ARTICLE

Modelling landscape genetic connectivity of the mountain pine beetle in western Canada[1]

Julian Wittische, Jasmine K. Janes, and Patrick M.A. James

Abstract: The current mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins, 1902) outbreak has reached more than 25 million hectares of forests in North America, affecting pine species throughout the region and substantially changing landscapes. However, landscape features that enhance or limit dispersal during the geographic expansion associated with the outbreak are poorly understood. One of the obstacles in evaluating the effects of landscape features on dispersal is the parameterization of resistance surfaces, which are often constructed based on biased expert opinion or by making assumptions in the calculation of ecological distances. In this study, we assessed the impact of four environmental variables on MPB genetic connectivity across western Canada. We optimized resistance surfaces using genetic algorithms and models of maximum likelihood population effects, based on pairwise genetic distances and ecological distances calculated using random-walk commute-time distances. Unlike other methods for the development of resistance surfaces, this approach does not make a priori assumptions about the direction or shape of the relationships between environmental features and their cost to movement. We found highest support for a composite resistance surface including elevation and climate. These results further the understanding of MPB movement during an outbreak. Additionally, we demonstrated how to use our results for management purposes.

Key words: range expansion, gene flow, random walk resistance, linear mixed-effect model, insect outbreaks.

Résumé : L'épidémie actuelle du dendroctone du pin ponderosa (DPP; *Dendroctonus ponderosae* Hopkins, 1902) s'étend sur plus de 25 millions d'hectares de forêts en Amérique du Nord; elle touche les espèces de pin à travers la région et modifie substantiellement les paysages. Cependant, les caractéristiques du paysage qui favorisent ou limitent la dispersion durant l'expansion géographique associée à l'épidémie sont peu connues. Un des obstacles pour évaluer les effets des caractéristiques du paysage sur la dispersion est le paramétrage des surfaces de résistance, lequel est souvent réalisé à partir de l'opinion biaisée d'experts ou en faisant des hypothèses pour le calcul des distances écologiques. Dans cette étude, nous évaluons l'impact de quatre variables environnementales sur la connectivité génétique du DPP à travers l'ouest du Canada. Nous avons optimisé les surfaces de résistance à l'aide d'algorithmes génétiques et de modèles des effets les plus vraisemblables sur les populations, sur la base de distances génétiques et de distances écologiques appariées calculées à l'aide des distances déterminées par la méthode de durée du trajet et de marche aléatoire. Contrairement aux autres méthodes d'élaboration des surfaces de résistance, cette approche ne fait pas d'hypothèses a priori concernant la direction ou la forme des relations entre les caractéristiques environnementales et leur coût de changement. Nous avons trouvé le meilleur support pour une surface de résistance composite incluant l'altitude et le climat. Ces résultats améliorent la compréhension du mouvement du DPP au cours d'une épidémie. De plus, nous avons démontré de quelle façon utiliser nos résultats à des fins d'aménagement. [Traduit par la Rédaction]

Mots-clés : expansion de l'aire de répartition, flux génétique, résistance de marche aléatoire, modèle linéaire à effet mixte, épidémies d'insecte.

Introduction

Dispersal is an important determinant of ecological and evolutionary dynamics due to its influence on population connectivity (Taylor et al. 1993). In turn, connectivity has significant implications for population (Martin and Fahrig 2016) and species persistence (Thomas 2000). Understanding dispersal is also important for the effective management and conservation of populations and communities faced with ongoing global change and increasingly fragmented and degraded habitats (Haddad et al. 2015). Dis-

persal models are particularly needed to help us better forecast range expansions of alien invasive and native irruptive species (Rejmanek and Richardson 1996). Irruptive and invasive species represent non-negligible threats to biodiversity and the provisioning of ecosystem services at a global scale (Simberloff et al. 2013). Improved understanding of how abiotic and biotic conditions influence dispersal of outbreaking or invasive species is of fundamental value to natural resource managers.

One species of particular concern in the boreal forest ecosystem of western North America is the mountain pine beetle (MPB;

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Table 1. Summary of predictor variables used in the optimization and selection process and the associated hypotheses.

Data	Sources	Hypothesis[a]	References
Elevation	SRTM, GMTED, NRCAN, registry.opendata.aws, open.canada.ca	(–): limited dispersal at high elevation	Amman et al. 1973
		(–): relief could act as a barrier for wind-dispersed MPB	de la Giroday et al. 2011
Pine volume	NRCAN/CFS, open.canada.ca	(+): preference for high-volume stands could increase effective dispersal	Safranyik et al. 2010; James et al. 2011
Drought	NRCAN/CFS, open.canada.ca	(–): severe drought decreases survival and brood production by depleting or drying phloem tissue	Amman 1972; Safranyik and Wilson 2006
		(+): drought weakens trees, which lowers their defenses and could increase effective dispersal	Berg et al. 2006; Raffa et al. 2008
Climate suitability index	NRCAN/CFS	(+): climatic limitations to successful reproduction would hinder effective dispersal	Carroll et al. 2004; Bentz et al. 2010; James et al. 2011

Note: SRTM, Shuttle Radar Topography Mission (NASA and NGA); GMTED, Global Multi-resolution Terrain Elevation Data (USGS and NGA); NRCAN, Natural Resources Canada; CFS, Canadian Forest Service.

[a]The minus (–) or plus (+) represents a hypothetical negative or positive relationship between the predictor and dispersal.

Dendroctonus ponderosae Hopkins, 1902; ITIS.org Taxonomic Serial Number 114918). The MPB is a highly mobile, native, and irruptive forest insect pest whose outbreaks have significant ecological and economic consequences as it feeds on the majority of pine species in its range, including, among others, lodgepole pine (*Pinus contorta* Douglas ex Loudon), sugar pine (*Pinus lambertiana* Douglas), western white pine (*Pinus monticola* Douglas ex D. Don), and ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), and is able to maintain outbreaks in healthy stands (Safranyik and Wilson 2006). MPB usually attack weak or damaged trees as do other bark beetle species; however, once MPB populations increase beyond a threshold, MPB populations are able to overcome tree defenses. MPB populations may then erupt into self-propagating large-scale outbreaks (Safranyik and Wilson 2006). MPB outbreaks represent one of the most significant biotic threats to Canadian forests (Raffa et al. 2008; Boucher et al. 2018). Since the early 2000s, outbreaking populations of the MPB have undergone rapid expansion from their historical range (Cullingham et al. 2011; de la Giroday et al. 2012). Eastward outbreak spread rates exceeded 80 km·year⁻¹ in certain years (Cooke and Carroll 2017). Models combining atmospheric dispersal and weather found that long-distance dispersal events greater than 50 km are plausible (Ainslie and Jackson 2011). At the new edge of its range, close to the Alberta–Saskatchewan border of Canada, the outbreak has now reached novel habitats and has the potential to spread further in the boreal forests, both eastward and northward, and is currently threatening forest resources in these areas (Safranyik et al. 2010; Cullingham et al. 2011; Sambaraju et al. 2012; Janes et al. 2014).

Despite being able to monitor the extent and rate of spread of the current outbreak (e.g., Cooke and Carroll (2017), we have limited knowledge about what hinders or facilitates MPB dispersal and movement and, thus, population connectivity (Taylor et al. 1993). Previous studies conducted in western Canada have shown that MPB populations belong to two clusters, a northern cluster and a southern one (James et al. 2011; Samarasekera et al. 2012; Janes et al. 2014). The northern cluster showed reduced genetic diversity relative to the southern one, which indicates a more recent colonization (Samarasekera et al. 2012). The importance of environmental features such as elevation, climate, and host volume on MPB dynamics and local population connectivity has been described previously (Bentz et al. 2010; James et al. 2011; de la Giroday et al. 2011). Drought has also been shown to increase host

tree vulnerability and may influence MPB population connectivity (Berg et al. 2006; Raffa et al. 2008). Although multiple landscape features likely influence MPB population connectivity (Table 1), we have yet to quantify the relative importance of each of these features to MPB movement across the Canadian portion of its range and how they influence outbreak spread.

Due to the challenges of directly monitoring small organisms such as forest insects, population connectivity is increasingly estimated using indirect methods that quantify intergenerational gene flow using molecular markers (Broquet and Petit 2009). Dispersal can be considered effective when it creates gene flow, which for mobile animal species often requires dispersing individuals to reproduce in a population after having dispersed (Broquet and Petit 2009). Because the genetic information used by indirect methods that estimate dispersal is affected by gene flow, they provide estimates of "effective" dispersal (Clobert et al. 2009). In general, the greater the gene flow is, the greater the presumed effective dispersal and, hence, the greater the functional connectivity between populations (Clobert et al. 2009).

When gene flow is combined with information on landscape resistance within a landscape genetics framework (Manel et al. 2003), one can also infer which landscape features hinder or facilitate movement among populations. Resistance may represent the physiological cost of moving through the landscape, the mortality for the organism moving through the landscape, and (or) the behavioral response of an organism to crossing the landscape (Bonte et al. 2012).

In this study, we investigate how landscape resistance influences MPB population genetic connectivity using landscape genetics to increase our understanding of the spatial dynamics of MPB outbreaks. We specifically sought to identify the landscape features that have affected MPB movement in the recent outbreak region in western Canada.

An important challenge in resistance-based models of landscape connectivity is that model outcomes are sensitive to the parametrization of resistance surfaces (Rayfield et al. 2010; Spear et al. 2010). Often, such parameterization relies heavily on expert opinion, which has been shown to be unreliable at times (Rayfield et al. 2010; Koen et al. 2012) and occasionally to perform worse than random null models of resistance (Charney 2012). To overcome the issues associated with parameterizing of resistance surfaces, we used a machine-learning approach (Peterman 2018) to identify the optimal model of MPB landscape genetic connectiv-

Fig. 1. Populations sampled across Alberta and British Columbia. Sampled sites are represented by black circles. See Table 2 for site abbreviations. [Colour online.]
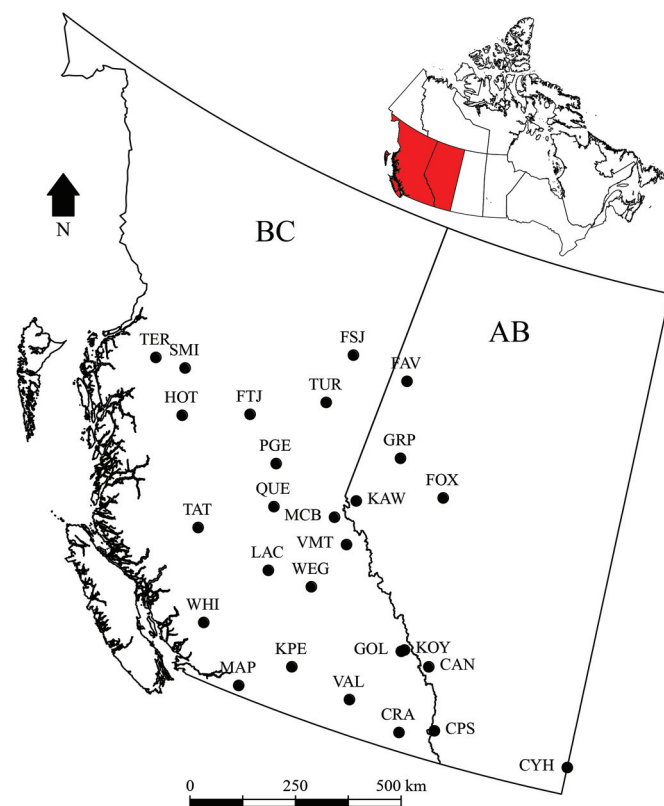
ity. We compared millions of potential resistance surfaces resulting in a link-based landscape genetics model of MPB genetic connectivity. We sought to identify the best fit between genetic and ecological distance matrices. The identified best resistance surfaces were used to predict future expected population connectivity and likely routes of expansion. This information could allow for a better prioritization of preventive management efforts.

Methods

Study area and genetic data

To address our research questions, we used the genetic dataset of Janes et al. (2014). These data include 532 MPB individuals from 27 sites throughout Alberta and British Columbia, Canada (Fig. 1; Table 2). These sites included both historical and recently colonized parts of the MPB range circa 2006–2010 (Janes et al. 2014). We used the same 764 single nucleotide polymorphisms (SNPs) that had been manually scored and screened for linkage disequilibrium and deviation from Hardy–Weinberg equilibrium (Janes et al. 2014). Allele frequencies for all populations were used to estimate genetic differentiation between populations using a sample size corrected estimator of F_{ST} (Weir and Cockerham 1984). The number of individuals and observed heterozygosity are displayed in Table 2. Additional details can be found in Janes et al. (2014).

Environmental data

We investigated the influence of elevation, climate, drought, and pine volume on population connectivity quantified using a matrix of pairwise F_{ST} values (Table 1). Environmental data were represented as continuous raster layers for the full extent of the study area at a spatial resolution of 10 km. We chose an elevation raster built from multiple sources (Table 1) and retained areas above sea level. Pine volume represents the volume of pine trees (m^3) per hectare. We used the climate moisture index to represent

drought (Hogg 1997). This index measures the absolute difference between precipitation and potential evapotranspiration. Finally, we used the mean climate suitability index (CSI) to incorporate the effect of climate on the MPB. We used the CSI mean of the period from 1991 to 2020 to cover both the start of the current outbreak and the start of the expansion to Saskatchewan. CSI is a synthetic measure built using multiple climatic variables known to determine MPB development, survival, and attack success (Safranyik et al. 2010). We made no a priori assumptions regarding the magnitude, shape, scale, or direction of influence of environmental resistance on gene flow. Instead, through application of our chosen optimization algorithm, we let the data tell us how environment affects MPB gene flow.

Optimization process

We used a genetic algorithm optimization approach provided by the ResistanceGA package (Peterman 2018) to convert information on landscape spatial environmental heterogeneity into movement costs (Spear et al. 2010; Zeller et al. 2012). Genetic algorithms are an example of machine learning that represents a suite of general approaches used to extract functional relationships from data without prior assumptions (Hastie et al. 2017). Machine-learning methods have been incorporated in the biologist toolset with very diverse applications (Tarca et al. 2007; Peters et al. 2014). For example, in this study, we used machine learning to improve resistance surfaces in an iterative way. The genetic algorithm that we used is an evolutionary example of a machine-learning algorithm. It is evolutionary in that we can consider the different resistance surfaces as individuals in a population undergoing evolution. The evolution starts with our population (i.e., set of resistance surfaces), which is part of a generation. As in a natural population, the fitness (model performance) of individuals varies. The fittest individuals survive natural selection (model performance threshold) and the characteristics (parameters) that allowed them to survive are therefore preserved. The genomes of surviving individuals are then mutated and recombined: a new generation has been created. Mutation represents a divergent force that partly changes the parameters of the top resistance surfaces to avoid local parameter optima and explore a different parameter space. Crossover represents a convergent force that will concentrate the characteristics of two good resistance surfaces to produce possibly superior new solutions. This whole process is repeated for a number of generations until the population reaches a fitness level that does not improve for several generations. The ResistanceGA package (Peterman 2018) that we used depends on the GA package (Scrucca 2013, 2017) to implement its genetic algorithms.

Throughout the optimization process, genetic distances were regressed against ecological distances using linear mixed-effects models with a maximum likelihood population effects parameterization, an approach that overcomes the issue of non-independence of pairwise distances (MLPE; Clarke et al. 2002; Row et al. 2017; Shirk et al. 2018). MLPE does so by including a population covariance random-effects term that accounts for the non-independent error structure associated with pairwise distances (Clarke et al. 2002).

We calculated pairwise matrices of ecological distances between sample sites through a random-walk commute-time algorithm. Commute-time distances represent the expected length of paths travelled by random walkers during a round trip between two nodes (Göbel and Jagers 1974) and are proportional to resistance distances calculated through electrical circuit theory (Doyle and Snell 1984). Although several environmental variables can contribute to the surface used in a model (composite surface), one predictor is used. In addition to all of the resistance surfaces built from landscape features, we examined an intercept-only model (null model), as well as a simple geographical distance surface where the resistances of all cells in the resistance surface are set to

Table 2. Sampling size and observed heterozygosity for all sampling sites.

Sampling site	Sample size	Observed heterozygosity	Longitude	Latitude	Year
Canmore (CAN)	9	0.371	–115.3364	50.9323	2010
Crowsnest Pass (CPS)	21	0.355	–114.5525	49.6574	2007/2008
Cypress Hills (CYH)	18	0.357	–110.0363	49.5931	2007
Fairview (FAV)	21	0.364	–119.3860	56.5994	2008
Fox Creek (FOX)	23	0.362	–116.6348	54.4806	2008/2010
Kakwa–Wilmore (KAW)	21	0.376	–119.6004	53.8036	2006/2008
Grande Prairie (GRP)	21	0.364	–118.6135	54.9924	2008/2010
Cranbrook (CRA)	20	0.362	–115.6460	49.4086	2010
Ft. St. James (FSJ)	20	0.355	–121.7120	56.7043	2006
Ft. St. John (FTJ)	19	0.363	–124.4203	54.6452	2006
Golden (GOL)	21	0.370	–116.3816	51.0744	2007
Houston (HOT)	21	0.360	–126.6527	53.9940	2006
Kelowna–Peachlands (KPE)	21	0.370	–119.6690	49.9965	2006/2010
Kootnay–Yoho (KOY)	20	0.365	–116.2908	51.1229	2006/2007
Lac Le Hache (LAC)	20	0.389	–121.5984	51.7307	2006
Manning Park (MAP)	21	0.353	–121.0697	49.2162	2006
McBride (MCB)	19	0.379	–120.1266	53.3116	2006
Prince George (PGE)	17	0.377	–122.8080	53.9065	2006
Quesnel (QUE)	20	0.385	–122.2741	53.0370	2006
Smithers (SMI)	21	0.356	–127.3505	54.9289	2010
Tatla Lake (TAT)	21	0.372	–124.4130	51.9715	2006
Terrace (TER)	16	0.363	–128.5000	54.8365	2010
Tumbler Ridge (TUR)	21	0.355	–121.9848	55.5387	2010
Valhalla (VAL)	18	0.370	–117.5181	49.7503	2006
Valemount (VMT)	22	0.383	–119.3816	52.8532	2007/2010
Wells Grey (WEG)	20	0.386	–120.0120	51.7411	2006
Whistler (WHI)	20	0.338	–122.9251	50.1678	2006

Note: See Supplementary data[2] for F_{ST} values (Table S1), commute-time distances (Table S2), and geographic distances (km) (Table S3) for all pairs of populations in this table.

one (i.e., isolation-by-distance). This gave us a total of 17 different resistance models to parameterize through the genetic algorithm. Single-surface models were used to evaluate the individual hypotheses described in Table 1. Following individual optimizations, we constructed and evaluated multiple composite surfaces (i.e., surfaces made up of different combinations of the individual surfaces) to identify an overall best integrated model.

The first step of the optimization process for a single surface is to generate a random initial set of resistance surfaces. These surfaces are created by applying a transformation to each spatial environmental variable that is hypothesized to influence genetic connectivity. Possible transformation functions included eight exponential-based functions, each of which is defined by two parameters: shape and maximum resistance. We used saturating monotonic functions (origin-fixing linear left end, a saturating middle, and an asymptote right end) and unimodal functions (origin-fixing linear left end, a hump-shaped middle, and a zero-approaching right end), as well as the reverse, inverse, and inverse–reverse of both functions (Peterman 2018). For each transformation, initial values for the shape and maximum resistance parameters were chosen randomly (ResistanceGA defaults; Peterman 2018). At the end of this first step, we evaluated the set of potential resistance surfaces for their ability to model our pairwise genetic response matrix on the basis of their log-likelihood values. The top 5% of those resistance surfaces were retained (ResistanceGA defaults; Peterman 2018).

Next, we sought to identify global parameter optima for this set of retained resistance surfaces using genetic algorithms. Optima were identified through "evolution" of the model parameters through the processes of "mutation" (probability = 0.2) and "crossover" (probability = 0.9). All steps were repeated until no improvement in log-likelihood was found for 25 iterations. This process

was applied to each landscape variable and combinations of variables, giving us 17 parameterized candidate models.

Model selection and performance

We selected the best model from our set of candidate models using the Akaike information criterion corrected for sample size (AICc) and associated Akaike weights (ω_{AICc}). A bootstrapping analysis was then conducted to validate the selection of our models (Peterman 2018). The goal of the bootstrapping procedure was to assess how sensitive our conclusions were to outliers (sites). To do this, 75% (ResistanceGA defaults; Peterman 2018) of our populations were randomly resampled without replacement 1000 times. For each iteration (i.e., sample) of the bootstrapping, we ranked the previously optimized models according to their log-likelihood when using this sample (1 meaning the best model and 2 meaning the second best model) and recorded which model was the best model. Average ranking and frequency of model being the top model were calculated for each model over all 1000 bootstrap iterations. To assess the absolute performance of the top model, we evaluated its marginal R^2 (fixed factors) and its conditional R^2 (fixed and random factors).

Finally, we sought to verify whether our best model based on all populations (Fig. 1) would still be considered a top model when examining population connectivity only within the northern genetic cluster. This cluster is of special interest because the current MPB outbreak is expanding from this cluster (James et al. 2011; Samarasekera et al. 2012; Janes et al. 2014). To do so, we re-ran the bootstrapping analysis described above only within this cluster.

Model applications — origin of the Hinton MPB population and potential for eastward expansion

For both applications, we modelled connectivity using circuit theory and visualized our previous results using electrical current

Fig. 2. Single-surface optimization results for each environmental variable: (A) elevation, (B) pine volume, (C) drought, and (D) climate suitability index (CSI). The frequency distributions of cost values and original environmental values are shown on the sides of the graphs.
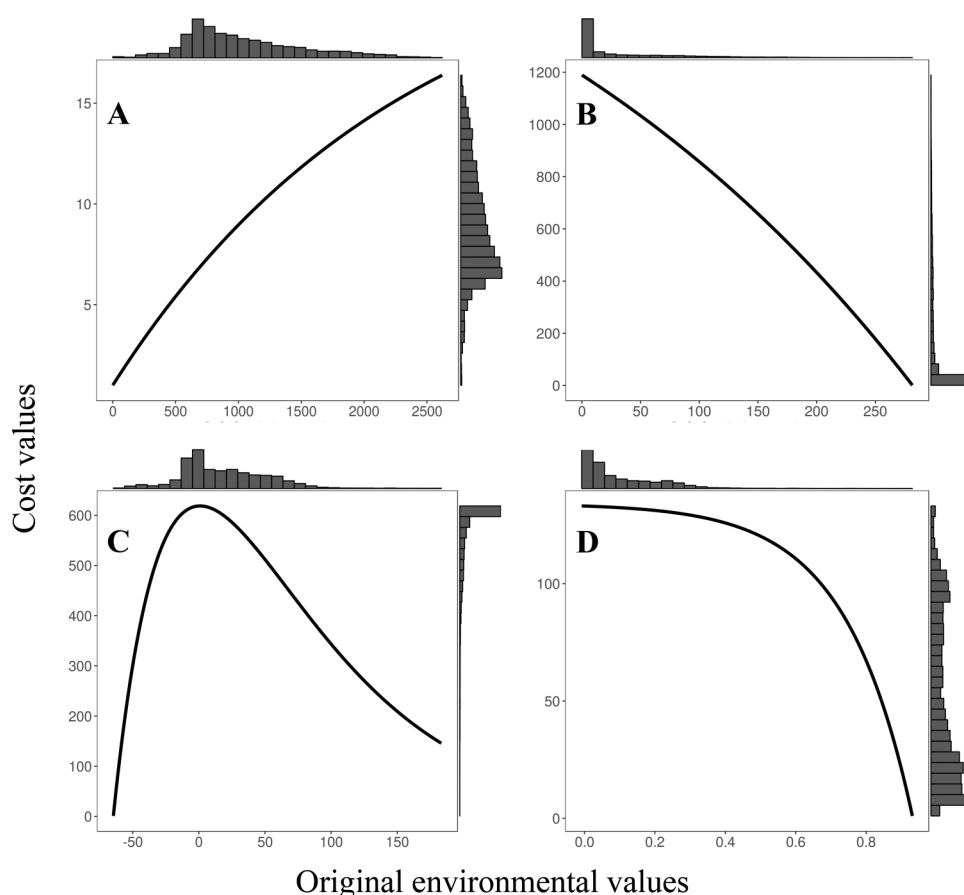
maps (McRae et al. 2008). Here, electrical current is analogous to the probability of movement through the landscape (Doyle and Snell 1984). The resulting current map illustrates the most likely paths of colonization (McRae et al. 2008). For both applications, we used infested areas as sources of current and areas at future risk of being attacked as grounds in virtual electrical circuits connected by resistors based on the values of the best model obtained.

Forested areas in and around the municipality of Hinton, Alberta, which depends heavily on forestry, are currently at risk of being attacked by the MPB (e.g., Weber 2017). Local government has great interest in understanding from where an MPB outbreak would most likely originate. We therefore sought to demonstrate the utility of our final model of MPB connectivity to predict relative genetic connectivity between Hinton and several potential source populations: Jasper, Edson, and Grande Prairie (Fig. 4). Based on the current maps, we then infer the likely origin of beetles moving into the Hinton area.

We also applied our approach to forecast MPB landscape connectivity between the outbreak range in Alberta in 2008 and forested areas east of there that represent potential further range expansion (Safranyik et al. 2010). For this larger scale application, we set the area damaged by the MPB in 2008 (Fig. 5) as an electrical source and the Saskatchewan–Manitoba border as a ground in an electrical circuit. Movement paths were only considered possible over parts of the landscape that contained pine. Because of the possibility of pine volume becoming more important to MPB spread in areas east of the Rockies (Safranyik et al. 2010; Cooke and Carroll 2017), we forecast future MPB spread using a pine-only optimized resistance surface, in addition to the best composite surface obtained through the model selection.

Results

Single environmental surface optimizations

The objective of the genetic algorithm is to identify the best parameter values to describe the relationships between individual landscape variables and gene flow. The transformation functions selected by the genetic algorithm for single surfaces largely support our hypotheses (Table 1). We identified a monotonically decreasing cost to movement with increasing pine volume and CSI values. Pine volume showed a decreasing relationship with cost that nears a linear relationship (Fig. 2B). In contrast, CSI showed a more marked plateau of high cost for low values of CSI. Thus, the rate at which CSI cost decreases is more pronounced at higher values of climate suitability (Fig. 2D). The negative effect of elevation is also captured with a transformation showing that the rate of elevation-cost increases is lower at higher elevations (Fig. 2A). Drought was fitted with a unimodal transformation with a maximum value at a drought value of 0, which indicates that the highest costs to beetle genetic connectivity are found in conditions with neither moisture deficit nor excess (Fig. 2C). The lowest costs are associated by severe drought (negative values).

Composite environmental surface optimizations — integrated model

Building on these individual surfaces, we sought to identify an optimal composite cost surface that could be used to model MPB genetic connectivity. The results of the model optimization using log-likelihood selection (Table 3) indicate that a composite surface built from elevation and CSI costs creates the ecological distance with the strongest effect on genetic distance. Indeed, this surface

Table 3. Model selection and bootstrap analysis results sorted by Akaike weights.

Model	LL	k	ΔAICc	ω_{AICc}	Rank	Top %
Elevation + CSI	919.13	5	0.00	0.94	2.72	44.3
Elevation + drought	915.67	5	6.90	0.03	3.48	32.4
Elevation + pine + CSI	918.63	7	8.02	0.02	3.62	1.7
Elevation + drought + CSI	918.59	7	8.10	0.02	3.83	13.9
Full model	918.63	9	16.71	0.00	5.1	0.2
Elevation + pine + drought	913.69	7	17.91	0.00	5.09	2.6
Elevation + pine	908.55	5	21.16	0.00	7.45	0.5
Pine + drought	905.83	5	26.59	0.00	9.39	0.0
Drought	903.25	3	28.71	0.00	10.12	0.0
Pine	902.63	3	29.94	0.00	12.24	0.1
Drought + CSI	903.73	5	30.79	0.00	9.38	1.0
Pine + drought + CSI	905.53	7	34.15	0.00	10.5	1.2
Pine + CSI	902.03	5	34.19	0.00	13.1	1.2
Geographical	897.66	2	34.58	0.00	13.74	0.1
Elevation	898.51	3	38.18	0.00	12.65	0.1
CSI	897.66	3	39.89	0.00	13.58	0.7
Null	796.89	1	233.77	0.00	/	/

Note: "Model" indicates the environmental cost surface(s) included in the optimized models; "LL" is the log-likelihood value of the model; k indicates the number of parameters used in each model; AICc is the AIC value of the model corrected for the number of parameters optimized (k) and the sample size; ΔAICc is the difference between the AICc of the model and the minimum AICc across all models; ω_{AICc} is the Akaike weight of the model; "Rank" is the average rank achieved by the model; 1 is the top rank in each iteration; "Top %" is the frequency of the model reaching the top rank. Models with equal "Top %" values were then sorted by rank. CSI, climate suitability index.

had by far the largest Akaike weight and no other models had a comparable (difference ≤ 2) AICc (Table 3).

Results from the bootstrap analysis (Table 3) supported the likelihood-based inference and found that the elevation + CSI model best describes MPB genetic connectivity. Indeed, the elevation + CSI composite surface was ranked as the best model in 44.3% of bootstrap iterations, with an average rank of 2.72, making it the only surface that is, on average, among the top three models. The second most supported model was elevation + drought, with 32.4% of iterations identified as the most supported model (Table 3). Rankings for other models diverge slightly between the full sample and bootstrap analyses. Akaike weights are more evenly distributed among models in the bootstrap analysis. Hence, support was attributed to more complex models with similar log-likelihoods to the best model in the full sample analysis in spite of penalties on complex models. However, out of those complex models, only elevation + drought + CSI achieved a high average rank and was regularly the top model in the bootstrap analysis (Table 3). The surface based on a homogeneous cost to movement (geographical distance) did not outperform any composite surface (Table 3). The best model for population connectivity in the northern cluster is the same as for the whole dataset: elevation + CSI.

Properties of the best surface: elevation + CSI

In the best surface, CSI and elevation costs contribute approximately 70% and 30%, respectively, of the total cost of travelling through a cell. The model using this surface as a predictor achieves a marginal R^2 of 0.67 and a conditional R^2 of 0.80, denoting a good performance. When visualizing the elevation + CSI composite surface that best explains genetic connectivity in our dataset (Fig. 3), one can notice large areas with low costs in the north. The influence of the Rocky Mountains (high elevation) can be seen, with intermediate costs to movement covering much of the central part of our study area. The eastern part of our study area shows less heterogeneity in cost to movement, which is likely the result of reduced variation in elevation relative to British Columbia and western Alberta (Fig. 3).

### Model application I — origin of the Hinton MPB population

Based on our genetically informed and machine-learning optimized model of landscape connectivity, we found that Jasper is

Fig. 3. Composite surface from our best model (elevation + CSI), projected on the study area. Lighter areas represent areas that offer less resistance and therefore facilitate movement. [Colour online.]
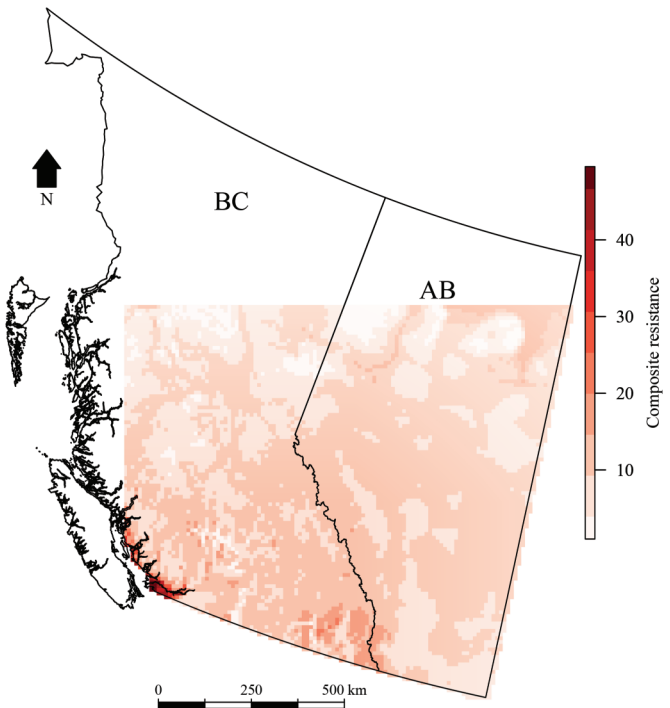
the most likely source of beetles in Hinton and that Hinton, Jasper, and Edson are part of a connectivity corridor (Fig. 4). Indeed, connectivity, as measured by commute-time distances, was the highest between Hinton and Jasper (Fig. 4). Connectivity was also strong between Edson and Hinton, with a difference of 7451.9 relative to the Hinton–Jasper distance. Grande Prairie was rather isolated from Hinton according to our model, with a difference of 372964.3 relative to the Hinton–Jasper distance.

Fig. 4. Electrical current map based on the best model (elevation + CSI). The current intensity represents the expected concentration of movement between the populations: the lighter the colour or shading, the more movement we expect. [Colour online.]
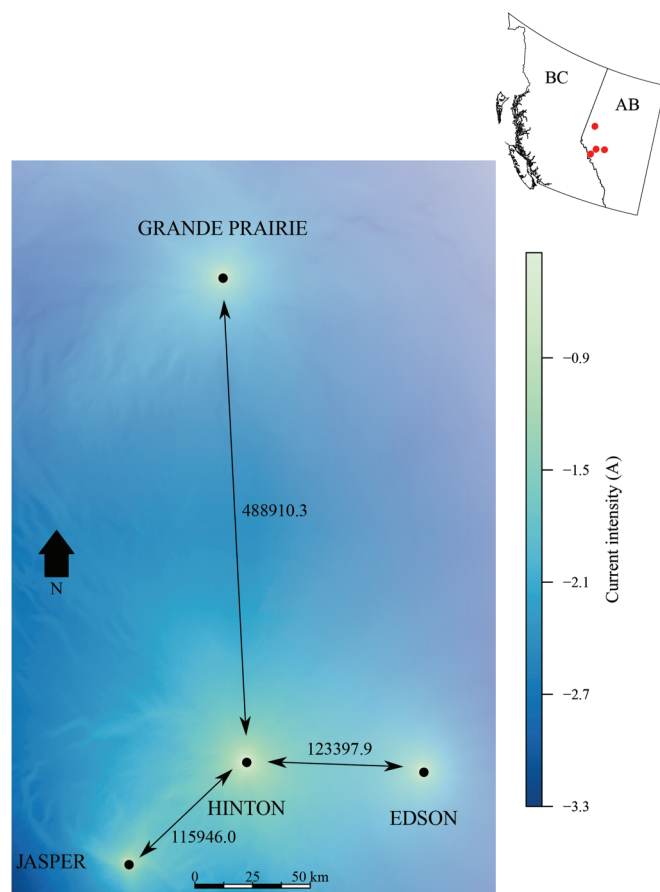
Model application II — potential for eastward expansion

Predictions using both our final selected model and a pine-only model indicate that there are few obstacles to beetle movement between the 2008 outbreak limit and the eastern border of Saskatchewan (Fig. 5). In predictions using our model based on elevation and CSI, there is higher connectivity in several large corridor areas: southeast of Wood Buffalo National Park (Alberta), southeast of Fort McMurray (Alberta), and a corridor crossing the Alberta and Saskatchewan border and following the southern limit part of the pine distribution (Fig. 5A). Prediction using a model based exclusively on pine volume (Fig. 5B) indicated that beetle connectivity is overall more homogeneous with fewer evident corridors, although one can recognize corridors identified using the elevation + CSI model.

Discussion

Improving our understanding of connectivity and movement is essential for the effective management of forest pest species. However, outbreaking populations pose many challenges such as expansion into novel habitats that limit applicability of expert opinion. We applied a novel machine-learning approach within a landscape genetics framework to characterize movement and population connectivity in the mountain pine beetle, one of the most damaging forest insect pests in western Canada. Through single-surface models, we were able to support the hypotheses and describe how environmental heterogeneity translates into movement cost. Considering all combinations of these variables in addition to the single-surface models, we found that pine beetle

population connectivity is driven by a combination of elevation and climate. Using machine-learning tools that make no a priori assumptions about how landscape heterogeneity affects movement, we were also able to demonstrate the predictive strength of our MPB connectivity model in two management-relevant contexts.

Single environmental surface optimizations

The real value of our single-surface analyses goes beyond simply confirming the direction of landscape effects on gene flow (Table 1): it lies in the parameterization of the shape and the maximum value of those relationships. As hypothesized, elevation was negatively associated with gene flow: resistance increased with elevation (Fig. 2A). This negative association could be explained by higher mortality of pines due to beetle attack at lower elevation, enhancing reproduction of beetles and effective dispersal (Amman et al. 1973). Very high elevations are also associated with a decrease in climate suitability for the pine (Smithers 1961), which would affect the resources available to the MPB. Beyond an effect on reproduction, low-elevation valleys have been previously shown to facilitate beetle dispersal (de la Giroday et al. 2011). Although elevation emerged as an important predictor of beetle connectivity in our study area, given the lack of significant topography east of the Rocky Mountains, elevation will not likely be a significant factor influencing pine beetle outbreak spread.

Pine volume was positively associated with gene flow: resistance decreased with greater pine volume (Fig. 2B). High-volume stands are generally thought to be more susceptible to MPB attack (Safranyik et al. 2010) and to result in higher beetle reproductive rates (Safranyik and Wilson 2006). Consequently, one expects lower pine volume east of the Rocky Mountains, where the beetle is currently spreading, to constrain MPB spread.

The single-surface optimization of drought produced the only surface with a non-monotonic parameterization (Fig. 2C). The lowest costs to movement are associated with the driest and wettest conditions, whereas the highest costs are associated with intermediate levels of drought. High levels of drought are expected to facilitate movement and MPB populations growth because drought-induced stress decreases the defenses of mature host trees (Berg et al. 2006; Raffa et al. 2008). The fact that resistance to movement decreases also under the moistest conditions could be a statistical artefact associated with the complex edges of the coast that support the wettest areas (Koen et al. 2010) or be due to higher MPB brood production associated with increased water storage in pines, possible when excess water is available (Amman 1972; Safranyik and Wilson 2006). Taken independent of any other factors, drier conditions east of the Rocky Mountains might be expected to facilitate MPB spread.

Finally, we found that resistance decreased with higher values of climate suitability (Fig. 2D). Relative to the other monotonic relationships (e.g., elevation and pine volume), the effect of climate suitability on gene flow is less linear, with a plateau of high resistance followed by a sharper decrease of resistance than, for example, the pine single surface (Fig. 2). Climate is known to strongly affect MPB (Carroll et al. 2004; Bentz et al. 2010) at several stages of its life cycle. The nonlinear relationship between climate suitability and resistance (Fig. 2D) likely reflects the physiological limit of MPB at lower temperatures. Replicated executions of the genetic algorithm, which ran without assumptions about the functional relationships between gene flow and landscape context, supported the signs of the relationships that we hypothesized from the literature.

Composite environmental surface optimizations — integrated model

Building a multisurface composite landscape genetics model and going beyond individually optimized resistance surfaces is important because using a single surface in a landscape genetics

Fig. 5. Electrical current map based on an extrapolation to Alberta and Saskatchewan of (A) our best model (elevation + CSI) and (B) a model based on pine volume. The core infested area used as a source is represented in black. The electrical ground is the Saskatchewan–Manitoba border. The current intensity represents the expected concentration of movement between the populations: the darker the colour or shading, the more movement we expect. [Colour online.]
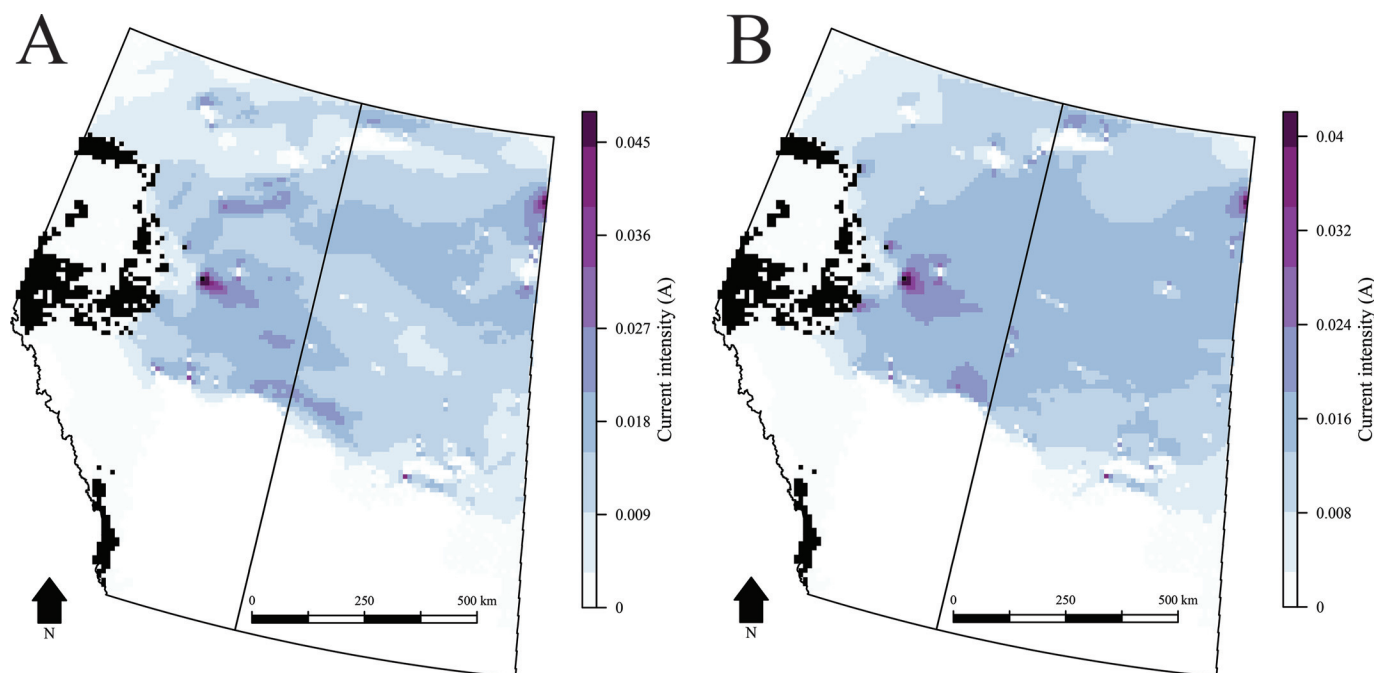
model assumes that only this variable influences genetic connectivity, which is rarely the case (Spear et al. 2010). A combination of elevation and CSI was the best model according to model selection, which was corroborated by our bootstrapping procedure. Elevation was consistently included in the best models, which indicates its importance to MPB gene flow.

Our results shed light on how the MPB outbreak may have exceeded its previous range. While topography has not changed during the last century, climate has (Intergovernmental Panel on Climate Change (IPCC) 2014). Previous research has shown that MPB outbreak dynamics in British Columbia has been driven mainly by increasing temperature during the last century (Carroll et al. 2004; Raffa et al. 2008; Sambaraju et al. 2012). Our study builds on this previous research by accurately describing how climate affects the movement aspect of outbreak dynamics. Indeed, given the increasingly more suitable climate, our model may explain how the MPB was able to move so quickly east of the Rockies in recent times (Janes et al. 2014; Cooke and Carroll 2017).

Our results differ from a previous landscape genetics study on the MPB at the leading edge of the outbreak (James et al. 2011). Using a neighbourhood-based analysis of landscape connectivity, in a central subset of our study area, James et al. (2011) found that pine volume was an important predictor of connectivity for a northern genetic cluster of populations. Pine volume was not included in our best models. Our optimized models of how cost varies in response to both climate and elevation may have captured some of the effect of pine volume. Indeed, ecological distances calculated from the pine volume surface are strongly correlated to ecological distances calculated from the composite elevation and climate surface (Mantel correlation, 0.87; p value <10^{-7}). The costs to movement from both surfaces are also correlated (Pearson correlation, 0.18; p value <10^{-16}). A part of the variation in genetic connectivity that is explained by pine volume may therefore be shared with climate and elevation.

Model applications

Our first model application attempted to resolve a local-scale question about the likely origin of beetles found in Hinton, Alberta. Our connectivity analysis suggests that the beetles most likely originated from Jasper (Fig. 4). Hinton is also well connected with Edson, and there seems to be a large corridor of high connectivity from Jasper to Edson. A recent study also showed that beetles east of Hinton are genetically similar to beetles from Jasper (Trevoy et al. 2018). Also, the latest MPB population forecast survey in Alberta showed that based on larval mortality, beetle numbers were strongly increasing in an area ranging from Jasper to the Edson forest area (Alberta Agriculture and Forestry 2017), which is similar to the highly conductive area that we described (Fig. 4). From a management perspective, this model could be used to forecast connectivity between attacked and unattacked stands and to prioritize well-connected, but not yet attacked, stands for pre-emptive harvest.

Our second model application examined potential routes of eastward expansion at a larger, interprovincial scale (Fig. 5A). Through our exploratory analysis, there appears to be few constraints to beetle movement to the east when considering connectivity models, based on elevation and climate, or based on pine volume. Several large-scale high-connectivity corridors exist, notably through the southern part of the pine distribution (Fig. 5), which has been previously described as conductive (Safranyik et al. 2010). Although producing reliable models for predicting further expansion is challenging (Cooke and Carroll 2017), the low variation of the factors associated with MPB dynamics in the elevation + CSI model or the pine volume model sets the stage for future connectivity. According to the elevation and climate model or the pine volume model, managing the outbreak and mitigating its consequences would be difficult. Indeed, in the absence of localized, pinch-point areas of high connectivity, deciding in which areas to prioritize management efforts would be less straightforward and management efforts could be less efficient in slowing or reducing the consequences of an MPB outbreak.

Limits to our approach

An important consideration in the application of any spatial statistical model is that it can be difficult to reliably make predictions in areas outside the scope of the original data. The concern about model transferability, i.e., applying a model built using a spatial dataset to a subset of those data or to a different dataset, is widespread in ecological studies (Wenger and Olden 2012; Yates et al. 2018). A challenge with transferring models to new data is that predictions can be affected by many factors not necessarily included in the original model such as changing biotic interactions, sampling biases, and landscape dissimilarity between the original and novel landscapes (Wenger and Olden 2012; Yates et al. 2018). This is especially true in studies dealing with species distribution (Petitpierre et al. 2017; Moon et al. 2017).

In the case of our model of MPB population connectivity, we do not know if the functional relationships between landscape heterogeneity and gene flow are the same outside our study area (Fig. 1). For example, drought is likely to be more severe in the future in the continental zone of western Canada (Wang et al. 2014), which may ultimately reduce rather than increase the rate of MPB spread as moderate drought would (Amman 1972; Safranyik and Wilson 2006). This relationship, however, remains uncaptured by our models built using data from noncontinental regions. Additionally, the cost associated with pine volume could change across the landscape as the main species of pine switches across western Canada, thereby changing biological interactions (Safranyik et al. 2010). For example, MPB could move at a different pace in jack pine relative to lodgepole pine forests due to differences in reproduction and physiology. The uncertainty inherent with these new interactions justifies continued work on MPB connectivity, especially in novel habitats.

A final important consideration is that we assume isotropic resistance to movement, i.e., the resistance between two locations is the same regardless of the direction being travelled; however, anisotropic movement and asymmetric resistance to movement and gene flow can play a significant role in shaping spatial patterns of genetic variation (Holderegger and Gugerli 2012). To our knowledge, no work has successfully incorporated directional processes explicitly in models of genetic connectivity, although recent efforts towards this goal have been made (Landguth et al. 2017). Within the MPB system, wind (direction and speed) has been hypothesized to influence the dynamics of long-distance dispersal (Ainslie and Jackson 2011; de la Giroday et al. 2012). We think that being able to use wind in combination with other isotropic landscape features would constitute the most well-rounded approach to modeling MPB. Incorporating directional processes such as wind in a landscape genetics model of the MPB is a natural, yet challenging, next step to better understanding the spatial dynamics of this complex system.

Conclusion

Using machine learning, we found that elevation and climate together constitute the best predictors of gene flow and movement of the MPB in western Canada. Using this model of landscape connectivity, we demonstrated that the beetles that recently colonized forests around Hinton, Alberta, most likely originated in Jasper and travelled in a high-connectivity corridor spanning from Jasper to Edson, in accordance with recent genetic analyses and government survival-based reports. This gives us confidence in the ability of our model to accurately predict population connectivity and gene flow within the spatial scope of the data that we used. Finally, using our results outside the scope of the study area, we found that pine forests in eastern Alberta and Saskatchewan may provide homogeneous routes of colonization for the MPB if it continues its expansion. Future avenues of research include incorporating directional processes such as wind into the landscape genetic model and evaluating uncertainty in long-term forecasts of the spread of MPB populations in novel habitats.

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