Panmictic population genetic structure of Northern British Columbia mountain goats (*Oreamnos americanus*) has implications for harvest management

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Abstract

Species that inhabit fragmented habitats are expected to exhibit spatial genetic structure with respect to geographic distance and landscape features. These patterns are also shaped by a variety of temporal processes, namely post-glacial recolonization, and those operating at more contemporary scales, such as sex-biased dispersal. We quantified the spatial population genetic structure of mountain goats (*Oreamnos americanus*) in northern British Columbia. We observed little genetic differentiation among mountain ranges across northern British Columbia, suggesting a panmictic subpopulation. Genetic diversity values increased slightly with latitude and bottleneck signatures were strongest in the south; these signatures are indicative of southward post-glacial colonization consistent with a northern glacial refugium. Mountain ranges were the most important predictor of genetic relatedness, suggesting large valleys impeded gene flow, and specific landscape features were not correlated to genetic variation. We used a case study in the Skeena Region of British Columbia to show how these data can directly inform local management recommendations. This study provides insight and much needed clarification of the genetic population structure of North American mountain goats and illustrates the limited impact of geographic distance and landscape features on gene flow in the northern half of the range.

Keywords

British Columbia, gene flow, genetic diversity, isolation-by-distance, landscape resistance, mountain goat

Introduction

Large-scale historical events such as continent-wide glaciation have impacted species-wide levels of genetic variation in North America (Brunsfeld et al. 2001; Shafer et al. 2010), but fine-scale landscape features have resulted in localized impacts (e.g. Parks et al. 2015; Worley et al. 2004). The distribution of genetic diversity will often vary across geographical distances and between landscape features, as limits to dispersal and movement result in the loss of genetic diversity via genetic drift. Population genetic analyses allow us to directly quantify the influence of such geographic and landscape variables (Manel et al. 2003) where at selectively neutral loci, population genetic structure is mainly determined by the interplay between genetic drift and migration. Population structure typically follows an isolation-by-distance (IBD) pattern (Jenkins et al. 2010) that explains the majority of the genetic variation seen among populations (Shafer and Wolf 2013). In fragmented populations, an isolation-by-resistance (IBR) pattern can be observed (Shirk et al. 2010); here, specific landscape features and individual preferences (i.e. habitat selection), along with the length of time on the landscape, play prominent roles in shaping genetic differentiation (Landguth et al. 2010; Bradburd and Ralph 2019).

The landscape a species inhabits can have widespread effects on genetic population structure (e.g. Kyle and Strobeck 2002; Manel et al. 2003; Worley et al. 2004; Holderegger and Wagner 2008) where small subpopulations separated by untraversable areas are more vulnerable and have an increased risk of extirpation (Kyle and Strobeck 2002; Parks et al. 2015). In the mountainous area of western North America, a high degree of genetic differentiation is often seen among alpine mammal populations on "sky islands" relative to contiguous mountain ranges (Worley et al. 2004; Galbreath et al. 2009; Shafer et al. 2011a; Gunderson et al. 2012). The fragmentation of mountain ranges can lead to limited dispersal resulting in reduced gene flow (e.g. Lomolino and Davis 1997). Conversely, a permeable landscape might allow for increased gene flow thereby increasing effective population size, adaptive potential, and the ability to respond to environmental change (Krosby et al. 2010). Moreover, climate-driven changes are projected to progress more rapidly in alpine ecosystems, leading to changes in biodiversity resulting from shifts in temperature, precipitation, and plant phenology (Sala et al. 2000; Yoccoz et al. 2011). This precipitates the need to accurately quantify the population genetic structure in alpine specialists to ensure the long-term adaptive and evolutionary potential.

Mountain goats (*Oreamnos americanus*) are large, long-lived alpine and sub-alpine ruminants that are endemic to the mountainous regions of northwestern North America (Festa-Bianchet and Côté 2008). Previous work has detected low to high levels of differentiation and large overlapping subpopulations that encompass entire mountain ranges (Shafer et al. 2011a). Contemporary long-distance dispersal has been suggested (Shafer et al. 2011b), with some radio-collared animals moving considerable distances (>70km) through suboptimal habitat (Festa-Bianchet and Côté 2008; Matthews and Heath 2008). In the southern portion of the range, landscape heterogeneity is the primary driver of genetic patterns (Shirk et al. 2010), whereas in southeast Alaska the effect of the landscape is considerably less pronounced (Shafer et al. 2012). Thus, mountain goats have shown a diverse array of population genetic patterns across their range, with the relationship in the core part of their range (British Columbia) only explored at an extremely coarse scale (Shafer et al. 2011a).

Little is known about mountain goat populations in northern British Columbia (BC), as reflected by a high degree of uncertainty surrounding population estimates (Festa-Bianchet and Côté 2008) and subpopulation delineations (Shafer et al. 2011a). Mountain goats are a managed species in BC, with ample interest in mountain goat hunting; annual revenue from license fees and species tags, approach half of one million dollars (Mountain Goat Management Team 2010). Mountain goats are ranked S3 or Blue Listed in BC, indicating they are of *special concern* (Conservation Data Centre 2016) due to their long

generation time, low reproductive rate, and potential negative responses to hunting that is not conservatively managed, and industrialization (Mountain Goat Management Team 2010). Previous work showed minimal differentiation in northern BC (Shafer et al. 2011a), but the scale was too large, and sample sizes too small, to inform regional management. Our study therefore aimed to evaluate the fine-scale genetic structure of mountain goats in northern BC, which accounts for approximately 25% of the global mountain goat population. We focussed on quantifying the drivers of genetic population structure of mountain goats located in northern BC to allow for biologically relevant population management. Lastly, we used an adjacent three-mountain complex in the Skeena region, an administrative boundary for natural resource management, as a case study to demonstrate how fine-scale genetic data can inform management decisions.

Methods

Study area and sampling

In 2018 we captured and radio-collared 24 mountain goats (n_{BM}=12, n_{NM}=9, n_{GM}=3) on three different mountain complexes with known herds using aerial net-gun capture (Carpenter and Innes 1995) northeast of Smithers, BC (Blunt Mountain- BM, Netalzul Mountain- NM, and Goat Mountain- GM). We took 6mm ear-punch biopsies and 10-12 faecal pellets from each captured mountain goat. The objective of the captures was to determine if genetic tools can be utilized to inform mountain goat population management on a refined scale in northern BC. Reduced numbers on BM have become a recent concern and is one of the reasons this case study was initiated. We non-invasively collected fresh pellets from mountain goats on the mountain complexes in 2019 (n_{BM}=1, n_{NM}=4, n_{GM}=17) used in the collar study area. We placed pellet samples on ice, then stored at -80ºC. These samples (i.e. 24 collared and 22 pellets) are hereafter referred to as the management case study - see Box 1.

We used this study site to centre larger analyses on harvested mountain goat samples from within a 500km radius available in our repository, collected from harvested individuals from 2010-2017. The resulting area was approximately 248,000km^2 (Fig. S1). Average summer temperatures ranged from 12.6 ºC – 15ºC, while average winter temperatures range from -9.4ºC – -2.2 ºC (Environment Canada). The study area constitutes northern boreal mountains and is subject to infrequent aerial surveys and exhibits high uncertainty in population estimates (i.e. 16,000–35,000 in the Skeena region). There are no major roads, however logging occurs, and forest service roads are present. Individuals part of the larger analysis were assigned to a one of six main mountain ranges *a priori* based on sample collection coordinates (Fig. S1); hereafter referred to as population. We extracted DNA from air-dried ear tissue using a DNeasy Blood and Tissue Kit (Qiagen, Valencia, California, USA) following manufacturer's protocol and subsequently stored at -20 ºC. Pellet samples were treated similarly and extracted using a QIAamp PowerFecal DNA Kit (Qiagen, Valencia, California, USA).

Genotyping

We amplified seventeen microsatellite loci in three PCR multiplex reactions using previously published PCR parameters (Shafer et al. 2011a). Genotyping occurred on an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, California, USA) and we analyzed loci using the program Geneious 10.1.2 (Kearse et al. 2012). Pellet samples used in the case management study were genotyped in triplicate, calls for each locus were compared across three replicates, and if there were disagreements, the peaks were compared visually, and the weak ones removed (RFU < 250). If more than one replicate at a marker had discrepancy between heterozygosity or homozygosity after three replicates, the marker was scored 0 following White et al. (2019). We removed individual samples and loci with >50% missing data.

Diversity statistics

We assessed deviation from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) for each locus and population using GENEPOP v4.2 in R (Rousset 2008). We maximized our sample size to minimize the effect of any HWE departures on biological conclusions and downstream analyses (Waples 2015). If a given locus was not in HWE for ≥ 3 populations, it was removed. We estimated mean number of alleles and mean number of private alleles with a rarefaction approach implemented in the software ADZE (Szpiech et al. 2008). The number of alleles, heterozygosity, inbreeding, and genetic differentiation indices were determined using the program GenAlEx v6.5 (Peakall and Smouse 2006) on the *a-priori* defined populations. Arlequin v3.5 was used to assess significance of F_{ST} using 10,000 permutations (Excoffier and Lischer 2010). GENHET was utilized to calculate measures of individual heterozygosity (Coulon 2010). BOTTLENECK V1.2.02 was used to assess whether any populations had undergone a bottleneck using both a Stepwise Mutation Model (SMM) and a Two Phase Model (TPM) (Cornuet & Luikart 1996; Piry et al. 1999). Populations that exhibited a significant heterozygosity excess were considered to have experienced a recent genetic bottleneck. We used a principal component analysis (PCA) to visualize population genetic structure and estimated the effective population size (N_e) using a single point in time, bias-corrected version of the linkage disequilibrium method available in NeEstimator V2.1 (Waples and Do 2008; Do et al. 2014).

Drivers of differentiation

We estimated isolation-by-distance (IBD) at the population level by taking the natural logarithm of the Euclidean distance between sampling area centroids and compared this to population F_{ST} and Nei's *D*. PCA attempts to detect population structure by reducing genetic data into uncorrelated principal components (Reichs et al. 2008) and can be regressed against geographic variables to assess spatial relationships (e.g. Hindley et al. 2018). We generated a PCA and used the PC scores to run a linear model with latitude to determine if there was any effect of a latitudinal gradient on allele frequencies. Additionally, we modeled latitude against standardized individual heterozygosity.

At the individual level, we estimated relatedness between individuals using the pairwise relatedness coefficient *r* (Lynch and Ritland 1999). IBD for each of the six populations was assessed independently, by comparing individual pairwise relatedness to pairwise Euclidean distance. Spatial genetic autocorrelation was assessed via a Moran's I correlogram at 20km distance bins on males and females separately. We then generated three additional matrices coding for pairwise geographic distances, occupation of the same mountain range (1 or 0), and pairwise least cost paths (LCPs) reflective of landscape features. The LCP used slope and elevation derived from a 25 x 25m Digital Elevation Model (GeoBC 2002) scored according to Shirk and Wallin (2009) and a water body of any size (GeoBC 2019) scored as a fixed cost of 25. We ran a multiple regression using the package ecodist (Goslee and Urban 2007), and tested for correlation using a Spearman rank correlation test. All statistical analyses were conducted in R v.3.6.1 unless otherwise stated.

Migration and population structure

We used a multi-locus coalescence genealogy Bayesian approach to estimate migration rates using the program Migrate v4.4.3 (Beerli 2009). Runs used one long chain of 1000000 recorded genealogies with a sampling increment of 20 and a burn-in of 10,000 as per Beerli (2006). An unweighted pair-group method based on F_{ST} using arithmetic averages (UPGMA) as a start tree and static heating with default temperature were used. A Brownian motion approximate of an SMM based on nuclear microsatellite data was also used. Migration was reported as the mutation scaled immigration rates. $\boldsymbol{\theta}$ was also reported as measured by $\boldsymbol{\theta} = 4N_e\mu$.

The Bayesian clustering program STRUCTURE v.2.3.4 was used to identify subpopulations (Pritchard et al. 2000). Admixture models within STRUCTURE were created for K = 1-7 (number of clusters) with a burn-in of $5x10^5$ followed by $1x10^6$ Markov chain Monte Carlo cycles with 20 replicate runs for each value of K. The results of the runs for each K were sorted and averaged with CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007). This process was completed once with the LOCPRIOR parameter set to 1, which

defines *a priori* population assignments for known groups, and once with the LOCPRIOR parameter set to 0. Hierarchical structure analysis was performed as per Vähä et al. (2007) and Janes et al. (2017). K was inferred using the ΔK (Evanno et al. 2005) in combination with the absolute value of ln $P(X \mid K)$ (Pritchard et al. 2000) as per the recommendations of Gilbert et al. (2012) and Janes et al. (2017).

Results

Microsatellite genotyping and quality control

Of the 17 microsatellite markers genotyped, average loci success was 97.5% and ranged from 87.2%-100%. We removed one locus due to missing data. Two pairwise comparisons of loci out of 120 comparisons were found to be in LD (1.7%). Three loci were found to be significantly out of HWE in three or more populations and were removed from subsequent analyses. 24 samples from collared individuals in the Skeena region and 139 samples obtained from our laboratory database were included. An additional 37 samples were taken from Shafer et al. (2011a) as they fit the above criteria. We note here the results were quantitatively similar with 16 loci (Table S1, 2, S2).

Diversity statistics

Expected heterozygosity (H_E) ranged from 0.41 to 0.46, while observed heterozygosity (H_O) ranged from 0.40 to 0.45 across all loci and sampling localities (Table 1). Generally, diversity appeared highest in the Cassiar and Omineca populations and lowest in the Kitimat-Hazelton (Kit-H), Rocky, and Skeena populations (Table 1). Estimates of effective population size were similar, with the exception of the Rocky population (Table 1). Sample size and the lower range of N_e estimates were not correlated when computing a non-parametric Spearman correlation test (S=6, ρ=0.83, p=0.06). N_e estimates were correlated to migrate-n inferred $\boldsymbol{\theta}$ (t_4=10.37, p<0.001) as expected. Under the TPM, the Skeena and KitH populations displayed results consistent with a genetic bottleneck effect using both the sign and Wilcoxon tests (Table S3). While no population structure was present in our PCA (Fig. S2), we detected a relationship between PC2 and latitude (Fig. 1a), indicating allele frequencies were distributed across a latitudinal gradient. A weak relationship was also observed between standardized heterozygosity and latitude (Fig. 1b). Four samples were filtered out in the PC-latitude regression as outliers and one sample was omitted in the heterozygosity regression due to unknown sex.

Drivers of differentiation

Nei's D and F_{ST} among populations were found to be positively correlated (S=30, ρ=0.95, p<0.001) and only F_{ST} was reported; population F_{ST} ranged from 0.004 to 0.055 (Table 2). No isolation-by-distance pattern was observed at the population or individual level (Fig. S3a, S3b, S4), but a pattern of spatial autocorrelation was seen at the individual level (Fig. 2). Our spatial autocorrelation results suggest that male relatedness was relatively consistent regardless of distance, whereas female relatedness decreased with distance (Fig. 2).

The multiple linear regression detected an effect of three predictor variables on individual genetic relatedness ($F_{3,19697}$= 60, p <0.001). We found that mountain range correlated to genetic relatedness: individuals on different mountain ranges were more genetically different than individuals on the same mountain range, although the variance explained was small (Table 3). Covariance among predictor variables ranged from -7.3×10^{-6} to 1.2×10^{-5}. Pairwise Euclidean distances were significantly correlated to pairwise least cost path distances (t_{19699}=519.1, r=0.96, p<0.001), indicating landscape resistance was similar to the geographic distance.

Population structure and migration

With respect to migrate-n estimates, the effective sample sizes and autocorrelation values obtained demonstrated that our analysis reached convergence. The mutation-scaled immigration rates ranged from

0.42 – 4.3 individuals when evaluated using a multi-locus coalescence genealogy Bayesian approach. Both migration metrics were consistent with the general trend of genetic homogeneity among mountain goats in northern BC (Table 4).

The ΔK method supported K=4, but K=2 and K=3 were also explored due to the large relative ΔK value, (Fig. S5) while the most supported number of clusters using the ln Pr(X|K) method similarly supported K=4 (Fig. S5). When the LOCPRIOR parameter was implemented, K=3 was supported (Fig. S5). Regardless of K-value explored, genetic admixture was present among northern BC mountain goats (Fig. 3). Plotting various K-values across our sample map resulted in no clear subdivisions or population structure (Fig. S6-S11).

Discussion

Alpine environments possess geo-physical barriers not present in other ecosystems that might lead to high levels of genetic differentiation (Worley et al. 2004; Haanes et al. 2011a; Gunderson et al. 2012). Refugial origin and mountain ranges have significantly influenced genetic differentiation, which highlights the need to consider both spatial and temporal factors when modeling genetic differentiation in alpine specialists (Shafer et al. 2011a). With alpine ecosystems projected to experience a disproportionate impact as a result of climate change through large changes in biodiversity and temperature (Sala et al. 2000), there is a clear need to understand the broad and fine-scale genetic patterns and drivers of these patterns on native wildlife to ensure proper management and conservation of adaptive and evolutionary potential.

We elucidated the landscape of genetic variation and population substructure of mountain goats in northern BC and showed that landscape features had minimal influence on genetic patterns. We observed similar diversity estimates to that across the range of mountain goats (Shafer et al. 2011a), and to that of the Caw Ridge, Alberta population (Ortego et al. 2011). The fine-scale analysis directly addressed management questions of relevance to northern BC (see Box 1), and ultimately, we clarified the temporal and spatial drivers shaping mountain goat genetic diversity in northern BC.

Box 1 – Management case study - the Skeena Region

Three areas of interest as it pertains to harvest are Netalzul Mountain (NM), Goat Mountain (GM), and Blunt Mountain (BM), located in WMU 6-8 (Fig. S12). The most recent estimates on population sizes in BM are 64, in NM are 100 and GM are 65. BM is currently managed as a special bow-only season and there are no limits on the number of mountain goats harvested per season. GM and NM are Limited Entry Hunt (LEH) zones. For example, three tags were issued for 2019-2020 on GM and 17 on NM. If harvest occurred in full for a given season, there would be fewer tags issued in the following year. Managers would benefit from understanding the extent to which these three complexes are isolated from one another in terms of movement of individual goats between mountain complexes. We used tissue (n=24) and non-invasive pellet samples (n=10) and successfully genotyped 13 microsatellite loci.

Genetic evidence suggested no population subdivision in the study area (Fig. S13), suggesting gene flow is common. The specific mountain complex that the sample came from was the variable most related to genetic relatedness (β=0.0043, R^2=0.0014, $p>0.05$), indicative of valleys being a minor barrier to gene flow (Fig. 4). If the mountains were to be merged into one managed population, it would be advisable to follow common harvest recommendations (e.g. (Rice and Gay 2010; Mountain Goat Management Team 2010)) specifically, populations <50 should not be harvested, but larger populations (>100) or populations where the proportion of males in the harvest is between 90-100% may sustain ≤4% harvest. BC limits harvest based on population size and aims to minimize female harvest, adaptively managing populations when female harvest exceeds 30%, which does fit within these recommendations (Mountain Goat Management Team 2010).

Broad-scale patterns of genetic diversity

Large dynamic processes that influence population distributions and connectivity have strong effects on genetic diversity and population structure (Hewitt 1996, 2000; Haanes et al. 2011b; Shafer et al. 2011a). In North America, glacial processes elicited widespread impacts on species distributions, forest compositions, and genetic diversity patterns (Brunsfeld et al. 2001; Roberts and Hamann 2015). For example, glacial patterns resulted in both morphological and genetic differentiation in thinhorn sheep (Worley et al. 2004; Loehr et al. 2006), divergence in vole species (Fletcher et al. 2019), and phylogeographic patterns consistent with the presence of cryptic refuges (Fleming and Cook 2002; Loehr et al. 2006; Aubry et al. 2009; Zigouris et al. 2013). Colonization post-glaciation resulted in a weak cline of mountain goat allele frequencies across northern BC (Fig. 1); we hypothesize that as individuals moved from a northern glacial refuge across the recently deglaciated landscape, allele frequencies organized in a similar fashion, resulting in individuals' further north being more genetically diverse compared to the individuals located further south. This is seen also with multiple populations in the south (i.e. KitH and Skeena) experiencing bottlenecks and having relatively low N_e values. Collectively, this supports the presence of a second, northern glacial refugium (Shafer et al. 2011a), as opposed to a single southern refugia that would have resulted in a cline of decreasing genetic diversity from south to north (Hewitt 1996, 2000).

Mountain goats in northern BC display a largely genetically homogenous pattern (Fig. 3); surprisingly, there was no discernable patterns of genetic distance with respect to IBD at this scale, as F_{ST} and pairwise relatedness values were similar between neighbouring populations. When evaluating IBD independently within each population, the same held true, as no IBD pattern was detected (Table 1). In evaluating rates of migration between populations, they too were consistent with a pattern of genetic homogeneity in northern BC. This contrasts observations in related alpine ungulates that have shown that the irregular habitat distribution, female philopatry, and dispersal ability generally leads to relatively structured populations (Worley et al. 2004; Galbreath et al. 2009). However, Knowles et al. (2016) noted that differences in dispersal abilities did not result in different patterns of population structure in five alpine mammals in Alaska. The largely homogenous pattern observed, we argue, is the product of past landscape changes, specifically deglaciation and rapid recolonization. Landguth et al. (2010) suggested that landscape conditions >100 generations in the past should still be detectable via population genetic analyses; here, a glacial response would exceed that timescale, but combined with high gene-flow, could explain the limited landscape signatures. Longer-lived highly mobile species might also not show effects of fragmentation on a conservation-relevant timescale (Landguth et al. 2010), which would fit with a similar analysis conducted on Alaskan mountain goats (Shafer et al. 2012).

Fine-scale patterns of genetic diversity

While broad scale approaches can inform general management unit designations (Moritz 2002), additional fine-scale patterns and factors can identify key habitat and biological features relevant to management. Mountain goats are highly polygynous, and dispersal is male-biased (Rideout and Hoffmann 1975). This places emphasis on the ability of males to facilitate gene flow, which is important in mountain goats as only a few males obtain the majority of paternities (Mainguy et al. 2009). Our data exhibited near-zero spatial autocorrelation among males, suggesting male-based dispersal, while females tended to be more related, suggesting female philopatry (Fig. 2). There was also more variation present in the female values of spatial autocorrelation, relative to the males, possibly reflective of philopatric calving or kidding ranges (Roffler et al. 2012, 2014). Spatial autocorrelation trends among Norwegian moose, (Haanes et al. 2011b) black bear (*Ursus americanus*), (Schwartz and McKelvey 2009) and roe deer

(*Capreolus capreolus*) (Bonnot et al. 2010) all exhibited similar sex and distance-based patterns to mountain goats.

In Washington, Shirk et al. (2010) found a high correlation between genetic distance and landscape resistance of mountain goats; conversely, Shafer et al. (2012) found that least cost paths and landscape resistance had a relatively minimal relationship with genetic relatedness of mountain goats in Alaska. Our findings align with the latter, in that LCPs were not strongly correlated with genetic relatedness, indicating that landscape resistance was not the likely causal factor for genetic differentiation. Parts of the Cascade Range in Washington were not fully covered by ice in the last glacial maximum (Riedel 2017), possibly explaining the differing signals; the ice-free Cascade Range has likely been colonized much longer than BC and Alaska, providing enough time for the landscape barriers to generate structure via drift. It is also possible that, due to the presence of multiple highways in the Cascade region, landscape resistance is driven by individuals not attempting to cross such barriers. Landscape features such as roads and other physical movement barriers can often be detected quickly with individual-based landscape genetic approaches (Landguth al. 2010), and with the exception of forestry, our study area has a very different human footprint to that of Washington (Shirk et al. 2010).

Conservation and management implications

The high rates of gene flow in northern BC and the large degree of panmixia in mountain goats across mountain ranges mean that management at local scales can continue to function without utilizing genetically informed boundaries. Harvest regulations should follow Rice and Gay (2010), but tailored to region specific patterns, such as access and harvest pressure, as noted by Mountain Goat Management Team (2010). These general findings are also reflected in the management case study (Box 1). Lastly, an important factor to consider is the ability of mountain ranges to reduce gene flow, which makes the exact scale at which we can manage populations slightly more nuanced: specifically, herds within northern BC mountain ranges can largely be assumed panmictic, while there is some disruption to gene flow between large mountain ranges that should continue to be monitored.

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Figure Captions

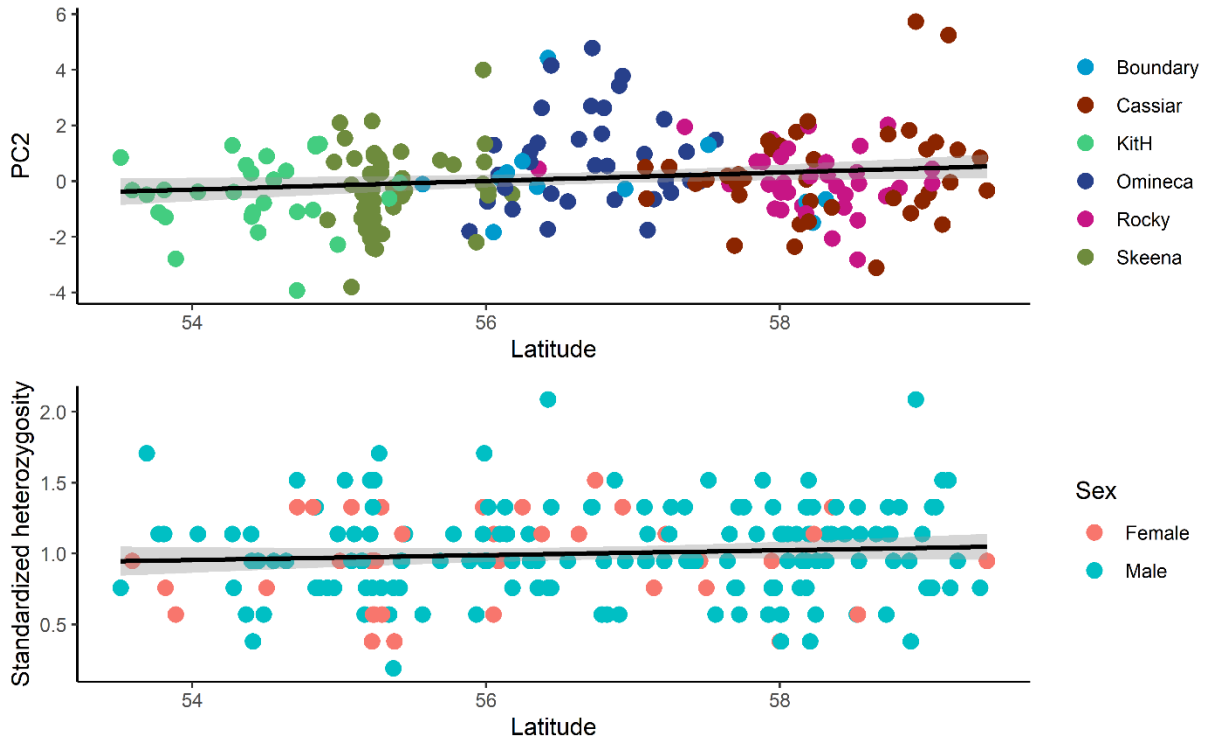
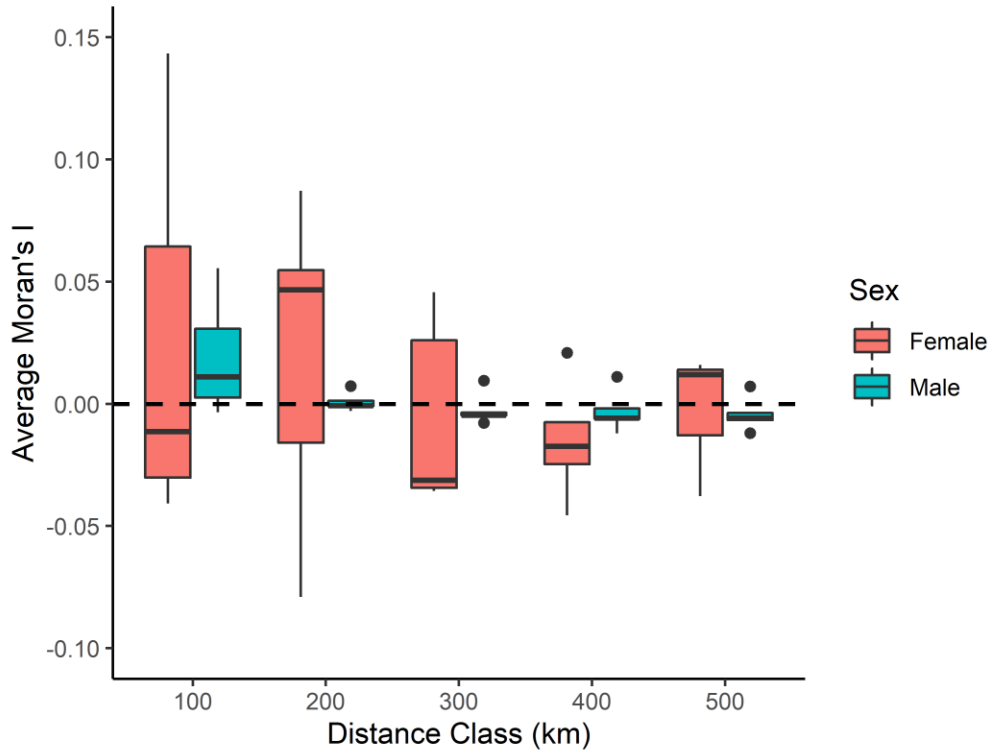


Fig. 1 Principal Component Analysis (PCA) of latitude versus PC2 of mountain goat allele frequencies (n=198). Two individuals were filtered out as outliers. Using a linear regression, a significant positive relationship was noted between latitude and PC2 ($F_{1,196}$=4.92, R^2=0.02, p=0.028). Scatter plot of latitude versus observed heterozygosity of mountain goat individuals, coloured by sex (n=199). One individual was filtered out due to unknown sex. Using a linear regression, a weak relationship is noted between latitude and observed heterozygosity ($F_{1,197}$=3.38, R^2=0.001, p=0.24)



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520 **Fig. 2** Boxplot of spatial autocorrelation as measured by average Moran's I versus Euclidean spatial
521 distance in distance classes of 100km for both male and female individuals (n=199). The dotted black line
522 depicts the null hypothesis that individuals are not spatially similar (Moran's I = 0). One individual from
523 the database was omitted due to unknown sex.

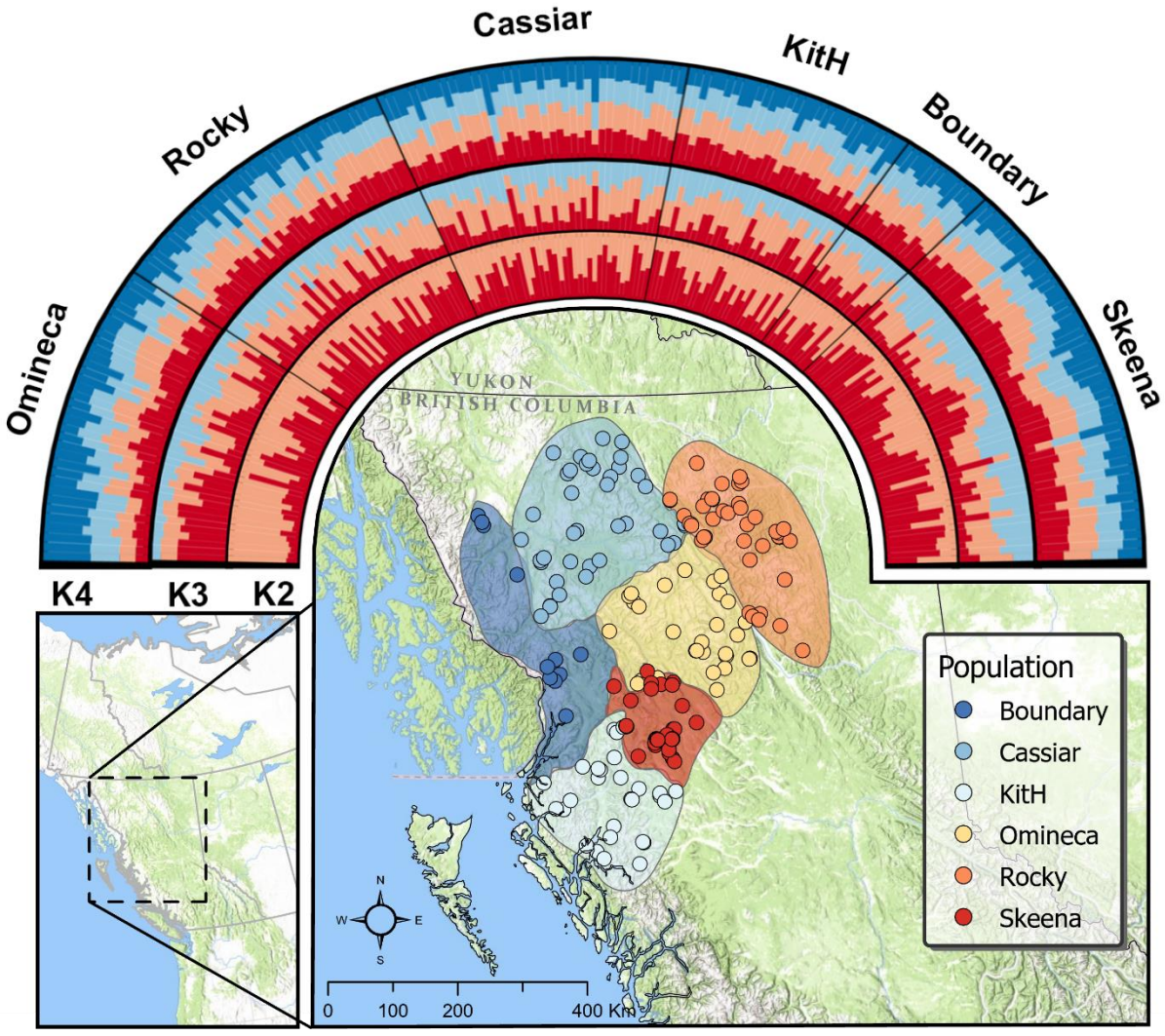

Fig. 3 Map of mountain goat samples used and classified according to mountain range in northern British Columbia (n=200) overlayed with K=2, K=3, and K=4 Distruct Structure plots. Colours used in the map are reflective of population, not Structure assignment. Irrespective of which K-value was depicted, panmixia is evident; it is also clear that the Omineca and Skeena populations cluster differently than the other four populations, possibly reflective of their relatively central distribution

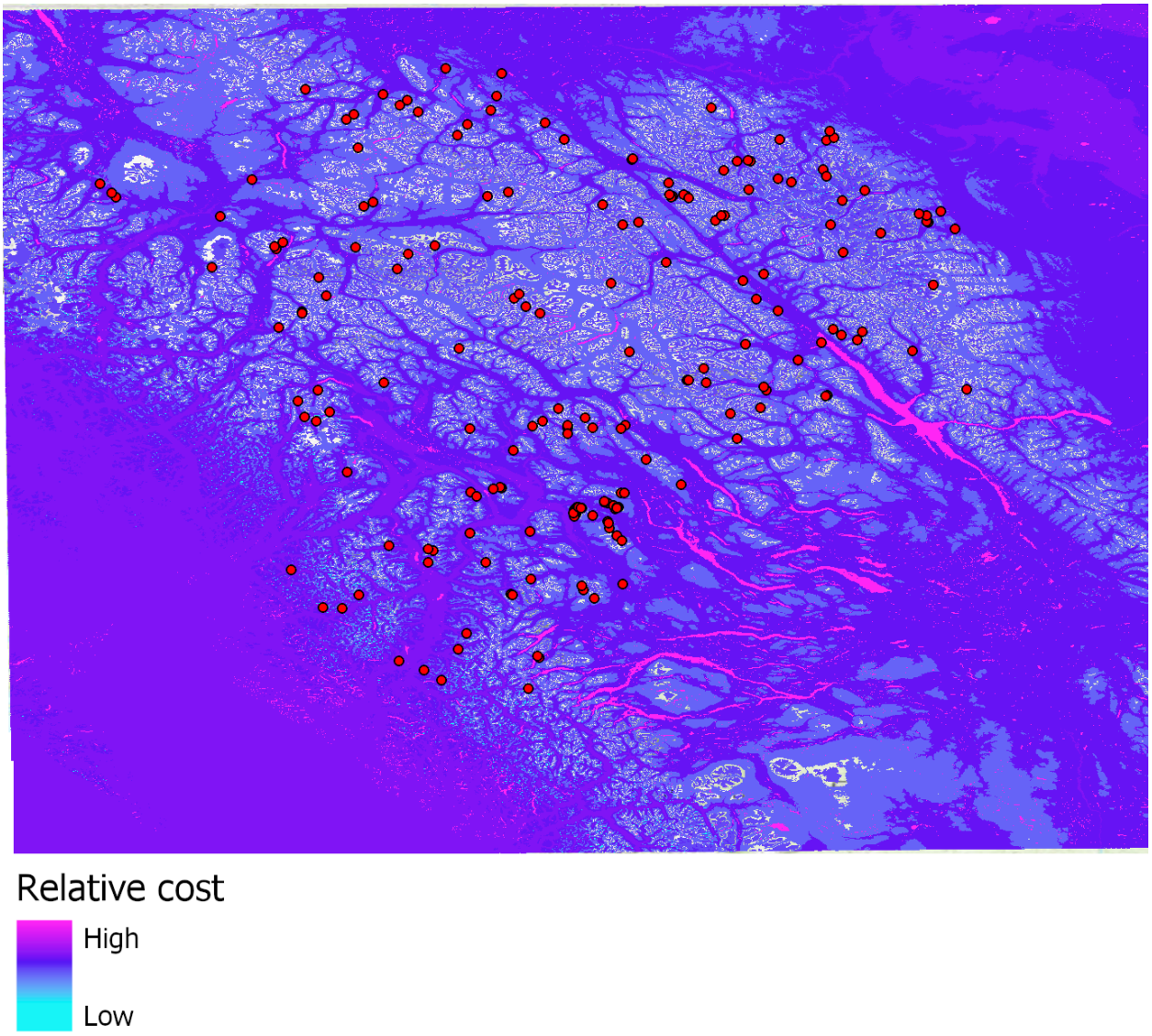

Fig. 4 Map of mountain goat (*Oreamnos americanus*) genetic sample locations (n=200) across northern BC (red dots) along with landscape cost derived from a 25m x 25m digital elevation raster. Cost was calculated using elevation, slope, and presence of water bodies in ArcGIS Pro 2.3.

Tables

Table 1. Diversity statistics for mountain goats (*Oreamnos americanus*) for six mountain ranges located across northern BC (n=200). Data were generated using Genalex v6.503. R^2 and associated p-value are with respect to linear regressions of the Lynch and Ritland *r* coefficient and pairwise Euclidean distance between individuals.

Population	No. of Samples	No. of rarefacted alleles	Observed H_E	Expected H_E	F_{IS}	N_e (95%CI)	Isolation-by-distance	
							R^2	p-value
Boundary	12	4.1 ± 0.61	0.40 ± 0.048	0.46 ± 0.054	0.084 ± 0.052	7.6 – 12.8	-0.001	0.87
Cassiar	39	4.0 ± 0.56	0.43 ± 0.57	0.46 ± 0.509	0.088 ± 0.043	37.2 – 45.8	-6.2 x 10^{-4}	0.46
Kit-H	29	4.2 ± 0.64	0.40 ± 0.055	0.45 ± 0.058	0.11 ± 0.04	25.2 – 30.7	-7.2 x 10^{-4}	0.40
Omineca	35	4.2 ± 0.55	0.45 ± 0.069	0.45 ± 0.064	-0.015 ± 0.046	29.6 – 32.1	-1.5 x 10^{-3}	0.76
Rocky	38	4.1 ± 0.48	0.41 ± 0.073	0.46 ± 0.72	0.093 ± 0.051	324.8 – INF	6.6 x 10^{-4}	0.46
Skeena	47	3.5 ± 0.48	0.40 ± 0.068	0.41 ± 0.067	0.015 ± 0.051	40.7 – 55.1	3.3 x 10^{-4}	0.24

Table 2. Pairwise F_{ST} for mountain goats (*Oreamnos americanus*) in six mountain ranges located across northern BC (n=200). Lower matrix is data generated using 13 loci, upper matrix is data generated using 16 loci. Data were generated using Genalex v6.503 and Arlequin v3.5. Significance was evaluated using 10,000 permutations and $p<0.05$.

	Boundary	Cassiar	Kitimat-Hazelton	Omineca	Rocky	Skeena
Boundary	-	0.038	0.047	0.055*	0.045*	0.050*
Cassiar	0.037	-	0.012	0.007*	0.016	0.021*
Kitimat-Hazelton	0.041	0.004	-	0.010*	0.009	0.018*
Omineca	0.051*	0.005*	0.008*	-	0.010*	0.026*
Rocky	0.041	0.011	0.010	0.009*	-	0.023*
Skeena	0.053*	0.017*	0.015*	0.023*	0.022*	-

Table 3. Summary statistics from the multiple linear regression of Lynch's relatedness coefficient (*r*) and the predictor variables of mountain goats (*Oreamnos americanus*) across northern BC (n=200) using 13 microsatellite loci. When assessed using permutations, mountain range was found to be the most significant variable predicting genetic relatedness. Pairwise Euclidean distances were significantly correlated to pairwise least cost path distances (t_{19699}=519.1, r=0.96, $p<0.001$), indicating landscape resistance was similar to the Euclidean paths among individuals.

Predictor variable	β value	r^2	P value
Euclidean Distance	-3.1 x 10^{-5}	0.004	>0.05
Mountain Range	3.4 x 10^{-2}	0.009	<0.001
Least Cost Path	6.6. x 10^{-10}	0.004	>0.05

552 Table 4. Gene flow as measured by mutation scaled immigration rates between populations of mountain
553 goats as identified using Migrate v4.4.3. This matrix represents the percentage of gene flow **from** the
554 column name.

	Boundary	Cassiar	Kit-H	Omineca	Rocky	Skeena
Boundary	-	1.06	2.69	1.31	1.66	1.86
Cassiar	4.29	-	3.85	2.56	1.29	3.15
Kit-H	1.84	0.51	-	0.42	2.44	1.08
Omineca	3.66	2.08	3.80	-	2.09	1.60
Rocky	4.19	4.30	3.80	4.01	-	3.03
Skeena	0.71	0.72	1.79	3.21	0.76	-

555