4
Lake Kenibuna	UAM 100867	1432377	1279108	1156776	80.8
Lake Kenibuna	UAM 100773	1564207	1427745	1276077	81.6
Lake Kenibuna	UAM 100847	745895	699382	591534	79.3
Lake Kenibuna	UAM 100839	1259324	1187048	1027264	81.6
Lake Kenibuna	UAM 100795	1213196	1163741	1008900	83.2
Lake Kenibuna	UAM 100796	1265215	1183067	1047871	82.8
Pika Camp*	Hik 441	75194	67780	16611	22.1
Pika Camp	Hik 446	1778613	1661328	1544253	86.8
Pika Camp	Hik 1355	1163164	947935	911105	78.3
Pika Camp*	Hik 1555	2101	1310	81	3.9
Pika Camp	Hik 1628	892219	860407	717744	80.4
Pika Camp	Hik 1649	1199435	1111021	1007959	84.0
Pika Camp	Hik 431	1606076	1533478	1412937	88.0
Pika Camp	Hik 492	1972543	1823294	1673905	84.9
Rock Lake	UAM 56066	1521653	1361724	1256627	82.6
Rock Lake	UAM 56099	1689457	1529948	1388376	82.2
Rock Lake	UAM 56814	768798	717441	614318	79.9
Rock Lake	UAM 102366	1264786	1142843	1081822	85.5
Rock Lake	UAM 102416	1587067	1370691	1314836	82.8
Rock Lake	UAM 56094	2071655	1911803	1694215	81.8
Rock Lake	UAM 56093	1943258	1790527	1609661	82.8

Table S1.2. Continued

b) hoary marmot

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Chitistone Pass	UAM 102368	4175093	3721281	3277407	78.5
Chitistone Pass*	UAM 102367	23459	19005	2787	11.9
Crescent Creek	UAM 58238	2891363	2569302	2156068	74.6
Crescent Creek	UAM 58239	3378236	3055098	2659358	78.7
Crescent Creek	UAM 58240	1482726	1306520	1034978	69.8
Crescent Creek	UAM 58241	1454473	1349589	1094736	75.3
Juneau	UAM 103473	2309775	2086943	1637808	70.9
Juneau	UAM 103474	978148	920620	779223	79.7
Juneau	UAM 103474	1930842	1800242	1578255	81.7
Juneau	UAM 103477	2603674	2391162	2115972	81.3
Juneau*	UAM 112351	299081	255796	118433	39.6
Juneau	UAM 112457	1501074	1436536	1196659	79.7
Juneau	UAM 112458	2301993	2192907	1958944	85.1
Juneau	UAM 48486	3250757	3014975	2585267	79.5
Kachemak Bay	UAM 112579	1941004	1816697	1509501	77.8
Kachemak Bay	UAM 112581	1599324	1491559	1230613	76.9
Kachemak Bay	UAM 112585	1539848	1473460	1270921	82.5
Kachemak Bay	UAM 112587	2780169	2529547	2182927	78.5
Kachemak Bay	UAM 113736	2761288	2594333	2357346	85.4
Kachemak Bay	UAM 113737	1400848	1323389	1107606	79.1
Kachemak Bay	UAM 113738	3114599	2954957	2689035	86.3
Kachemak Bay	UAM 113739	3415085	3043041	2630326	77.0
NWBC	UAM 112316	1140170	1085547	889298	78.0
NWBC	UAM 33803	2000829	1893993	1679877	84.0
NWBC	UAM 35130	2363572	2025866	1743681	73.8
Sud Island	UAM 103489	2172259	2059729	1749002	80.5
Sud Island	UAM 103490	2392986	2137562	1761507	73.6
Sud Island	UAM 103491	942613	877060	729171	77.4
Sud Island	UAM 111786	820156	694019	459919	56.1
Sud Island	UAM 112286	2503546	1845158	1502658	60.0
Sud Island	UAM 112288	1763105	1581073	1341696	76.1
Sud Island	UAM 112289	2008293	1895603	1630050	81.2
Sud Island	UAM 112290	1608895	1412409	1186261	73.7
Sud Island	UAM 112291	1506953	1430160	1142606	75.8
Sud Island	UAM 112293	1091236	1002018	811950	74.4
Thompson Pass	UAM 112326	1350412	1217425	950532	70.4
Thompson Pass	UAM 114143	1057980	918237	618237	58.4
Thompson Pass	UAM 115723	2400149	1954568	1693644	70.6

Table S1.2. Continued

b) hoary marmot (continued)

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Thompson Pass	UAM 115799	384976	367886	247580	64.3
Thompson Pass	UAM 115798	1275007	1221186	1013227	79.5
Thompson Pass	UAM 115800	837170	739427	512216	61.2
White Mountains	UAM 112353	2666327	2545939	2306311	86.5
White Mountains	UAM 112367	485606	459186	354633	73.0
White Mountains	UAM 112368	1458152	1383635	1139011	78.1
White Mountains	UAM 112369	1187556	1127253	979705	82.5
White Mountains	UAM 113907	1595556	1511218	1288350	80.7
White Mountains	UAM 113925	1113309	973708	821577	73.8
White Mountains	UAM 113930	1025217	938816	779845	76.1
Wickersham Dome	UAM 106211	531030	495055	361265	68.0
Wickersham Dome	UAM 106220	1288189	1221690	958705	74.4
Wickersham Dome	UAM 111555	1597633	1478101	1236201	77.4
Wickersham Dome	UAM 111557	2284430	2176256	1866427	81.7
Wickersham Dome	UAM 111561	578449	491016	349298	60.4
Wickersham Dome	UAM 111626	1993445	1882727	1590029	79.8
Wickersham Dome	UAM 111634	1595443	1529830	1371388	86.0

Table S1.2. Continued

c) singing vole

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Agaik Lake	78759	1245748	1192849	1008072	80.9
Agaik Lake	78751	1063364	1000389	872326	82.0
Agaik Lake*	78882	69710	51383	8558	12.3
Agaik Lake*	79097	192823	180426	46904	24.3
Agaik Lake*	78769	0	0	0	0.0
Agaik Lake	78770	2144684	1908104	1540348	71.8
Agaik Lake*	78772	93857	88625	22012	23.5
Agaik Lake	78764	2182020	2098908	1734529	79.5
Bold Peak	64352	2763337	2647126	2362820	85.5
Bold Peak	64359	3139842	2634124	2211552	70.4
Bold Peak	64376	2511774	2356268	2074653	82.6
Bold Peak	64353	1760470	1600104	1351777	76.8
Bold Peak	64384	542020	507571	383240	70.7
Chisana	57749	1836055	1750878	1503459	81.9
Chisana	57755	1412663	1351333	1130278	80.0
Chisana	57771	1628878	1568161	1314936	80.7
Copter Peak	56344	2871946	2744864	2541071	88.5
Copter Peak	56692	1749818	1680151	1381528	79.0
Copter Peak	56694	2314324	2221718	1791135	77.4
Copter Peak	56697	2052972	1964401	1715161	83.5
Copter Peak	56698	2139152	2053671	1717708	80.3
Copter Peak	56608	2595374	2482323	2202431	84.9
Copter Peak	56682	1177012	1121109	889907	75.6
Copter Peak*	56690	340366	324265	222233	65.3
Glacier Lake*	103430	1123068	1074395	943930	84.0
Glacier Lake	103411	2127302	2029338	1816454	85.4
Glacier Lake*	103435	706667	675189	580045	82.1
Glacier Lake*	103466	1450806	1245284	1009346	69.6
Glacier Lake*	103296	3478514	3319767	2932958	84.3
Glacier Lake	103448	4015317	3816907	3533824	88.0
Glacier Lake	98984	1379118	1323044	1128008	81.8
Glacier Lake	103409	1470251	1380845	1077291	73.3
Kenai Peninsula	98727	298923	287670	170740	57.1
Kenai Peninsula	98726	1507798	1435008	1178250	78.1
Kenai Peninsula	98935	856073	818291	673112	78.6
Kenai Peninsula*	98983	392847	367861	242073	61.6
Kenai Peninsula*	98982	4935364	4602939	4205670	85.2

Table S1.2. Continued

c) singing vole (continued)

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Kenai Peninsula	103414	345954	333897	161805	46.8
Max Lake	85628	2206793	2046470	1762883	79.9
Max Lake*	85792	278247	260878	160930	57.8
Max Lake	85682	2041326	1917509	1695312	83.0
Max Lake	85673	2087364	2006728	1771304	84.9
Max Lake	85565	1941810	1842761	1590306	81.9
Max Lake	85798	1362261	1249234	830593	61.0
Max Lake	85566	2000747	1894574	1659892	83.0
Max Lake	85567	1302352	1242384	981572	75.4
Lake Peters	64403	3061139	2920843	2535887	82.8
Lake Peters	64399	1331660	1280024	1133350	85.1
Lake Peters	64394	1787114	1712595	1531030	85.7
Lake Peters	64392	3867715	3593991	3259856	84.3
Lake Peters	64400	1588608	1531051	1235872	77.8
Lake Peters*	64389	996409	939191	823590	82.7
Lake Peters*	64387	8	5	0	0.0
Lake Peters	64398	703258	669168	573443	81.5
Polychrome Pass	62810	3184428	3059239	2795632	87.8
Polychrome Pass*	61389	247550	234273	129214	52.2
Polychrome Pass	61393	3156332	2830994	2526822	80.1
Polychrome Pass*	61347	161326	138668	30831	19.1
Polychrome Pass	61380	1689102	1624824	1415306	83.8
Polychrome Pass	61396	2118811	1936125	1671602	78.9
Polychrome Pass	61394	3856161	3229118	2815792	73.0
Polychrome Pass	61379	1694407	1624187	1345771	79.4

Table S1.2. Continued

d) brown lemming

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Cape Bathurst	58011	2181110	1802340	1522749	69.8
Cape Bathurst	58012	1580241	1468034	1225111	77.5
Cape Bathurst	58013	2078402	1957699	1682637	81.0
Cape Bathurst	58014	4472777	4230626	3802044	85.0
Colville River	43141	1599264	1515084	1297159	81.1
Colville River	43142	2609547	2443650	2075982	79.6
Colville River	43136	2320965	2063005	1742611	75.1
Colville River	43143	2602071	2389598	2138446	82.2
Colville River	43135	3082884	2912486	2594638	84.2
Colville River	43138	1464662	1370499	1165464	79.6
Colville River	43144	3048080	2850887	2582016	84.7
Mt. Fairplay	58053	2258730	1966099	1628967	72.1
Mt. Fairplay	58054	1727535	1606816	1318602	76.3
Mt. Fairplay	58055	2108648	1992821	1665164	79.0
Mt. Fairplay	58056	2506500	2355555	2043386	81.5
Mt. Fairplay	58057	1380789	1293338	985927	71.4
Mt. Fairplay	58058	2567981	2331657	1859751	72.4
Mt. Fairplay	58045	1707137	1574218	1303069	76.3
Mt. Fairplay	58044	1562098	1449789	1237396	79.2
Ivvavik*	56357	1312801	1077727	815617	62.1
Ivvavik*	56364	816480	733276	534923	65.5
Ivvavik	56373	1270218	1170593	915786	72.1
Ivvavik	56378	2719317	2587197	2295805	84.4
Ivvavik	56401	1234046	1133511	916694	74.3
Ivvavik	56356	1171825	1074588	812951	69.4
Ivvavik	56374	923955	841750	673865	72.9
Ivvavik	56379	2494885	1993457	1586047	63.6
Kaluich Creek	65770	754912	643474	391797	51.9
Kaluich Creek	65746	2127845	1844893	1489698	70.0
Kaluich Creek	65769	1094771	981177	692040	63.2
Kaluich Creek*	65771	447228	385795	181046	40.5
Kaluich Creek	65776	849916	742544	490398	57.7
Kaluich Creek*	65890	432554	363595	145141	33.6
Kaluich Creek	65891	2338984	2081529	1721522	73.6
Kaluich Creek	65892	1679794	1517937	1194847	71.1
Nowitna River	24338	2790529	2345731	1939670	69.5
Nowitna River	24270	1359323	1316729	1139651	83.8

Table S1.2. Continued

d) brown lemming (continued)

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Nowitna River	24269	3148065	2910679	2568131	81.6
Nowitna River	24272	2570193	2347832	2007464	78.1
Nowitna River	24274	4988448	4786813	4400331	88.2
Nowitna River	24339	3635592	3314070	2823402	77.7
Nowitna River*	24340	183064	172544	50329	27.5
Nowitna River*	51184	2031501	1818278	1523549	75.0
Tangle Lakes	95691	1088657	1050452	853897	78.4
Tangle Lakes	95687	1599395	1349824	997277	62.4
Tangle Lakes	96259	1366867	1285408	1037812	75.9
Tangle Lakes	85888	2533203	2213693	1853710	73.2
Tangle Lakes	95316	2429157	2097732	1707190	70.3
Tangle Lakes	95678	1714539	1630744	1393076	81.3
Tangle Lakes	96502	1294599	1252331	925259	71.5
Tangle Lakes	96502	1468152	1403885	1182197	80.5
Tangle Lakes	96183	2115924	2001668	1712429	80.9
Twin Lakes	65836	2179184	1810076	1472669	67.6
Twin Lakes	65837	2039903	1972338	1730048	84.8
Twin Lakes	65884	2633276	2148424	1752454	66.6
Twin Lakes	66198	1476616	1348660	1072188	72.6
Twin Lakes	65866	2323863	2186020	1737499	74.8
Twin Lakes	65870	1794090	1667450	1393465	77.7
Twin Lakes	65883	1266294	1148511	889340	70.2

Table S1.2. Continued

e) arctic ground squirrel

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Debauch Mountain	100869	1665950	1508552	1083348	65.0
Debauch Mountain	88531	2539041	2304920	1783175	70.2
Debauch Mountain	100821	964607	891972	677443	70.2
Debauch Mountain	57515	2280127	2068845	1706787	74.9
Debauch Mountain	102516	2501834	2055468	1684069	67.3
Debauch Mountain	88533	1224799	1122132	846303	69.1
Debauch Mountain	22028	2533987	2303254	1908515	75.3
Debauch Mountain	114141	1623126	1468371	1078480	66.4
Donnelly Dome	35162	321372	293022	142705	44.4
Donnelly Dome*	114289	71748	63624	13998	19.5
Donnelly Dome*	114264	382885	345562	156738	40.9
Donnelly Dome	114286	1525375	1336820	950595	62.3
Donnelly Dome*	114137	49909	44436	10836	21.7
Donnelly Dome	57508	1028675	914726	541262	52.6
Donnelly Dome	57512	713801	567624	329049	46.1
Jawbone Lake	58653	4062466	3019426	2500724	61.6
Jawbone Lake	58661	1945591	1738220	1374569	70.7
Jawbone Lake	58668	1697941	1515211	1185605	69.8
Jawbone Lake	58675	3236187	2899104	2419762	74.8
Jawbone Lake*	85784	634907	555172	259412	40.9
Jawbone Lake	85789	2613955	2401305	1953609	74.7
Jawbone Lake*	85797	278639	249327	106078	38.1
Jawbone Lake	88529	1093107	973552	691818	63.3
Kongakut River	99001	792344	713021	468065	59.1
Kongakut River	100835	2099827	1934772	1655340	78.8
Kongakut River	100866	1320146	1222290	955879	72.4
Kongakut River	102515	1056931	974273	725081	68.6
Kongakut River	102533	423718	393452	208004	49.1
Kongakut River	64431	1358350	1261683	974231	71.7
Kongakut River	85788	1224341	1134635	911980	74.5
Kongakut River	88525	3020486	2685609	2336058	77.3
LACL	88530	3150858	2871630	2581820	81.9
LACL	64430	1620351	1495592	1253409	77.4
LACL	64432	1272894	1166930	824406	64.8
LACL*	85787	1338383	1222598	878723	65.7
Cape Lisburn	88523	2181335	1958066	1514022	69.4
Cape Lisburn*	88524	243046	221521	101895	41.9
Cape Lisburn	98413	2351696	2159376	1812471	77.1

Table S1.2. Continued

e) arctic ground squirrel (continued)

Population	Specimen ID	Raw read count	Post quality control	Analyzed reads	Percentage of raw reads used
Cape Lisburn	102517	2675803	2277962	1728722	64.6
Cape Lisburn	102529	1049995	955117	702246	66.9
Cape Lisburn	22027	860941	787348	597499	69.4
Cape Lisburn	22029	1094449	1002012	804845	73.5
Rock Creek	22030	2522345	2269311	1796819	71.2
Rock Creek	22031	662783	613912	411402	62.1
Rock Creek	24350	2337802	2115058	1797010	76.9
Rock Creek	24351	1423250	1300626	1006014	70.7
Rock Creek	24352	3402175	2676432	2317086	68.1
Rock Creek	31902	1797821	1593483	1236628	68.8
Rock Creek	35163	1800459	1640136	1287649	71.5
Rock Creek	85778	1898492	1727041	1338291	70.5
sWRST	85781	3106239	2773760	2419543	77.9
sWRST	87119	2063154	1881539	1462530	70.9
sWRST	87120	3355621	3057816	2536402	75.6
sWRST	88528	2194444	2002879	1590617	72.5
sWRST	98415	1104954	996271	721761	65.3
sWRST	98416	1981547	1830824	1479220	74.6
sWRST	98417	2718492	2507972	2052580	75.5
White Pass	102512	3142333	2825494	2397705	76.3
White Pass	102513	3617447	3329959	2857583	79.0
White Pass	113887	2208468	1996063	1565643	70.9
White Pass	114138	2438971	2214408	1943034	79.7
White Pass	98414	1401381	1299122	958374	68.4
White Pass*	85786	621340	555014	336888	54.2

Knowles et al., Quantifying the similarity between genes and geography across Alaska's alpine small mammals, Journal of biogeography.

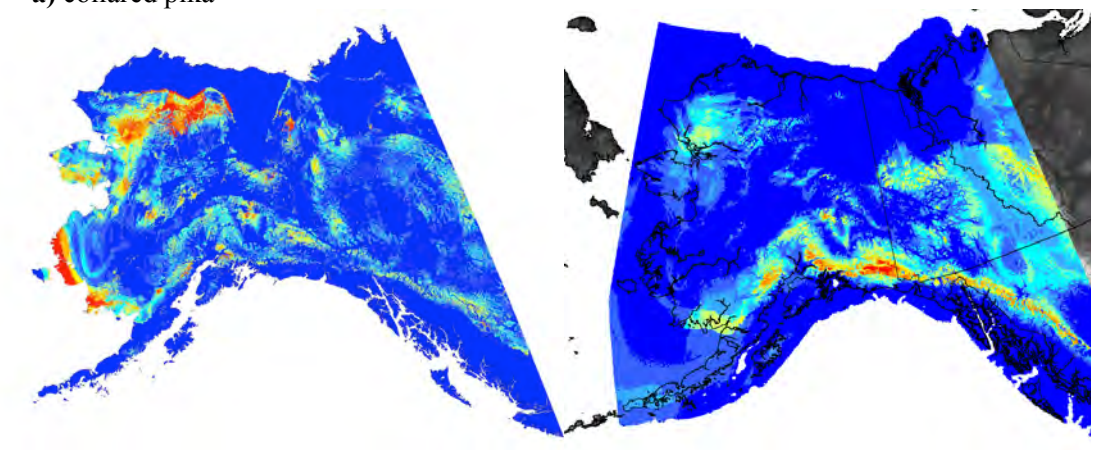
Appendix S2 Summaries of ENM settings and projections of current and LGM distributions

Details about the settings used in the ecological niche modelling (ENMs) are provided in Table S1, along with projections of the distributions of the five taxa (Fig. S1) for the present and last glacial maximum (LGM) in this appendix, Appendix S2.

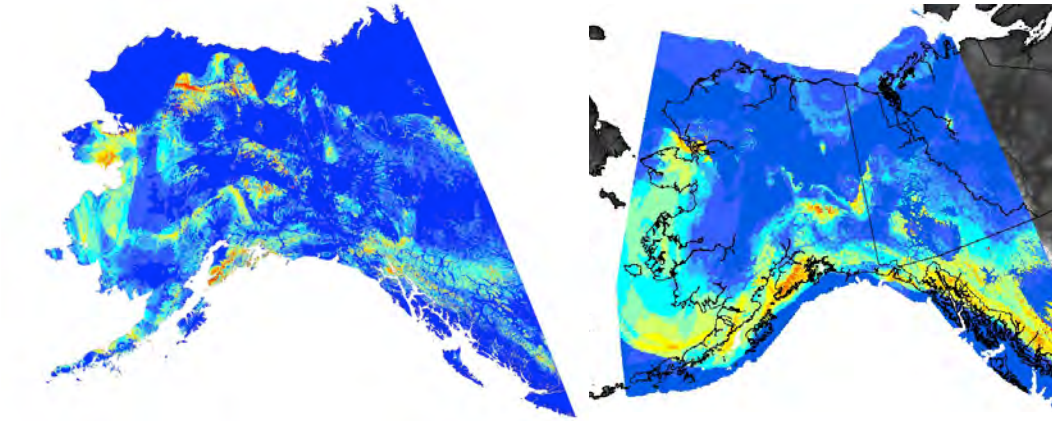
Table S2.1. For each of the five Alaskan mammal taxa, the number of vetted distribution points (# points) and variables used in niche modelling are shown; specifically, these include the bioclimatic variables used to construct LGM ENMs that are not out-of-range in the past compared to the present (LGM modeling variables), the bioclimatic variable used in LGM modelling that had the highest percent contribution to the ENM as determined by Maxent (Highest % contribution), and the bioclimatic variables that had >90% Pearson's r correlation with the variable with the highest percent contribution (>90% correlation). Present-day models for each species were constructed using all feature classes and a regularization parameter of 0.25; these parameter combinations were informed by *a priori* model testing in SDMToolBox. The bioclimatic variables include: Annual Mean Temperature (1); Mean Diurnal Range (2); Isothermality (3); Temperature Seasonality (4); Maximum Temperature of Warmest Month (5); Minimum Temperature of Coldest Month (6); Temperature Annual Range (7); Mean Temperature of Wettest Quarter (8); Mean Temperature of Driest Quarter (9); Mean Temperature of Warmest Quarter (10); Mean Temperature of Coldest Quarter (11); Annual Precipitation (12); Precipitation of Wettest Month (13); Precipitation of Driest Month (14); Precipitation Seasonality (15); Precipitation of Wettest Quarter (16); Precipitation of Driest Quarter (17); Precipitation of Warmest Quarter (18); and Precipitation of Coldest Quarter (19). See the Methods for more details.

Taxon	# points	LGM modelling variables	Highest % contribution	>90% correlation
collared pika	94	4,7,10,14,15,16,17	10	5
hoary marmot	290	1,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	10	5
singing vole	144	1,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19	10	5
brown lemming	135	1,4,5,6,9,15	15	NA
arctic ground squirrel	171	1,4,5,7,9,11,12,14,15,17,19	4	6,7,11

a) collared pika



b) hoary marmot



c) singing vole

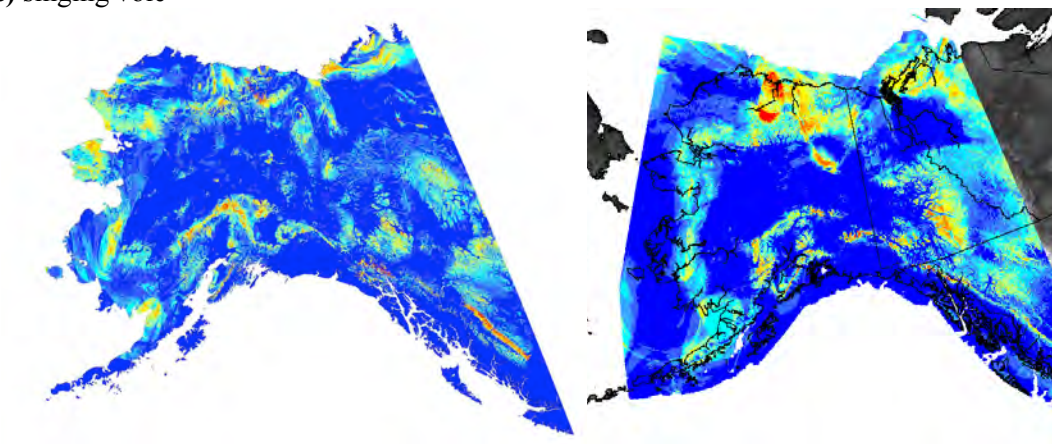
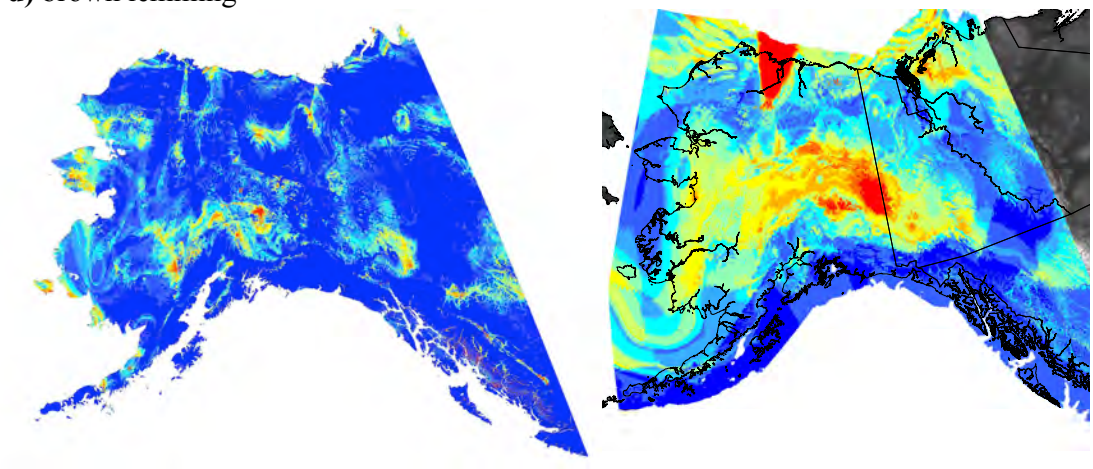


Figure S2.1. Projections of the current (left) and LGM (right) distributions for each the five mammal taxa. Warmer colours indicate higher suitability of habitat, while cooler colours indicate unsuitable habitat

d) brown lemming



e) arctic ground squirrel

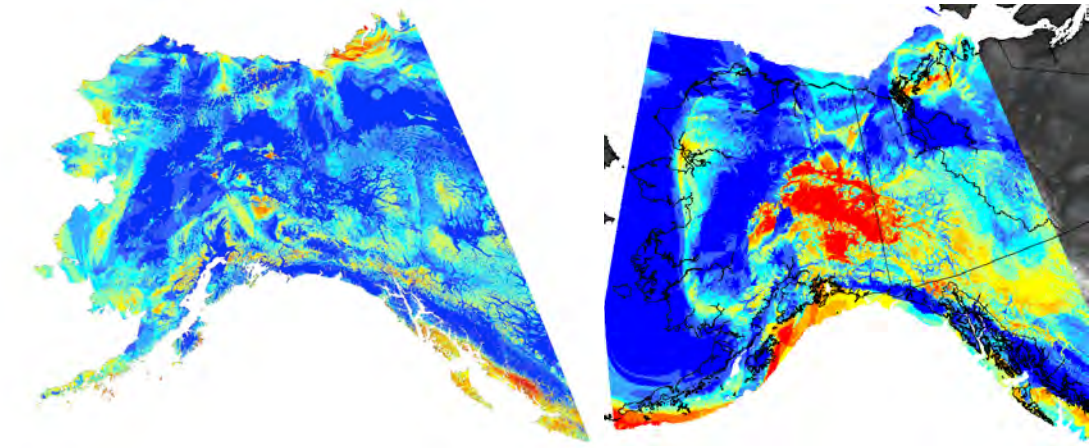


Figure S2.1. Continued.

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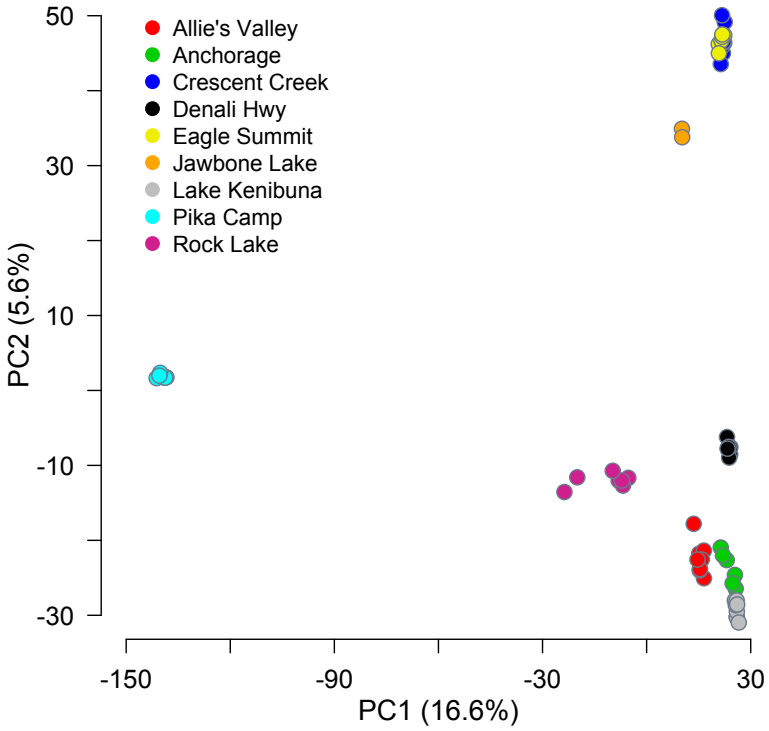
Appendix S3 PC-maps of genetic variation and summaries of genetic variation

Details about the patterns of genetic variation in each of the five taxa are given in this appendix, Appendix S3. This includes plots of genetic variation across individual from PC-analyses (Fig. S3.1), a comparison of taxa of the deviations from expectations based on the geographic sampling of individuals based on Procrustes analyses (Fig. S3.2), and sensitivity analyses of the strength of the association between genes and geography based on sequential exclusion of populations in Procrustes analyses (Table S3.1).

Figure S3.1. Distribution of individuals along PC1 and PC2 axes of genetic variation based on the analysis of polymorphic SNPs. Individuals are color coded according to their population identities.

a) collared pika



b) hoary marmot

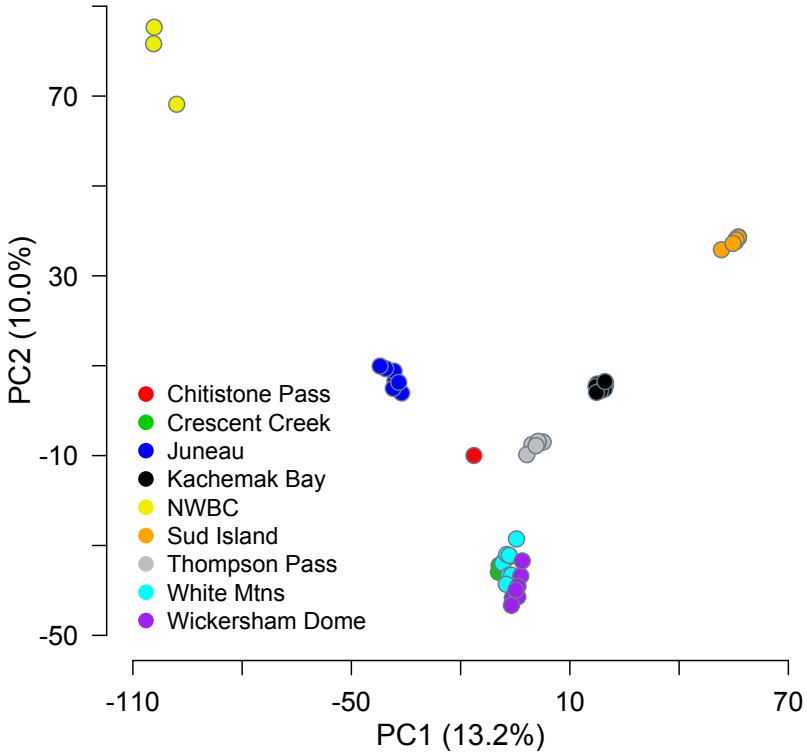
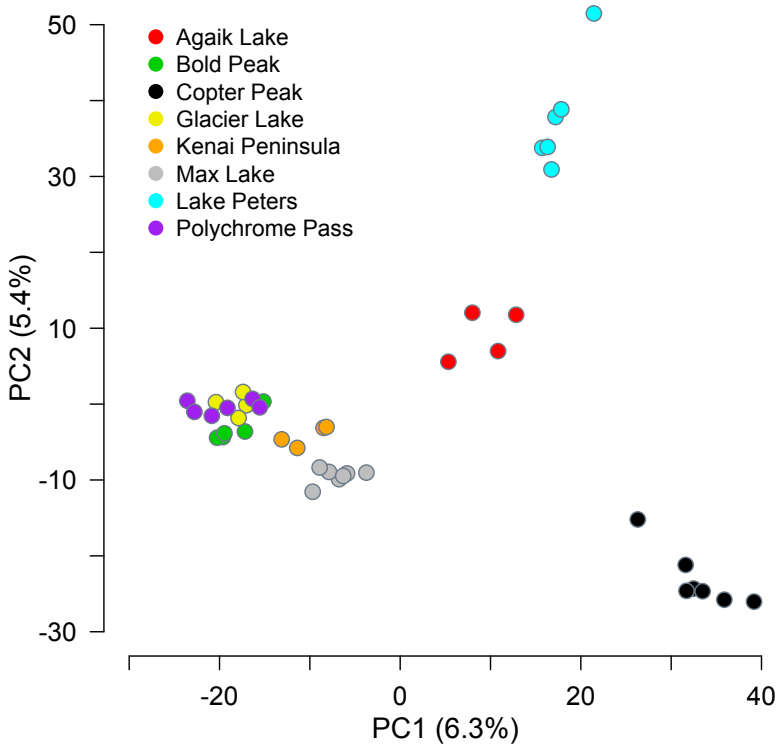


Figure S3.1. Continued

c) singing vole



d) brown lemming

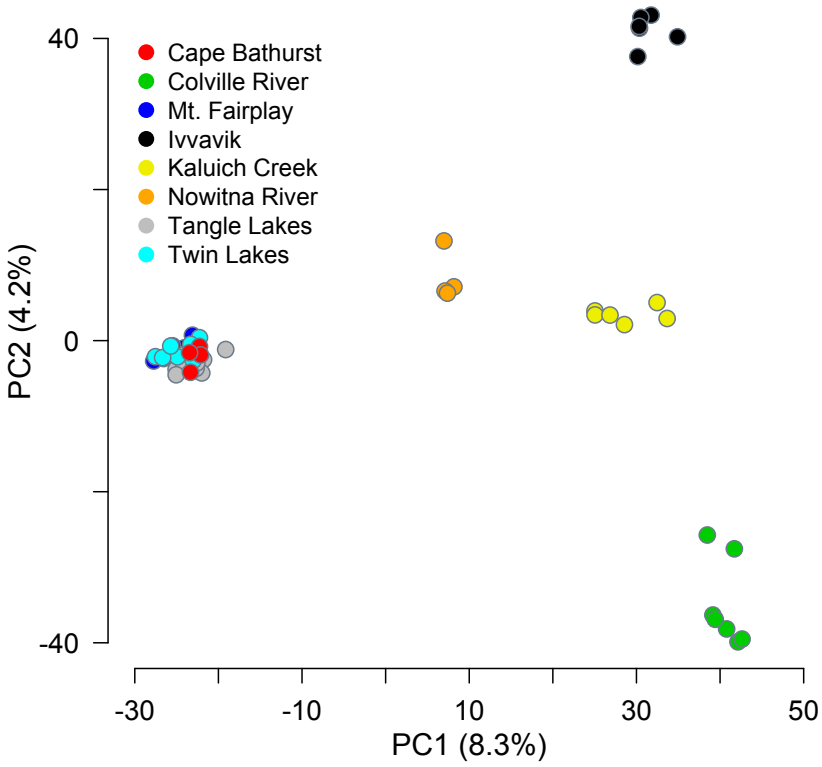


Figure S3.1. Continued
e) arctic ground squirrel

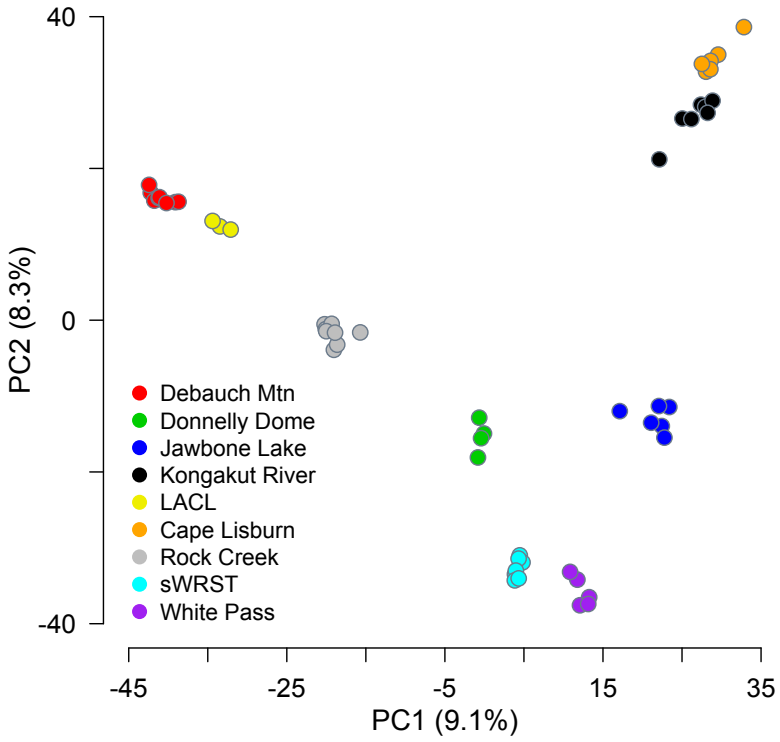


Figure S3.2. Comparison of the Procrustes-transformed PCA plots of genetic variation across species, where each taxon is colour-coded. Each individual (represented by a coloured circle) is mapped in PC space relative to the geographic location of its sampling location (denoted by arrowheads). The length of the lines connecting individuals in PC space to their populations represents the magnitude of the deviation from the expected pattern of genetic variation based on geography. All points (both individuals and sampling localities) are drawn using the Albers Equal Area Conic projection, and distances among the points are represented in kilometres.

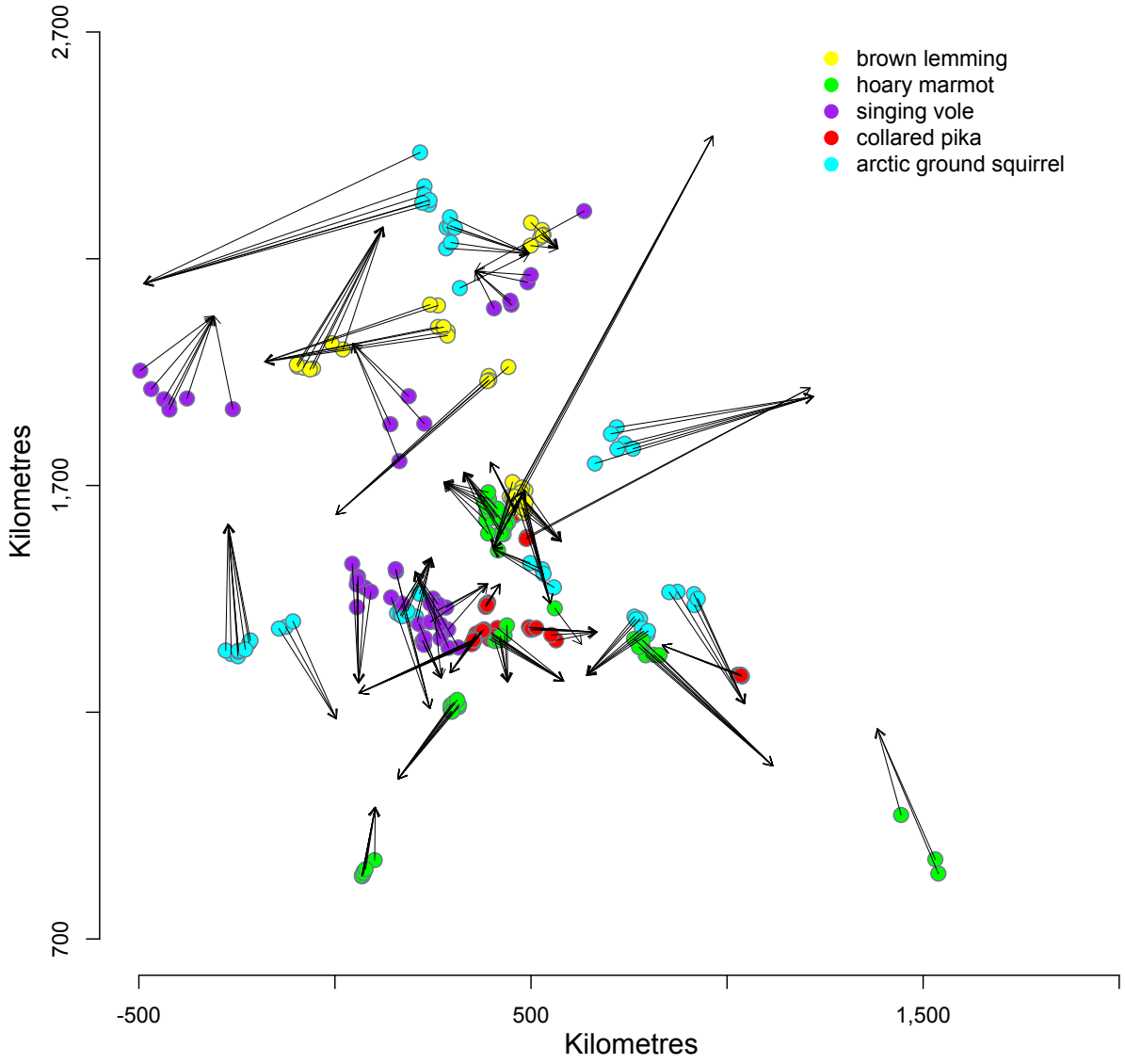


Table S3.1. Population summary statistics for the five Alaskan mammal species. Included is the: average number of individuals genotyped across the individual's loci (*N*); total number of nucleotide sites (polymorphic + fixed; Sites); percentage of polymorphic loci (% poly); average observed heterozygosity (H_{obs}); average nucleotide diversity (π); and Wright's inbreeding coefficient (F_{IS}).

a) collared pika

	N	Sites	% poly	H_{obs}	π	F_{IS}
Allie's Valley	6.9	5585637	0.08	0.00022	0.00024	0.000062
Anchorage	4.8	4971121	0.05	0.00016	0.00017	0.000037
Crescent Creek	6.1	6341035	0.08	0.00026	0.00027	0.000038
Denali Hwy	5.2	5107329	0.06	0.00019	0.00022	0.000058
Eagle Summit	5.4	5057421	0.05	0.00020	0.00020	-0.000001
Jawbone Lake	1.6	7092069	0.03	0.00018	0.00018	0.000002
Lake Kenibuna	7.1	5239023	0.04	0.00012	0.00011	-0.000015
Pika Camp	5.3	5305828	0.06	0.00019	0.00020	0.000024
Rock Lake	6.2	5610267	0.10	0.00030	0.00034	0.000087

b) hoary marmot

	N	Sites	% poly	H_{obs}	π	F_{IS}
Chitistone Pass	1.0	9148082	0.05	0.00051	0.00051	0.000000
Crescent Creek	3.4	8839899	0.09	0.00045	0.00041	-0.000077
Juneau	6.5	6505544	0.15	0.00050	0.00055	0.000114
Kachemak Bay	7.1	6964820	0.11	0.00042	0.00042	0.000008
NWBC	2.8	6319308	0.13	0.00064	0.00063	-0.000018
Sud Island	8.9	5994123	0.02	0.00012	0.00009	-0.000067
Thompson Pass	4.9	5709742	0.11	0.00043	0.00047	0.000070
White Mtns	6.1	5522559	0.12	0.00046	0.00047	0.000024
Wickersham Dome	6.0	5760755	0.10	0.00039	0.00040	0.000030

c) singing vole

	N	Sites	% poly	H_{obs}	π	F_{IS}
Agaik Lake	3.0	2051233	0.18	0.00044	0.00087	0.000740
Bold Peak	4.1	1720098	0.13	0.00032	0.00050	0.000374
Chisana	2.0	1033820	0.16	0.00057	0.00089	0.000530
Copter Peak	5.8	1856071	0.21	0.00050	0.00076	0.000614
Glacier Lake	3.1	2320533	0.15	0.00043	0.00070	0.000475
Kenai Peninsula	2.8	1330770	0.06	0.00022	0.00032	0.000164
Max Lake	5.8	1714620	0.21	0.00049	0.00076	0.000613
Lake Peters	4.6	1944776	0.20	0.00051	0.00080	0.000605
Polychrome Pass	4.7	2264512	0.19	0.00046	0.00077	0.000642

d) brown lemming

	N	Sites	% poly	H_{obs}	π	F_{IS}
Cape Bathurst	3.2	3131719	0.17	0.00054	0.00079	0.000438
Colville River	6.0	2492453	0.22	0.00061	0.00081	0.000467
Mt. Fairplay	6.5	2565557	0.28	0.00059	0.00091	0.000758
Ivvavik	4.8	2350735	0.17	0.00059	0.00069	0.000199
Kaluich Creek	4.4	2492971	0.25	0.00063	0.00097	0.000696
Nowitna River	3.1	3232862	0.24	0.00068	0.00108	0.000693
Tangle Lakes	7.5	1924798	0.25	0.00056	0.00081	0.000603
Twin Lakes	5.7	2095602	0.23	0.00053	0.00082	0.000654

e) arctic ground squirrel

	N	Sites	% poly	H_{obs}	π	F_{IS}
Debauch Mtn	6.7	4759046	0.12	0.00037	0.00043	0.000128
Donnelly Dome	2.7	3101928	0.10	0.00038	0.00050	0.000196
Jawbone Lake	4.9	5469875	0.18	0.00057	0.00069	0.000238
Kongakut River	6.0	3966933	0.18	0.00052	0.00061	0.000221
LACL	2.7	4693453	0.10	0.00043	0.00048	0.000081

Cape Lisburn	4.9	4598436	0.12	0.00037	0.00047	0.000199
Rock Creek	6.6	4991411	0.19	0.00057	0.00065	0.000198
sWRST	6.1	5026303	0.13	0.00040	0.00050	0.000228
White Pass	4.4	5362339	0.13	0.00042	0.00054	0.000241

Table S3.2. Association statistics between genetic PCAs with all populations compared to genetic PCAs when single populations are excluded (i.e., *t'*), and between genetic PCAs and geography with the exclusion of individual populations (i.e., *t''*). The excluded populations are listed in the first row, and columns contain both the association statistics and the rotation in degrees (θ) that best aligns the 2 matrices. Positive values of θ indicate clockwise rotations and negative values indicate counterclockwise rotations. Note that θ-values marked with asterisks are not directly comparable with other values of θ within species because the PCAs that excluded those respective populations resulted in fundamentally different distributions of populations in PC space.

a) collared pika, $t_0 = 0.71$, $\theta = 73.1$

	Allie's Valley	Anchorage	Crescent Creek	Denali Hwy	Eagle Summit	Jawbone Lake	Lake Kenibuna	Pika Camp	Rock Lake
t'	0.99	1.00	0.99	1.00	0.99	1.00	0.99	0.89	1.00
θ	-1.1	-1.6	3.6	-0.4	2.8	0.3	-2.8	-11.1	0.5
t''	0.76	0.68	0.70	0.71	0.70	0.79	0.69	0.77	0.71
θ	65.6	73.0	73.5	73.0	71.0	77.5	75.5	65.4	71.6

b) hoary marmot, $t_0 = 0.90$, $\theta = -73.5$

	Chitistone Pass	Crescent Creek	Juneau	Kachemak Bay	NWBC	Sud Island	Thompson Pass	White Mtns	Wickersham Dome
t'	1.00	1.00	1.00	1.00	0.96	0.81	1.00	1.00	0.99
θ	0.4	-0.2	6.1	-4.4	28.6	46.9	-3.2	-1.7	-3.3
t''	0.90	0.88	0.95	0.92	0.96	0.84	0.92	0.86	0.83
θ	-73.9	-73.3	-73.7	-69.9	51.4	-79.1*	-70.5	-74.1	-73.4

c) singing vole, $t_0 = 0.89$, $\theta = 30.2$

	Agaik Lake	Bold Peak	Copter Peak	Glacier Lake	Kenai Peninsula	Max Lake	Lake Peters	Polychrome Pass
t'	1.00	1.00	0.86	1.00	1.00	1.00	0.78	1.00
θ	-0.6	2.6	44.6	-2.1	0.9	0.7	17.9	-2.2

t''	0.90	0.88	0.78	0.91	0.91	0.91	0.86	0.92
θ	27.6	33.0	-12.6*	26.0	31.1	29.5	49.2*	27.3

d) brown lemming, $t_0 = 0.60$, $\theta = 33.2$

	Cape Bathurst	Colville River	Mt. Fairplay	Ivvavik	Kaluich Creek	Nowitna River	Tangle Lakes	Twin Lakes
t'	1.00	0.92	1.00	0.95	1.00	1.00	1.00	1.00
θ	-0.1	21.7	0.0	13.2	1.4	0.0	0.7	0.0
t''	0.77	0.73	0.56	0.76	0.63	0.65	0.57	0.56
θ	-24.7	-34.4	32.3	-47.0	23.1	31.6	37.8	35.8

e) arctic ground squirrel, $t_0 = 0.83$, $\theta = 39.7$

	Debauch Mtn	Donnelly Dome	Jawbone Lake	Kongakut River	LACL	Cape Lisburn	Rock Creek	sWRST	White Pass
t'	0.99	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00
θ	-58.9	3.5	36.6	-26.5	15.0	-24.3	14.9	-0.2	-11.0
t''	0.80	0.83	0.83	0.81	0.82	0.92	0.83	0.84	0.81
θ	-25.9*	43.1	-2.8*	-59.2	-26.9	-80.0	54.6	36.3	27.0