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Spatial genetic structure of the mountain pine beetle (*Dendroctonus ponderosae*) outbreak in western Canada: historical patterns and contemporary dispersal

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Abstract

Environmental change has a wide range of ecological consequences, including species extinction and range expansion. Many studies have shown that insect species respond rapidly to climatic change. A mountain pine beetle epidemic of record size in North America has led to unprecedented mortality of lodgepole pine, and a significant range expansion to the northeast of its historic range. Our goal was to determine the spatial genetic variation found among outbreak population from which genetic structure, and dispersal patterns may be inferred. Beetles from 49 sampling locations throughout the outbreak area in western Canada were analysed at 13 microsatellite loci. We found significant north-south population structure as evidenced by: (i) Bayesian-based analyses, (ii) north-south genetic relationships and diversity gradients; and (iii) a lack of isolation-by-distance in the northernmost cluster. The north-south structure is proposed to have arisen from the processes of postglacial colonization as well as recent climate-driven changes in population dynamics. Our data support the hypothesis of multiple sources of origin for the outbreak and point to the need for population specific information to improve our understanding and management of outbreaks. The recent range expansion across the Rocky Mountains into the jack/lodgepole hybrid and pure jack pine zones of northern Alberta is consistent with a northern British Columbia origin. We detected no loss of genetic variability in these populations, indicating that the evolutionary potential of mountain pine beetle to adapt has not been reduced by founder events. This study illustrates a rapid range-wide response to the removal of climatic constraints, and the potential for range expansion of a regional population.

Keywords: bark beetle, dispersal, mountain pine beetle, population genetics, population structure, Scolytinae

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Introduction

There is growing evidence that environmental change has, and is expected to continue to have a wide range of ecological consequences, including species extinctions (Thomas *et al.* 2004) and range expansions (Walther *et al.* 2002, 2009), either by invasions into new habitats or by the elimination of barriers to expansion from native sites. Indeed, range expansions are a potent driver of further ecological change. Kenis *et al.* (2008) reviewed publications on the biological effects of invasions by 72

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insect species and found ~80% reported significant effects. These included direct effects of herbivores, parasitoids and predators on local species as well as indirect effects such as competition with native species, the introduction of new pathogens and the cascading effects of altering plant and animal communities. Given the biological impacts of range expansion, developing an understanding of the nature of range expansion is critical.

Climate change has facilitated poleward and elevational range expansions/shifts in many insects, and has been well documented in Lepidoptera (butterflies and moths), Odonata (dragonflies and damselflies) (Parmesan 2006) and more recently in the eruptive bark beetle mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) (Safranyik *et al.* 2010; Cullingham *et al.* 2011). This beetle is native to the pine forests of western North America with its distribution extending from central BC to northern Mexico. It is one of the most destructive forest insect pests in North America (Safranyik & Carroll 2006). Fire suppression and limited harvest of lodgepole pine over the past century have led to large, contiguous areas with a high density of trees vulnerable to beetle attack (Konkin & Hopkins 2009). In combination with a northern shift in climatic suitability, this has created ideal conditions for mountain pine beetle population expansion (Safranyik & Carroll 2006; Clark *et al.* 2010; Cudmore *et al.* 2010). These factors have led to an ongoing and unprecedented mountain pine beetle outbreak in western Canada that has affected over 16 million hectares of pine forests (Kurz *et al.* 2008). Most of the mortality has involved the primary host, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), but most pine species are acceptable hosts (Wood 1982). The current outbreak had expanded into lodgepole pine and lodgepole x jack pine (*Pinus banksiana* Lamb.) hybrid stands in northern Alberta by 2006 (Safranyik & Carroll; Raffa *et al.* 2008; Cullingham *et al.* 2011), and recently into pure jack pine of the boreal forest (Cullingham *et al.* 2011). These events support predictions of potential further range expansion of MPB into eastern Canada and eastern and central United States (Logan & Powell 2001; Mock *et al.* 2007; Safranyik *et al.* 2010), and also provide an excellent opportunity to investigate population genetic consequences of mass migration by an eruptive herbivore.

Bark beetle epidemics make large contributions to global carbon dioxide emissions (Kurz *et al.* 2008) and inflict severe economic damage on forest industries and forestry-dependent communities (Wagner *et al.* 2006). Current predictions related to future climate change suggest that the frequency and severity of other bark beetle outbreaks, e.g. Douglas-fir beetle, *D. pseudotsugae* (Hopkins), and spruce beetle, *Dendroctonus rufipennis* (Kirby), will increase in the future (Raffa *et al.* 2008). It is therefore vital to study the dynamics of the spread of the current outbreak, both to improve our understanding and management of current and future bark beetle outbreaks, and to study the effects of climate change-facilitated range expansion of native fauna (Valéry *et al.* 2009).

The epidemiology of the mountain pine beetle is well understood (Safranyik & Carroll 2006). In the endemic population phase, populations exist at low densities and only colonize low-vigour trees, e.g. those suppressed by competition or disease. Through processes that suppress the health of trees or that increase beetle population numbers, an incipient-epidemic phase is reached where healthy, large diameter pines can be successfully killed. Consecutive years of population increases allow beetles to reach the epidemic phase, characterized by infestations over large spatial and temporal scales. Through extreme cold-weather events and/or resource depletion, epidemic populations eventually crash and revert to the endemic phase.

Mountain pine beetle outbreaks may arise locally from the expansion of numerous endemic-phase populations, or as a result of long distance dispersal from epicentres (Aukema *et al.* 2006). Long distance bark beetle dispersal is thought to be a passive process in which emerging beetles are caught in updrafts (Chapman 1962; Furniss & Furniss 1972; Safranyik *et al.* 1989). This moves them above the canopy (Safranyik *et al.* 1992), from where they may be transported hundreds of kilometres by atmospheric winds (Jackson *et al.* 2008; Ainslie & Jackson 2011). A complex combination of the two modes is also possible (Namkoong *et al.* 1979). As *D. ponderosae* is found in the endemic population phase in many regions of BC (Wood & Unger 1996; Nelson *et al.* 2007), it has been suggested that some of the recent isolated outbreaks in Alberta have originated via dispersal from numerous localized outbreaks in adjacent areas of BC. There is also a widespread perception that the current epidemic originated and spread from an epicentre in Tweedsmuir Provincial Park (located south of the Houston site; Fig. 1) in the mid-1990s, as this was one of the first regions to erupt. The relative roles of dispersal from a single epicentre and coalescence of multiple local outbreaks in determining the overall extent of the outbreak is an area of ongoing study. Both may be important. Indeed, in a spatiotemporal analysis of the current epidemic, Aukema *et al.* (2006) found evidence for both a true epicentre in Tweedsmuir Provincial Park and simultaneous geographically isolated outbreaks in southern BC. Examination of genetic structure can differentiate among these alternate hypotheses, with genetic homogeneity across a

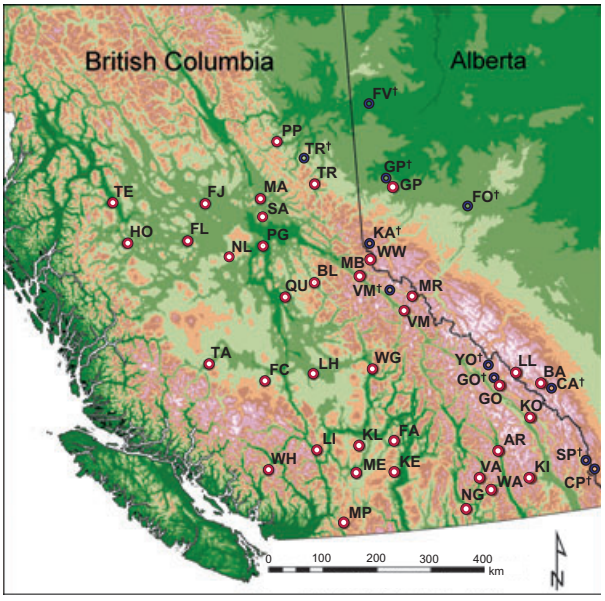

Fig. 1 Map of mountain pine beetle sampling locations in BC and Alberta. Sampling locations in 2005/06 are represented by light colour circles (red) and 2007/08 sampling locations are represented by dark (blue) circles. One location, Cypress Hills (CH) on the Alberta Saskatchewan border (GPS coordinate 49.6130, -110.1884 sampled in 2008) is not shown in the map. The location name, GPS location, year sampled and number of beetles genotyped (*N*) are given in Table 1.

landscape supporting a single epicentre and genetic structure correlated with geographic distribution supporting multiple outbreaks.

Our understanding of the development of the current epidemic is hampered by a paucity of data regarding long distance dispersal (Safranyik & Carroll 2006). Mark-recapture techniques to characterize long distance dispersal and their contribution to outbreak development are not economically feasible (e.g. Salom & McLean 1990), and prior genetic techniques (e.g. RAPD—Calpas *et al.* 2002) have not produced informative results. However, microsatellites provide a powerful tool for investigating population structure, colonization patterns and characterization of migration and dispersal patterns (Balloux & Lugon-Moulin 2002). Most population genetic studies of bark beetles support the idea that significant geographic barriers, such as mountain ranges (e.g. Horn *et al.* 2006) and large deserts (e.g. Mock *et al.* 2007), can prevent or limit inter-population gene flow, causing genetic differentiation among population. Studying patterns of gene flow can provide critical information for both preventative and reactive forest management, and may prove useful for predicting future climate-induced range changes. Specifically, if populations that breached the geographic barrier of the Rocky Mountains show similar genetic diversity to source populations, it is likely that evolutionary potential is high, allowing rapid adaptation and further expansion to the east. Furthermore, a lack of genetic structure and a high amount of gene flow may indicate that management efforts in one region would be applicable across a species' range (Schrey *et al.* 2011). In contrast, evidence of genetic structure may indicate the need for area-specific management strategies. MPB outbreaks throughout western North America provide a unique opportunity to explore the effects of genetic heterogeneity on an organism's response to climate change at the landscape level.

The aim of this study was to characterize the spatial genetic structure and dispersal patterns of *D. ponderosae* over the current epidemic area in western Canada using microsatellites. More specifically, the first objective was to examine the hypotheses that mountain ranges in British Columbia serve as barriers to gene flow, resulting in significant patterns of genetic differentiation concordant with geographic distribution. This will provide an assessment of the historic gene flow among the indigenous beetle populations in western Canada. The second objective was to use measures of genetic similarity to characterize dispersal patterns, and thereby infer the origin(s) and spread of the current outbreak. The third objective was to assess whether or not range expansion across the Rocky Mountain barrier was associated with significant loss of genetic variation, which has implications for establishment potential and further north and east range expansion.

Materials and methods

Site selection and beetle collection

Beetles were collected from lodgepole pine or lodgepole x jack pine hybrids in British Columbia and Alberta from 2005 to 2008, either in the winter or spring prior to summer dispersal in each year (Fig. 1). Sample sites were selected based on current and past mountain pine beetle outbreak activity. In 2005 and 2006, a wide range of sites were sampled. In 2007 and 2008, sampling primarily targeted the newly infested areas at the eastern edge of the outbreak, with the intention of identifying the origin of recent dispersal flights. Attacked trees in Alberta were selected from fall aerial survey data collected by the Alberta Ministry of Sustainable Resource Development. Trees within 80 km of log yards were not sampled, to minimize possible bias because of anthropogenic transport of potentially infested trees. During the entire period, a total of 85 sites were sampled. Following Balloux & Lugon-Moulin (2002), sample sites in close proximity, those with similar landscapes and lacking obvious geographic

barriers, were initially analysed separately. These sites were pooled into a single sample location if there were no significant spatial or temporal evidence of divergence (F_{ST} and F_{IS}). A total of 47 geographic sample locations were identified, but to enable comparisons between all 2005/06 and 2007/08 sample locations, sites sampled in 2005/06 in Golden (GO) and Grande Prairie (GP) were not pooled with those collected in 2007/08. This resulted in 49 sample locations that were used for analysis of population structure (Table 1).

At each site, beetles were exclusively sampled from lodgepole pine or from lodgepole x jack pine hybrids to avoid the potentially confounding influence of beetles taken from different host trees (Langor & Spence 1991; but see Mock *et al.* 2007). At the time that the beetle samples were collected in Alberta, MPB had not yet spread to forests containing jack pine. Before sampling, trees were inspected for MPB attack and colonization by identification of diagnostic entrance holes in the bark, followed by bark removal to confirm the presence of MPB larval galleries. We sampled 13–20 infested trees separated by a minimum of 10 m at each site. In most cases, beetles were collected from separate galleries from each of the four sides of the tree. For each tree, a GPS location was taken and beetles were collected in 95% ethanol on site (2005/06 summer collections) or a 10 cm bark disc containing a gallery was removed and stored at 4 °C for processing in the lab (2007/08 winter collections). All samples were stored at −20 or −80 °C prior to genetic analysis.

DNA extraction and evaluation

One beetle per gallery was randomly selected for genetic analysis to ensure each analysed beetle had different parents. DNA was extracted using a standard phenol/chloroform procedure (Sambrook & Russell 2001) or a DNeasy 96 Blood and Tissue Kit (Qiagen, Toronto, ON, USA) using the manufacturers protocol. DNA was resuspended in Tris-EDTA (pH 8.0) or eluted in the supplied buffer and the concentration normalized using a NanoDrop® ND-1000 UV-Vis Spectrophotometer (Thermo Scientific, Waltham, MA, USA).

Microsatellite amplification

A total of 4607 beetles were genotyped at 16 beetle-specific microsatellite loci using four co-amplification (four loci each) procedures (Davis *et al.* 2009). Amplified fragments were co-loaded into two injections on an AB 3730 DNA analyzer and band sizes were determined relative to GeneScan-500 LIZ (AB) and scored using GeneMapper software. One locus, *MPB012*, proved unreliable and one locus, *Dpo486*, was shown to be sex linked (Davis *et al.* 2009). Both were removed from further analysis.

Hardy–Weinberg equilibrium and linkage disequilibrium

Genotypic data from each site were checked for Hardy–Weinberg Equilibrium (HWE) across loci and sites using an expansion of Fisher's exact test. To ensure that all loci were independently assorting at all sites, linkage disequilibrium (LD; Slatkin & Excoffier 1996) was assessed using a likelihood ratio test. Statistical significance was evaluated both before and after sequential Bonferroni correction for multiple tests (Holm 1979; Rice 1989). All analyses were conducted using Arlequin 3.1.1 (Excoffier *et al.* 2005).

Genetic diversity

Gene diversity and allelic richness were used to describe patterns of genetic diversity across the study area. Observed and expected heterozygosity were calculated for each sample location using the microsatellite toolkit (Park 2001). We modelled mean expected heterozygosity and allelic richness for each sample location as a function of latitude using linear regression. Allelic richness was corrected for variation in sample size through rarefaction (Petit *et al.* 1998) implemented in fstat 2.9.3.2 (Goudet 2001) and sampling locations with fewer than 30 beetles were excluded. Patterns of genetic diversity were studied for the entire study area as well as within the main clusters identified by Bayesian analysis for population structure as described below.

Population structure

Population genetic structure was examined using three Bayesian approaches. We first used structure 2.3.1 (Pritchard *et al.* 2000; Falush *et al.* 2003) assuming an admixture model and correlated allele frequencies. Analyses were done without prior sampling information. After examining the effects of parameters on outcome and variance, each run with structure was performed with 10 000 burn-in and 10 000 MCMC steps. Default values were maintained for all other parameters. Population structure was tested at K values ranging from 1 to 49 with ten replicates, followed by 20 replicates each at $K = 1–10$. The best value of K was chosen using the second order rate of change (ΔK) method suggested by Evanno *et al.* (2005). To correctly assess the membership proportions (q values) for clusters identified by structure, the results of 20 replicates at the best fit K were post-processed using clumpp 1.1.2 (Jakobsson & Rosenberg 2007). These values were used

Table 1 Sampling locations (49), by region, for the mountain pine beetle with GPS locations, year sampled, number of beetles genotyped (N) (number of sites, in locations with more than one collection are given in brackets), mean observed heterozygosity (H_o), mean expected heterozygosity (H_e), mean number of alleles (N_A), allelic richness (A_R) and inbreeding coefficient (F_{IS}) are shown

Location	Code	Latitude (N)	Longitude (W)	Year Sampled	N	H_o	H_e	N_A	A_R	F_{IS}
Rocky Mountains										
Pine Pass	PP	55.6352	122.2522	2006	38	0.492	0.496	4.69	4.52	NS
Willmore Wilderness	WW	53.3421	119.4744	2006	37	0.514	0.533	5.46	5.26	NS
Kakwa†	KA†	53.8036	119.6004	2007/08	280 (6)	0.522	0.524	7.92	5.22	NS
Mount Robson	MR	52.8949	118.7348	2005	45	0.583	0.609	6.69	6.32	NS
Banff	BA	51.1779	115.5588	2006	52	0.633	0.626	6.69	5.95	NS
Lake Louise	LL	51.4172	116.1793	2006	42	0.610	0.629	6.46	6.12	NS
Canmore†	CA†	50.9852	115.3086	2007/08	472 (7)	0.609	0.627	11.31	6.55	0.028***
Kootenay	KO	50.6435	115.9786	2005/06	44 (2)	0.643	0.644	6.54	6.16	NS
Golden	GO	51.2402	116.6555	2005	39	0.653	0.624	7.08	6.67	NS
Golden†	GO†	51.3094	116.7834	2008	274 (3)	0.621	0.625	10.92	6.60	NS
Yoho†	YO†	51.1229	116.2908	2008	154 (2)	0.645	0.635	9.31	6.51	NS
Crowsnest Pass†	CP†	49.7485	114.5360	2007/08	99	0.639	0.637	8.00	6.14	NS
Sparwood†	SP†	49.8046	114.8557	2008	217 (3)	0.612	0.631	10.92	6.53	0.029**
Northeast of Rocky Mountains										
Tumbler Ridge	TR	54.9301	121.2959	2005/06	32 (2)	0.519	0.515	4.92	4.92	NS
Tumbler Ridge†	TR†	55.2598	121.4616	2008	307 (4)	0.485	0.488	6.92	4.63	NS
Grande Prairie	GP	54.7540	118.9333	2006	33	0.462	0.478	4.77	4.73	NS
Grande Prairie†	GP†	54.9332	119.1002	2007/08	434 (6)	0.482	0.489	7.46	4.64	NS
Fox Creek†	FO†	54.6456	116.6522	2007/08	129 (3)	0.500	0.494	6.23	4.68	NS
Fairview†	FV	56.4020	119.2572	2007/08	367 (7)	0.492	0.490	6.62	4.47	NS
Nechako Plateau										
Fort St. James	FJ	54.6452	124.4203	2005	44	0.467	0.484	4.46	4.25	NS
Francois Lake	FL	54.0318	124.9387	2006	53	0.463	0.461	4.46	4.07	NS
Houston	HO	53.9940	126.6527	2006	50	0.486	0.481	5.00	4.56	NS
Telkwa	TE	54.6674	127.0887	2006	51	0.463	0.479	4.54	4.22	NS
West of Rocky Mountains										
Mackenzie	MA	54.6963	122.8210	2005	50	0.512	0.503	5.00	4.66	NS
Prince George	PG	53.9065	122.8077	2005	48	0.492	0.516	5.92	5.42	NS
Salmon Valley	SA	54.2957	122.8949	2006	12	0.474	0.476	3.46	NI	NS
Norman Lake	NL	53.7497	123.4426	2006	65	0.473	0.484	5.31	4.51	NS
McBride	MB	53.3116	120.1266	2005	50	0.523	0.541	6.15	5.60	NS
Valemount	VM	52.6739	119.0190	2005	47	0.604	0.614	7.00	6.39	NS
Valemount†	VM†	52.8994	119.3538	2008	197 (3)	0.568	0.585	9.23	6.11	0.030*
Cariboo-Chilcotin										
Quesnel	QU	53.0370	122.2741	2006	55	0.510	0.532	6.08	5.28	NS
Bowron Lake	BL	53.2488	121.4172	2006	50	0.515	0.539	6.38	5.74	NS
Farwell Canyon	FC	51.6665	122.9033	2006	56	0.501	0.531	5.77	5.20	0.056*
Tatla Lake	TA	51.9715	124.4130	2006	49	0.487	0.490	5.31	4.89	NS
Lac La Hache	LH	51.7307	121.5984	2006	48	0.554	0.567	6.31	5.77	NS
Wells Gray	WG	51.7411	120.0120	2006	50	0.623	0.620	7.08	6.43	NS
Coast Mountains										
Whistler	WH	50.1678	122.9251	2006	43	0.572	0.621	5.69	5.36	0.079**
Cascade Mountains										
Manning Park	MP	49.2162	121.0697	2006	46	0.604	0.638	7.15	6.44	0.055*
Thompson-Okanagan										
Lillooet	LI	50.4566	121.6350	2006	48	0.571	0.585	6.77	6.13	NS
Merritt	ME	50.0352	120.6562	2006	49	0.614	0.627	7.23	6.54	NS
Kamloops	KL	50.4859	120.5316	2006	45	0.619	0.642	7.23	6.56	NS
Falkland	FA	50.5200	119.6018	2006	52	0.623	0.619	7.31	6.51	NS
Kelowna	KE	49.9965	119.6693	2006	43	0.601	0.603	7.08	6.53	NS
Kootenays										
Nancy Greene	NG	49.2591	117.9275	2006	47	0.660	0.641	7.15	6.50	NS
Valhalla	VA	49.7503	117.5181	2006	41	0.587	0.606	7.15	6.68	NS

Table 1 *Continued*

Location	Code	Latitude (N)	Longitude (W)	Year Sampled	N	H_o	H_e	N_A	A_R	F_{IS}
West Arm	WA	49.5244	117.2324	2006	13	0.621	0.641	5.00	NI	NS
Argenta	AR	50.1578	116.9173	2006	48	0.596	0.624	7.54	6.76	0.045*
Kimberley	KI	49.5841	116.1417	2005	49	0.625	0.633	7.08	6.45	NS
Southeastern Alberta										
Cypress Hills[†]	CH[†]	49.6130	110.1884	2008	13	0.604	0.638	4.85	NI	NS

NI, not included. NS, nonsignificant.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$(significant after the sequential Bonferroni correction).
[†]Locations with beetle, fungal and host samples collected in an integrated fashion.

to generate pie charts separately for each location to illustrate the geographical pattern of the clusters. A line was drawn to visualize the possible boundary between divergent clusters. STRUCTURE and the Evanno method capture only the uppermost level of structure when hierarchical levels of structure exist within a population (Evanno *et al.* 2005). Therefore, each cluster was further analysed for nested sub-structures and evaluated with the Evanno method as described above.

Although STRUCTURE (Pritchard *et al.* 2000) is commonly used for the analysis of population structure, it may not correctly identify population structure when overall F_{ST} is small (Latch *et al.* 2006; Waples & Gaggiotti 2006; Chen *et al.* 2007). To further explore population structure, we used TESS 2.3 (Durand *et al.* 2009) which implements a Bayesian clustering algorithm that uses spatial information to ascertain spatial population structure and performs well with F_{ST} values between 0.03 and 0.05 (Chen *et al.* 2007). With TESS, runs were done with 10 000 burn-in and 25 000 total sweeps and default values were maintained for all other parameters. We assumed no admixture and started the analysis using $K = 2$; K values were increased until the estimated number of clusters stabilized based on no further changes in the Deviance Information Criterion (DIC). Ten replicates were done for each K value. Taking the value at which DIC stabilized as the upper bound for the model with admixture, 100 replicates were done (assuming admixture) at $K2$–K(upper bound) (Fedy *et al.* 2008). The estimated membership probabilities of the 20 highest likelihood runs of best fit K were averaged using CLUMPP (Jakobsson & Rosenberg 2007) to correct for between-run discrepancies common to cluster analyses (Chen *et al.* 2007; Fedy *et al.* 2008).

BAPS (Corander *et al.* 2003, 2006; Corander & Marttinen 2006) also has been shown to be capable of identifying population structure when F_{ST} is small (Latch *et al.* 2006). BAPS determines optimal partitions for each K value and then merges the results according to the log-likelihood values to determine the best K value. Clustering analysis with the program BAPS 5.2 was done at the level of groups of individuals (population level), independently using two models (i.e. with and without spatial information models). Each analysis was done selecting 2–49 as K values (2–10 continuously and the rest with five value intervals up to 45 and then 49 as final K). Five repetitions were done at each K value.

Genetic differentiation

We partitioned genetic variance among and within clusters using analysis of molecular variance (AMOVA) carried out in ARLEQUIN 3.11 (Excoffier *et al.* 2005) based on pairwise F_{ST} corrected for unequal sample size using the method of Weir & Cockerham (1984). To study differentiation among clusters, two independent nested AMOVAs were carried out in which groups of locations were based on the results of the Bayesian analyses. Sample locations were grouped at $K = 2$ (STRUCTURE results) and $K = 4$ (BAPS results) independently. In each analysis, variance components were calculated (i) among groups (F_{CT}), (ii) among locations within groups (F_{SC}), and (iii) within sampling locations (F_{IS}). Furthermore, independent AMOVAs were done for each cluster and each subcluster to compare the level of genetic differentiation. Each AMOVA was run with 10 000 permutations at 0.05 significance levels.

To summarize the population structure and relationships among locations, a neighbour-joining tree was constructed using the program POPTREE2 (Takezaki *et al.* 2010). For the tree construction, Nei's genetic distance was used with 1000 bootstrap replicates, resampling loci, to assess node confidence.

Gene flow

Relationships between genetic and linear geographic distances [i.e. isolation-by-distance (IBD)], were examined using a Mantel test (Mantel 1967). Mantel tests implemented in GENEPOP 3.3 (Raymond & Rousset 1995) were done using the 'Isolde' option with 10 000 permutations. To visualize IBD patterns, $F_{ST}/(1-F_{ST})$ estimates

from GENEPOP were regressed against the logarithm of geographic distance (Rousset 1997). Following Garnier *et al.* (2004), IBD patterns were studied for the whole study area, as well as within and between the clusters and subclusters identified in the Bayesian analyses.

Gene flow among locations was assessed using pairwise F_{ST}. We considered nominally nonsignificant pairwise F_{ST} to indicate recent and/or historical gene flow between that pair of sample locations. We also used the program BARRIER 2.2 (Manni *et al.* 2004) to identify and graphically visualize barriers to gene flow. BARRIER uses Monmonier's (1973) maximum-difference algorithm to identify likely gene flow barriers (Manni *et al.* 2004).

To trace the origin of MPB expansion into northern Alberta, beetles from locations that represent recent infestation were assigned to a 'resource dataset' (i.e. all data minus the assigned location and secondly, to explore the temporial patterns, all data minus locations of interest) using assignment tests in GENECLASS 2 (Piry *et al.* 2004). Beetles from Fox Creek ($FO^{\dagger}$), Fairview ($FV^{\dagger}$) and two Grande Prairie locations (GP and $GP^{\dagger}$) were tested respectively, assigning one sampling location at a time. Individual and population assignments were done using likelihood-based assignment methods (Paetkau *et al.* 1995).

Historical demography

Signatures of bottlenecks and/or population expansion were tested in each sample location with a minimum of 30 beetles using the program BOTTLENECK 1.2.02 (Cornuet & Luikart 1997). We considered both the stepwise mutation model (SMM) and the two-phased mutation model (TPM). For the TPM, the variance was set at 30% leaving 70% proportion of SMM in TPM. Wilcoxon signed-rank tests were used to determine whether deviations from mutation-drift equilibrium (MDE) were statistically significant.

Results

Hardy–Weinberg equilibrium and linkage disequilibrium

Averaged across all sites for each of the 14 loci, observed and expected heterozygosity ranged from 0.215–0.820 to 0.145–0.821 respectively (Table 2). Prior to population genetic analysis of the 49 sampling locations, HWE and LD were examined at each of the 85 sampling sites. Deviations from HWE at 13 of the loci were not consistent across 85 sites, i.e. no sites had more than two loci out of HWE and only 71 out of 1190 total tests (5.97%) were significant before correction for multiple tests ($P < 0.05$ at $\alpha < 0.05$). Only three tests were significant after the sequential Bonferroni correction was applied for each locus across sites (i.e. $P < 0.05$ at $\alpha < 0.05/85$). Hence, those 13 loci were regarded as loci in HWE. One locus, MPB054, displayed a significant deviation from HWE. MPB054 was monomorphic in 14 sites, whereas tests for HWE showed a significant deviation in another 41 sites ($P < \alpha < 0.05$), and in 19 sites after the sequential Bonferroni correction was

Table 2 Loci typed. Total number of alleles (N_A), mean expected heterozygosity (H_e), mean observed heterozygosity (H_o), number of loci deviated from HWE before and after (in brackets) sequential Bonferroni correction, and fixation indices [F_{IS}, F_{ST} and significant values (***$P < 0.001$) are shown]

					Fixation indices			
Locus	N_A	H_e	H_o	HWE	F_{IS}	P	F_{ST}	P
Dpo028	19	0.461	0.439	5	0.042	***	0.056	***
Dpo103	26	0.820	0.821	3 (1)	NS		0.034	***
Dpo160	38	0.702	0.696	5 (1)	NS		0.023	***
Dpo453	22	0.680	0.663	14	0.022	***	0.008	***
Dpo479	11	0.655	0.657	5	NS		0.070	***
Dpo530	9	0.660	0.644	6 (1)	0.030	***	0.016	***
Dpo566	12	0.298	0.299	2	NS		0.019	***
Dpo760	14	0.594	0.588	9	NS		0.031	***
Dpo780	16	0.553	0.550	5	NS		0.026	***
Dpo793	14	0.557	0.552	3	NS		0.089	***
MPB011	10	0.566	0.537	4	0.050	***	0.014	***
MPB017	20	0.411	0.403	4	NS		0.024	***
MPB038	14	0.321	0.319	3	NS		0.076	***
MPB054	11	0.215	0.145	41 (19)	0.349	***	0.067	***

NS, nonsignificant.

applied across sites. Illustrated by the large and significant F_{IS} value across all sites, these deviations were because of locus-specific heterozygote deficiencies that may suggest the presence of a null allele. Therefore, locus MPB054 was excluded from further analysis.

Significant LD ($P < \alpha < 0.05$) was detected between some pairs of loci in some sites, i.e. out of 7735 total comparisons (14 loci at each of the 85 sites), only 91 tests (1.17%) were significant before the correction for multiple tests. These were not clustered at any pair of loci. None of these tests were significant after the sequential Bonferroni correction for multiple tests, at any level (i.e. at all loci across all sites, $\alpha < 0.05/7735$ comparisons, or at all loci within a site, $\alpha < 0.05/91$ comparisons) suggesting that these loci segregate independently.

Genetic diversity

Mean observed and expected heterozygosity among the 49 sampling locations varied between 0.46–0.65 and 0.46–0.64 respectively (Table 1). Mean expected heterozygosity and allelic richness by sample location declined from south to north with latitude (Fig. 2).

Population structure

We identified two geographically distinct clusters using STRUCTURE (Fig. 3) which were supported by the ΔK criterion (Evanno *et al.* 2005) and were geographically distinct. In most locations, >80% of individuals had similar cluster membership. We were unable to detect further substructure within either cluster.

We identified a similar boundary between southern and northern clusters at $K = 2$ using the program TESS (not shown in Fig. 4). However, the lowest DIC value before the plateau was observed at $K = 3$, which would yield an east-west subdivision of the southern cluster into southwest (SW) and southeast (SE) clusters as well as the northern cluster (Fig. 4). The location Lac La Hache (LH) close to the boundary between northern and southern clusters was grouped differently in $K = 2$ and $K = 3$ outputs.

Our population level analysis using BAPS (without spatial information) identified four clusters whereas BAPS (with spatial information) identified three (Fig. 4). These comprise the same main north and south clusters identified using STRUCTURE and TESS, as well as further subclustering of each main cluster. Similar to TESS, the south was divided into SW and SE subclusters by BAPS. Two locations at the boundary between the southern subclusters were grouped differently in BAPS and TESS (Fig. 4). In contrast to TESS, the northern cluster was split into lower (NL) and upper (NU) subclusters by

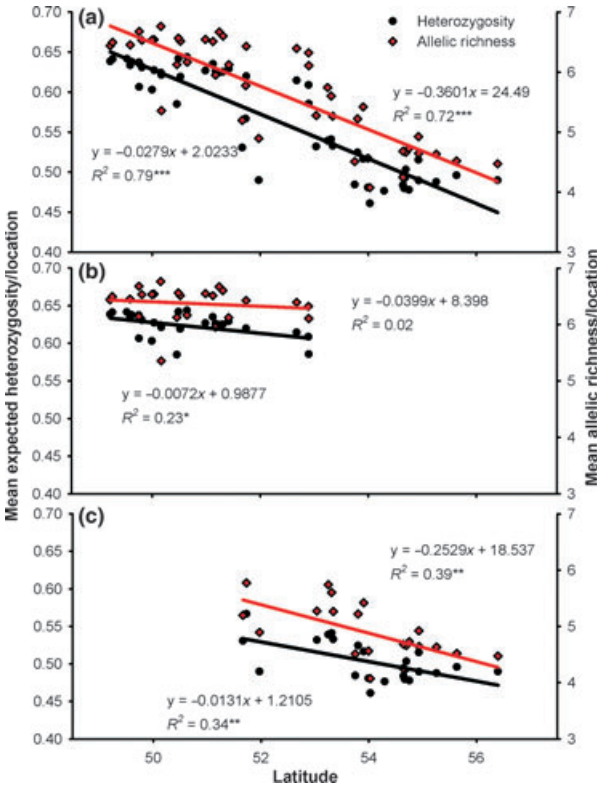

Fig. 2 Genetic diversity. (a) Decrease of mean expected heterozygosity (H_e) and allelic richness from south to north. (b) Pattern of genetic diversity within southern cluster. (c) Pattern of genetic diversity within northern cluster. R^2 significance is shown by $^*P < 0.05$, $^{**}P < 0.005$, $^{***}P < 0.0005$.

BAPS (without spatial information) analysis. Hereafter, we refer to $K = 2$ for the two main clusters identified using the program STRUCTURE and $K = 4$ for the four subclusters identified using the program BAPS.

In the neighbour-joining tree, locations were designated according to predicted STRUCTURE, TESS and BAPS assignments (Fig. 5). A clear division was noted between the northern and southern clusters defined by TESS (98% bootstrap support), with the NU and SE subclusters defined by BAPS forming weakly supported terminal monophyletic groups.

Genetic differentiation

Overall, genetic differentiation was low (AMOVA $F_{ST} = 0.037$), but significant ($P < 0.00001$). We observed significant genetic differentiation between the northern and southern clusters (nested AMOVA at $K = 2$ STRUCTURE clusters; $F_{CT} = 0.057$, $P < 0.00001$). Similarly, there was significant genetic differentiation between $K = 4$ clusters identified using BAPS ($F_{CT} = 0.045$, $P < 0.00001$). The level of population structure was

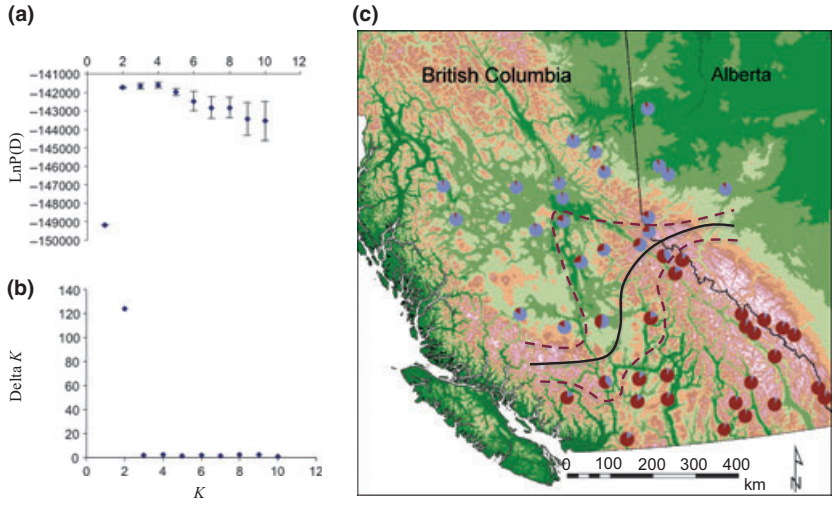

Fig. 3 STRUCTURE analysis of mountain pine beetles individuals in Western Canada. (a) Mean log probability of data LnP(D) over 10 runs for each K value as a function of K (error bars represent standard deviation). (b) Evanno's *ad hoc* statistic; ΔK as a function of K (over 20 replicates). (c) North and south clusters. Pie charts are based on proportion of membership of each predefined sampling location in each of the $K = 2$ clusters with prior sampling data not used. Solid line represents the boundary or the 0.50/0.50 membership isocline between two main clusters. The 80% membership isoclines in each cluster are represented by the dashed lines.

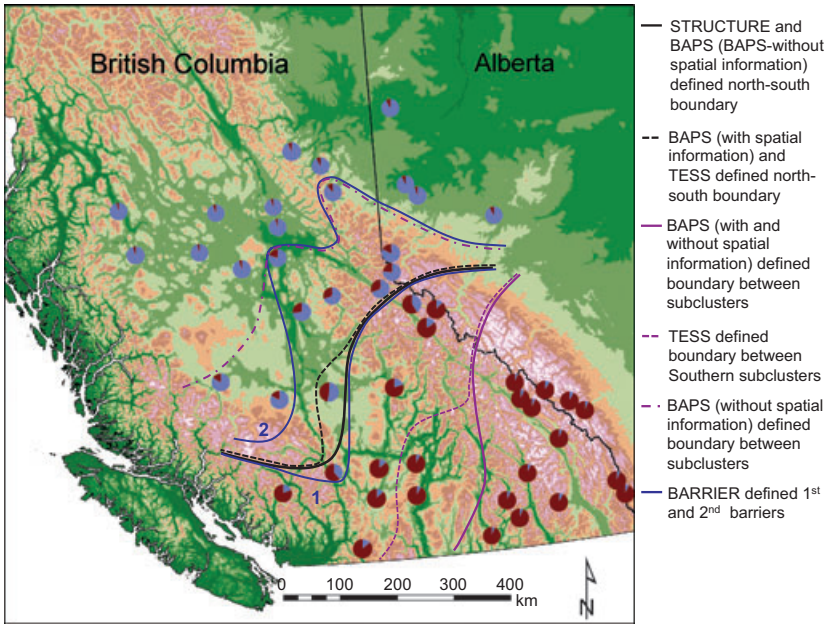

Fig. 4 Subclustering pattern of MPB in western Canada. Results of the TESS, BAPS (with and without spatial information), and BARRIER analyses were overlaid on top of STRUCTURE results. Pie charts are based on STRUCTURE results at $K = 2$.

slightly greater among locations within the southern main cluster ($F_{ST} = 0.0075$, $P < 0.00001$) than within the northern cluster ($F_{ST} = 0.0048$, $P < 0.00001$). Furthermore, the genetic differentiation between subclusters (F_{CT}) within the southern cluster was slightly higher (0.0080) than that in the northern cluster (0.0064) (both $P < 0.00001$). When each subcluster was analysed independently, the highest among-location variation was found within the SW ($F_{ST} = 0.0085$, $P < 0.00001$) and the lowest was found within the NU subcluster ($F_{ST} = 0.00122$, $P = 0.0018$). Among location variation within the SE and NL subclusters were intermediate at $F_{ST} = 0.0018$ ($P < 0.00001$) and 0.0028 ($P < 0.00001$) respectively.

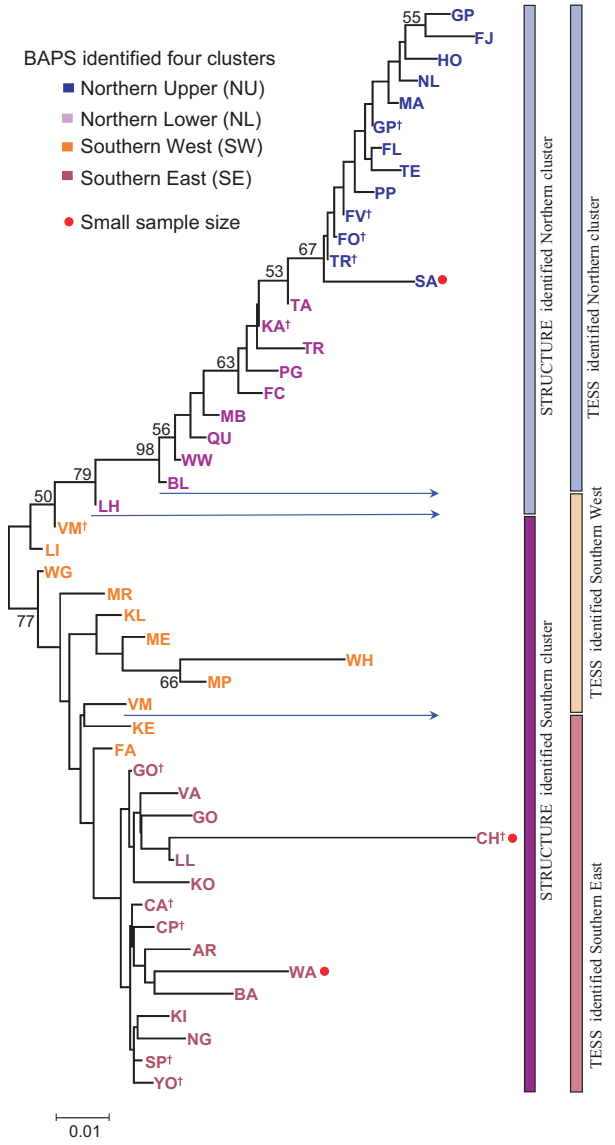

Fig. 5 Neighbour-joining tree of MPB sampling locations based on pairwise Nei's genetic distance. Bootstrap values >50% are shown are the respective nodes. STRUCTURE, TESS and BAPS identified clusters were overlaid on the tree. Sampling locations with samples sizes <15 are noted by red dotes.

The gradient of declining diversity from south to north was apparent within each cluster, but more pronounced in the north (Fig. 2). The relationship was statistically significant for both heterozygosity and allelic richness within the northern cluster (Fig. 2c) whereas in the southern cluster only the gradient in expected heterozygosity was significant (Fig. 2b). Furthermore, when locations were pooled into a northern or southern cluster (2338 and 2269 beetles, respectively), more alleles/locus (and hence more private alleles) were detected in the southern cluster (16.92 mean alleles per locus, 6.62 private alleles) than in the northern cluster (10.69 mean alleles per locus, 0.39 private alleles).

Gene flow

There was a highly significant IBD relationship across the whole range studied (Fig. 6a). The slope of the relationship between comparisons within the southern cluster was steeper than within the northern cluster (Fig. 6a). IBD between locations in the two main clusters was highly significant (Fig. 6b). A strong and significant IBD effect also could be observed between subclusters within the southern group whereas the IBD effect between the two subclusters within the northern group was relatively low. Within each of the four subclusters, significant IBD patterns were detected in SE, SW and NL, but not within the NU subcluster (Fig. 6c,d).

When program BARRIER was used to identify likely barriers to gene flow, the primary barrier corresponded to the boundary between the two main clusters whereas the secondary barrier corresponded to the boundary between the two subclusters in the northern group (Fig. 4).

Routes of gene flow were also examined using non-significant pairwise F_{ST} values, which may reflect recent gene flow between sampling locations. The percentage of pairwise F_{ST} values not significantly different from 0 (considering locations with sample sizes of at least 30) was 37.7% (N = 276 comparisons) within the southern cluster, and 31.2% within the northern cluster (N = 231 comparisons). In contrast, almost all pairwise F_{ST} values between locations in the two main clusters were significantly >0 (except for five locations pairs that were close to the boundary out of 528 total comparisons; Fig. 7a). When comparisons within each of the four subclusters were considered, 40% (SW) 67.9% (SE), 68.8% (NL) and 71.2% (NU) of the pair-wise F_{ST} comparisons were not significantly different from 0. In contrast, the percentage of nonsignificant comparisons between locations in SW and SE was 17.5% and between locations in NU and NL was 8.3%. All pairwise F_{ST} values (at P = 0.05) involving Whistler (WH) were significant.

The samples collected from new and expanding locations of the current epidemic in Alberta [Fox Creek (FO), Fairview (FV) and Grande Prairie (GP); Wood & Unger 1996; Safranyik & Carroll 2006; Raffa *et al.* 2008)], were genetically differentiated from all southern cluster locations, and genetically indistinct from most northern ones (Fig. 7b). For example, Tatla Lake and Fox Creek were not significantly differentiated, despite the large geographical distance (~596 km) between the two locations.

Assignment tests (GENECLASS) were also used to explore possible source locations for sampling locations northeast of the Rocky Mountains. Individuals from the

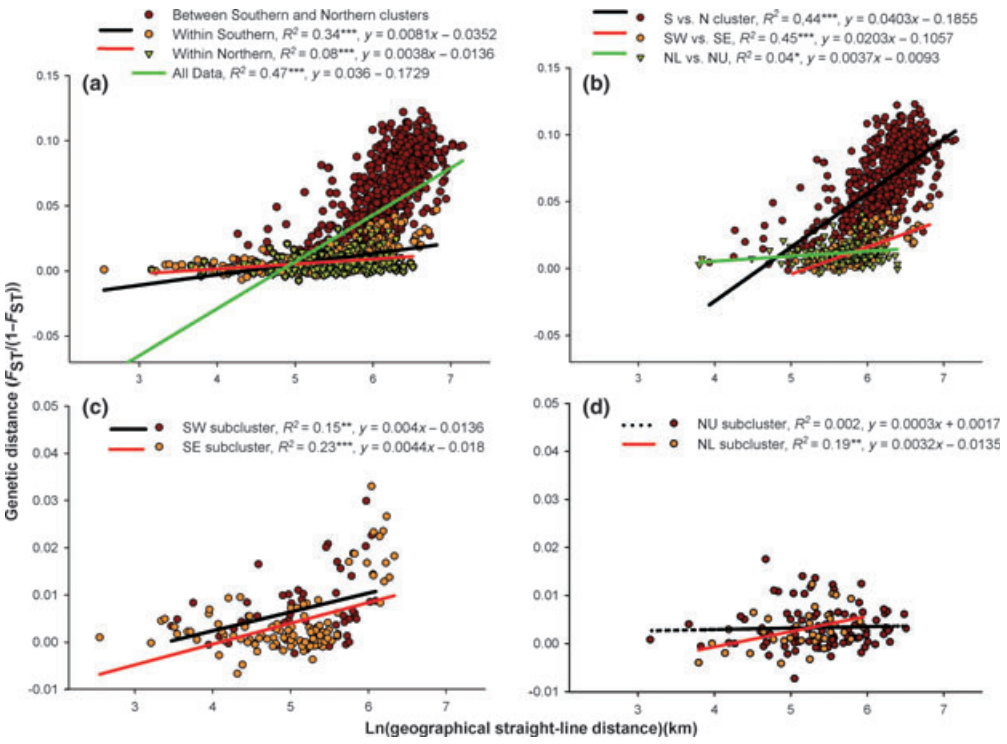

Fig. 6 Isolation-by distance (IBD) analysis within (w/n) and between (b/w) clusters identified. Regression of genetic differentiation [estimated by $F_{ST}/(1-F_{ST})$] against logarithm of geographical distances (km) based on Rousset (1997). (a) IBD across the study area and within each main clusters; (b) IBD between clusters; (c) IBD within southern subclusters; (c) IBD within northern subclusters. R^2 significance is shown by $^*P < 0.05$, $^{**}P < 0.005$, $^{***}P < 0.0005$.

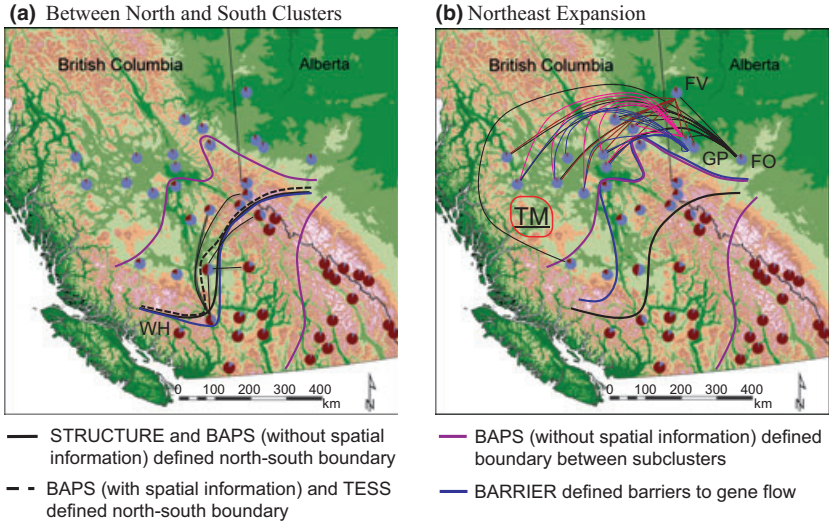

Fig. 7 Interconnected sampling locations. Solid lines between locations represent connections (i.e. nonsignificant pairwise F_{ST}), (a) between sampling locations of the southern and northern clusters and (b) connections to expansion sampling locations in Fairview ($FV^{\dagger}$), Fox Creek ($FO^{\dagger}$), Grande Prairie ($GP^{\dagger}$ and GP). Results were overlaid on the relevant STRUCTURE, BAPS, TESS and BARRIER results (Fig. 4). Pie charts are based on STRUCTURE results at $K = 2$. The relative location of Tweedsmuir Provincial Park (TM) to the sampling locations is shown.

2007/2008 sampling locations Tumbler Ridge, Fairview, Fox Creek, Grande Prairie and from the 2006 Grande Prairie locations were assigned to all other sampling locations. Consistent with the shallow genetic divergence noted, few exclusions occurred in the probability-based analysis. Likelihood-based analyses, however, indicated

Table 3 Results of likelihood-based assignment tests for locations in northern Alberta compared to all other locations. The rank (top 5) and score (%) are estimated by GENECLASS2. The scores given are based on frequency based likelihood-based method (Paetkau *et al.* 1995). Locations codes are found in Table 1

Location tested	Source location & assignment score (%)	Rank 1	2	3	4	5
FO†	Assigned to	TR†	GP†	FV†	KA†	MA
	Score	98.65	1.34	0.01	0	0
FV†	Assigned to	GP†	TR†	FO†	KA†	FL
	Score	100	0	0	0	0
GP†	Assigned to	TR†	FV†	FO†	PP	MA
	Score	100	0	0	0	0
GP	Assigned to	GP†	FO†	TR†	MA	FJ
	Score	95.25	3.28	0.99	0.25	0.21

that individuals were most likely of the NU subcluster origin. For 70.2% of 1270 individuals tested the top likelihood score was of NU origin whereas 98.2% was of northern cluster origin. Similar percentages were observed for all five sampling locations tested.

In the sampling location level analysis, sampling locations northeast of the Rocky Mountains were assigned only to the other tested locations in the NU cluster at scores greater than 95% (Table 3). When the same tests were done after removing all tested locations (Table 4), all of the 2007/08 locations assigned to the 2006 Francois Lake sampling location (NU cluster, scores >99%).

Table 4 Results of likelihood-based assignment tests for locations northeast of the Rocky Mountains compared to all other locations*. The rank (top 3) and Score (%) are estimated by GENECLASS2. The scores given are based on frequency based likelihood-based method (Paetkau *et al.* 1995). Locations codes are found in Table 1

Location tested	Source location & assignment score (%)	Rank 1	2	3
FO†	Assigned to	FL	PP	TE
	Score	99.72	0.28	0
FV†	Assigned to	FL	MA	PP
	Score	99.98	0.02	0
GP†	Assigned to	FL	MA	PP
	Score	100	0	0
TR†	Assigned to	FL	MA	PP
	Score	100	0	0
GP	Assigned to	MA	FJ	FL
	Score	97.91	2.09	0

*The locations GP, GP†, FO†, FV† and TR† were not included in the reference dataset.

In contrast, the 2006 Grande Prairie sample was assigned to a 2005 Mackenzie location (NU subcluster, scores >97%).

Historical demography

No signature of a recent bottleneck event was detected in any location. However, significant deviations ($P < 0.05$) from mutation drift equilibrium may suggest population expansion (i.e. expected heterozygosity less than heterozygosity at equilibrium), which was found under the stepwise mutation model in all locations except Whistler (WH). Under the two-phase model (TPM), evidence for expansion was detected in 27 locations including most of the locations at the eastern edge of the epidemic (Table 1).

Discussion

The mountain pine beetle in western Canada exhibits significant population genetic structure. We identified a clear north-south clustering pattern using all three Bayesian approaches. Only one location at the boundary between the main northern and southern clusters, Lac La Hache (LH), was inconsistently classified. Approximately, 5.7% ($P < 0.00001$) of the genetic variance was partitioned by AMOVA between the northern and southern clusters, and the primary barrier to gene flow delineated by the program BARRIER corresponded with the north-south cluster boundary. Furthermore, patterns of pairwise $F_{ST} > 0$ and the presence of private alleles within each of the two main clusters also indicate restricted gene flow (Allendorf & Luikart 2007). This indicates that the strongest barrier to gene flow within the studied area exists between the north and south clusters.

The observed population structure may be explained by a number of nonmutually exclusive hypotheses, including:

1 The existence of physical or climatic barriers,
2 Differing selective pressures between the northern and southern habitats,
3 The post-glacial expansion of mountain pine beetles into the northernmost portions of their historic range.

Previous studies of the mountain pine beetle support the role of geographic barriers, such as mountain ranges and large distances, in limiting gene flow and causing divergence among populations (Stock & Guenther 1979; Langor & Spence 1991; Kelley *et al.* 2000; Mock *et al.* 2007). Similar findings have also been noted in studies of other bark beetles (Coleoptera: Curculionidae: Scolytinae) in North America (*e.g.*, Stock *et al.* 1979; Roberds *et al.* 1987; Kelley *et al.* 1999; Six *et al.* 1999; Cognato *et al.* 2003;

Maroja *et al.* 2007) and Europe (e.g. Stauffer *et al.* 1999; Duan *et al.* 2004; Ritzerow *et al.* 2004; Faccoli *et al.* 2005; Horn *et al.* 2006). In this study, however, there exists neither a large distance nor an obvious geographic barrier that separates the northern and southern clusters. Excluding the recent expansion locations northeast of the Rocky Mountains, the northern cluster beetles are generally found on the Chilcotin, Cariboo and Nechako Plateaus, in an area jointly known as the Fraser or Central Plateau. Here, the primary host, lodgepole pine, is found in large continuous forest stands (Taylor & Carroll 2004). In contrast, the beetles in the southern cluster are found in more mountainous habitats, where the suitable host trees are generally found in a more patchy spatial distribution along the valley slopes (Ritchie 2008).

It is not clear why the transition from mountain habitat to the northern plateau would limit gene flow from the southern beetles into this region, although biological or climatic factors may be involved. Ongoing studies are looking at the possible roles of host availability, host genotype, the presence and diversity of fungal associates and other geographic or climatic features.

A hypothesis of post-glacial expansion predicts that populations are the oldest in the southern part of Western Canada, as these areas would have been colonized first following glacial retreat (Abbott & Brochmann 2003; Beatty & Provan 2010). In the presence of limited gene flow, newly founded populations are expected to contain lower levels of diversity. Genetic diversity should, thus, decline from south to north. Such a pattern has been demonstrated in many taxa (Hewitt 1999, 2004; Schoville *et al.* 2011), including species endemic to the Pacific Northwest (e.g. Green *et al.* 1996) indicating this is a common scenario in post-glacial colonization. The predicted genetic pattern is concordant with the observed diversity gradient, i.e. reduction in heterozygosity, allelic diversity and numbers of private alleles, from south to north reported in this study and in a previous range-wide study of mtDNA and AFLP variation (Mock *et al.* 2007). Based on a smaller, but more widely spaced, number of sampling locations, Mock *et al.* (2007) reported a decrease in genetic diversity north and south from central popularions in Idaho/Utah. The current study allows a fine scale analysis of this pattern at the northern extent of the range in western Canada. The gradient is more pronounced within the northern cluster than the southern cluster. Colonization within the northern cluster seems to follow the pattern predicted in the stepping stone colonization model (Slatkin 1991). Long-term persistence of beetles in the southern cluster, and hence, a likely series of complex historic events, may have disrupted this pattern within the southern cluster.

In terms of post-Pleistocene expansion, our results suggest that *Dendroctonus ponderosae* repopulated Western Canada from a single refugium south of the continental ice sheet. The existence of such a refugium during the last glaciation is supported by genetic (Marshall *et al.* 2002; Fazekas & Yeh 2006; Godbout *et al.* 2008) and fossil pollen data (MacDonald & Cwynar 1985; Cwynar & MacDonald 1987) for *Pinus contorta* var. *latifolia,* the beetle's primary host. The mountain pine beetle may have also persisted in minor coastal refugia, which were populated by *P. contorta* var. *contorta*, the shore pine (Heusser 1960; Peteet 1991; Fazekas & Yeh 2006; Godbout *et al.* 2008). Furthermore, recent genetic and pollen evidence support another possible refugium of flora and fauna during the last glaciation, in the Beringia region (Brubaker *et al.* 2005; Anderson *et al.* 2006; Beatty & Provan 2010). However, our study does not support a spread of beetles from that region (i.e. no decline in diversity from the northwest).

The evidence for population structure within clusters was not as strong as that found between clusters. Subclustering within the southern cluster was identified by both TESS and BAPS, whereas subclustering within the northern cluster was identified only by BAPS. The second likely barrier to gene flow identified by BARRIER supported the subclustering of the northern cluster defined by BAPS. The genetic differentiation between subclusters in either the northern or southern subclusters (F_{CT} = 0.0064 and 0.008, respectively) was seven to nine times lower than that found between the clusters (F_{CT} = 0.057). In the southern cluster, this structure may simply reflect the spatial IBD trends observed in the data and not have any further biological significance. In the northern cluster, however, where IBD trends are weaker (and even lacking in the NU subcluster), this structure is most likely the signature of the rapid northeastern expansion of the beetles in the current outbreak. In this regard, the NU subcluster can be viewed as an expanding group that originated in the northern cluster.

Among the four subclusters, the NU subcluster is characterized by a lack of IBD, the lowest genetic differentiation among locations (F_{ST}), and the least genetic diversity. Collectively, these findings indicate a lack of equilibrium between genetic drift and gene flow and are consistent with the recent expansion of MPB. Pairwise F_{ST} values in the NU subcluster vary within a small range (Fig. 6b) and are generally nonsignificant, indicating a nonequilibrium situation in which gene flow dominates over drift (Hutchison & Templeton 1999). Hence, the lack of IBD in the NU subcluster is most likely because of both long distance dispersal events and recent age. Low levels of differentiation can be because of high gene flow among locations and/or the recent origin of beetles from one or a few common sources. As Namkoong *et al.* (1979) reported, a region-

wide homogenization of population allele frequencies typically occurs when epidemics spread from epicentres.

The comparative lack of mountain ranges in the north vs. the south, as well as the contiguous cover of susceptible hosts over the large Central Plateau of northern BC, may have facilitated more gene flow in the north once climatic constraints were removed (Carroll *et al.* 2004). Field observations combined with the results of this study support the assumption that the mountain pine beetle outbreaks in the NU cluster are mainly because of long-distance dispersal from an epicentre. Large numbers of mountain pine beetles were not reported northeast of the Rocky Mountains in northern Alberta prior to the current outbreak. These represent the best locations to study assumptions of dispersal. Indeed, the movement of beetles into this region was so pronounced in the summer of 2006 (corresponding to the 2007 sample) that it was described as ''beetle rain''. Assignment tests clearly show that the likely origin of the 2007/2008 samples northeast of the Rocky Mountains were from NU subcluster locations west of the Rocky Mountains. Previous studies have reported the long-distance dispersal events of bark beetles by atmospheric winds (Furniss & Furniss 1972; Safranyik *et al.* 1992; Jackson *et al.* 2008; Westfall & Ebata 2008) and beetles have been captured moving eastward over the Rocky Mountains (Jackson *et al.* 2008). Consistent with observational data (D. Lux, personal communication), the pre-2007 Grande Prairie samples were assigned to a different location west of the Rocky Mountains, suggesting multiple waves of immigration.

The results show that the beetles in northern Alberta are mainly or completely from northern BC. Tweedsmuir Provincial Park, located in west-central BC, has been implicated as a primary epicentre of the current outbreak (Aukema *et al.* 2006). Although the data set did not include beetles from the park itself, the Houston site just to the north of the park and Tatla Lake just south of the park may be considered surrogates for the Tweedsmuir beetles. Indeed, the Tatla Lake area is close to one of the first regions that erupted in the mid-1990s during the onset of the current epidemic. As both these locations are part of the NU subcluster, our results are consistent with the Tweedsmuir Park area being an epicentre and the primary source of the NU cluster of the outbreak.

Consistent with the large population density of MPB outbreak populations, no loss of genetic variation was associated with the northeastern range expansion. Similar results have been noted in other eruptive insects (Berthier *et al.* 2006; Chapuis *et al.* 2008) and other invasions with high numbers of founders or multiple waves of founders (Dlugosch & Parker 2008; Uller & Leimu 2011). The retention of the genetic variation suggests that the newly established population will possess the full evolutionary potential of the source population, and thus may have a higher likelihood of adapting to the novel host environment than populations experiencing founder effects. However, a recent meta-analysis of 119 human-mediated range expansions did not find a relationship between genetic variation and invasiveness (Uller & Leimu 2011) suggesting that genetic variation alone does not predict the success of range expansion. Despite observational evidence of successive waves of immigrants in multiple years, the evidence does not support a role for the southern cluster in the northeast range expansion. Beetles either have not dispersed from the southern cluster to northern Alberta or the southern beetles have not survived in northern Alberta because of lack of adaptations to this less climatically suitable region. Furthermore, the genetic similarity with the northern cluster beetle would predict that the expansion and source populations have similar biological characteristics and should respond in the same way to management efforts.

Although Aukema *et al.* (2006) found evidence for a northern epicentre in Tweedsmuir Provincial Park, they also found simultaneous geographically isolated outbreaks in southern BC. The existence of genetic diversity gradients and substructure during the outbreak clearly support multiple epicentres across BC. Furthermore, the presence of IBD patterns indicates the long-term persistence of beetle populations at locations throughout most of the study area. If IBD exists in an area of concern it reveals that equilibrium has most likely been reached between the gene flow and genetic drift (Slatkin 1993), a situation that may take thousands of generations to develop (Johnson *et al.* 2007). The factors governing the epidemics in the locations in the southern cluster seem to be mainly because of the expansion of numerous endemic-phase native populations. An extended temporal analysis of variation would be required to assess whether the current outbreak will lead to the homogenization of gene frequencies among the southern outbreaks or not. However, the existence of IBD suggests the historic importance of geographic barriers, presumably mountain ranges, to limit gene flow. The isolated nature of locations in the southern cluster is confirmed by the high among-location differentiation and the low percentage of nonsignificant pairwise F_{ST} comparisons. The Whistler (WH) sampling location can be viewed as an extreme example of an isolated outbreak in the southern cluster. Among all locations studied, Whistler showed unique characteristics including being the only location with all pairwise F_{ST} values significant and a lack of evidence of population expansion with the program BOTTLENECK. Whistler is close to the west coast of BC. The predominant west to east atmospheric wind direction

during the summers would not favour passive beetle movement into this location from the more easterly locations sampled.

Range expansion of the mountain pine beetle northeastward across the Rocky Mountains and into the lodgepole and subsequent jack pine forests of the boreal forest is a major concern (Rice *et al.* 2007; Cullingham *et al.* 2011). Climate modelling predicts that climatic suitability for the beetles will continue to increase in this region (Carroll *et al.* 2004; Safranyik *et al.* 2010). Mountain pine beetle outbreaks are not considered endemic to these forests and a series of recent successful invasions into northern Alberta have been recorded (Raffa *et al.* 2008; Cullingham *et al.* 2011). Our study clearly shows that the spread of beetles into northern Alberta has occurred mainly from northern BC. Our results point to the need for further investigations as to the adaptive differences among beetles in western Canada that may explain their current geographic distribution (and possibly the limitations of) as well as their successful dispersal into the boreal forest of Canada. Finally, our results indicate that MPB, like other eruptive organisms (Berthier *et al.* 2006; Chapuis *et al.* 2008), retains most of its genetic variability during mass dispersal events, and hence northern Alberta populations are likely to have retained the evolutionary potential necessary for adapting to the novel host jack pine. With continued climate change reducing climatic constraints, a further range extension into eastern Canada and United States, as predicted by Logan & Powell (2001), will not be associated with loss of genetic diversity if current outbreak conditions remain.

Most studies on insect range expansion have focused on invasions of exotic ants or bees into new environments (Kenis *et al.* 2009) or on range shifts mainly in Lepidoptera and Odonata (Parmesan 2006). This study describes the pattern of range expansion in a native eruptive insect herbivore. It illustrates a rapid range-wide response to the removal of climatic constraints, and the potential for range expansion of a regional population. Similar to MPB, many other insect species have a high reproductive potential and dispersal ability. In light of ongoing climate change, the potential for range expansion of other pest and nonpest insect species is likely high.

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This study was multi-institutional project operated under the umbrella of a mountain pine beetle systems genomics (TRIA) project. At the time of the study G.D.N.G.S and N.V.B. were M.Sc. students at the University of Northern BC whose research focused on the genomics and population genetics of the MPB outbreak occurring around them. B.S.L. is a Professor at the University of Northern BC with a research focus on forest insects. J.E.K.C. is an Associate Professor at the University of Alberta. She is a tree biologist whose research is mainly focused on understanding how environmental cues affect growth and development of forest trees. C.S.D. has a keen interest in marker development and applying new molecular techniques to studies of molecular ecology. P.M.A.J. was a postdoctoral researcher with the TRIA project. He is currently an Assistant Professor at the University of Montreal were he studies spatial ecology with particular emphasis on forest disturbance dynamics. D.W.C. is a Professor of wildlife genetics at the University of Alberta. K.E.M. is an Associate Professor in conservation genetics and molecular ecology at Utah State University. B.W.M. is an Associate Professor at University of Northern BC with research interests in molecular ecology and evolution.

Data accessibility

Sample locations and microsatellite data: DRYAD entry doi: 10.5061/dryad.9s4r4g90.