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ARTICLE

Source and spread dynamics of mountain pine beetle in central Alberta, Canada

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Abstract

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Curculionidae) is a significant destructive force in the pine forests of western Canada and has the capacity to spread east into a novel host tree species, jack pine (Pinaceae). New populations have been documented in central Alberta, Canada, but the source populations for these outbreaks have yet to be identified. In this study, we use genetic data to identify parent populations for recent outbreak sites near Slave Lake, Lac La Biche, and Hinton, Alberta. We found the northern population cluster that entered Alberta near Grande Prairie was the source of the most eastern established population near Lac La Biche, and the range expansion to this leading-edge population has been too rapid to establish evidence of population structure. However, some dispersal from a population in the Jasper and Hinton area has been detected as far north and east as Slave Lake, Alberta. We also identified two potential source populations for the current outbreak in Hinton: most beetles appear to be from Jasper National Park, Alberta, but some also originated from the northern population cluster. These findings demonstrate the dynamic dispersal capabilities of mountain pine beetle across the Alberta landscape and the potential hazard of increased dispersal to newly established leading-edge populations.

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), is a tree-killing bark beetle that has become one of the most significant destructive forest pests in western North America (Natural Resources Canada 2017). Historically, mountain pine beetle populations in Canada have been confined largely to British Columbia and southwestern Alberta within the range of their primary host, lodgepole pine (Pinaceae) (Safranyik *et al.* 2010). However, in the early 2000s, populations expanded and established in northwestern Alberta (Natural Resources Canada 2017), aided by wind updrafts (Jackson *et al.* 2008; Janes *et al.* 2014). The species' eastward spread has continued, resulting in more than $Cdn 500 million being spent on mitigating damage in Alberta alone (Whittaker 2018). Northeastern Alberta is of particular concern because this is where lodgepole pine transitions to jack pine, a naïve host species that provides a potential entry point into the boreal pine forests of eastern Canada and the northern United States of America (Cullingham *et al.* 2011; Bleiker *et al.* 2014).

Various genetic markers have been used to map mountain pine beetle population structure and range expansions in British Columbia (Mock *et al.* 2007) and Alberta (Langor and Spence 1991;

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Cullingham *et al.* 2012; Samarasekera *et al.* 2012; Janes *et al.* 2014, 2016, 2018; Batista *et al.* 2016). These studies have shown that mountain pine beetle spread into Alberta was composed of two incursions that are genetically distinct (Samarasekera *et al.* 2012; Janes *et al.* 2014; Batista *et al.* 2016) and a third incursion that is genetically intermediate (Trevoy *et al.* 2018). The southern resident population has ranged as far north as Banff and Canmore (Hopping and Mathers 1945), and a more recently established northern population extends eastwards past Grande Prairie (Janes *et al.* 2014). The intermediate population recently entered Alberta by way of Jasper National Park, and its genetic similarity to lab-produced hybrids between the northern and southern populations suggests that it resulted from admixture between them (Trevoy *et al.* 2018).

Epidemic populations have been identified in Hinton, west–central Alberta, and Slave Lake, indicating continued northeastward range expansion in Alberta. Mountain pine beetle has now also been detected at low densities on the eastern edge of Alberta near the border with Saskatchewan, Canada in novel jack pine habitat (MacCormick 2020). It is uncertain if beetles detected near Saskatchewan came from low-density, locally established populations from previous long-range dispersal events or directly from larger outbreak populations to the west. These recently detected populations have not yet been included in demographic studies on mountain pine beetle spread. Determining their sources would allow optimisation of pheromone monitoring (Miller *et al.* 2005), guide forest management practices to limit localised population increases (Safranyik and Carroll 2006), and better inform assessments of outbreak risk (Bleiker 2019). In the present study, we use genome-wide single nucleotide polymorphisms to characterise population structure and identify dispersal and spread of mountain pine beetle in northern Alberta, particularly in newly detected northeastern populations.

Methods

Beetle sampling, DNA extraction, and sequencing

A total of 306 specimens were collected at 44 different sites from nine locations between 2014 and 2018, and specimens were assigned to populations based on proximity to other collection localities (Supplemental materials, Table S1). Beetles were preferentially taken from different trees or egg galleries to reduce the influence of genetic structuring due to the inclusion of siblings from single families. Once collected, beetles were preserved in 90–95% ethanol and placed in a freezer at −20 °C until DNA extraction.

DNA extraction used the Qiagen DNEasy Blood & Tissue kit (Qiagen, Germantown, Maryland, United States of America) with an optional RNAse A treatment. Library preparation of samples collected in 2014–2015 followed the two-enzyme genotyping-by-sequencing protocol of Poland *et al.* (2012), and the library preparation of samples collected in 2016–2018 followed double digest restriction-site associated DNA sequencing protocol of Peterson *et al.* (2012), according to the general procedure outlined in Campbell *et al.* (2017). Single-end sequencing of the 2014–2015 samples was performed on an Illumina HiSeq 2000 (Illumina, Inc., San Diego, California, United States of America) at the Institut de biologie intégrative et des systèmes (IBIS) at Université Laval, Quebec City, Québec, Canada, whereas single-end sequencing of the 2016–2018 samples was performed on an Illumina NextSeq 500 (Illumina, Inc.) at the University of Alberta Molecular Biology Service Unit, Edmonton, Alberta, Canada.

Data filtering and single nucleotide polymorphism identification

Initial data demultiplexing was conducted in Stacks, version 2.0b (Rochette *et al.* 2019) on the Graham cluster of Compute Canada (Toronto, Ontario, Canada). The *PstI* restriction sites on the 5′ end of each DNA sequence that was read were trimmed using cutadapt, version 1.9.1 (Martin 2011). Samples sequenced on a NextSeq 500 had a final read length of 67 base pairs after trimming. Following Campbell *et al.* (2017), longer reads produced on a HiSeq 2000 (Illumina, Inc.)

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were additionally truncated on the 3′ end to match the length of the NextSeq-generated data. The trimmed sequence reads were then aligned to the female mountain pine beetle draft genome (Keeling *et al.* 2013) using the alignment algorithm Burrows–Wheeler Aligner Maximal Exact Match (BWA-MEM), version 0.7.17 (Li and Durbin 2009). Alignment quality was checked using SAMtools, version 1.9 (Li *et al.* 2009).

Single nucleotide polymorphisms were identified using the ref_map.pl script in Stacks (Catchen *et al.* 2011; Rochette *et al.* 2019). We specified a minimum minor allele frequency of 0.01 and adhered to the *r80* principle recommended by Paris *et al.* (2017), which requires a locus to be present in at least 80% of the individuals in a population in order to be retained in the final data set. At each locus, only a single, random single nucleotide polymorphism was retained. Further filtering of single nucleotide polymorphism data and samples was conducted in VCFtools, version 0.1.14 (Danecek *et al.* 2011). Specifically, loci were excluded if they had a genotype quality score below 30 or if a single nucleotide polymorphism locus had more than 5% missing data globally. Initial exploratory principal component analysis recovered clustering along the first principal component that appeared to be driven by sex (consistent with Trevoy *et al.* 2019), which largely confounded population-level clustering (Supplemental materials, Fig. S2). To remove this signal, we filtered for linkage disequilibrium, following Abdellaoui *et al.* (2013). Linkage disequilibrium was calculated for all pairwise single nucleotide polymorphism combinations using the dartR package (Gruber and Georges 2019) in R (R Core Team 2018). For any groups of single nucleotide polymorphisms that were in linkage disequilibrium ($R^2 > 0.5$), we retained only one random single nucleotide polymorphism from each to reduce the impact on population-clustering analyses. Finally, we did not distinguish between putatively adaptive and neutral loci for population-clustering analyses because a combination of both has been shown to more accurately reflect population structure in mountain pine beetle (Batista *et al.* 2016).

Principal component analysis groups specimens based on the extent of covariance in their associated data, and often individuals that are closely related can confound population structure due to their high rate of covariance (Alhusain and Hafez 2018). Although our sampling procedure was designed to reduce the incidence of multiple specimens from a single family, data visualisation using principal component analysis indicated tight clustering patterns for two groups, consisting of a total of seven individuals, that were consistent with family-level structure (Price *et al.* 2010; Supplemental materials, Fig. S1). Three clustered individuals came from a single tree (sibling group 1; Supplemental materials, Fig. S1), and four clustered individuals came from two close trees (sibling group 2; Supplemental materials, Fig. S1). No patterns in missing data or poor locus coverage were identified that could explain this structuring. Because female mountain pine beetles are capable of producing multiple egg galleries from a single mating (Reid 1958), these clustered individuals were assumed to be siblings. To reduce the influence of such family structure on population-level analyses, all but one individual in each set of closely related specimens were removed from the data set.

Population structure analysis

To explore and identify potential signs of population structure across northern Alberta, we used several approaches. A principal component analysis on all samples that passed filtering was performed in the R package adegenet (Jombart 2008; Jombart and Ahmed 2011) and plotted with ggplot2 (Wickham 2016). This was used to detect single nucleotide polymorphism covariance between specimens and to identify population structure among the specimens without *a priori* population assignment. We also used this set of samples to calculate observed heterozygosity, expected heterozygosity, and pairwise population differentiation due to genetic structure (F_{ST}) in the R package dartR, and the R package Genepop (Raymond and Rousset 1995; Rousset 2008) was used to calculate population differentiation based on genetic diversity using an exact G-test of genic differentiation with a Bonferroni correction based on the 36 pairwise tests.

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To assess fine-scale population structure across the northernmost locations, we created a northern data set by removing all southern- and intermediate-cluster population samples, including any putative dispersers. We performed a principal component analysis on this northern data set, then used discriminant analysis of principal components (Jombart *et al.* 2010) in adegenet to detect potential weak signals of population structure using *a priori* population assignments based on collection locality and verified by the prior principal component analysis. We then performed isolation-by-distance analysis using the R packages Geosphere (Hijmans 2019) and SNA (Butts 2016) and calculated a Mantel test in adegenet.

The program Structure, version 2.3.4 (Pritchard *et al.* 2000; Falush *et al.* 2003, 2007; Hubisz *et al.* 2009), was used to infer genetic population structure among all populations. We subsampled the full data set to 125 individuals that were arbitrarily selected to represent potential sample-site variation (10 to 16 individuals from each location) in order to reduce bias due to differences in sampled population sizes (Puechmaille 2016). In this data set, we attempted to include as many samples as possible for each population while maintaining a roughly equal sample size among the many sampling locations. We used the admixture model without specifying *a priori* population or location information, and we tested values of K from 1 to 10 with one million Markov chain Monte Carlo generations and a burn-in period of 250 000. We replicated the analysis for each value of K a total of 10 times and then used CLUMPAK (Kopelman *et al.* 2015) to average the 10 independent replicates for each value of K. The optimal value of K was assessed using both the difference between the likelihoods of subsequent K values (ΔK) (Evanno *et al.* 2005) and the mean estimated natural logarithm of the probability of each K value (Ln(PrK)) (Pritchard *et al.* 2000). We then ran a principal component analysis using this subset of data to ensure our Structure results were comparable to the principal component analysis of the full data set described above.

Results

After filtering, 299 individuals and 2872 genomic single nucleotide polymorphisms were retained for data analysis (Supplemental materials, Table S1). Average individual read depth was 58.3 (minimum depth = 12.6, maximum depth = 217.3; Supplemental materials, Table S1). Pairwise F_{ST} between populations ranged from approximately 0 to 0.13 (Table 1), with Canmore found to be the most distinct population. Tests for differences in pairwise population genetic differentiation also identified Canmore as having allelic distributions that significantly differed from those of all other tested populations and found some significant differences between intermediate and northern locations (Table 1). Observed heterozygosity was similar among populations, ranging from 0.14 to 0.19, and differences between expected and observed heterozygosity were minimal (Table 1). Some of the most recently detected populations, such as Battle Lake and Lac La Biche, had higher heterozygosity than some older, established populations, such as Grande Prairie and Edson, but no clear trend was evident (Table 1).

In the principal component analysis for the full data set of 299 individuals (Fig. 1A), beetle sex had strong signal that overwhelmed population structure (Supplemental materials, Fig. S2). All but three specimens could be sexed using methods outlined in Trevoy *et al.* (2019). For the three ambiguous specimens, we removed all loci containing missing data from sex-related scaffolds, but they remained intermediate between the male and female clusters (Supplemental materials, Fig. S2). Despite this, after filtering for linkage disequilibrium, these specimens clustered as expected, based on sampling location. To focus on geographic population structure, sex-based signal was successfully removed from the data set by filtering for linkage disequilibrium.

After filtering, the first principal component (PC1), which often relates to geographic location in genetic assessments of population structure (see Abdellaoui *et al.* 2013), explained 3.6% of the variation in the single nucleotide polymorphism data and distinguished northern and southern

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Table 1. Pairwise population differentiation *P*-values (above diagonal), F_{ST} (below diagonal), and observed (Ho) and expected (He) population heterozygosity.

Gen D / F_{st}	Battle Lake	Canmore	Edson	Grande Prairie	Hinton	Jasper	Lac La Biche	Slave Lake	Whitecourt	*n*	Ho	He
Battle Lake	–	0.018	**0.000**	**0.000**	1.000	1.000	**0.000**	**0.000**	0.187	52	0.19	0.19
Canmore	0.053	–	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	48	0.18	0.18
Edson	0.032	0.128	–	1.000	**0.000**	**0.000**	1.000	1.000	1.000	49	0.15	0.17
Grande Prairie	0.032	0.131	0.002	–	**0.000**	**0.000**	1.000	1.000	1.000	53	0.15	0.17
Hinton	0.002	0.065	0.019	0.018	–	1.000	**0.000**	**0.000**	**0.000**	32	0.14	0.19
Jasper	0.001	0.056	0.028	0.028	0.002	–	**0.000**	**0.000**	0.918	27	0.18	0.19
Lac La Biche	0.036	0.134	0.003	0.003	0.021	0.031	–	1.000	1.000	10	0.17	0.17
Slave Lake	0.030	0.126	0.001	0.001	0.017	0.024	0.003	–	1.000	12	0.14	0.18
Whitecourt	0.021	0.113	0.001	0.001	0.012	0.018	0.003	0.001	–	11	0.16	0.18

Statistics were calculated using *n* individuals for each population group. Significantly differentiated population pairs (in bold) had genic differentiation values of $P < 0.001$ after Bonferroni correction.

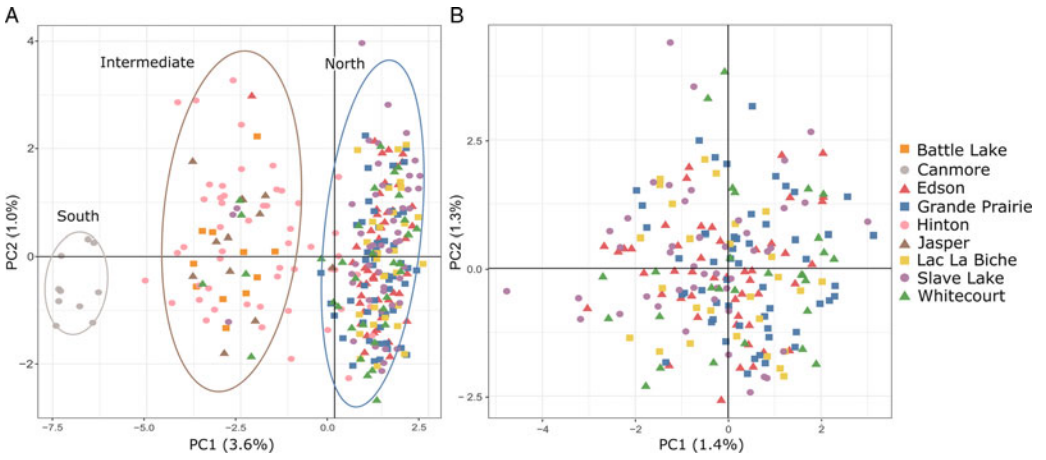


Fig. 1. Principal component analyses results. **A**, Results for all sampling locations and individuals ($n = 299$) and **B**, results for northern locations (Edson, Grande Prairie, Lac La Biche, Slave Lake, and Whitecourt), with all intermediate-cluster individuals removed ($n = 201$). In **A**, ellipses were added to emphasise the south, intermediate, and north clusters. These genetic population clusters were divided at PC1 = −5.5 and PC1 = −0.06 for assignment of individuals in Supplemental materials, Table S1.

populations as well as a distinct intermediate group between the two; for this study, we used PC1 = −5.5 and −0.06 to delimit the intermediate cluster. The second principal component explained 1.0% of the remaining variance and related to variation within, rather than between, populations.

No population structure was detected in either principal component analysis or discriminant analysis of principal components when we focussed on a northern data set that included 206 specimens, after removing individuals from the intermediate and southern clusters (Fig. 1B; Supplemental materials, Fig. S3). Isolation-by-distance analysis of the northern locations likewise did not indicate any patterns of population differentiation based on geographic distances (Mantel test: $P = 0.75$).

The ΔK values from the Structure analysis indicated an optimal K value of 2, and Ln(PrK) indicated an optimal K of 2 or 3 (Supplemental materials, Fig. S4). A K value of 2 distinguished northern and southern population clusters and identified a genetically and geographically intermediate population of specimens from Jasper, Battle Lake, and Hinton (Fig. 2); K values of three and higher neither further resolved this intermediate population nor indicated any other meaningful geographic clustering. Thus, $K = 2$ was considered to be optimal (Supplemental materials, Fig. S4). Structure analysis also indicated some individuals that did not cluster according to the locations in which they were collected; one individual that was collected near Edson and one that was collected near Slave Lake grouped with the intermediate population. Principle component analysis using this subset of 125 samples also produced similar divisions to the Structure analysis and closely resembled the patterns shown in Fig. 1A, indicating that the results of the Structure analysis were consistent with the population structure identified through principal component analysis of the full data set.

Based on the principal component analysis of the full data set ($n = 299$), we identified several additional individuals that were collected in the northern populations but grouped with the intermediate population cluster, bringing the totals to three beetles from Slave Lake, five from Whitecourt, and one from Edson (Supplemental materials, Table S1 and Fig. S5). By chance, none of these Whitecourt individuals were sampled in the subset Structure analysis of 125 individuals; however, a larger Structure analysis of all 299 specimens indicated that these individuals were

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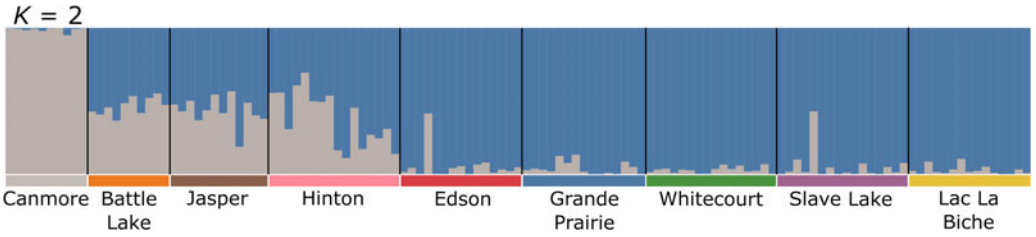


Fig. 2. Structure analysis for equivalently sized population subsets, totalling 125 individuals. $K = 2$ was the best supported number of populations. Based on individual assignments, the Edson and Slave Lake populations each include a single admixed individual with a roughly equal assignment to both the northern and southern genetic clusters.

admixed (Supplemental materials, Fig. S4) and was largely consistent with the results of the principal component analysis presented in Fig. 1A. We also identified 11 specimens collected in Hinton and one collected in Jasper that grouped with the northern cluster. Of these putative dispersers, 81% were female and 19% were male (Supplemental materials, Table S1); the sex ratio of these geographically mismatched individuals is consistent with known sex biases in mountain pine beetle (Blomquist *et al.* 2010; James *et al.* 2016; Fig. 3). No putative dispersers from the intermediate population were found among the newly established Lac La Biche specimens.

Discussion

Our study used population structure to investigate the dispersal dynamics of mountain pine beetle in central Alberta, identifying primary source populations as well as fine-scale dispersal from other regions. We found the same distinct north–south beetle genetic population structure that was previously described for Alberta (Janes *et al.* 2014; Batista *et al.* 2016; Trevoy *et al.* 2018; Figs. 1 and 2). When we focussed on individuals from northern locations, however, we found no evidence of population structure (Fig. 1B). This finding is consistent with a high rate of dispersal and gene flow between these regions. The long-range dispersal capability of mountain pine beetle (Jackson *et al.* 2008) likely promotes genetic admixture, particularly from west to east, and may have inhibited the further development of genetically distinct populations in this region.

The extensive dispersal of mountain pine beetle also applies to mixing of population clusters. Although we saw no admixture involving the southern cluster, mingling was evident among the north and intermediate populations. We identified several putative dispersers with affinities to Jasper and Hinton in sites across the northern locations, including as far to the northeast as Slave Lake (Fig. 3; Supplemental materials, Table S1). This illustrates the considerable dispersal capability of these populations and their potential contribution to range expansion in the north. The majority of putative dispersers that we identified were female, which could potentially increase establishment success rate because female beetles can be mated before they disperse (Bleiker *et al.* 2013) and are the pioneering sex in *D. ponderosae* (Blomquist *et al.* 2010). Specimens collected in Hinton and one specimen at Jasper showed the reverse pattern, with some beetles having affinities to the northern cluster, indicating that several individuals likely came from a northern source (Fig. 3). These results highlight the importance of considering multiple source populations when determining infestation origins in newly established regions.

Admixture and high dispersal rates from the north and intermediate populations towards the northeast may have important genetic ramifications. In particular, dispersal from the genetically intermediate Jasper and Hinton region is likely to increase genetic diversity in the currently expanding eastern range of mountain pine beetle, which would otherwise be solely composed of the genetically homogenous northern population. Although this introduces the possibility of potential benefits from increased genetic diversity in the leading-edge populations, high rates

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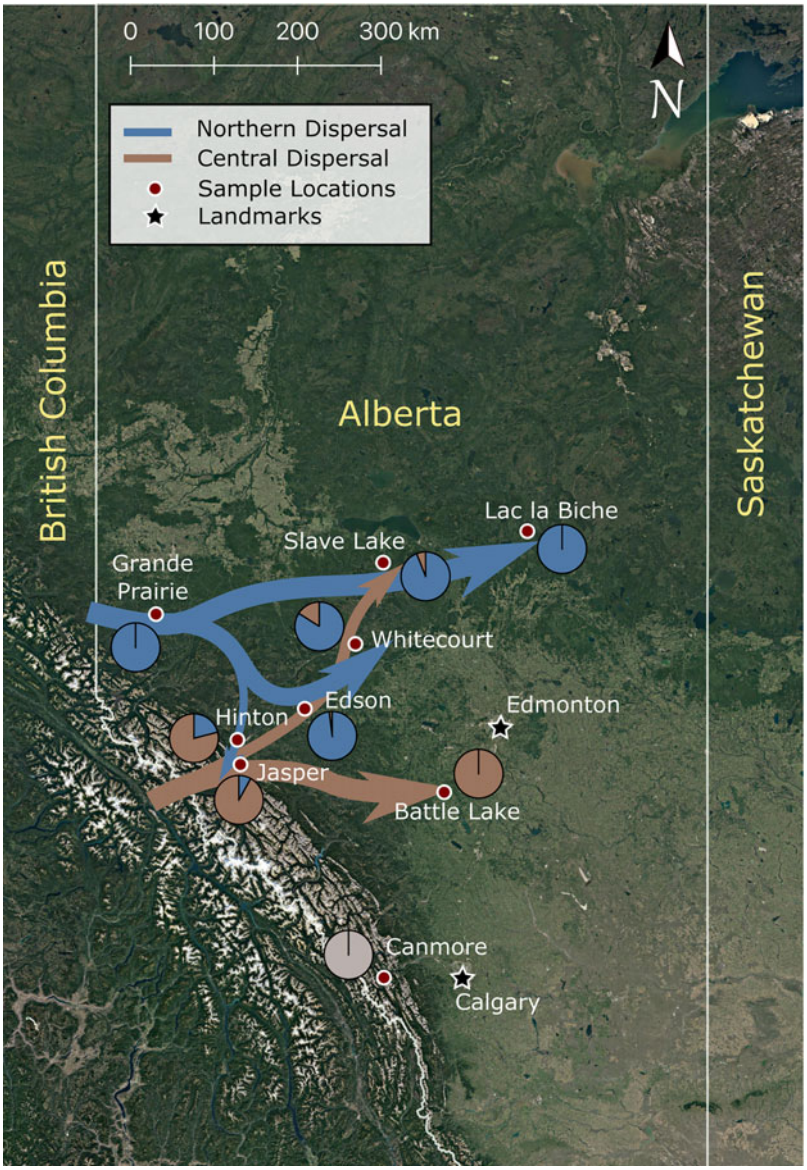


Fig. 3. Population expansion dynamics inferred from genetic evidence based on 299 mountain pine beetle specimens collected from sites across Alberta, Canada. Pie charts for each sampling location are coloured by proportion of individuals assigned to the north (blue), intermediate (brown), and south (grey) population clusters, as determined using principal component analysis (Fig. 1A).

of dispersal and gene flow may also prevent local adaptation (Lenormand 2002). Regardless, genetic differences between regions allow us to monitor new populations and to identify the magnitude and composition of the spread of mountain pine beetle towards the northeast from different genetic sources.

Currently, the leading edge of the mountain pine beetle range is found in jack pine forests near Lac La Biche (MacCormick 2020), and this population is genetically indistinguishable from other northern populations as far west as Grande Prairie. This uniformity can be explained by high rates

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of dispersal and regular waves of reinforcing conspecifics from other populations. In another forest pest, the spruce budworm (*Choristoneura fumiferana* Clemens) (Lepidoptera: Tortricidae), reinforcing waves of dispersers from neighbouring populations may allow endemic populations to become epidemic (Larroque *et al.* 2020). Although their life histories differ, mountain pine beetle and spruce budworm have similar overall outbreak dynamics, with large increases in population size causing epidemic conditions (Royama 1984; Larroque *et al.* 2020). In jack pine forests, mountain pine beetle can face intense competition from heterospecifics, such as wood-boring beetles (Klutsch *et al.* 2016). This may serve to mediate local population growth, but populations near Slave Lake likely make contributions to the Lac La Biche infestation. Continued recruitment in this region risks establishing large, potentially epidemic populations in the eastern jack pine forests.

Mountain pine beetle dispersal has been difficult to predict, but our study has helped to identify large-scale dispersal patterns in central Alberta. We demonstrate that the current Hinton infestation was derived from two sources, these likely being Jasper and, to a lesser degree, Grande Prairie. Although we found no evidence of any dispersal from the southern population cluster, there was a general trend of population expansion from the Jasper region towards the northeast, with occasional dispersal as far northeast as Slave Lake. To date, control efforts in Alberta have been largely successful at slowing the spread of mountain pine beetle, but the beetle nonetheless remains capable of extensive and rapid range expansion. Long-range dispersal may limit population structure within the northernmost regions, but it also may contribute to epidemic population development. Continued focus on reducing current outbreaking populations may be necessary to minimise long-range dispersal and reinforcement of populations at the beetle's leading edge in Alberta.

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Data availability. Raw sequence data in the form of fastq files are available in the National Center for Biotechnology Information Sequence Read Archive (NCBI SRA) under the accession number PRJNA656769 (https://www.ncbi.nlm.nih.gov/sra/PRJNA656769).

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.4039/tce.2020.83.

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