Influence of landscape features on the microgeographic genetic structure of a resident songbird.

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Abstract

Variation in landscape features influence individual dispersal and as a result can affect both gene flow and genetic variation within and between populations. The landscape of British Columbia, Canada, is already highly heterogeneous due to natural ecological and geological transitions, but disturbance from human mediated processes has further fragmented continuous habitat, particularly in the central plateau region. In this study, we evaluated the effects of landscape heterogeneity on the genetic structure of a common resident songbird, the black-capped chickadee (*Poecile atricapillus*). Previous work revealed significant population structuring in British Columbia which could not be explained by physical barriers, so our aim was to assess the pattern of genetic structure at a microgeographic scale and determine the effect of different landscape features on genetic differentiation. A total of 399 individuals from 15 populations were genotyped for fourteen microsatellite loci revealing significant population structuring in this species. Individual and population based analyses revealed as many as nine genetic clusters with isolation in the north, the central plateau and the south. Moreover, a mixed modelling approach that accounted for non-independence of pairwise distance values revealed a significant effect of land cover and elevation resistance on genetic differentiation. These results suggest that barriers in the landscape influence dispersal which has led to the unexpectedly high levels of population isolation. Our study demonstrates the importance of incorporating additional landscape features when interpreting patterns of population differentiation. Despite taking a microgeographic approach, our results have opened up additional questions concerning the processes influencing dispersal and gene flow at the local scale.

Introduction

Dispersal and gene flow are crucial for maintaining population connectivity and species persistence, while also preventing population differentiation and species divergence. The heterogeneity and patchiness of landscapes can influence the ability of an individual to disperse between populations. If dispersal is restricted by barriers in the landscape, the resulting decrease in population connectivity can lead to discrete, isolated groups. Over time, these isolated groups may experience reduced genetic diversity and become genetically distinct (Baguette and Van Dyck, 2007). Landscape genetics offers new approaches to explicitly test the influence of landscape elements on genetic structure to identify barriers corresponding to structured populations (Manel *et al.,* 2003, Holderegger and Wagner, 2008; Sork and Waits, 2010; Manel and Holderegger, 2013).

Large physical structures (e.g. mountain ranges and large water bodies) as well as stretches of unsuitable habitat are obvious barriers to dispersal and subsequent gene flow. The influence of barriers can vary within and among species so it is important to be able to identify the specific factors influencing genetic differentiation of target groups prior to implementing management strategies (With *et al.,* 1997). For example, using a landscape genetics approach, Frantz *et al.* (2012) found that motorways influenced genetic structuring in red deer (*Cervus elaphus*), but not wild boars (*Sus scrofa*); as a result, considering fragmentation effects of motorways would be primarily targeted at conservation efforts on only the former species. The effects of landscape features can also vary across a species range, as in the ornate dragon lizard (*Ctenophorus ornatus*), where land clearing was associated with genetic differentiation in one area, but not another (Levy *et al.,* 2012). Smaller, less conspicuous structures or environmental variables, such as microclimate, may also influence gene flow. Through landscape genetics, effects of multiple factors on

contemporary patterns of genetic structure can be examined across different spatial scales and across species with varying dispersal capabilities, allowing us to better understand how organisms interact with their environment, and how they may respond to future environmental change.

In current landscapes, habitat fragmentation from natural and human-mediated processes can influence the potential for animals to disperse and thus affect the spatial distribution of genetic variation at both large and small geographical scales. Contemporary factors such as insect outbreaks (e.g. mountain pine beetle *Dendroctonus ponderosae*) and habitat degradation (e.g. forestry operations, agricultural conversion) have reduced population connectivity by removing suitable breeding/dispersal habitat (Martin *et al.*, 2006). For instance, a combination of already-restricted range of the northern spotted owl (*Strix occidentalis caurina*) in the Pacific North West coupled with the removal of dense, late successional forest has left the species federally threatened (COSEWIC, 2008; Blackburn *et al.*, 2003; Yezerinac and Moola, 2006).

British Columbia (Canada) has a complex climatic and vegetation history following the Last Glacial Maximum (26.5 – 19 thousand years ago). When this is combined with broad-scale climatic gradients (i.e. moisture, temperature and topography - Meidinger and Pojar, 1991) in the province, the result is major regional transitions that create rich and heterogeneous landscapes (Gavin and Hu, 2013; Figure 1). The province contains six ecozones and 14 biogeoclimatic zones (see Figure 10 in Meidinger and Pojar, 1991). A major longitudinal moisture gradient formed by the Coastal Mountains is characterised by dominant maritime moist conifer forest in the west, transitioning to sagebush steppe in the rain-shadow of the south central interior, to mixed conifer and pine forest in the east. The interior regions are further influenced by a latitudinal gradient with increasing summer moisture from south to

north. This results in desert steppe in the south transitioning to subboreal and boreal spruce forest in the north. This natural heterogeneity is further increased by high levels of habitat fragmentation resulting from current forestry and agricultural practices occurring within the province.

To determine how these natural and anthropogenic factors influence population structure, we conducted a microgeographic landscape genetic assessment of a common resident songbird, the black-capped chickadee (*Poecile atricapillus*) in British Columbia. Our previous work identified population genetic structuring in central British Columbia, but the sampling regime and range-wide scale of the study meant that smaller geographical barriers were less noticeable (Adams and Burg, 2015). Here, a fine-scale transect sampling approach allowed for a more detailed examination of the landscape patterns and processes influencing population genetic structuring and a larger number of microsatellite markers were used to better capture the spatial distribution of genetic variation (Runde *et al.*, 1987; Selkoe and Toonen, 2006). The study area is comprised of a number of different habitats and environmental conditions, so studying genetic variability in a non-migratory species with limited dispersal potential will allow us to investigate the role of habitat heterogeneity on the ecology and evolution of populations. The aims of the study were to identify where the genetic breaks occur and to evaluate the processes driving differentiation. This led to three main hypotheses; 1) fine scale population genetic differentiation will be evident in the black-capped chickadee due to the inclusion of additional sampled populations and microsatellite loci; 2) given the level of topographical and climatic variability found within the province, dispersal and gene flow are influenced by landscape features and environmental variables, and 3) habitat fragmentation resulting from anthropogenic disturbance (e.g. forestry and agriculture) isolates populations in central and southern British Columbia.

Materials and Methods

Study Species

The black-capped chickadee is a resident songbird, common throughout most of North America with a range that covers a large and complex geographical area. Black-capped chickadees are an important study species because they are generalists and thrive in a variety of environmental conditions, although they prefer mixed deciduous and coniferous woodland (Smith, 1993). If specific landscape processes are found to have a negative impact on chickadees, this would indicate that other species (particularly specialists) may also be affected. As primary cavity nesters, chickadees are dependent on advanced decaying trees or snags in mature forests. Their diet requirements also vary seasonally with a preference for mixed berries, seeds and insects in the winter in comparison to a completely insectivorous diet during the breeding season (Runde *et al.*, 1987). Although chickadees do reside and breed in disturbed areas, studies have found these low quality habitats negatively affect reproduction (Fort *et al.*, 2004a), territoriality (Fort *et al.*, 2004b), song output (van Oort *et al.*, 2006), song consistency and perception (Grava *et al.*, 2013a) and song structure (Grava *et al.*, 2013b) in this species. Elevation and the presence of other chickadee species (e.g. mountain chickadees) can also influence their distribution and habitat preference (Campbell *et al.*, 1997). Collectively, this information highlights the importance of a number of factors related to habitat quality (e.g. mature, dense woodland) on species persistence.

Sample collection

We included samples from seven populations collected as part of our previous study (i.e. FtStJ1, PG, NWBC, NBC, BCR, SAB1 and SAB2; Table 1; Adams and Burg, 2015). We

collected additional samples during the 2012 breeding season using a transect-based approach along HWY 16, the main east-west corridor in north-central British Columbia. Birds were captured using mist nets and call playback, and samples of blood (< 100 µl from the brachial vein) and/or feathers were obtained from each individual. This resulted in approximately 20 individual birds sampled from each of an additional six locations (i.e. HAZ, HOU, FF, FrL, CLU and FtStJ2; Table 1). Where possible, sampling sites were confined to a 10 km radius. Feather samples were also obtained from two more populations: Vancouver (VAN) and Kelowna (KEL). With all individuals combined, sampling took place over ten breeding seasons (2003 – 2010, 2012 and 2013) and a total of 405 individuals from 15 populations were collected (Figure 1; Table 1; Supplementary Table S1). Each bird was banded with a numbered metal band to prevent re-sampling and all blood/ feather samples were stored in 95% ethanol and, on return to the laboratory, stored at -80ºC.

DNA extraction and microsatellite genotyping

DNA was extracted from blood ethanol mix (10 µl) or feather samples using a modified Chelex protocol (Walsh, 1991). Each individual was genotyped for 14 polymorphic microsatellite loci (Supplementary Table S2) and DNA was amplified for all loci (including new loci Pij02, VeCr05 and CTC101) using the same two-step annealing PCR conditions outlined in Adams & Burg (2015); the exception was for Pij02, where the two-step annealing temperatures were adjusted from 50°C and 52°C to 52°C and 54°C. All procedures following DNA amplification were conducted as in Adams and Burg (2015).

Most individuals were successfully genotyped for all 14 variable microsatellite loci. Seven populations were missing genotypes for locus PmanTAGAn45, four populations for Ppi2, two populations for Titgata02, and two populations for Pij02. All analyses were carried

out with and without these four loci to determine if missing data influenced levels of observed population differentiation. In addition, we conducted analyses with and without the feather sampled populations (KEL and VAN) as the DNA extracted from feathers were of lower quality which resulted in missing data and created the potential for genotyping errors from low amplification success for some loci.

Genetic analyses

Genetic diversity

A total of 399 individuals remained after removing those genotyped for ≤ 5 loci. Errors within the data (i.e. input errors, allelic dropout, stutter and null alleles) were assessed in MICRO-CHECKER v2.2 (van Oosterhout *et al.,* 2004). Allelic richness was calculated in FSTAT v2.9.2.3 (Goudet, 2001) and tests for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were performed in GENEPOP v4.0.10 (Raymond and Rousset, 1995; Rousset, 2008) using default Markov chain parameters (100 batches, 1000 iterations and 1000 dememorisation steps). Both observed and expected heterozygosities were calculated in GenAlEx v6.5 (Peakall and Smouse, 2012) to determine the levels of population genetic diversity. Lastly, levels of significance were adjusted using the modified False Discovery Rate (FDR) correction (Benjamini and Yekutieli, 2001).

Population genetic structure analyses

We used multiple approaches to gain insight into the genetic structure of the black-capped chickadee. We used two clustering methods: GENELAND v4.0.0 (Guillot *et al.,* 2005a) and STRUCTURE v2.3.4. (Pritchard et al., 2000). Both use Bayesian models to assign individuals to genetic clusters by maximising HWE and minimising LD, but differ in the way

191 they use spatial information. STRUCTURE relies solely on genetic data (with the option of
192 predefining populations with location priors) whereas GENELAND incorporates individual
193 spatial coordinates.

194 Implemented in the program R v 3.1.3 (R Development Core Team, 2015),
195 GENELAND was run in two steps following the recommended protocol of Guillot *et al.*
196 (2005a, b). First, we ran the program for ten replicates for each *K* (1 – 10) using the
197 correlated allele frequencies and null allele models and 100,000 McMC iterations, a thinning
198 interval of 100 and a maximum rate of Poisson process of 399 (equal to the sample size). The
199 uncertainty attached to spatial coordinates was fixed to 20 km (i.e. the precision of our sample
200 locations; 10 km radius) and the maximum number of nuclei in the Poisson–Voronoi
201 tessellation was fixed to 1197 (three times the sample size). The number of clusters (*K*) was
202 inferred from the modal *K* and the run with the highest mean posterior probability. A second
203 run was then conducted with the inferred *K* fixed and all parameters left unchanged to allow
204 individuals to be assigned to clusters. To determine the robustness of this model,
205 GENELAND was run multiple times with different parameters (e.g. with and without the
206 correlated allele frequencies and null allele models; and 50,000, 100,000 and 200,000 McMC
207 iterations).

208 STRUCTURE was run with the admixture model, correlated allele frequencies (Falush
209 *et al.*, 2003) and locations as priors (locpriors). To determine the optimal number of clusters
210 (*K*), we conducted ten independent runs (100,000 burn in followed by 200,000 McMC
211 repetitions) for each value of *K* (1-10). Results were averaged using STRUCTURE
212 HARVESTER v0.6.6 (Earl and vonHoldt, 2012) and both delta *K* (ΔK; Evanno *et al.*, 2005)
213 and LnPr(X|K) were used to determine the true *K*. Any populations with individuals showing
214 mixed ancestry (e.g. 50% Q to cluster 1, and 50% Q to cluster 2) were rerun individually with

two populations representing each of the two clusters involved in the mixed ancestry to determine correct assignment. This is important to check because as *K* increases above the true *K* value, Q values will often decrease and split clusters (Pritchard *et al.*, 2000). This splitting of populations must be clarified prior to additional testing. Finally, if multiple populations were assigned to the same genetic cluster, those populations were rerun to test for additional substructure using the same parameters as the initial run, but only to a maximum of five runs for each *K* value.Pairwise F_{ST} values were then calculated in GenAlEx v6.5 to investigate the degree of genetic differentiation among the predefined populations. We also calculated D_{EST} (Jost, 2008) in SMOGD v1.2.5 (Crawford, 2010), an alternative measure of diversity that accounts for allelic diversity and is shown to measure genetic differentiation more accurately than traditional F_{ST} when using polymorphic microsatellite markers (Heller and Siegismund, 2009). We compared measures of D_{EST} and F_{ST} to determine the true level of genetic differentiation. Since the theoretical maximum of 1 for F_{ST} is only valid when there are two alleles, population wide F'_{ST}, standardised by the maximum F_{ST} value, was calculated in GenAlEx v6.5. To further assess genetic structure among populations, we carried out a Principal Coordinate Analysis (PCoA) using both F_{ST} and D_{EST} in GenAlEx v6.5.

Landscape genetics

Parameterization of landscape variables

To assess the functional connectivity among populations, we evaluated four competing models: 1) the null model of isolation by geographical distance (or IBD; Wright, 1943), 2) isolation by elevation resistance, 3) isolation by land cover resistance and 4) isolation by combined elevation and land cover resistance (i.e. both land cover and elevation raster layers

were combined into one resistance layer, termed ‘land-elevation’ herein). Pairwise resistance distances were calculated among all sampling sites using spatial datasets and an eight neighbour connection scheme in CIRCUITSCAPE v4.0 (McRae, 2006). This method is based on circuit theory and uses resistance distances to assess all possible pathways between two focal points (or populations) to better map gene flow across the landscape and measure isolation by resistance (IBR).

Categorized land cover and digital elevation maps (DEM), circa 2000, were obtained from GEOBASE (www.geobase.ca) and resistances to habitat types were assigned using ArcMap, ESRI© (Table 2). Land cover data were categorised into six cover types. The lowest resistance values were assigned to suitable chickadee habitat known to facilitate dispersal (i.e. forest cover, particularly broadleaf and mixed forests) whereas other land cover types were classified as being moderately permeable (i.e. coniferous forest, shrubland and grassland), or completely impermeable (i.e. unsuitable habitat which included agricultural land and water) to dispersal (Table 2). For elevation, five different ranges were assigned resistance values based on elevations where chickadees have previously been observed. For example, low resistances were given to low elevation ranges (< 1500 m), whereas higher resistance values were given to higher elevations where chickadees are rarely observed (> 1500 m) (Table 2). The program outputs a cumulative ‘current map’ to portray the areas where resistance to gene flow is either high or low. Populations SAB1 and SAB2 were excluded from these analyses as geo-referenced coordinates were outside the spatial extent of the data. Given the size of our study area, all resistance surfaces were based on a 2 x 2 km resolution.

Landscape effects

We implemented a linear mixed-effect modelling approach based on the maximum-likelihood population-effects (MLPE) model (Clarke *et al.*, 2002) using the 'lmer' function in the package 'lmer4' v1.1.8 (Bates *et al.*, 2015) in R v 3.1.3 (R Development Core Team, 2015). This approach is superior to the Mantel test to identify the landscape variable(s) which best explain population genetic differentiation. This is because these tests are often described as having low statistical power (Legendre and Fortin, 2010) and, more importantly, fail to account for non-independence of each pairwise observation within the distance matrix (Yang, 2004).

Nine predefined models were used to test for effects of different landscape variables on both estimates of pairwise genetic distance (i.e. F_{ST} and D_{EST}). When fitting MLPE models, the 'lmer' function was modified so the random factor would account for multiple memberships (i.e. two individual populations for each pairwise distance) following van Strien *et al.* (2012). Explanatory variables were centred around their mean, and parameter estimation was performed with the residual maximum-likelihood (REML) criterion (Clarke *et al.*, 2002). For each parameter estimate 95% confidence intervals were calculated. Models satisfied the assumptions of normality and constant variance, and showed no evidence of multicollinearity. In landscape genetics, a common technique is to use the Akaike Information Criterion (AIC) for model selection (Storfer *et al.*, 2007). However, use of REML precludes the use of AIC; therefore we used the marginal R^2 statistic developed by Nakagawa and Schielzeth (2013) in the R package, MuMIn v 1.14.0 (Barton, 2014), to select the best fitting and most parsimonious model (*c.f.* van Strien *et al.*, 2012).

Results

Genetic structure

286 Genetic diversity

287 Among all loci and populations, the total number of alleles ranged from 3 – 46 alleles
288 (Supplementary Table S2). Observed heterozygosity at each site and across all loci ranged
289 from 0.584 (KEL) to 0.683 (SAB1, followed closely by SAB2 at 0.681), and expected
290 heterozygosity ranged from 0.572 (KEL) to 0.717 (FtStJ1; Supplementary Table S3).
291 Accounting for differences in sample size, allelic richness ranged from 2.42 (PG) to 2.79
292 (FtStJ1 and FF; Table 1). Eleven of the fifteen populations contained at least one private
293 allele (Table 1); FtStJ1 contained the highest number of private alleles (PA = 11) followed by
294 NBC and SAB2 (PA = 5). Null alleles were detected at a low frequency for a number of loci
295 and were not consistent across populations with the exception of two loci: VeCr05 (0 – 25%)
296 and Cuμ28 (31 – 71%). We found a large difference between observed and expected
297 heterozygosities across populations for locus VeCr05 (*Ho*: 0.185, *He*: 0.306), but not for
298 Cuμ28 (*Ho*: 0.485, *He*: 0.502, Supplementary Table S3). Exclusion of VeCr05 and/ or Cuμ28
299 did not alter the results, and so all 14 loci were included in the final dataset. Thirteen
300 deviations from HWE (Supplementary Table S3) and two pairs of loci in disequilibrium were
301 identified after corrections for multiple tests. All deviations were the result of a heterozygote
302 deficit. Significant LD was found between loci Titgata02 and CTC101 ($P \leq 0.001$) within
303 FtStJ1 and between loci Escu6 and Titgata02 ($P \leq 0.001$) within SAB1. As LD was not
304 consistent across populations and genotypes showed no association, it is possible that LD is
305 the result of a type 1 error. Results were not substantially affected after removing either the
306 underrepresented loci or the feather sampled populations (see summary statistics in
307 Supplementary Table S4).

308

309 Population genetic structure analyses

The two clustering analyses failed to converge on the total number of genetic clusters (*K*), however a number of groupings were similar across analyses. A hierarchical STRUCTURE analysis inferred seven genetic clusters (Supplementary Figure S1a) using both mean log likelihood (Pr(X|K) = -17544.9) and Δ*K* (Supplementary Figure S1b). A larger number of groupings was found in GENELAND; eight runs suggested $K = 9$ and two runs suggested $K = 10$. As the highest posterior probability was for $K = 9$ (-958) we took this as being the true estimation of *K*. For population membership and boundary graphs see Supplementary Figure S2. The genetic clusters included single populations (BCR, CLU, FtStJ1, NBC, NWBC, and PG), as well as groups of populations (KEL and VAN, SAB1 and SAB2, and all remaining populations; Figure 1). Five of the groupings were identical to those identified in STRUCTURE (BCR, NWBC, PG, FtStJ1 and VAN+KEL; Supplementary Figure S1). The distinction of PG and FtStJ1 is concordant with patterns observed in our previous study (Adams and Burg, 2015).

Pairwise F_{ST} and D_{EST} values showed a significant positive correlation ($R^2 = 0.692$, $P = 0.003$). Pairwise F_{ST} values ranged from 0.009 to 0.316 (Table 3) and after corrections for multiple tests, 86 of the 105 tests were significant indicating a high level of genetic differentiation among populations. Similar levels of population structure were detected using D_{EST} which ranged from 0.005 to 0.329 (Table 3). Overall F'_{ST} was 0.240 (Supplementary Table S5).

Distinct clustering of populations in PCoA was only found using D_{EST} values. The first principal coordinate analysis with all 15 populations resulted in clear separation of populations KEL and VAN from all other populations, as well as differentiation from each other, with the first two axes explaining 50.59% and 17.04% of the variation (Figure 2a) respectively. Isolation of KEL and VAN is concordant with GENELAND. It is important to

note that these two populations contained some missing genotype information. Since PCoA is sensitive to missing data, we removed KEL and VAN from analyses to identify additional structure. Concordant with some of the patterns observed in GENELAND, we see separation of PG as well as NWBC and BCR (Coordinate 1 = 31.05%, Coordinate 2 = 19.93%; Figure 2b).

Landscape genetics

MLPE models were ranked based on marginal R^2 (Table 4). For F_{ST}, the best fitting model included land-elevation (R^2 (mar) = 0.879; Table 4a), whereas for D_{EST} the model with the highest R^2 included both land-elevation and geographical distance (R^2 (mar) = 0.711; Table 4b). All variables in the best models had a positive effect on genetic distance. Over all models, those including either land cover or land-elevation as explanatory variables produced consistently high R^2 values for both F_{ST} ($\geq$ 0.874) and D_{EST} ($\geq$ 0.660). The effects of geographical distance and elevation varied across all models. Only once was there a significant effect of the parameter elevation (model 7 for D_{EST}), and although geographical distance was significant in all models for D_{EST}, (including the top two models) for F_{ST} geographical distance was significant in only two of the nine models. This may be explained by the different properties of the response variables (i.e. F_{ST} is based on allele frequencies whereas D_{EST} is based on allelic diversity) and emphasizes the importance of comparing measures of genetic distance. D_{EST} corrects for sampling bias and as the sample sizes varied between sites, this may explain the differences between the two. The effect of geographical distance on D_{EST} was consistent across all models, and suggests an isolation by distance (IBD) effect. Meanwhile, land cover and land-elevation had a clear significant effect on all models and across both measures of genetic distance. This suggests that while the combined

effect of both land cover and elevation resistances on genetic distance is significant, ultimately, land cover resistance is the largest factor contributing to variation in population genetic differentiation.

Discussion

Fine-scale genetic structure of the black-capped chickadee

Populations of black-capped chickadees in British Columbia are spatially structured from restricted population connectivity as supported by individual based (Bayesian clustering analyses), population based (F_{ST}, PCoA) and landscape based analyses (CIRCUITSCAPE and MLPE modelling). Intensive sampling and additional microsatellite loci used in this study resulted in a finer resolution of observed genetic structure. Here, nine genetic clusters were inferred in comparison to four clusters in our previous study (Adams and Burg, 2015) and population genetic differentiation was observed in all regions of British Columbia from the north (NWBC) to the interior (CLU, NBC, FtStJ1, PG) and in the south (VAN and KEL, BCR).

Despite their vagility and generalist behaviour, black-capped chickadees are a highly sedentary species, showing strong aversion to crossing gaps in suitable habitat and this characteristic appears to have a significant impact on dispersal across fragmented landscapes (Desrochers and Hannon, 1997). Population genetic structure is an expected evolutionary consequence of species inhabiting fragmented landscapes (Shafer *et al.*, 2010), especially in species with restricted dispersal (Unfried *et al.*, 2012) like black-capped chickadees. Spontaneous and highly irregular, large distance movements (i.e. irruptions) are observed in juveniles (Weise and Meyer 1979), and occasionally in adults (Brewer *et al.*, 2000), and adults will sometimes move down from high altitude localities in response to severe weather

conditions or food availability (Campbell *et al.,* 1997). However, black-capped chickadees rarely disperse long distances; although a maximum dispersal of 2000 km was recorded for one bird in a recapture study on 1500 individuals; less than 2% of birds dispersed more than 50 km from banding locations, and over 90% remained in the location they were initially banded (Brewer *et al.,* 2000). Distances between adjacent populations in this study are within the potential dispersal range, yet genetic differentiation was observed between populations separated by both small (e.g. ~30 km between FtStJ1 and FtStJ2) and large (e.g. ~390 km between PG and HAZ) distances (Figure 1). The observed patterns suggest that at smaller geographical distances, other factors such as habitat heterogeneity and fragmentation resulting from both natural and anthropogenic causes may be influencing dispersal and gene flow.

Effects of landscape features on genetic differentiation

A landscape genetic approach revealed the complexity of black-capped chickadee population structuring from just two spatial datasets (elevation and land cover), which highlights the importance of incorporating landscape level data into studies of gene flow in addition to using traditional measures of IBD. Despite the relatively weak resolution of model based analyses, both land cover (suitable forest cover) and elevation (low- mid elevation valleys) appear to be important factors in explaining the observed patterns of genetic differentiation in black-capped chickadees. The models that included land cover combined with elevation (land-elevation) best explained genetic differentiation for F_{ST} and D_{EST} in two separate analyses, but it is likely that land cover is the most influential factor (Table 4). As forest generalists, dispersal for black-capped chickadees is largely dependent upon the availability of woodland corridors (Bélisle and Desrochers 2002, Desrochers and Bélisle 2007). For example, differences in forest cover can be observed between genetically differentiated populations in

406 Fort St. James (FtStJ1 and FtStJ2). Timber harvesting of the abundant lodgepole pine (*Pinus*
407 *contorta*) significantly reduces the amount of suitable forest in the south (FtStJ2) in
408 comparison to the north (FtStJ1) where the forest is managed and protected from logging
409 (Fondahl and Atkinson, 2007).

410 Populations were sampled on either side of a distinct mountain (Pope Mountain;
411 approximately 1400 m elevation) and large water body (Stuart Lake) which may act as
412 connectivity barriers. Elevation may therefore be a significant factor, as black-capped
413 chickadees are often associated with low-elevation riparian corridors in British Columbia, and
414 tend to be replaced ecologically at higher elevations by mountain chickadees (*Poecile*
415 *gambeli*) (Foote *et al.*, 2010). Low resistance dispersal routes also corresponded to areas of
416 low elevation (i.e. within the central plateau and to the south; Figure 3). Black-capped
417 chickadees frequently breed between 270 m and 1500 m elevation with the highest elevation
418 recorded at 2300 m in British Columbia (Campbell *et al.*, 1997). As black-capped chickadees
419 are forest dependent and found at lower elevations, it is not surprising that the lack of forest
420 cover and high elevations would impede gene flow. The same two landscape features are
421 important in facilitating black bear (*Ursus americanus*) dispersal in northern Idaho (Cushman
422 *et al.*, 2006).

423 Differences in land cover and elevation may reflect multiple biogeoclimatic zones
424 across the region; characterised by variation in climate, topography and vegetation. As our
425 populations are distributed across a number of these zones, it is possible that habitat
426 discontinuity is playing a bigger role in genetic differentiation, than physical geographical
427 barriers. For example, genetic differentiation in the north (NWBC) could be explained by
428 local environmental conditions. NWBC is situated within the boreal-black and white spruce
429 biogeoclimatic zone, characterised by long, extremely cold winters and short, warm summers,

and is isolated from other sampling sites by the Skeena and Omineca Mountains. To the south of NWBC, there is a sharp transition from boreal-black and white spruce to Engelmann spruce-subalpine fir to interior cedar-hemlock (Parish, 1995). The Engelmann spruce-subalpine fir zone occupies the highest forested elevations in British Columbia. Our landscape analyses revealed high pairwise resistance values (results not shown) between NWBC and nearby populations for both elevation and land cover, suggesting limited dispersal. This is also evident from both CIRCUITSCAPE (Figure 3), where there are little to no connections between NWBC and nearby populations, and the effect of IBD on pairwise D_{EST} values (Table 4b). Our resistance map of elevation (Supplementary Figure S3a) supports isolation of NWBC. Therefore high variability in habitat and climatic conditions combined with high elevations and large geographic distances may explain the genetic differentiation of this population, as when gene flow is low, isolated populations may adapt to local environmental conditions as a result of divergent selection pressures (Cheviron and Brumfield, 2009). However, it is important to note that many neighbouring populations to NWBC have not been sampled and so these observations could be a function of sampling regime rather than specific landscape effects. To confirm these speculations, more robust sampling in and around this area is necessary.

Genetic clustering of KEL and VAN was supported by high, yet non-significant pairwise F_{ST} (0.316). Black-capped chickadee subspecies delimitations by size and colouration might explain this grouping; VAN birds are grouped within the Oregon subspecies (*P. a. occidentalis*); KEL birds within the Columbian subspecies (*P. a. fortuitus*) and all other populations in this study within the larger-sized long-tailed subspecies (*P. a. septentrionalis*) (Smith, 1991). While we expected to see reduced gene flow between KEL and VAN because of the presence of two prominent north-south mountain ranges bisecting the two sampling

sites, there were inconsistencies among analyses (i.e. differentiation was indicated by F_{ST} and PCoA analyses, but not by Bayesian clustering analyses). It is possible that low valleys within the Coastal Range act as important corridors to dispersal between these two populations. The genetic status of KEL and VAN, however, will require validation with additional sampling.

Dispersal in fragmented landscapes

Loss of genetic diversity from habitat loss can impede a species' ability to adapt to changes in their environment, and lead to reductions in reproductive fitness and population size (Frankham, 1995; Haag *et al.*, 2010; Woltmann *et al.*, 2012; Finger *et al.*, 2014). As such, loss of forests within low- to mid-elevation areas from both natural and anthropogenic processes could have a significant impact on chickadee dispersal, and thus on the health of chickadee populations. One reason for reduced dispersal in fragmented habitats is predation risk. Both St Clair *et al.* (1998) and Desrochers and Hannan (1997) found that black-capped chickadees are less willing to cross gaps of > 50 m of unsuitable habitat. In areas of central British Columbia where logging and other activities have fragmented chickadee habitat, dispersal would be restricted. The size and abundance of cut-blocks from forestry activities may be restricting dispersal; however, explicit testing at an even smaller spatial scale is required. Unexpectedly, our resistance map (Figure 3) displayed a large area in the central plateau (between FrL and CLU) where movement is impeded. This area corresponds to an area of increased agriculture which could explain differentiation of CLU in GENELAND analyses as well as lower observed allelic diversity and observed heterozygosities (FF, FrL and FtStJ2; Tables 1 and S3).

Natural contributors to habitat fragmentation may also explain patterns of genetic structure observed here. Bark beetle outbreaks have been observed in western Canada since the 1900s (Swaine, 1918). Current outbreaks are spreading quickly with warmer/milder winters facilitating their expansion across western Canada. The mountain pine beetle outbreak has destroyed huge portions of mature pine forests throughout British Columbia, particularly in the central plateau region within elevations of 800 and 1400 m (Safranyik and Wilson, 2006). Habitat loss could be leading to high levels of population isolation here, particularly in low-mid elevation forested valleys which serve as dispersal corridors. In fact, a number of populations within this region are showing signs of reduced genetic diversity, particularly the PG population (Ho = 0.594, He = 0.669; Table 1), suggesting that some populations may be experiencing a bottleneck as a result of restricted gene flow. Thus, despite being common, widely distributed and of little conservation concern (IUCN Red List), isolated chickadee populations may be undergoing microevolutionary processes which may eventually lead to local adaptation.

Conclusions

Weak population genetic differentiation is expected for common and widespread species with the ability to disperse among habitat patches (i.e. bird flight), but our findings suggest that variation and/or changes in the environment can impact genetic differentiation in mobile species, resulting in microgeographic population structuring.

Dispersal and gene flow among black-capped chickadee populations appear to be affected by variation in landscape topography and forest cover; features critical to chickadee survival and reproductive success. Climatic differences among sampling sites may also create differential selective pressures. The importance of including landscape features when

assessing connectivity and population differentiation is particularly relevant when identifying vulnerable populations and management units, as over time isolated populations may diverge through local adaptation or inbreeding. In the face of climate change, biogeographic zones will change and forest tree species are under threat of shifting and narrowing distributions (Hebda, 1997; Hamann and Wang, 2006; Wang *et al.,* 2012) which could in turn, have an impact on black-capped chickadee populations. Changes in precipitation and winter temperature have already driven shifts in the geographic patterns of abundance of bird populations in western North America (Illán *et al.,* 2014).

Overall, when assessing patterns of genetic differentiation of populations, a smaller sampling scale and the inclusion of more loci can provide additional patterns of genetic structure. More importantly, incorporating both landscape features and environmental variables when explaining patterns can significantly improve our understanding of how species evolve in response to changes in their environment.

Conflict of Interest

The authors declare no conflict of interest.

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Data Accessibility

All microsatellite genotypes will be archived prior to publication.

Supplementary Information

Supplementary information is available at Heredity's website.

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717

718 **Table 1.** Sampling location information including site abbreviation (Abbrev.), geographical
719 location (latitude (Lat) and longitude (Long)) and sample size (*N*). Microsatellite summary
720 statistics for each population and all loci including: observed (Ho) and expected (He)
721 heterozygosities, number of private alleles (PA) and allelic richness (AR).

Location	**Abbrev.**	**Lat (°N)**	**Long (°W)**	***N***	**Ho**	**He**	**PA**	**AR**
Revelstoke	BCR	50.9807	-118.1817	54	0.652	0.708	4	2.66
Northern BC	NBC	54.8883	-127.7665	43	0.647	0.690	5	2.68
Cluculz Lake	CLU	53.9102	-123.5496	20	0.654	0.703	4	2.70
Fort Fraser	FF	53.9629	-124.5331	11	0.644	0.672	0	2.79
Francois Lake	FrL	54.0488	-125.6988	20	0.622	0.668	1	2.64
Fort St. James Town	FtStJ 2	54.4183	-124.2743	18	0.623	0.667	0	2.69
Hazelton	HAZ	55.2829	-128.0470	20	0.622	0.682	1	2.66
Houston	HOU	54.4043	-126.6433	18	0.620	0.666	1	2.72
Kelowna	KEL	49.9200	-119.3950	8	0.584	0.572	0	-
Northwest BC	NWBC	58.3003	-130.6677	17	0.658	0.689	2	2.63
Vancouver	VAN	49.2644	-123.0816	33	0.649	0.625	0	-
Fort St. James John Prince Research Station	FtStJ 1	54.6453	-124.3949	61	0.666	0.717	11	2.79
Prince George	PG	53.8936	-122.8289	30	0.594	0.669	1	2.42
Southern Alberta 1	SAB1	49.3455	-114.4153	30	0.683	0.677	3	2.60
Southern Alberta 2	SAB2	49.0694	-113.8561	22	0.681	0.707	5	2.71

722

723 Table 2. Landscape models and corresponding resistance values assigned to each cover type or range in CIRCUITSCAPE analyses. Model

724 hypotheses are also provided.

Model	Resistance values assigned to cover types/ ranges	Hypothesis
Null	Uniform landscape (all cells given a value of 1)	Isolation by Distance
Land cover	Mixed forest = 1 Broadleaf forest = 2 Coniferous forest = 5 Shrubland = 10 Grassland/ wetland/ bryoids = 100 Unsuitable habitat (incl. agricultural land) = 1000	Isolation by Resistance
Elevation	0 - 800 m = 1 801 - 1000 m = 5 1001 - 1500 m = 10 1501 - 2300 m = 100 2301 - 3454 m = 1000	Isolation by Resistance
Land-elevation	Combined land cover and elevation resistance maps using "raster calculator"	Isolation by Resistance

725 **Table 3.** Pairwise F_{ST} values (below diagonal) and harmonic mean estimates of D_{EST} (above diagonal) for 15 black-capped chickadee

726 populations based on 14 microsatellite loci. Bold values indicate significance after corrections for multiple tests.

	BCR	**NBC**	**CLU**	**FF**	**FrL**	**FtStJ2**	**HAZ**	**HOU**	**KEL**	**NWBC**	**VAN**	**FtStJ1**	**PG**	**SAB1**	**SAB2**
BCR	-	0.045	0.032	0.038	0.040	0.056	0.035	0.062	0.224	0.041	0.149	0.037	0.106	0.031	0.021
NBC	**0.014**	-	0.015	0.018	0.030	0.043	0.029	0.048	0.217	0.043	0.162	0.043	0.091	0.015	0.009
CLU	**0.017**	**0.020**	-	0.017	0.019	0.042	0.023	0.037	0.239	0.051	0.184	0.017	0.063	0.019	0.008
FF	**0.056**	0.054	0.058	-	0.034	0.039	0.010	0.011	0.218	0.070	0.190	0.020	0.096	0.026	0.010
FrL	**0.087**	**0.097**	0.097	0.130	-	0.048	0.040	0.052	0.202	0.070	0.167	0.049	0.098	0.030	0.024
FtStJ2	**0.088**	0.094	**0.100**	0.129	0.159	-	0.050	0.063	0.166	0.066	0.123	0.046	0.103	0.033	0.038
HAZ	**0.057**	**0.063**	0.058	0.094	**0.136**	**0.135**	-	0.044	0.202	0.052	0.157	0.029	0.094	0.039	0.018
HOU	**0.065**	**0.063**	**0.072**	0.096	**0.140**	**0.140**	**0.116**	-	0.279	0.059	0.211	0.046	0.102	0.048	0.021
KEL	**0.195**	**0.204**	**0.207**	**0.235**	**0.264**	0.253	**0.226**	**0.262**	-	0.243	0.168	0.240	0.329	0.243	0.222
NWBC	**0.018**	**0.019**	**0.025**	**0.065**	**0.101**	**0.099**	**0.069**	**0.067**	**0.212**	-	0.175	0.050	0.103	0.048	0.043
VAN	**0.172**	**0.183**	**0.189**	**0.217**	**0.246**	**0.234**	**0.218**	**0.234**	0.316	**0.188**	-	0.164	0.237	0.156	0.178
FtStJ1	**0.011**	**0.014**	**0.012**	0.053	**0.092**	**0.090**	**0.057**	**0.064**	**0.200**	**0.017**	**0.177**	-	0.091	0.013	0.025
PG	**0.035**	**0.033**	**0.034**	0.080	**0.118**	**0.121**	**0.087**	**0.081**	**0.237**	**0.036**	**0.211**	**0.031**	-	0.073	0.043
SAB1	**0.014**	**0.014**	**0.017**	0.055	**0.095**	**0.094**	**0.062**	**0.066**	**0.208**	**0.022**	**0.187**	**0.009**	**0.037**	-	0.005
SAB2	**0.013**	**0.013**	**0.019**	0.056	0.092	**0.094**	0.061	**0.065**	**0.201**	**0.021**	**0.183**	**0.013**	**0.030**	0.012	-

727

728 **Table 4.** Results of maximum-likelihood population effects (MLPE) model selection after accounting for non-independence of pairwise
729 distance observations. For all models, pairwise F_{ST} (a) and D_{EST} (b) values were the response variable. Models are ranked based on
730 marginal R^2 value (high to low) with the best fitting model having the highest R^2 value. For each explanatory variable included in the
731 model, values ($x10^{-4}$) are presented as regression slopes ± 95% confidence interval. Values in bold indicate significant parameter estimates
732 (i.e. 95% confidence intervals which do not overlap zero). Explanatory variables not included in the model are indicated by '--'.

a)	Regression Slope Est. ± 95% Confidence Intervals				
Model	Distance	Elevation	Land cover	Land-elevation	Marginal R^2
4	--	--	--	**0.83 ± 0.04**	0.879
9	0.01 ± 0.01	--	--	**0.83 ± 0.04**	0.878
7	--	2.05 ± 5.42	**0.83 ± 0.04**	--	0.875
6	0.01 ± 0.01	--	**0.83 ± 0.04**	--	0.875
3	--	--	**0.89 ± 0.04**	--	0.875
8	**0.03 ± 0.02**	-7.38 ± 10.72	**0.81 ± 0.04**	--	0.874
5	**0.23 ± 0.11**	94.38 ± 45.94	--	--	0.158
1	0.05 ± 0.06	--	--	--	0.022
2	--	-12.00 ± 27.41	--	--	0.008

b)	Regression Slope Est. ± 95% Confidence Intervals				
Model	Distance	Elevation	Land cover	Land-elevation	Marginal R^2
9	**0.08 ± 0.05**	--	--	**0.59 ± 0.14**	0.711
6	**0.08 ± 0.05**	--	**0.59 ± 0.14**	--	0.710
7	--	**24.19 ± 20.31**	**0.65 ± 0.14**	--	0.709
8	**0.12 ± 0.10**	-17.46 ± 42.29	**0.56 ± 0.16**	--	0.694
4	--	--	--	**0.06 ± 0.37**	0.667
3	--	--	**0.64 ± 0.15**	--	0.660
5	**0.27 ± 0.11**	-80.24 ± 48.16	--	--	0.173
1	**0.11 ± 0.07**	--	--	--	0.129
2	--	16.96 ± 29.46	--	--	0.022

733

Titles and legends to figures

Figure 1. Sampling locations of the black-capped chickadee (*Poecile atricapillus*) in British Columbia (See Table 1 for abbreviations) with inferred clusters from GENELAND (K = 9) denoted by the patterned circles (and colours in the online version). The nine genetic clusters are 1) NWBC, 2) NBC, 3) FtStJ1, 4) PG, 5) CLU, 6) HAZ, HOU, FF, FrL and FtStJ2, 7) BCR, 8) VAN and KEL, and 9) SAB1 and SAB2.

Figure 2. Principal coordinate analysis conducted in GenAlEx based on pairwise D_{EST} values for (a) all 15 populations (coordinates 1 and 2 explained 50.59% and 17.04% of the variation respectively) and (b) after removal of populations KEL and VAN (coordinates 1 and 2 explained 31.05% and 19.93% of the variation respectively).

Figure 3. Map showing the resistance grid output from CIRCUITSCAPE analyses for the resistance surface of land cover and elevation combined (land-elevation) as this variable best explained genetic differentiation in other analyses. A close up of the central plateau region is included (bottom).

Table 1. Sampling location information including site abbreviation (Abbrev.), geographical location (latitude (Lat) and longitude (Long)) and sample size (N). Microsatellite summary statistics for each population and all loci including: observed (Ho) and expected (He) heterozygosities, number of private alleles (PA) and allelic richness (AR).

Table 2. Landscape models and corresponding resistance values assigned to each cover type or range in CIRCUITSCAPE analyses. Model hypotheses are also provided.

Table 3. Pairwise F_{ST} values (below diagonal) and harmonic mean estimates of D_{EST} (above diagonal) for 15 black-capped chickadee populations based on 14 microsatellite loci. Bold values indicate significance after corrections for multiple tests.

Table 4. Results of maximum-likelihood population effects (MLPE) model selection after accounting for non-independence of pairwise distance observations. For all models, pairwise F_{ST} (a) and D_{EST} (b) values were the response variable. Models are ranked based on marginal R^2 value (high to low) with the best fitting model having the highest R^2 value. For each explanatory variable included in the model, values ($x10^{-4}$) are presented as regression slopes ± 95% confidence interval. Values in bold indicate significant parameter estimates (i.e. 95% confidence intervals which do not overlap zero). Explanatory variables not included in the model are indicated by '--'.

Supplementary Information

Figure S1. (a) A hierarchical STRUCTURE analysis inferred six genetic groups with additional substructuring found for FtStJ1 and SAB1, as illustrated in the histograms (right). Each vertical line represents one individual and the colour(s) of each line represents the proportion of assignment of that individual to each genetic group. Inferred genetic groupings (coloured pie charts) were overlaid onto a map for better visualisation (left). Overall population assignment

was verified by (b) log likelihood plots (LnPr(X|K)) and (c) delta *K*. Runs involving only two populations could not be plotted.

Figure S2~~1~~. GENELAND output including the modal number of clusters (*K* = 9), map of population membership, and map boundaries for each of the nine clusters inferred.

Figure S3~~2~~. Maps showing the resistance grid output from CIRCUITSCAPE analyses for the resistance surfaces (a) elevation and (b) land cover.

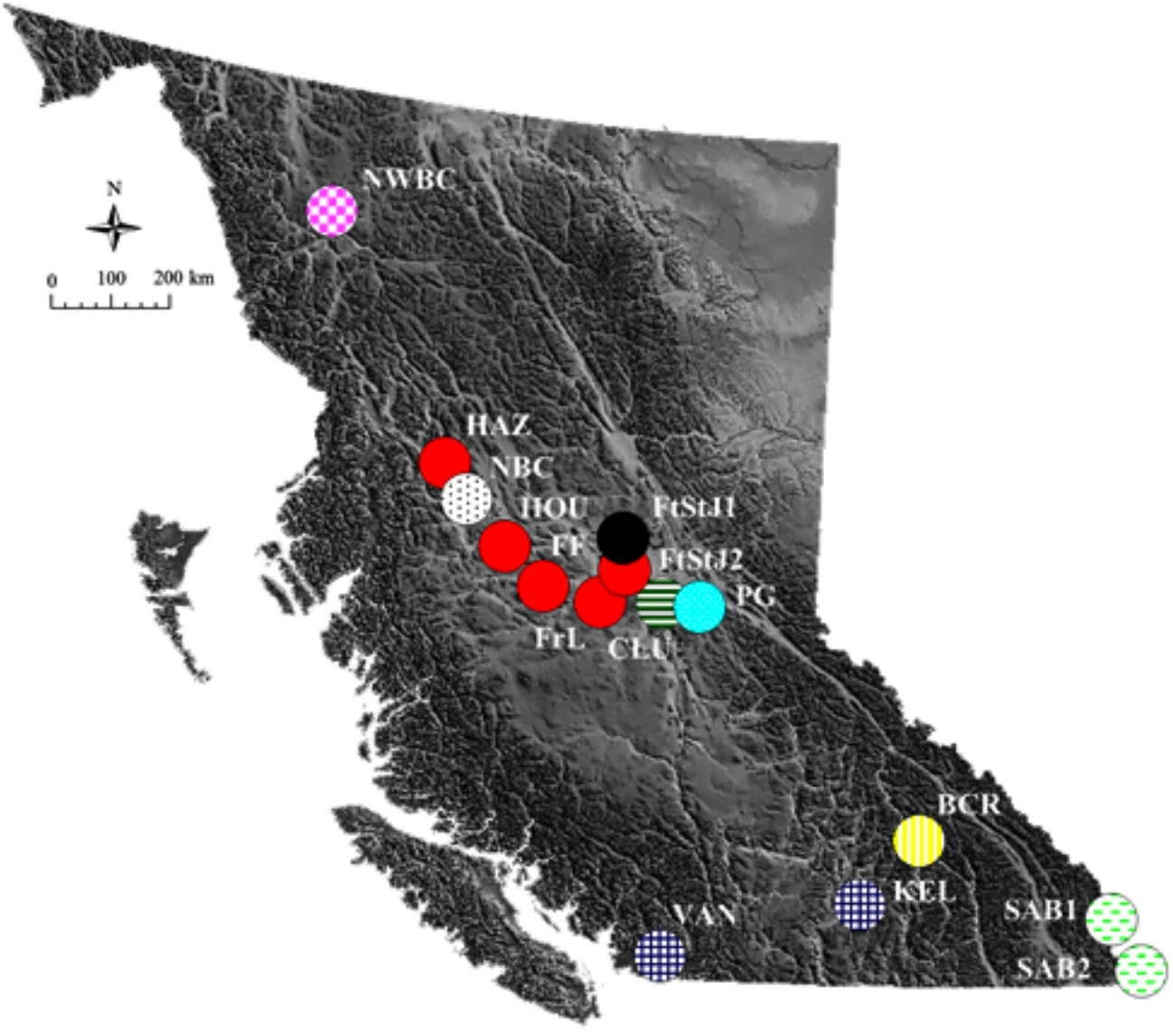
Table S1. Details of black-capped chickadee sampled. Samples in grey were removed from analyses. Sources include Burg lab (wild), and University of Northern British Columbia (UNBC).

Table S2. Repeat type (if known), primer sequence, allele size range (bp), number of alleles (*Na*) and $MgCl_2$ concentration for each microsatellite locus used to genotype black-capped chickadee individuals. * indicates new primer designed during this study.

Table S3. Expected (*He*) and observed (*Ho*) heterozygosities, total number of alleles (*Na*) for 15 populations of black-capped chickadees at 14 microsatellite loci. Summaries are provided for across loci and across populations. Bold values indicate deviations from HWE. See Table 1 for sampling site abbreviations.

Tables S4. A comparison of the summary statistics after the removal of feather sampled populations KEL and VAN and underrepresented microsatellite loci. These include a) mean observed and expected heterozygosities across populations and b) loci as well as c) pairwise FST values.

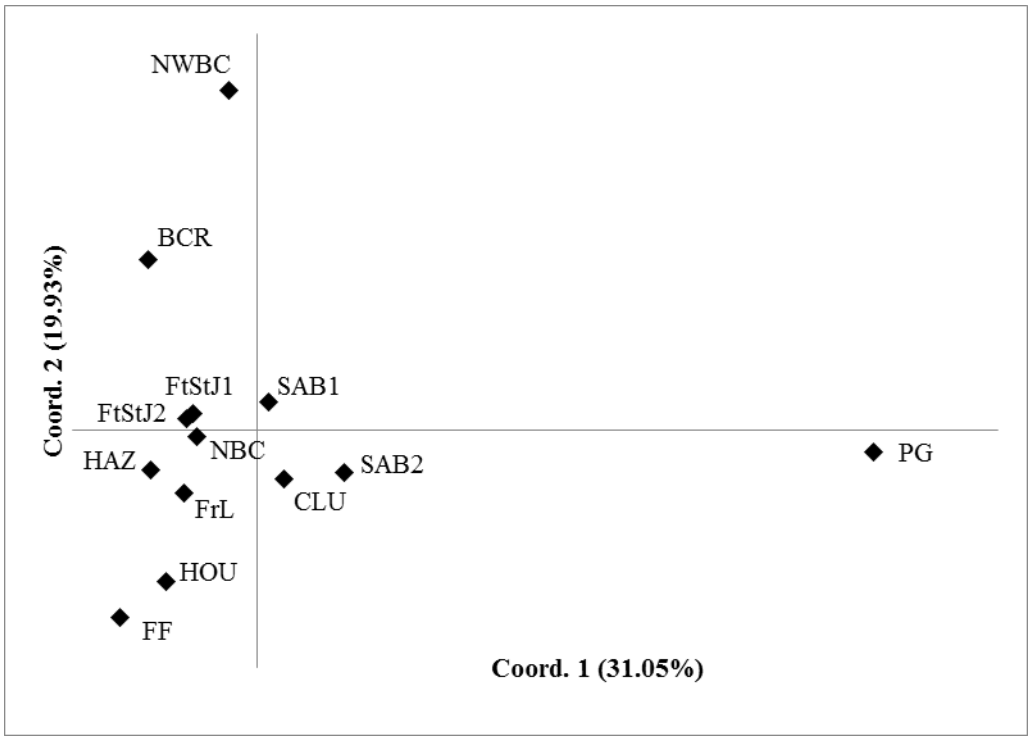
Table S54. Pairwise F'_{ST} values for 15 black-capped chickadee populations based on 14 microsatellite loci with significant values in bold ($P \leq 0.05$).

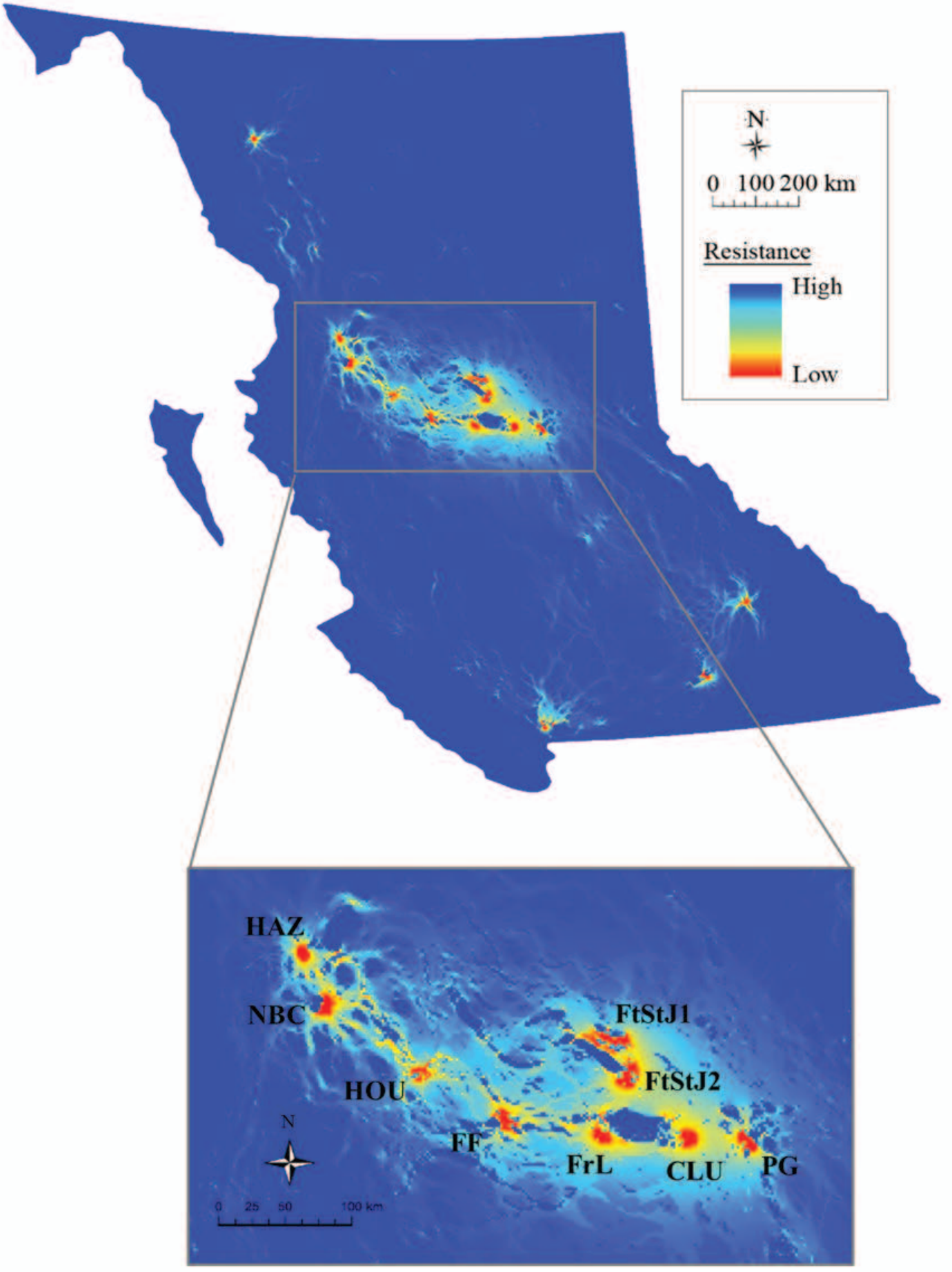

N
0 100 200 km
NWBC
HAZ
NBC
HOU
FtStJ1
FF
FtStJ2
PG
FrL
CLU
BCR
KEL
VAN
SAB1
SAB2

(a)

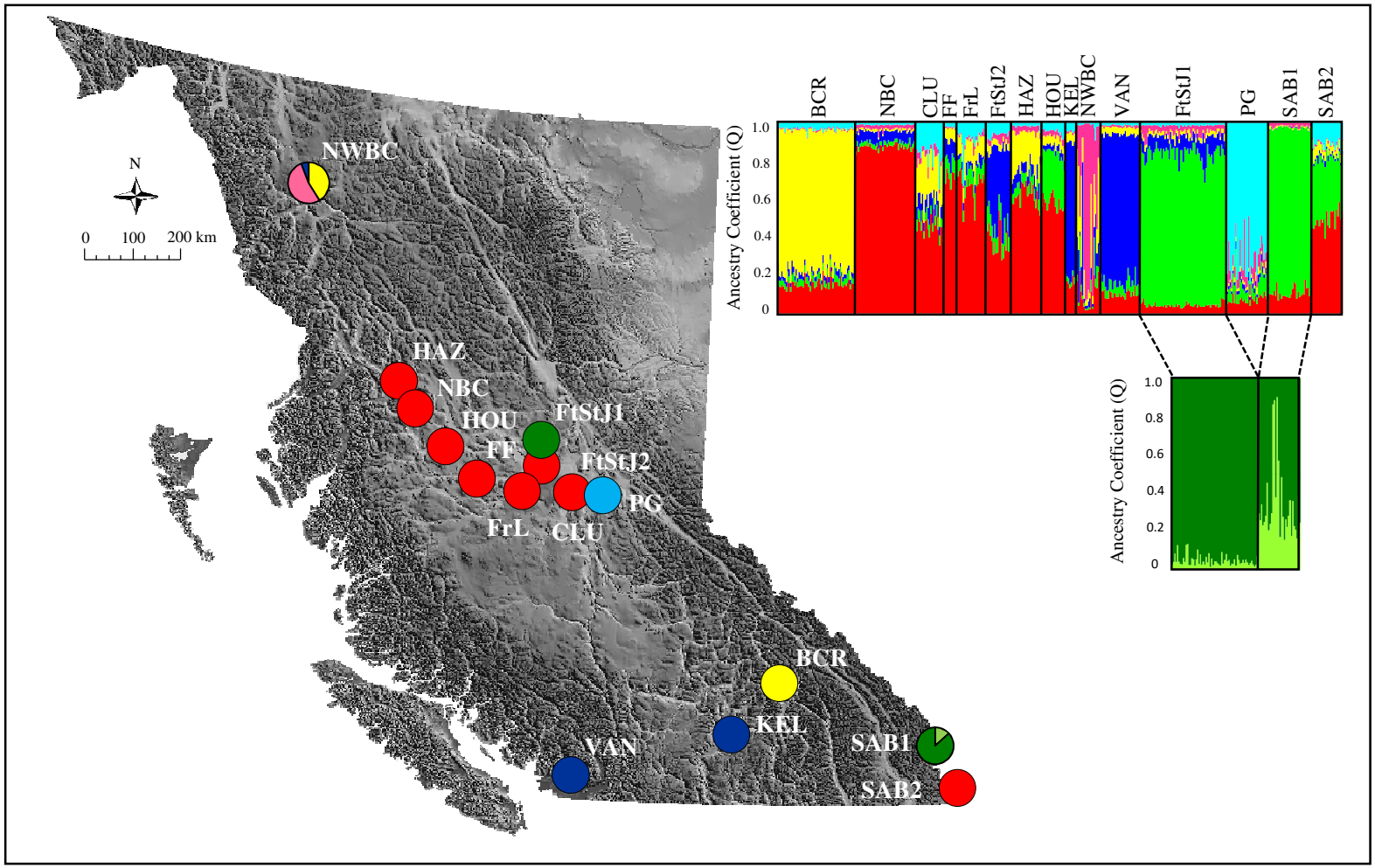
VAN
PG
SAB1
NWBC
FtStJ1
BCR
FtStJ2
SAB2
NBC
CLU
HAZ
HOU
FrL
FF
KEL
Coord. 2 (17.04%)
Coord. 1 (50.59%)

(b)

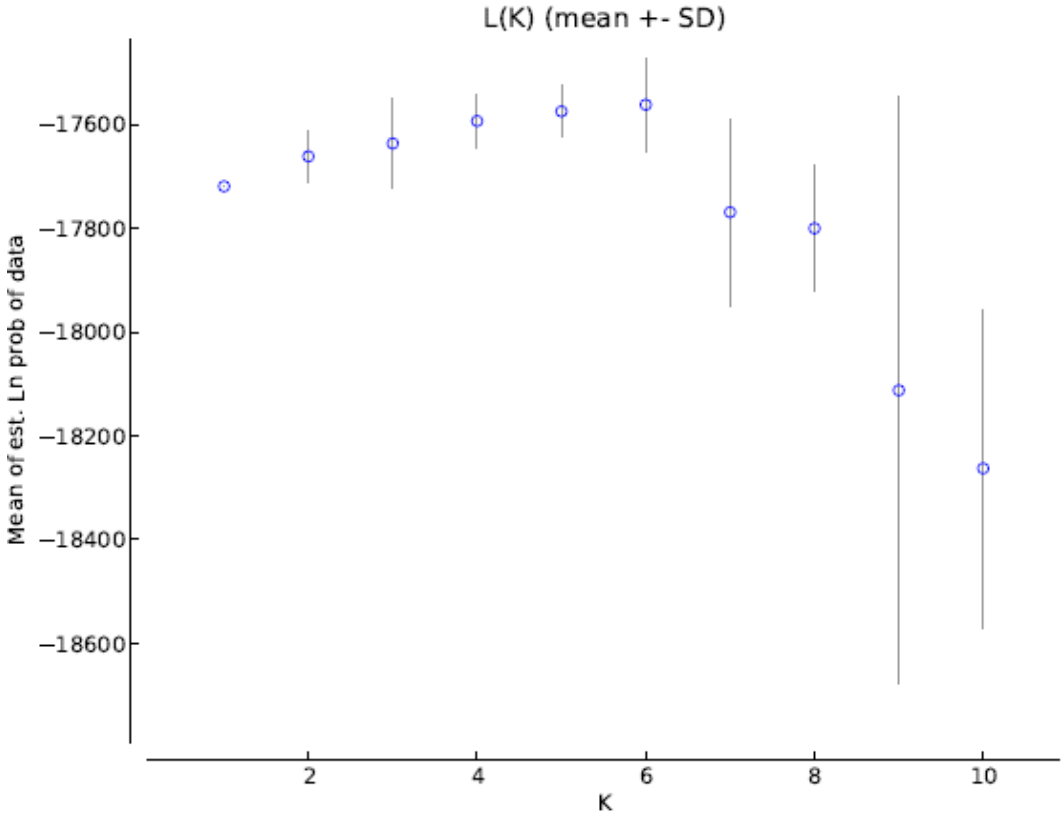

NWBC
BCR
FtStJ1
SAB1
FtStJ2
NBC
HAZ
SAB2
PG
CLU
FrL
HOU
FF
Coord. 2 (19.93%)
Coord. 1 (31.05%)


N
0 100 200 km
Resistance
High
Low
HAZ
NBC
HOU
FF
FrL
CLU
PG
FtStJ1
FtStJ2
N
0 25 50 100 km

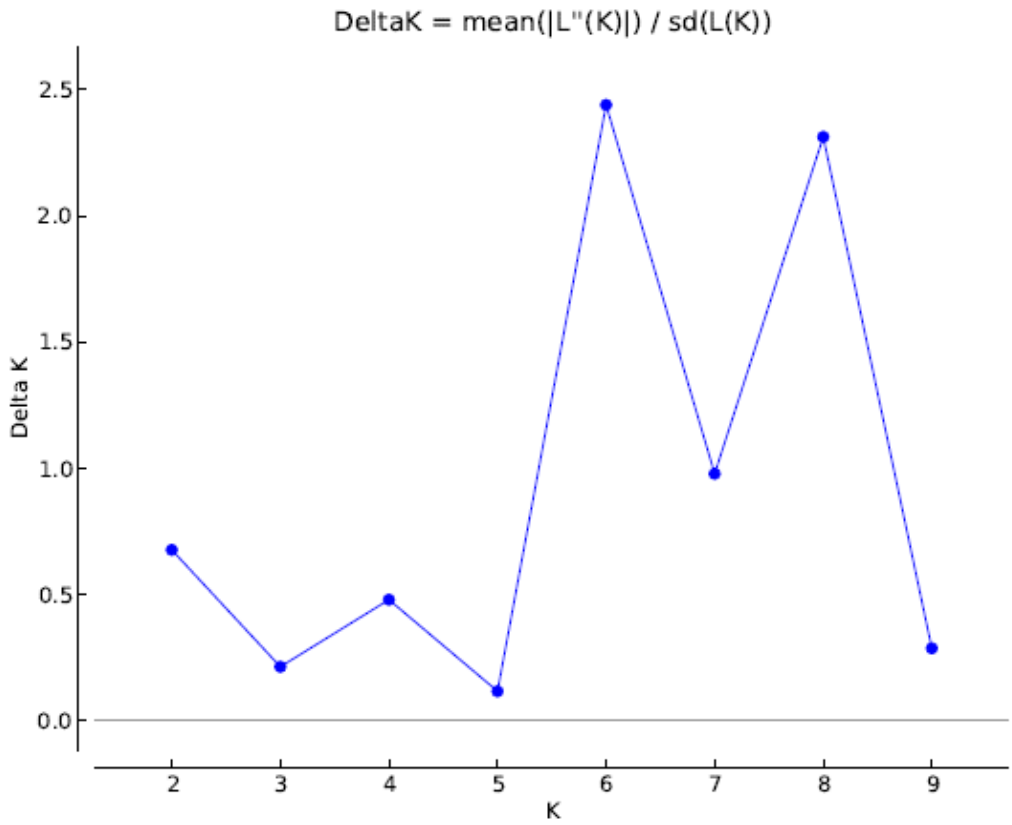
(a)

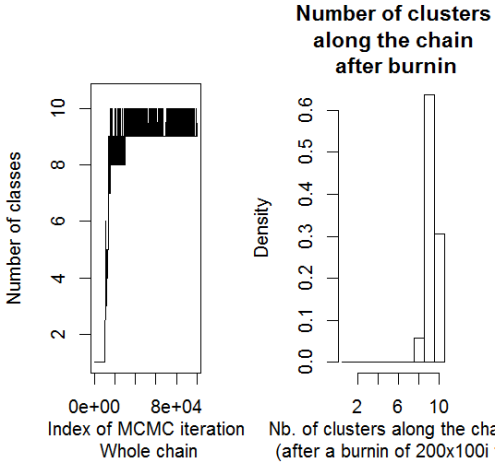

N
0 100 200 km
NWBC
HAZ
NBC
HOU
FF
FrL
FtStJ1
FtStJ2
PG
CLU
BCR
KEL
VAN
SAB1
SAB2
BCR NBC CLU FF FrL FtStJ2 HAZ HOU KEL NWBC VAN FtStJ1 PG SAB1 SAB2
Ancestry Coefficient (Q)
1.0
0.8
0.6
0.4
0.2
0
Ancestry Coefficient (Q)
1.0
0.8
0.6
0.4
0.2
0

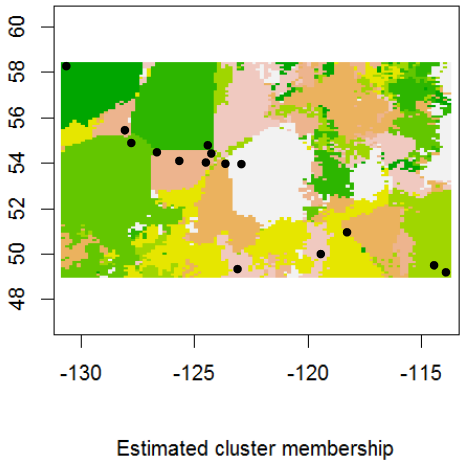
(b)


L(K) (mean +- SD)
Mean of est. Ln prob of data
−17600
−17800
−18000
−18200
−18400
−18600
2
4
6
8
10
K

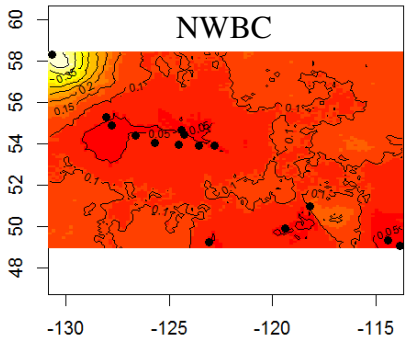
(c)

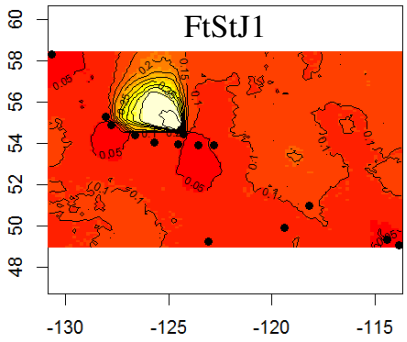

DeltaK = mean(|L''(K)|) / sd(L(K))
Delta K
2.5
2.0
1.5
1.0
0.5
0.0
2
3
4
5
6
7
8
9
K

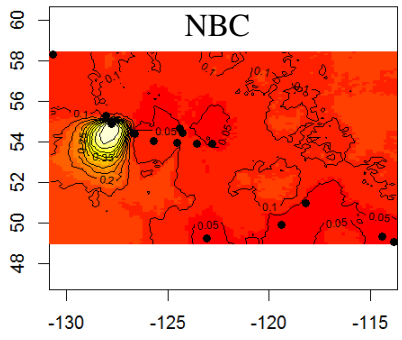


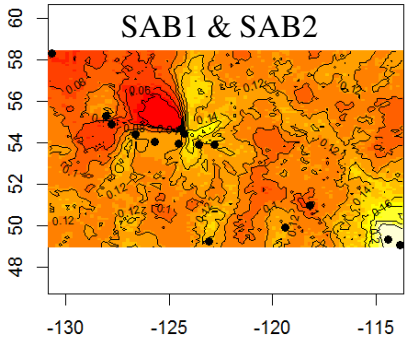


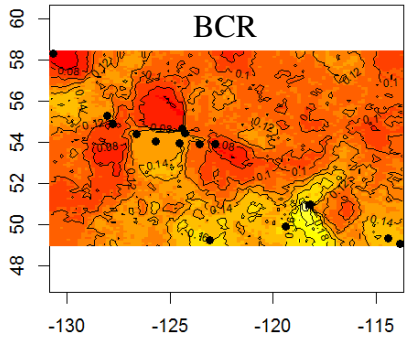
Estimated cluster membership

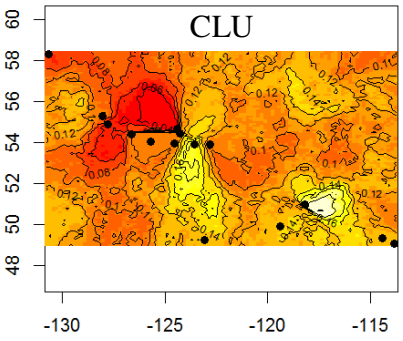


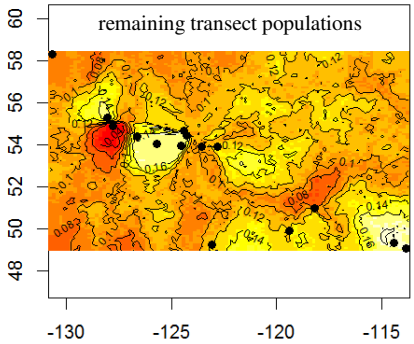


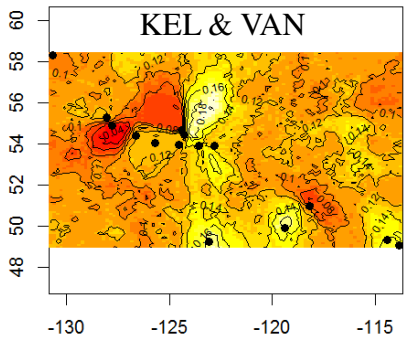


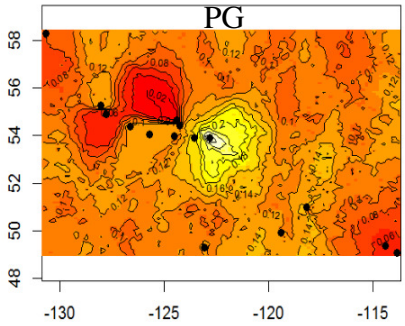


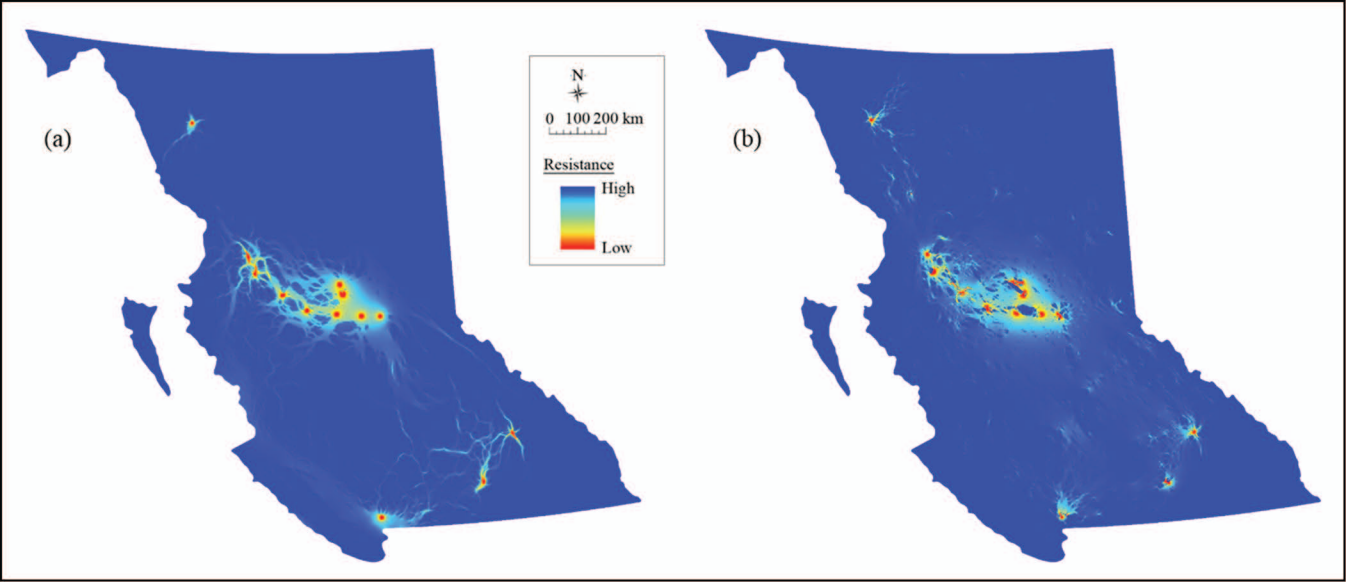











(a)
N
0 100 200 km
Resistance
High
Low
(b)

Population	ID	Location	Lat (N)	Long (W)
BCR	BCR001	Revelstoke, BC	50.981	-118.182
BCR	BCR002	Revelstoke, BC	50.981	-118.182
BCR	BCR003	Revelstoke, BC	50.983	-118.179
BCR	BCR004	Mt Revelstoke Ski Chalet, BC	51.007	-118.191
BCR	BCR005	Mt Revelstoke Ski Chalet, BC	51.007	-118.191
BCR	BCR006	Mt Revelstoke Ski Chalet, BC	51.014	-118.203
BCR	BCR007	Mt Revelstoke Ski Chalet, BC	51.014	-118.203
BCR	BCR008	Mt Revelstoke Ski Chalet, BC	51.006	-118.182
BCR	BCR009	Revelstoke field, BC	50.982	-118.180
BCR	BCR010	Revelstoke Resort, BC	50.970	-118.172
BCR	BCR011	Revelstoke Resort, BC	50.970	-118.174
BCR	BCR012	Begbie Falls Revelstoke, BC	50.944	-118.205
BCR	BCR013	Mount MacPherson Revelstoke, BC	50.942	-118.223
BCR	BCR014	9 mile Revelstoke, BC	50.897	-118.114
BCR	BCR015	Smokey Bear Revelstoke, BC	50.989	-118.278
BCR	BCR016	Frisby Rd Revelstoke, BC	51.066	-118.194
BCR	BCR017	Frisby Rd Revelstoke, BC	51.066	-118.194
BCR	BCR018	Frisby Rd Revelstoke, BC	51.052	-118.219
BCR	BCR019	Frisby Ridge Rd Revelstoke, BC	51.059	-118.206
BCR	BCR020	Frisby Ridge Rd Revelstoke, BC	51.059	-118.206
BCR	BCR021	Frisby Ridge Rd Revelstoke, BC	51.141	-118.209
BCR	BCR022	Frisby Ridge Rd Revelstoke, BC	51.059	-118.223
BCR	BCR023	Frisby Ridge Rd Revelstoke, BC	51.062	-118.224
BCR	BCR024	Frisby Ridge Rd Revelstoke, BC	51.062	-118.224
BCR	BCR025	Frisby Ridge Rd Revelstoke, BC	51.062	-118.224
BCR	BCR026	Frisby Ridge Rd Revelstoke, BC	51.065	-118.226
BCR	BCR027	Frisby Ridge Rd Revelstoke, BC	51.063	-118.232
BCR	BCR028	Frisby Ridge Rd Revelstoke, BC	51.063	-118.232
BCR	BCR029	Frisby Ridge Rd Revelstoke, BC	51.049	-118.229
BCR	BCR030	Frisby Ridge Rd Revelstoke, BC	51.049	-118.229
BCR	BCR031	Frisby Ridge Rd Revelstoke, BC	51.052	-118.226
BCR	BCR032	Frisby Ridge Rd Revelstoke, BC	51.056	-118.225
BCR	BCR033	West Bridge, Revelstoke BC	51.003	-118.218
BCR	BCR034	Machete Island 2, Revelstoke, BC	50.971	-118.202
BCR	BCR035	Westside RD 2, Revelstoke BC	51.013	-118.237
BCR	BCR036	Westside RD 2, Revelstoke BC	51.013	-118.237
BCR	BCR037	Bridge Creek, Revelstoke BC	50.994	-118.172
BCR	BCR038	Westside RD 1, Revelstoke BC	51.004	-118.228
BCR	BCR039	Williamson Lake, Revelstoke, BC	50.970	-118.175
BCR	BCR040	Williamson Lake, Revelstoke, BC	50.970	-118.175
BCR	BCR041	Williamson Lake, Revelstoke, BC	50.970	-118.175
BCR	BCR042	Williamson Lake, Revelstoke, BC	50.970	-118.175
BCR	BCR043	Revelstoke City Park, BC	50.984	-118.198
BCR	BCR044	Revelstoke City Park, BC	50.984	-118.198
BCR	BCR045	Revelstoke City Park, BC	50.984	-118.198
BCR	BCR046	Begbie Dyke, Revelstoke, BC	50.996	-118.315

BCR	BCR047	Begbie Dyke, Revelstoke, BC	50.996	-118.315
BCR	BCR048	Begbie Dyke, Revelstoke, BC	50.996	-118.315
BCR	BCR049	Begbie Dyke, Revelstoke, BC	50.996	-118.315
BCR	BCR050	Revelstoke City Park, BC	50.984	-118.198
BCR	BCR051	Westside Road, Revelstoke, BC	51.004	-118.228
BCR	BCR052	Westside Road, Revelstoke, BC	51.004	-118.228
BCR	BCR053	Westside Road, Revelstoke, BC	51.004	-118.228
BCR	BCR054	Westside Road, Revelstoke, BC	51.004	-118.228
NBC	CBC001	Smithers, BC	54.785	-127.151
NBC	CBC002	Smithers, BC	54.785	-127.151
NBC	CBC003	Smithers, BC	54.785	-127.151
NBC	CBC004	Smithers, BC	54.785	-127.151
NBC	CBC005	Smithers, BC	54.785	-127.151
NBC	CBC006	Smithers, BC	54.785	-127.151
NBC	CBC007	Smithers, BC	54.785	-127.151
NBC	CBC008	Smithers, BC	54.785	-127.151
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NBC	CBC010	Smithers, BC	54.785	-127.151
NBC	CBC011	Smithers, BC	54.785	-127.151
NBC	CBC012	Smithers, BC	54.785	-127.151
NBC	CBC013	Smithers, BC	54.785	-127.151
NBC	CBC014	Smithers, BC	54.785	-127.151
NBC	CBC015	Smithers, BC	54.785	-127.151
NBC	CBC016	Smithers, BC	54.785	-127.151
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NBC	CBC019	Smithers, BC	54.785	-127.151
NBC	CBC020	Smithers, BC	54.785	-127.151
NBC	CBC021	Smithers, BC	54.785	-127.151
NBC	CBC022	Smithers, BC	54.785	-127.151
NBC	CBC023	Smithers, BC	54.785	-127.151
NBC	CBC024	Smithers, BC	54.785	-127.151
NBC	CBC025	3928 Mountainview Ave, Thornhill BC	54.506	-128.543
NBC	CBC026	Ferry Island, BC	54.512	-128.574
NBC	CBC027	Stockner's Residence; Kispiox BC	55.468	-127.735
NBC	CBC028	Stockner's Residence; Kispiox BC	55.468	-127.735
NBC	CBC029	Tyee Lake, Telkwa BC	54.707	-127.040
NBC	CBC030	Tyee Lake, Telkwa BC	54.707	-127.040
NBC	CBC031	Tyee Lake, Telkwa BC	54.707	-127.040
NBC	CBC032	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC033	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC034	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC035	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC036	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC037	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC038	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC039	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036

NBC	CBC040	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC041	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC042	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
NBC	CBC043	4567 Tyee Lake Rd., Telkwa BC	54.725	-127.036
CLU	CBC-CLU131	Cluculz Lake- Brookside camp, BC	53.913	-123.593
CLU	CBC-CLU132	Cluculz Lake- Brookside camp, BC	53.913	-123.593
CLU	CBC-CLU133	Cluculz Lake - West Meier Road, BC	53.875	-123.638
CLU	CBC-CLU134	Cluculz Lake - West Meier Road, BC	53.875	-123.638
CLU	CBC-CLU135	Cluculz Lake - West Meier Road, BC	53.875	-123.638
CLU	CBC-CLU136	Cluculz Lake - West Meier Road, BC	53.875	-123.638
CLU	CBC-CLU137	Finmore Rd - Cluculz Lake, BC	53.940	-123.580
CLU	CBC-CLU138	Finmore Rd - Cluculz Lake, BC	53.950	-123.573
CLU	CBC-CLU139	Cobb Lake, Cluculz, BC	53.962	-123.557
CLU	CBC-CLU140	Cobb Lake Road, Cluculz, BC	53.962	-123.557
CLU	CBC-CLU141	Cobb Lake Road, Cluculz, BC	53.962	-123.557
CLU	CBC-CLU142	Cobb Lake Road, Cluculz, BC	53.962	-123.566
CLU	CBC-CLU143	Finmore Rd - Cluculz Lake, BC	53.935	-123.576
CLU	CBC-CLU144	Beverly Lake Forest Road, Cluculz, BC	53.923	-123.575
CLU	CBC-CLU145	Tapping Road, Cluculz, BC	53.885	-123.573
CLU	CBC-CLU146	Tapping Road, Cluculz, BC	53.885	-123.573
CLU	CBC-CLU147	Tapping Road, Cluculz, BC	53.890	-123.521
CLU	CBC-CLU148	Lloyd Road, Cluculz, BC	53.868	-123.494
CLU	CBC-CLU149	Lloyd Road, Cluculz, BC	53.875	-123.502
CLU	CBC-CLU150	Lloyd Road, Cluculz, BC	53.875	-123.502
FF	CBC-FF120	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF121	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF122	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF123	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF124	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF125	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF126	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF127	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF128	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF129	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FF	CBC-FF130	Lily Lake Road - Fort Fraser, BC	53.963	-124.533
FrL	CBC-FrL062	17224 Colleymount Rd, Francois Lake, BC	54.040	-125.991
FrL	CBC-FrL063	17224 Colleymount Rd, Francois Lake, BC	54.040	-125.991
FrL	CBC-FrL064	Colleymount Road, Francois Lake, BC	54.040	-125.987
FrL	CBC-FrL065	Colleymount Road, Francois Lake, BC	54.040	-125.987
FrL	CBC-FrL066	Colleymount Road, Francois Lake, BC	54.040	-125.987
FrL	CBC-FrL067	Colleymount Road, Francois Lake, BC	54.040	-125.987
FrL	CBC-FrL068	Colleymount Road, Francois Lake, BC	54.040	-125.987
FrL	CBC-FrL069	30867 Collymount Road, Francois Lake, BC	54.019	-125.184
FrL	CBC-FrL070	30867 Collymount Road, Francois Lake, BC	54.019	-125.184
FrL	CBC-FrL071	30867 Collymount Road, Francois Lake, BC	54.019	-125.184
FrL	CBC-FrL072	30867 Collymount Road, Francois Lake, BC	54.019	-125.184
FrL	CBC-FrL073	Collymount Road, Francois Lake, BC	54.005	-126.265

FrL	CBC-FrL074	Collymount Road, Francois Lake, BC	54.005	-126.265
FrL	CBC-FrL075	Collymount Road, Francois Lake, BC	54.005	-126.265
FrL	CBC-FrL076	Collymount Road, Francois Lake, BC	54.005	-126.265
FrL	CBC-FrL077	Collymount Road, Francois Lake, BC	54.005	-126.265
FrL	CBC-FrL078	Collymount Road, Francois Lake, BC	54.005	-126.265
FrL	CBC-FrL079	Collymount Road, Francois Lake, BC	54.005	-126.265
FrL	CBC-FrL080	Collymount Road, Francois Lake, BC	54.005	-126.265
FrL	CBC-FrL081	Collymount Road, Francois Lake, BC	54.005	-126.265
FtStJ2	CBC-FSJ 044	Necoslie Road, Fort St James, BC	54.416	-124.220
FtStJ2	CBC-FSJ 045	Necoslie Road, Fort St James, BC	54.416	-124.220
FtStJ2	CBC-FSJ 046	Necoslie Road, Fort St James, BC	54.416	-124.220
FtStJ2	CBC-FSJ 047	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 048	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 049	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 050	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 051	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 052	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 053	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 054	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 055	4494 Sowchea Road, Fort St James, BC	54.427	-124.314
FtStJ2	CBC-FSJ 056	Hanley, Fort St James, BC	54.402	-124.287
FtStJ2	CBC-FSJ 057	4712 Sowchea Road, Fort St James, BC	54.426	-124.317
FtStJ2	CBC-FSJ 058	4712 Sowchea Road, Fort St James, BC	54.426	-124.317
FtStJ2	CBC-FSJ 059	4712 Sowchea Road, Fort St James, BC	54.426	-124.317
FtStJ2	CBC-FSJ 060	4712 Sowchea Road, Fort St James, BC	54.426	-124.317
FtStJ2	CBC-FSJ 061	4712 Sowchea Road, Fort St James, BC	54.426	-124.317
HAZ	CBC-HAZ082	Kispiox Salmon River Rd, BC	55.281	-127.669
HAZ	CBC-HAZ083	Kispiox Salmon River Rd, BC	55.281	-127.669
HAZ	CBC-HAZ084	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ085	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ086	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ087	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ088	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ089	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ090	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ091	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ092	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ093	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ094	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ095	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ096	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ097	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ098	New Hazelton College St., BC	55.251	-128.453
HAZ	CBC-HAZ099	Swannell Dr, New Hazelton, BC	55.264	-127.652
HAZ	CBC-HAZ100	Swannell Dr, New Hazelton, BC	55.264	-127.652
HAZ	CBC-HAZ101	Swannell Dr, New Hazelton, BC	55.264	-127.652
HOU	CBC-HOU102	Houston - Shady Campground, BC	54.416	-126.633

HOU	CBC-HOU103	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU104	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU105	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU106	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU107	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU108	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU109	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU110	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU111	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU112	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU113	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU114	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU115	Houston - Duck Pond, BC	54.391	-126.656
HOU	CBC-HOU116	Houston - Duck Pond, BC	54.391	-126.656
HOU	CBC-HOU117	Houston - Duck Pond, BC	54.391	-126.656
HOU	CBC-HOU118	Houston - Shady Campground, BC	54.416	-126.633
HOU	CBC-HOU119	Houston - Shady Campground, BC	54.416	-126.633
KEL	KEL001	Mission Creek, Kelowna, BC	49.867	-119.439
KEL	KEL002	Mission Creek, Kelowna, BC	49.867	-119.439
KEL	KEL003	Mission Creek, Kelowna, BC	49.867	-119.439
KEL	KEL004	Mill Creek, Kelowna, BC	49.972	-119.364
KEL	KEL005	Mill Creek, Kelowna, BC	49.972	-119.364
KEL	KEL006	Mill Creek, Kelowna, BC	49.972	-119.364
KEL	KEL007	Mill Creek, Kelowna, BC	49.972	-119.364
KEL	KEL008	Mission Creek, Kelowna BC	49.876	-119.430
NWBC	NWBC001	Telegraph Creek, BC	58.401	-131.212
NWBC	NWBC002	Telegraph Creek, BC	58.401	-131.212
NWBC	NWBC003	Telegraph Creek, BC	57.909	-131.224
NWBC	NWBC004	Telegraph Creek, BC	57.909	-131.224
NWBC	NWBC005	Dease Lake, BC	58.507	-130.023
NWBC	NWBC006	Dease Lake, BC	58.430	-129.987
NWBC	NWBC007	Dease Lake, BC	58.430	-129.987
NWBC	NWBC008	Dease Lake, BC	58.430	-129.987
NWBC	NWBC009	Dease Lake, BC	58.430	-129.987
NWBC	NWBC010	Dease Lake, BC	58.430	-129.987
NWBC	NWBC011	Dease Lake, BC	58.430	-129.987
NWBC	NWBC012	Dease Lake, BC	58.430	-129.987
NWBC	NWBC013	Telegraph Creek, BC	57.913	-131.210
NWBC	NWBC014	Telegraph Creek, BC	57.913	-131.210
NWBC	NWBC015	Telegraph Creek, BC	57.913	-131.210
NWBC	NWBC016	Telegraph Creek, BC	57.913	-131.210
NWBC	NWBC017	Telegraph Creek, BC	57.913	-131.210
VAN	VAN001	Jericho Park, Vancouver	49.269568	-123.195325
VAN	VAN002	Jericho Park, Vancouver	49.271095	-123.19865
VAN	VAN003	Stanley park, Vancouver, BC	49.294	-123.143
VAN	VAN004	Stanley park, Vancouver, BC	49.294	-123.143
VAN	VAN005	Stanley park, Vancouver	49.293847	-123.142856

VAN	VAN006	Memorial South, Vancouver	49.229783	-123.086267
VAN	VAN007	Memorial South, Vancouver, BC	49.230	-123.086
VAN	VAN008	Memorial South, Vancouver	49.229783	-123.086267
VAN	VAN009	Pacific Spirit, Vancouver, BC	49.270	-123.237
VAN	VAN010	Pacific Spirit, Vancouver, BC	49.270	-123.237
VAN	VAN011	Pacific Spirit, Vancouver, BC	49.270	-123.237
VAN	VAN012	Pacific Spirit, Vancouver, BC	49.270	-123.237
VAN	VAN013	Queen Elizabeth, Vancouver, BC	49.241	-123.116
VAN	VAN014	Queen Elizabeth, Vancouver, BC	49.241	-123.116
VAN	VAN015	Queen Elizabeth, Vancouver, BC	49.243	-123.113
VAN	VAN016	Queen Elizabeth, Vancouver, BC	49.243	-123.113
VAN	VAN017	Burnaby Lake, Vancouver, BC	49.240	-122.952
VAN	VAN018	Burnaby Lake, Vancouver, BC	49.240	-122.952
VAN	VAN019	Burnaby Lake, Vancouver, BC	49.240	-122.952
VAN	VAN020	Burnaby Lake, Vancouver, BC	49.244	-122.937
VAN	VAN021	Burnaby Lake, Vancouver, BC	49.244	-122.937
VAN	VAN022	Burnaby Lake, Vancouver, BC	49.245	-122.939
VAN	VAN023	Burnaby Lake, Vancouver, BC	49.245	-122.939
VAN	VAN024	Trout Lake, Vancouver, BC	49.256	-123.061
VAN	VAN025	Trout Lake, Vancouver, BC	49.256	-123.061
VAN	VAN026	Centre, Vancouver, BC	49.226	-123.021
VAN	VAN027	Centre, Vancouver, BC	49.226	-123.021
VAN	VAN028	Centre, Vancouver, BC	49.226	-123.021
VAN	VAN029	Centre, Vancouver, BC	49.226	-123.021
VAN	VAN030	Centre, Vancouver, BC	49.227	-123.014
VAN	VAN031	Centre, Vancouver, BC	49.227	-123.014
VAN	VAN032	Centre, Vancouver, BC	49.226	-123.016
VAN	VAN033	Centre, Vancouver, BC	49.226	-123.016
FtStJ1	BC-MI-037	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-038	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-039	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-040	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-041	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-042	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-043	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-044	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-045	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-046	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-047	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-048	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-049	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-050	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-051	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-052	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-053	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-054	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-055	John Prince Research Station, Ft St James BC	54.645	-124.395

FtStJ1	BC-MI-056	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-057	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-058	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-059	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-060	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-061	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-062	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-063	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-064	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-065	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-066	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-067	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-068	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-069	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-070	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-071	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-155	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-156	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-157	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-158	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-159	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-160	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-161	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-162	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-163	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-164	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-165	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-166	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-167	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-168	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-169	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-170	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-171	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-172	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-173	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-174	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-175	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-177	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-178	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-179	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-180	John Prince Research Station, Ft St James BC	54.645	-124.395
FtStJ1	BC-MI-184	John Prince Research Station, Ft St James BC	54.645	-124.395
PG	BC-PU-01	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-02	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-03	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-04	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-05	UNBC, Prince George BC	53.894	-122.829

PG	BC-PU-06	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-07	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-08	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-09	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-10	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-11	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-12	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-13	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-14	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-15	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-16	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-17	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-18	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-19	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-20	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-21	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-22	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-23	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-24	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-25	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-26	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-27	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-28	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-29	UNBC, Prince George BC	53.894	-122.829
PG	BC-PU-30	UNBC, Prince George BC	53.894	-122.829
SAB1	SAB001	West Castle, AB	49.345	-114.415
SAB1	SAB002	West Castle, AB	49.345	-114.415
SAB1	SAB003	West Castle, AB	49.345	-114.415
SAB1	SAB004	West Castle, AB	49.345	-114.415
SAB1	SAB005	West Castle, AB	49.345	-114.415
SAB1	SAB006	West Castle, AB	49.345	-114.415
SAB1	SAB007	West Castle, AB	49.345	-114.415
SAB1	SAB008	West Castle, AB	49.345	-114.415
SAB1	SAB009	West Castle, AB	49.345	-114.415
SAB1	SAB010	West Castle, AB	49.345	-114.415
SAB1	SAB011	West Castle, AB	49.345	-114.415
SAB1	SAB012	West Castle, AB	49.345	-114.415
SAB1	SAB013	West Castle, AB	49.345	-114.415
SAB1	SAB014	West Castle, AB	49.345	-114.415
SAB1	SAB015	West Castle, AB	49.345	-114.415
SAB1	SAB016	West Castle, AB	49.345	-114.415
SAB1	SAB017	West Castle, AB	49.345	-114.415
SAB1	SAB018	Syncline Ski Area, AB	49.391	-114.340
SAB1	SAB019	Syncline Ski Area, AB	49.391	-114.340
SAB1	SAB020	Syncline Ski Area, AB	49.391	-114.340
SAB1	SAB021	Syncline Ski Area, AB	49.391	-114.340
SAB1	SAB022	Syncline Ski Area, AB	49.391	-114.340

SAB1	SAB023	Syncline Ski Area, AB	49.391	-114.340
SAB1	SAB024	Field station cabin, AB	49.349	-114.411
SAB1	SAB025	North Lost Creek Rd, TWP 60-1, AB	49.472	-114.463
SAB1	SAB026	North Lost Creek Rd, TWP 60-1, AB	49.472	-114.463
SAB1	SAB027	North Lost Creek Rd, TWP 60-1, AB	49.472	-114.463
SAB1	SAB028	North Lost Creek Rd, TWP 60-1, AB	49.472	-114.463
SAB1	SAB029	North Lost Creek Rd, AB	49.472	-114.463
SAB1	SAB030	North Lost Creek Rd, AB	49.472	-114.463
SAB2	SAB031	Hwy 6, Waterton, S AB	49.106	-113.821
SAB2	SAB032	Hwy 6, Waterton, S AB	49.106	-113.821
SAB2	SAB033	Hwy 6, Waterton, S AB	49.106	-113.821
SAB2	SAB034	Hwy 6, Waterton, S AB	49.106	-113.821
SAB2	SAB035	Crandall Lake Campground, Waterton, S AB	49.097	-113.955
SAB2	SAB036	Crandall Lake Campground, Waterton, S AB	49.097	-113.955
SAB2	SAB037	Hwy 6, Waterton, S AB	49.084	-113.802
SAB2	SAB038	Hwy 6, Waterton, S AB	49.084	-113.802
SAB2	SAB039	Hwy 6, Waterton, S AB	49.084	-113.802
SAB2	SAB040	Hwy 6, Waterton, S AB	49.076	-113.791
SAB2	SAB041	Hwy 6, Waterton, S AB	49.076	-113.791
SAB2	SAB042	Belly River Campground, Waterton, S AB	49.022	-113.687
SAB2	SAB043	Belly River Campground, Waterton, S AB	49.022	-113.687
SAB2	SAB044	Marquis Hole Picnic Area, Waterton, S AB	49.069	-113.856
SAB2	SAB045	Marquis Hole Picnic Area, Waterton, S AB	49.069	-113.856
SAB2	SAB046	Marquis Hole Picnic Area, Waterton, S AB	49.069	-113.856
SAB2	SAB047	Marquis Hole Picnic Area, Waterton, S AB	49.069	-113.856
SAB2	SAB048	Marquis Hole Picnic Area, Waterton, S AB	49.069	-113.856
SAB2	SAB049	Marquis Hole Picnic Area, Waterton, S AB	49.069	-113.856
SAB2	SAB050	Marquis Hole Picnic Area, Waterton, S AB	49.069	-113.856
SAB2	SAB051	Marquis Hole, Waterton, S AB	49.069	-113.856
SAB2	SAB052	Belly River Campground Waterton, AB	49.023	-113.687

Source	Band/ Museum ID
Wild	2490-57684
Wild	2490-57685
Wild	bcch 3
Wild	2490-57686
Wild	2490-57687
Wild	2490-57688
Wild	2490-57689
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Wild	2490-57691
Wild	2490-57692
Wild	2490-57693
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Wild	2500-94928
Wild	2500-94930
Wild	2500-94931
Wild	2500-94932
Wild	2500-94933
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Wild	2490-57734
Wild	2490-57737
Wild	A

Locus	Repeat type	Sequence (5' to 3')	Size range (bp)	*Na*	$MgCl_2$ (mM)
PAT MP 2-14F	-	GAACAGATAAAGCCAAATTAC	125-167	19	2
PAT MP 2-14R		TAGTGAATGCTTGATTTCTTTG			
PAT MP 2-43F	-	ACAGGTAGTCAGAAATGGAAAG	141-211	28	1.5
PAT MP 2-43R		GTATCCAGAGTCTTTGCTGATG			
Escu6F	-	CATAGTGATGCCCTGCTAGG	120-248	26	1.5
Escu6R		GCAAGTGCTCCTTAATATTTGG			
Titgata02F	$(GATA)_{12}$	ATTGCTTGATATTTGAAAGCATA	116-276	17	2
Titgata02R		TTGTCTTTTGGGTTGCCTGA			
Titgata39F	$(GATA)_{10}$	CATGTATTTTCCAAAAGTAAATAT	222-258	11	2
Titgata39R		CTGCTATTCTGCAAACTTGTGG			
CcaTgu11F	-	TGCTTAGGAAATAGGAAGCACA	212-218	4	2
CcaTgu11R		CTGCAACTTAAGCARRGTTATGA			
PmanTAGAn71F	$(TAGG)_6(TAGA)_{11}$	TCAGCCTCCAAGGAAAACAG	157-193	10	2.5
PmanTAGAn71R		GCATAAGCAACACCATGCAG			
PmanTAGAn45F	$(TGA)_{10}$	CCCCTGGCTCTTTCATATCC	320-407	26	2
PmanTAGAn45R		GACAGGTGTTGGCACAAGG			
Ase18F	$(GT)_{12}$	ATCCAGTCTTCGCAAAAGCC	188-220	8	2.5
Ase18R		TGCCCCAGAGGGAAGAAG			
Cuμ28F	$(CA)_{12}$	GAGGCACAGAAATGTGAATT	182-186	3	2.5
Cuμ28R		TAAGTAGAAGGACTTGATGGCT			
Ppi2F	-	CACAGACCATTCGAAGCAGA	324-488	46	2.5
Ppi2R		GCTCCGATGGTGAATGAAGT			
VeCr05F	$(AC)_8$	ACACACTTATGTGCATGGGCT	288-340	4	2.5
VeCr05R		ATATTTCAGGTATGGGTTTGGTTC			
CtC101-F	$(CATC)_8$	GTCCAGTAGGTAGGTGTGATG	232-284	12	2.5
CtC101-R		TTATTTAGGTGCCAGAGAGATG			
Pij02F	$(GT)_{23}$	CACACCTACCTCATGGATCT	168-258	35	2.5
Pij02Rnew*		CTGCATCAACTCATGTCCTG			

Reference
Otter *et al.,* 1998
Otter *et al.,* 1998
Hanotte *et al.,* 1994
Wang *et al.,* 2005
Wang *et al.,* 2005
Olano Marin *et al.,* 2010
Saladin *et al.,* 2003
Saladin *et al.,* 2003
Richardson *et al.,* 2000
Gibbs *et al.,* 1999
Martinez *et al.,* 1999
Tarvin, 2006
Stenzler *et al.,* 2004
Saito *et al.,* 2005

		PAT MP-14	Titgata39	Escu6	Titgata02	PAT MP-43	Ase18	PmanTAGAn 71	Cuμ28
	Na	12	9	16	14	14	6	8	3
BCR	***Ho***	0.600	0.593	0.852	0.774	0.769	0.370	0.759	0.566
	He	0.647	0.691	0.911	0.854	0.856	0.338	0.782	0.496
	Na	11	7	19	14	17	6	8	3
NBC	***Ho***	0.711	0.744	0.833	0.814	0.907	0.256	0.674	0.372
	He	0.658	0.742	0.916	0.852	0.906	0.234	0.751	0.543
	Na	7	7	16	11	13	3	6	3
CLU	***Ho***	0.750	0.800	1.000	0.800	0.950	0.250	0.700	0.421
	He	0.685	0.765	0.901	0.865	0.864	0.226	0.715	0.445
	Na	5	6	10	10	9	2	5	3
FF	***Ho***	0.556	0.400	0.900	1.000	1.000	0.167	0.900	0.700
	He	0.673	0.690	0.875	0.883	0.846	0.153	0.700	0.565
	Na	3	6	15	10	12	4	8	3
FrL	***Ho***	0.500	0.800	**0.650**	0.900	0.950	0.450	0.800	0.400
	He	0.524	0.663	**0.891**	0.859	0.884	0.448	0.778	0.521
	Na	3	7	12	11	14	3	8	3
FtStJ 2	***Ho***	0.176	0.706	0.706	1.000	0.889	0.333	0.765	0.778
	He	0.403	0.775	0.874	0.893	0.889	0.290	0.765	0.554
	Na	5	9	13	11	13	2	8	3
HAZ	***Ho***	0.500	0.950	0.750	0.950	1.000	0.050	0.650	0.400
	He	0.540	0.821	0.886	0.801	0.878	0.049	0.760	0.521
	Na	8	6	15	10	14	3	7	2
HOU	***Ho***	0.714	0.800	0.722	0.933	0.833	0.313	0.857	0.353
	He	0.804	0.691	0.907	0.873	0.887	0.275	0.827	0.457
	Na	3	4	8	-	6	2	4	2
KEL	***Ho***	0.571	0.667	0.857	-	0.857	0.167	0.750	0.200
	He	0.439	0.722	0.847	-	0.776	0.153	0.750	0.420
	Na	7	9	12	8	8	4	5	2
NWBC	***Ho***	0.824	0.824	0.824	0.882	0.706	0.294	0.765	0.353
	He	0.720	0.754	0.891	0.773	0.775	0.346	0.721	0.484
	Na	5	3	13	-	8	4	6	3
VAN	***Ho***	0.520	0.333	0.850	-	0.826	0.500	0.882	0.667
	He	0.460	0.573	0.889	-	0.792	0.400	0.787	0.571
	Na	16	8	18	14	17	6	8	3
FtStJ 1	***Ho***	0.760	0.833	0.891	0.900	**0.733**	0.262	0.847	0.383
	He	0.741	0.759	0.912	0.875	**0.880**	0.266	0.781	0.458
	Na	11	7	17	11	14	5	6	3
PG	***Ho***	0.364	**0.607**	**0.583**	**0.478**	**0.481**	0.357	0.750	0.690
	He	0.748	**0.795**	**0.898**	**0.849**	**0.860**	0.528	0.633	0.499
	Na	10	6	20	11	13	2	7	3
SAB1	***Ho***	0.655	0.833	0.833	0.893	0.900	0.200	0.759	0.533
	He	0.640	0.686	0.902	0.839	0.882	0.180	0.727	0.455
	Na	7	8	16	10	13	3	8	3
SAB2	***Ho***	0.611	0.909	0.909	0.857	0.818	0.227	0.773	0.455

	He	0.702	0.791	0.912	0.815	0.863	0.241	0.778	0.538
Average for each locus	*Na*	8	7	15	10	12	4	7	3
	Ho	0.587	0.720	0.811	0.745	0.841	0.280	0.775	0.485
	He	0.626	0.728	0.894	0.735	0.856	0.275	0.750	0.502

Ppi2	**PmanTAGAn45**	**CcaTgu11**	**VeCr05**	**CtC-101**	**Pij02**	Pop. mean across all loci
24	20	3	3	9	17	11
0.745	0.900	0.389	0.184	0.887	0.744	0.652
0.932	0.900	0.494	0.329	0.804	0.876	0.708
23	16	3	2	8	19	11
0.757	0.762	0.286	0.200	0.907	0.829	0.647
0.839	0.843	0.431	0.224	0.844	0.882	0.690
16	16	3	2	9	16	9
0.750	**0.579**	0.250	0.350	0.850	0.700	0.654
0.807	**0.896**	0.501	0.439	0.838	0.900	0.703
8	-	2	2	8	13	6
0.333	-	0.300	0.111	1.000	1.000	0.644
0.861	-	0.455	0.278	0.850	0.914	0.672
-	-	2	3	6	14	7
-	-	0.200	0.278	0.750	0.786	0.622
-	-	0.495	0.285	0.801	0.870	0.668
-	-	3	2	9	15	8
-	-	0.500	0.000	0.833	0.786	0.623
-	-	0.551	0.245	0.843	0.918	0.667
12	-	2	2	7	14	8
0.333	-	0.600	0.316	0.750	0.833	0.622
0.907	-	0.480	0.499	0.805	0.915	0.682
11	-	2	1	10	15	8
0.667	-	0.222	0.000	0.778	0.867	0.620
0.833	-	0.346	0.000	0.880	0.880	0.666
-	-	3	2	4	-	4
-	-	0.750	0.400	0.625	-	0.584
-	-	0.531	0.480	0.602	-	0.572
13	-	3	2	7	13	8
0.563	-	0.588	**0.000**	0.824	0.882	0.658
0.859	-	0.469	**0.291**	0.817	0.860	0.689
-	-	4	2	8	-	6
-	-	0.789	0.240	0.882	-	0.649
-	-	0.609	0.365	0.804	-	0.625
26	16	4	2	10	22	12
0.846	**0.647**	0.492	**0.138**	0.800	0.786	0.666
0.896	**0.872**	0.511	**0.348**	0.817	0.923	0.717
2	5	3	2	9	9	7
1.000	1.000	0.621	0.069	0.571	0.750	0.594
0.500	0.750	0.499	0.238	0.815	0.750	0.669
9	15	2	2	10	19	9
0.826	0.833	0.467	0.167	0.800	0.862	0.683
0.813	0.877	0.464	0.299	0.851	0.861	0.677
16	12	3	2	11	14	9
0.667	0.727	0.364	0.318	0.955	0.947	0.681

0.909	0.819	0.501	0.268	0.874	0.892	0.707
11	8	3	2	8	13	
0.499	0.422	0.454	0.185	0.814	0.718	
0.610	0.456	0.489	0.306	0.816	0.763	

a) Average number of alleles (Na), observed and expected heterozygosities (Ho, He) across populations for each microsatellite locus.

	PAT MP-		**Titgata39**		**Escu6**		**Titgata02**		**PAT MP-**		**Ase18**		**PmanTAGAn71**		**Cuμ28**		**Ppi2**		**PmanTAGAn4**		**CcaTgu11**		**VeCr05**		**CtC-101**		**Pij02**	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Na	8	8	7	7	15	15	10	11	12	13	4	3	7	7	3	3	11	12	8	9	3	3	2	2	8	9	13	15
Ho	0.587	0.594	0.720	0.754	0.811	0.804	0.745	0.860	####	0.841	0.280	0.272	0.775	0.769	0.485	0.493	0.499	0.576	0.422	0.487	####	0.406	0.185	0.164	0.814	0.823	0.718	0.829
He	0.626	0.653	0.728	0.740	0.894	0.898	0.735	0.849	####	0.867	0.275	0.275	0.750	0.747	0.502	0.503	0.610	0.704	0.456	0.526	####	0.477	0.306	0.288	0.816	0.834	0.763	0.880

[+]including populations KEL and VAN
[-]KEL and VAN removed

b) Average number of alleles (Na), observed and expected heterozygosities (Ho, He) across loci for each population.

	BCR		**CBC**		**CLU**		**FF**		**FrL**		**FtStJ2**		**HAZ**		**HOU**		**KEL**		**NWBC**		**VAN**		**FtStJ1**		**PG**		**SAB1**		**SAB2**	
	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**	+	**x**
Na	11	8	11	8	9	7	6	5	7	6	8	6	8	6	8	7	4	4	8	6	6	6	12	9	7	8	9	8	9	7
Ho	0.652	0.597	0.647	0.589	0.654	0.632	0.644	0.603	0.622	0.547	0.623	0.569	0.622	0.597	0.620	0.559	0.584	0.584	0.658	0.600	0.649	0.649	0.666	0.614	0.594	0.509	0.683	0.615	0.681	0.634
He	0.708	0.635	0.690	0.625	0.703	0.638	0.672	0.608	0.668	0.629	0.667	0.619	0.682	0.624	0.666	0.607	0.572	0.572	0.689	0.627	0.625	0.625	0.717	0.647	0.669	0.651	0.677	0.609	0.707	0.647

[+]including all loci
[x]underrepresented loci removed

c) A comparison of calculated pairwise F_{ST} values after removing populations KEL and VAN (above diagonal) and underrepresented loci (below diagonal). Bold values indicate significance after corrections for multiple tests.

	BCR	**NBC**	**CLU**	**FF**	**FrL**	**FtStJ2**	**HAZ**	**HOU**	**KEL**	**NWBC**	**VAN**	**FtStJ1**	**PG**	**SAB1**	**SAB2**
BCR	-	0.014	0.017	**0.059**	0.096	0.097	**0.061**	**0.069**		**0.018**		**0.011**	**0.036**	**0.014**	**0.014**
NBC	0.013	-	0.021	0.057	0.107	0.104	**0.068**	**0.067**		**0.020**		**0.014**	**0.034**	**0.015**	**0.013**
CLU	**0.016**	**0.020**	-	**0.061**	**0.107**	0.112	0.062	**0.077**		**0.025**		**0.013**	**0.036**	**0.018**	**0.020**
FF	**0.018**	0.015	**0.021**	-	**0.149**	**0.147**	0.104	0.106		**0.069**		**0.056**	**0.087**	0.059	0.059
FrL	**0.053**	**0.061**	**0.063**	0.063	-	**0.189**	**0.157**	**0.162**		**0.112**		**0.102**	**0.133**	**0.105**	**0.101**
FtStJ2	**0.053**	**0.058**	**0.067**	**0.061**	**0.094**	-	**0.155**	**0.163**		**0.110**		**0.099**	**0.138**	**0.103**	**0.104**
HAZ	**0.020**	**0.025**	0.021	0.024	**0.069**	**0.068**	-	**0.131**		**0.074**		**0.060**	**0.096**	**0.066**	**0.065**
HOU	**0.028**	**0.025**	**0.036**	0.026	**0.073**	**0.074**	**0.048**	-		**0.072**		**0.068**	**0.088**	**0.071**	**0.069**
KEL	**0.168**	**0.177**	**0.182**	**0.177**	**0.208**	0.196	**0.167**	**0.205**	-						
NWBC	**0.017**	**0.017**	**0.024**	**0.028**	**0.067**	**0.065**	**0.032**	**0.030**	**0.186**	-		**0.018**	**0.038**	**0.022**	**0.022**
VAN	**0.144**	**0.154**	**0.162**	**0.157**	**0.188**	**0.175**	**0.157**	**0.175**	**0.264**	**0.160**	-				
FtStJ1	**0.009**	**0.013**	**0.011**	0.015	**0.057**	**0.055**	**0.019**	**0.026**	**0.173**	**0.016**	**0.148**	-	**0.032**	**0.009**	**0.013**
PG	**0.032**	**0.032**	**0.032**	0.040	**0.080**	**0.084**	**0.048**	**0.041**	**0.209**	**0.034**	**0.181**	**0.030**	-	**0.038**	**0.031**
SAB1	**0.013**	**0.014**	0.016	**0.017**	**0.060**	**0.059**	**0.025**	**0.029**	**0.182**	**0.021**	**0.159**	**0.009**	**0.037**	-	**0.012**
SAB2	**0.011**	**0.013**	0.018	0.016	**0.055**	**0.057**	0.022	**0.026**	**0.173**	**0.021**	**0.153**	**0.012**	**0.029**	0.011	-

	BCR	NBC	CLU	FF	FrL	FtStJ2	HAZ	HOU
BCR	-							
NBC	**0.044**	-						
CLU	**0.052**	**0.063**	-					
FF	**0.172**	0.169	0.180	-				
FrL	**0.271**	**0.301**	0.301	0.403	-			
FtStJ2	**0.273**	**0.293**	**0.312**	0.399	0.494	-		
HAZ	**0.178**	**0.197**	0.181	0.292	**0.422**	**0.418**	-	
HOU	**0.201**	**0.196**	**0.223**	0.297	**0.434**	**0.436**	**0.360**	-
KEL	**0.605**	**0.634**	**0.644**	**0.731**	**0.821**	0.787	**0.703**	**0.812**
NWBC	**0.054**	**0.059**	**0.076**	**0.201**	**0.314**	**0.307**	**0.213**	**0.208**
VAN	**0.536**	**0.568**	**0.588**	**0.675**	**0.764**	**0.727**	**0.676**	**0.726**
FtStJ1	**0.034**	**0.042**	**0.039**	0.165	**0.287**	**0.281**	**0.177**	**0.198**
PG	**0.108**	**0.102**	**0.107**	0.248	**0.365**	**0.376**	**0.271**	**0.251**
SAB1	**0.043**	**0.045**	**0.054**	0.172	**0.294**	**0.291**	**0.192**	**0.206**
SAB2	**0.041**	**0.041**	**0.060**	**0.173**	**0.285**	**0.291**	**0.191**	**0.201**

KEL	NWBC	VAN	FtStJ1	PG	SAB1	SAB2
-						
0.658	-					
0.983	0.582	-				
0.622	0.054	0.550	-			
0.735	0.112	0.655	0.096	-		
0.646	0.067	0.579	0.028	0.115	-	
0.625	0.066	0.569	0.041	0.092	0.036	-