

# Landscape resistance and American marten gene flow

Erin L. Koen · Jeff Bowman · Colin J. Garroway ·  
Stephen C. Mills · Paul J. Wilson

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**Abstract** Landscape heterogeneity can influence animal dispersal by causing a directional bias in dispersal rate, as certain landscape configurations might promote, impede, or prevent movement and gene flow. In forested landscapes, logging operations often contribute to heterogeneity that can reduce functional connectivity for some species. American martens (*Martes americana*) are one such species, as they are considered specialists of late-seral coniferous

forests. We assessed marten gene flow to test the hypothesis that habitat management has maintained landscape connectivity for martens in the managed forests of Ontario, Canada. We genotyped 653 martens at 12 microsatellite loci, sampled from 29 sites across Ontario. We expected that if forest management has an effect on marten gene flow, we would see a correlation between effective resistance, estimated by circuit theory, and genetic distance, estimated by population graphs. Although we found a positive relationship between effective resistance and genetic distance (Mantel  $r = 0.249$ ,  $P < 0.001$ ), marten gene flow was better described by isolation by Euclidean distance (Mantel  $r = 0.410$ ,  $P < 0.001$ ). Our results suggest that managed forests in Ontario are well connected for marten and neither impede nor promote marten gene flow at the provincial scale.

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E. L. Koen (✉) · C. J. Garroway  
Environmental and Life Sciences, Trent University, 2140  
East Bank Drive, Peterborough, ON K9J 7B8, Canada  
e-mail: erinkoen@trentu.ca

J. Bowman  
Wildlife Research & Development Section, Ontario  
Ministry of Natural Resources, Trent University DNA  
Building, 2140 East Bank Drive, Peterborough,  
ON K9J 7B8, Canada

*Present Address:*  
C. J. Garroway  
Edward Grey Institute, Department of Zoology,  
University of Oxford, South Parks Road, OX1 3PS  
Oxford, UK

S. C. Mills  
Northeast Science and Information Section, Ontario  
Ministry of Natural Resources, P.O. Bag 3020, 5520 Hwy.  
101 E., South Porcupine, ON P0N 1H0, Canada

P. J. Wilson  
Biology Department, Trent University, 2140 East Bank  
Drive, Peterborough, ON K9J 7B8, Canada

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## Introduction

Dispersal and gene flow are important processes influencing the persistence of populations because genetically isolated groups of individuals may be

prone to inbreeding depression and possible extinction (e.g., O'Grady et al. 2006). Landscape structure can facilitate or impede dispersal and gene flow by affecting animal movement patterns (Taylor et al. 1993; Broquet et al. 2006b; Perez-Espona et al. 2008). Thus, understanding the interactions between landscape structure and animal movement can often be important for the conservation of populations. The effects of landscape structure on gene flow can be assessed by creating a species-specific map, known as a resistance surface, which represents the likelihood of that species moving between landscape features. Resistance surfaces are often parameterized based on expert opinion or occurrence data, as direct field measurements of the ease of movement through the landscape are difficult to obtain (Spear et al. 2010; but see Driezen et al. 2007; Cushman and Lewis 2010). Fortunately, recent technological and analytical advances in the field of landscape genetics have made it possible to relate landscape structure directly to gene flow (Manel et al. 2003; Storfer et al. 2007). Similarities in multi-allelic loci between individuals sampled at many geographic sites can indicate gene flow among those sites; pairs of sites with few shared alleles are assumed to have little gene flow between them. We can use genetics to build resistance surfaces that represent gene flow (e.g., Cushman et al. 2006; Shirk et al. 2010; Wasserman et al. 2010; Garroway et al. 2011b), or conversely, to validate a resistance surface built with occurrence data as a model of gene flow (e.g., Schwartz et al. 2009).

American martens (*Martes americana*) are conventionally regarded as specialists of late successional coniferous forest (Buskirk and Powell 1994; Bowman and Robitaille 1997; but see Potvin et al. 2000), and are considered indicators of these forest conditions in the boreal forest (McLaren et al. 1998). In recent decades, forestry operations in Ontario, Canada have been required to adhere to guidelines that ensure a sufficient quantity and quality of habitat to support healthy populations of martens (Watt et al. 1996). To this end, researchers in Ontario have developed a model of marten habitat suitability (Elkie et al. 1999, 2009; Naylor et al. 1999) that has been used to guide forestry operations in the province. The habitat features associated with the presence of marten have been well characterised (e.g., Bowman and Robitaille 1997; Potvin et al. 2000; Fuller and Harrison 2005). Studies

at the scale of the forest stand describe the importance of forest structure for martens, such as canopy cover and abundance of tree snags (Buskirk and Powell 1994; Bowman and Robitaille 1997; Payer and Harrison 2003). Marten research at larger spatial scales has complemented stand-scale studies by considering the influence of landscape pattern, such as forest fragmentation and connectivity of suitable habitat, on marten movement and occupancy. For example, marten capture rates tend to be lower in fragmented habitats (Hargis and Bissonette 1997; Hargis et al. 1999) and forest patch size and isolation of patches influence the spatial distribution of martens on the landscape (Chapin et al. 1998). Whether habitat characteristics that predict marten occupancy act as barriers to dispersal, influencing gene flow and population genetic structure across the landscape, however, is largely unknown (but see Broquet et al. 2006a, b; Wasserman et al. 2010; Cushman et al. 2011). Our goal was to assess the hypothesis implicit in marten habitat planning in Ontario's managed forests, which aims to maintain landscape connectivity for martens across the province. Thus, we tested for an effect of marten habitat supply on genetic differentiation.

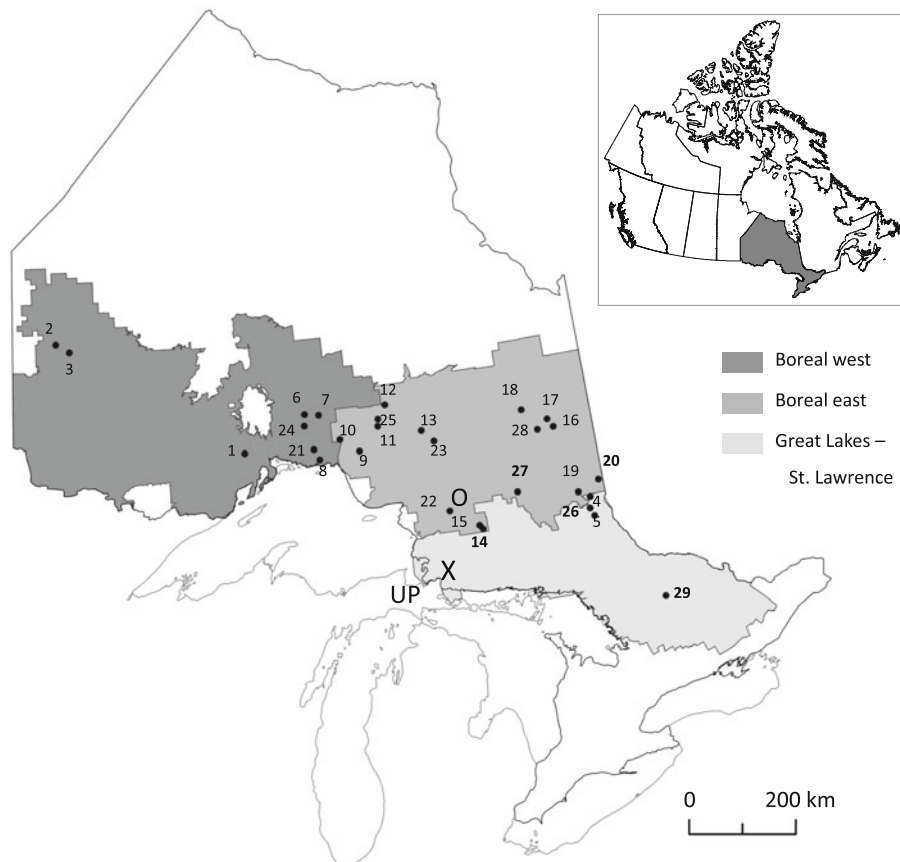
Given the abundance of studies suggesting that martens are specialists of late-seral coniferous forests, we expected that young and immature forests would act as a barrier for martens, and hence that landscape structure would have an effect on gene flow. We assessed the genetic structure of martens across Ontario; a spatial scale that is relevant to both gene flow and forest management decisions. We created a resistance surface based on marten habitat suitability models used by forest managers for Ontario, and we predicted marten gene flow based on this surface. We then compared the gene flow model with estimates of gene flow based on genetic data. If there is no effect of forest-management induced landscape structure on dispersal and gene flow in martens, then we expected either: (a) panmixia, where there is no genetic pattern, or (b) isolation-by-distance, where genetic differences increase with geographic distance because individuals mate with their neighbours. If forest-management induced landscape structure does influence marten dispersal, then we expected isolation by resistance: a relationship between the resistance surface and gene flow, where areas with low (high) resistance to movement will promote (impede) gene flow.

## Methods

### Study area and sampling design

We conducted our study across the 443,000 km<sup>2</sup> of commercially managed forests in Ontario, Canada (Fig. 1). The boreal west and boreal east forest regions of Ontario (Fig. 1) are dominated by coniferous and mixed stands composed of tree species such as jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam fir (*Abies balsamifera*) (Thompson 2000). Black spruce and jack pine account for 70% of the boreal forest area in Ontario (Thompson 2000). In the

Great Lakes-St. Lawrence forest region (GLSL; Fig. 1) of Ontario, there are over 45 tree species; dominant tree species include sugar maple (*Acer saccharum*), trembling aspen, yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), eastern white pine (*Pinus strobus*), balsam fir, eastern hemlock (*Tsuga canadensis*), and red oak (*Quercus rubra*). Sugar maple and poplar (*Populus* spp.) cover 45% of the GLSL forest region (Thompson 2000). Important natural disturbances vary across the province. The boreal forest is dominated by large stand-replacing fires, especially in the northwest, where fire return intervals are very rapid (e.g., as low as 50–60 years; Voigt et al. 2000; Ter-Mikaelian et al. 2009). GLSL forest has much longer fire return



**Fig. 1** Map of Ontario, Canada showing the regions covered by forest resource inventory data (shaded). The 29 sites sampled for marten are indicated by black dots with number labels. We sampled 11–27 martens per site. Sites labeled with bold font have pairwise  $D_{est}$  values  $>0.1$ . Algonquin Provincial Park (site

29) is the southwestern-most site. Chapleau Game Preserve is indicated by “O”. Sault Ste. Marie is indicated by “X”. The Upper Peninsula of Michigan, USA, is indicated by “UP”. The inset map shows Ontario’s location within Canada

intervals, and is dominated instead by small-scale gap dynamics (Voigt et al. 2000). Anthropogenic disturbances are primarily related to forestry. Approximately 1% of managed Crown forest is harvested each year, with about 87% of logging done using a clear cut system (principally in the boreal forest) and about 13% using a selection cut system (principally in the GLSL) (Ontario Ministry of Natural Resources, unpubl. data).

### American marten ecology

The American marten is a mid-sized carnivore of the family Mustelidae. In Ontario, marten home ranges in logged and unlogged areas, and across years of high and low prey density, range between 3.3–11.2 km<sup>2</sup> for males, and 1.0–12.7 km<sup>2</sup> for females (Thompson and Colgan 1987). Juvenile dispersal, estimated with radio telemetry, varies between 6–18 km for males (max 214 km) and 4–6 km (max 181 km) for females (Johnson et al. 2009). Juvenile dispersal from the natal home range begins in September (Johnson 2008). Martens have been harvested for fur in Ontario throughout its history, and in the current registered trapline system since the late 1940s.

We obtained 647 tongue tissue samples from martens harvested in 2004–2005 from Ontario Ministry of Natural Resources district offices. We also obtained hair samples from 32 martens livetrapped in Algonquin Provincial Park, Ontario, in the summer of 2004 as part of a study by Tully (2006) (Fig. 1). We grouped samples by the registered trapline that they were harvested in, as we did not know the exact location of each individual marten harvested. When our sampled traplines were adjacent, we grouped samples from these traplines and used the centroid of each trapline group. Herein, we refer to trapline and trapline group centroids as sites. Our sample consisted of 11–47 (average = 22.5, SD = 5.9) individual martens from each site ( $n = 29$  sites). The average site was 232 km<sup>2</sup> (SD = 209 km<sup>2</sup>, range = 69–936 km<sup>2</sup>). Site centroids were an average of 369 km apart (SD = 255 km, range = 10–1,307 km). We do not know of any marten translocations into our study area, although there are several accounts of marten translocations out of our study area that took place to help restore populations at various destinations (e.g., Berg 1982; Williams et al. 2007; Williams and Scribner 2010).

### Genotyping of microsatellite loci

We extracted DNA from tongue tissue using a QIAEasy tissue kit (Qiagen). We genotyped martens using 16 microsatellite loci previously developed for martens or for closely related species (Table 1): wolverine (*Gulo gulo*; Gg7, Gg443, Ggu101, Ggu216), otter (*Lontra canadensis*; Lut604), marten (*Martes americana*; Ma1, Ma2, Ma5, Ma11, Ma19), ermine (*Mustela erminea*; Mer041), and mink (*Neovison vison*; Mvis002, Mvi1321, Mvi1341, Mvi1354, Mvi2243). We amplified the 16 microsatellite loci in four multiplex reactions and one single locus reaction using the polymerase chain reaction (PCR). We performed amplifications in 10 µl volumes containing 2–5 ng of DNA, 2.0 mM MgCl<sub>2</sub>, 0.2 mM of each dNTP, 1× PCR buffer (Invitrogen), and 0.5 units of Taq polymerase (Invitrogen). We amplified all samples under the following conditions: 94°C for 5 min, 30 cycles of 94°C for 30 s, 51°C, 56°C, or 59°C for 45 s, 74°C for 30 s, and 65°C for 45 min. We visualized each reaction on an ABI 3730 automated genotyper (Applied Biosystems) with a size standard (ET-Rox 550; Applied Biosystems) run with each sample to determine base pair length. We scored genotypes, characterized as allele sizes, manually with the GeneMarker v1.7 software package (SoftGenetics).

### Analysis of genetic data

We used Bonferroni-corrected Chi-squared tests ( $\alpha = 0.0001$ ) to assess whether allele frequencies were in Hardy–Weinberg equilibrium within sites and for each locus with the Adegnet package 1.2 (Jombart 2008) for R (R Development Core Team 2008). We used software Genepop (web version 4.0.10; Rousset 2008) to assess linkage disequilibrium.

We expected that if the structure of the landscape was influencing gene flow, we would observe a positive relationship between landscape connectivity and genetic connectivity. We used several methods to measure genetic connectivity across the landscape. We used a Bayesian clustering technique to identify genetic clusters. We assessed relative genetic similarity between pairs of sites with both allelic diversity (Jost 2008) and network-based (conditional genetic distance [*cGD*]; Dyer and Nason 2004; Dyer et al. 2010) approaches. Finally, we used ordination to

**Table 1** Variability of 16 microsatellite loci used for profiling American marten (*Martes americana*)

Locus	NA <sup>a</sup>	HE <sup>b</sup>	HO <sup>c</sup>	HE – HO	Source
Gg7 <sup>d</sup>	10	0.811	0.672	0.139	Davis and Strobeck (1998)
Ggu101 <sup>d</sup>	1				Duffy et al. (1998)
Ggu216	9	0.828	0.794	0.034	Duffy et al. (1998)
Gg443	10	0.876	0.859	0.017	Walker et al. (2001)
Lut604	5	0.590	0.554	0.036	Dallas and Piertney (1998)
Ma1 <sup>d</sup>					Davis and Strobeck (1998)
Ma2	7	0.775	0.743	0.032	Davis and Strobeck (1998)
Ma5	10	0.782	0.749	0.033	Davis and Strobeck (1998)
Ma11	4	0.318	0.314	0.004	Davis and Strobeck (1998)
Ma19	7	0.791	0.763	0.028	Davis and Strobeck (1998)
Mer041	4	0.511	0.477	0.034	Fleming et al. (1999)
Mvis002 <sup>d</sup>	2				Fleming et al. (1999)
Mvi1321	6	0.587	0.566	0.021	Vincent et al. (2003)
Mvi1341	11	0.739	0.715	0.024	Vincent et al. (2003)
Mvi1354	7	0.737	0.729	0.008	Vincent et al. (2003)
Mvi2243	10	0.443	0.411	0.032	Vincent et al. (2003)
Mean		0.676	0.642	0.034	
SD		0.170	0.164	0.033	

<sup>a</sup> NA No. of alleles observed

<sup>b</sup> HE Expected heterozygosity

<sup>c</sup> HO Observed heterozygosity

<sup>d</sup> Locus was omitted from analyses

describe spatial patterns in genetic variability (Jombart et al. 2008).

#### Bayesian clustering

We used a Bayesian clustering approach in program Structure (version 2.3; Pritchard et al. 2000). This technique uses Markov chain Monte Carlo simulation to assign individuals to genetic populations without incorporating a priori knowledge of geographic source populations, such that the model assumptions of Hardy–Weinberg equilibrium within populations and linkage equilibrium between loci within populations are satisfied. We used a burn-in of 500,000 iterations, followed by  $1 \times 10^6$  iterations of the Markov chain Monte Carlo simulation. We used three independent simulations for each of  $\{K = 2, 3, 4\}$  in program Structure with an admixture model. We assigned individuals to a putative population when >80% of an individual's genome could be assigned to that population.

#### Pairwise comparisons with $D_{est}$

We used  $D_{est}$  (Jost 2008) to estimate pairwise differences in allele frequencies between sites with the software SMOGD (Crawford 2010).

#### Population graphs

We used a graph-theoretic approach to model gene flow between sites (Dyer and Nason 2004; Garroway et al. 2008; Dyer et al. 2010). We constructed networks of genetic connectivity among sample sites using the software package Geneticstudio (Dyer 2009). Briefly, we used individual genotypes to define multi-dimensional node centroids, representing the mean genetic individual sampled at a node (site), with unique coordinates in multi-dimensional space. Multi-dimensional distances between centroids define the edges of a saturated network (all nodes connected). We then pruned the saturated network based upon the concept of conditional independence, such that we

removed edges that did not contribute to the overall genetic covariance structure. Finally, from this network we calculated a conditional genetic distance (*cGD*) between nodes. This distance was the sum of edge weights along the shortest path through the network between pairs of nodes. For full details of network construction and network based *cGD* see Dyer and Nason (2004) and Dyer et al. (2010).

### *Spatial principal component analysis*

We described spatial patterns in genetic variability with a spatial principal component analysis (sPCA; Jombart et al. 2008) using the ADEGENET package 1.2 (Jombart 2008) in R. This technique uses both the variability and the spatial autocorrelation of allele frequencies to derive synthetic principal components describing spatial genetic structure. Spatial autocorrelation is estimated with Moran's *I* (Moran 1948, 1950), which estimates spatial structure in allele frequencies based on a connection network linking neighbouring sites; here, we used a Delaunay connection. The data used to derive the principal component axes are the product of the matrix of centered allele frequencies and a spatial weighting matrix (i.e., Moran's *I* values for sites connected by the network). We used tests to detect global and local patterns with 9,999 permutations as per Jombart et al. (2008). The null hypothesis is that allele frequencies on the connection network are distributed at random. Significant global (positive eigenvalues) structure would indicate that sites are more genetically similar to their neighbours than expected by chance and is indicative of either genetic clustering or allele frequency clines. Significant local structure (negative eigenvalues) is suggestive of local differentiation among neighbouring sites (Jombart et al. 2008).

### Resistance surface for marten

We classified habitats according to perceived quality for martens based on models previously developed for martens in Ontario (Table 2). We parameterized the surface with conductances rather than costs: we assigned habitats of low quality a score of 1, medium quality a score of 2, and high quality a score of three using attributes from forest resource inventory (FRI) data. These scores rank habitats with respect to the suitability for all marten habitat requirements (e.g.,

denning, resting, foraging). Accordingly, non-forested habitats were assigned a low quality conductance of one. We also identified several large bodies of water (e.g., Great Lakes, Lake Nipigon) as impermeable barriers, which we coded as zero. Forest Resource Inventory data were available for only the extent of managed forests in Ontario (shaded area of Fig. 1), even though forests existed beyond the FRI map. We used FRI data that were updated in 2004, the same year we collected our genetic data.

We used three previously developed marten habitat suitability models, based on literature and expert opinion, that were specific to the three forest regions of northern and central Ontario (Fig. 1). The landscape differs between the three forest regions (e.g., dominant vegetation cover), therefore the model variables differ between the three models (Table 2). Habitat features important for martens is thought to vary spatially. For example, marten use of jack pine dominated forests might be higher in the boreal west region than the GLSL region (Elkie et al. 1999). The models are not meant to be inconsistent; rather, they aim to define suitable marten habitat across the range of forest types. We used the Ontario Marten Analyst (Elkie et al. 1999) model for the boreal west region, the Ontario Wildlife Habitat Analysis Model (OWHAM; Naylor et al. 1999) for the boreal east region, and the OWHAM, updated with variables from the Ontario Landscape Tool (OLT; Elkie et al. 2009) for the GLSL region (Table 2). We implemented all three models using R code.

### Estimating resistance of the landscape to marten gene flow

We used circuit theory (McRae and Beier 2007; McRae et al. 2008) with software Circuitscape 3.5 (McRae and Shah 2009) to model landscape resistance for martens, based on our resistance surface. We first converted our vector-based map of forest stands to a raster of pixels (0.25 km<sup>2</sup> each). Smaller pixels resulted in more pixels than Circuitscape could compute. We changed the range of conductance values from 0–2 to 1–3 because Circuitscape interprets zero conductance as a barrier. We used the pair-wise mode in Circuitscape, connecting eight neighbours based on average conductance. We estimated effective resistance between all possible pairs of marten sample sites.



**Table 2** Non-spatial models of American marten (*Martes americana*) habitat suitability for three forest regions in Ontario

Region	Model	Input	Suitability Scale <sup>a</sup>
Boreal west	OMA <sup>b</sup>	Coniferous (%) Canopy closure (%) Tree height Stocking (%)	0–2
Boreal east	OWHAM <sup>c</sup>	Spruce, fir, and cedar (%) Canopy closure (%) Tree height Development stage <sup>d</sup>	0–3
Great Lakes–St. Lawrence	OWHAM/OLT <sup>e</sup>	Canopy closure (%) Development stage <sup>f</sup> Standard forest unit <sup>g</sup>	0–2

All models are based on attributes of Ontario Forest Resource Inventory data. In general, the most suitable marten habitat is considered to be mature or older coniferous forest with a closed canopy. Details of the specific models can be found in Elkie et al. (1999), Naylor et al. (1999), and Bowman and Robitaille (2005)

<sup>a</sup> Zero represents poor habitat. We forced the boreal east OWHAM from a 0–3 scale into a 0–2 scale so that all three models were on the same scale, and such that we retained as much consistency as possible between models: we combined suitability classes 1 and 2 for percent spruce, fir, or cedar, and tree height, and combined suitability classes 2 and 3 for percent canopy closure. Development stage was already on a 0–2 scale

<sup>b</sup> OMA Ontario Marten Analyst (Elkie et al. 1999)

<sup>c</sup> OWHAM: Ontario Wildlife Habitat Analysis Model (Naylor et al. 1999)

<sup>d</sup> According to Holloway et al. (2004) based on standard forest units

<sup>e</sup> OLT: Ontario Landscape Tool (Elkie et al. 2009)

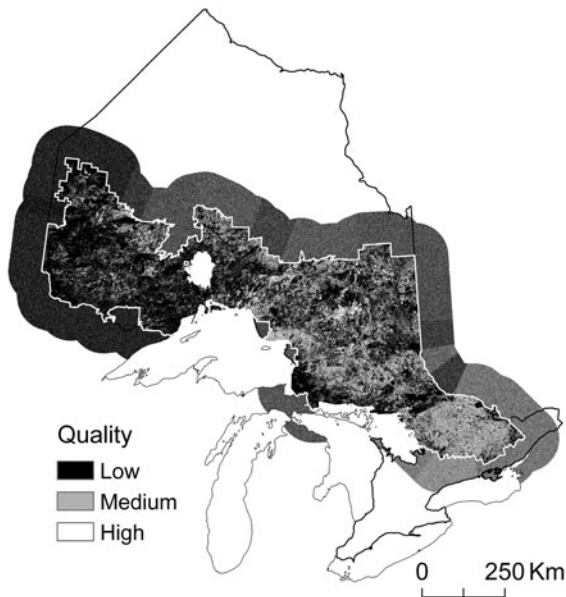
<sup>f</sup> According to Elkie et al. (2009) based on standard forest units

<sup>g</sup> We used suitability based on standard forest units (from the OLT model) rather than ecosite type (from the OWHAM) since the OLT model uses updated information on marten habitat use (Elkie et al. 2009)

Several of our sites were close to the edge of our resistance surface map (Fig. 1). The edge of the map acts as an artificial barrier, because although model organisms (random walkers) are constrained by the map edge, martens on the ground are able to move through areas beyond the map edge. Artificial edges on the map can result in an overestimate of effective resistance when using the circuit theory model (Koen et al. 2010). Koen et al. (2010) showed that placing a buffer composed of randomly-generated habitat quality data around the edge of the map reduced the bias. Here, we used a 100-km wide buffer around the edge of our resistance surface (Fig. 2). We classified map pixels within the buffer as low, medium, or high quality. As we did not know the true composition of the land-cover beyond the edge of the FRI map, we assigned pixel classifications randomly such that the proportion of each suitability class was the same as in the known map that bordered the buffer.

The relative value of our assigned habitat quality scores was arbitrary. To assess the effect of the value assigned to each habitat quality class (i.e., low, medium, high) on the relationship between predicted (effective resistance) and observed (*cGD*) gene flow, we varied the habitat quality values in our resistance surface (Table 3). We held the value of low quality habitat constant at 1, arbitrarily varied the value of medium quality habitat by multiples of 2, and high quality habitat by multiples of 3 or 4 (results for multiples of 4 are not shown).

We used simple Mantel tests (9,999 permutations; Mantel 1967) with the Vegan package (Oksanen et al. 2009) for R to compare pairwise estimates of *cGD* to both Euclidean distance and effective resistance (for all six resistance surfaces described in Table 3). We used partial Mantel tests to factor out the effect of Euclidean distance on the relationship between effective resistance and genetic distance, and to factor out



**Fig. 2** A resistance surface depicting habitat quality for martens in Ontario, Canada (outlined in white) with a 100-km wide buffer of randomly-distributed habitat quality data, as per Koen et al. (2010)

the effect of effective resistance on the relationship between Euclidean distance and genetic distance (Cushman et al. 2006). For these comparisons, we used only the resistance surface that correlated best with genetic distance based on the simple Mantel tests. The use of partial Mantel tests in landscape genetics has been questioned (Raufaste and Rousset 2001), but subsequent work has shown that Mantel and partial Mantel tests are appropriate for comparing genetic and resistance distance matrices (Cushman and Landguth 2010b; Legendre and Fortin 2010).

To discriminate between our hypotheses of isolation by distance and isolation by resistance, we required that Mantel tests that partial out the influence of one variable be significant, while the reverse test is not significant. For example, to accept that isolation by distance is a better explanation than isolation by resistance for the observed genetic structure, the relationship between Euclidean and genetic distance, with effective resistance partialled out, must be significant, while the relationship between effective resistance and genetic distance, with Euclidean distance partialled out, must not be significant (Cushman et al. 2006). Cushman and Landguth (2010b) found this approach to be powerful in discriminating between hypotheses that are driving the relationship and hypotheses that are simply correlated.

## Results

### Analysis of genetic data

We successfully genotyped 653 martens at 12 micro-satellite loci. We omitted 26 samples because  $\geq 4$  of the 12 loci did not amplify; 9 (31%) of these were from the Algonquin Provincial Park site for which we had hair rather than tissue samples. We omitted loci Ggu101 and Mvis002 because they were fixed for one or two alleles, respectively, across all individuals. We omitted locus Ma1 because the morphology of the electropherogram allele peaks made it difficult for us to distinguish between certain alleles. We omitted locus Gg7 because the observed heterozygosity was lower than expected (Table 1), suggesting potential

**Table 3** Mantel  $r$  statistics calculated between pairwise conditional genetic distance and effective resistance, and mean and standard deviation of effective resistance between all pairs of sites

Habitat quality value			Mantel $r$	Mean resistance	Standard deviation
Low	Medium	High			
1	2	3	0.249*	1.01	0.268
1	4	9	0.194*	0.810	0.249
1	8	27	0.146*	0.673	0.238
1	16	81	0.108	0.576	0.230
1	32	243	0.078	0.507	0.223
1	64	729	0.055	0.458	0.217

Values assigned to medium and high quality categories were varied by multiples of 2 and 3, respectively

\* Indicates the Mantel  $r$  statistic is significant ( $\alpha = 0.05$ )



null alleles during amplification. Five sites (1, 2, 4, 9, and 14) departed from Hardy–Weinberg equilibrium, each at only one locus, representing 1.4% of the total (348) comparisons; we did not remove these loci because doing so would greatly reduce the number of loci and thus our power to detect genetic structure. There was no evidence of linkage disequilibrium ( $P > 0.17$  for all pair-wise comparisons between loci).

#### Bayesian clustering

We were unable to detect genetic structure among sites with program Structure, suggesting that  $K = 1$ .

#### Pairwise comparisons and isolation by distance

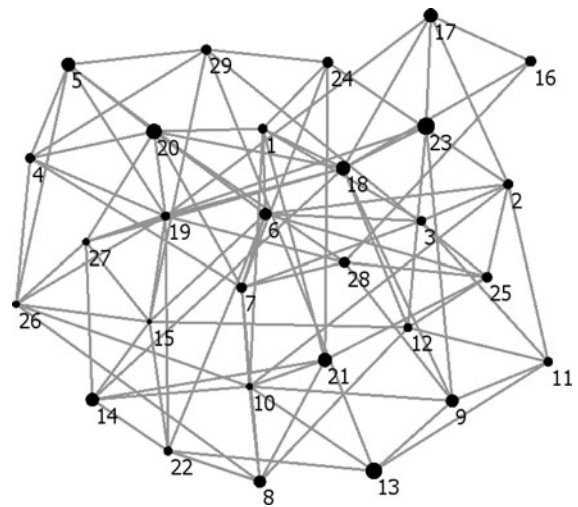
All pairwise estimates of genetic differentiation based on  $D_{est}$  (Jost 2008) were  $<0.1$  except four pairs of sites: 27 and 29 ( $D_{est} = 0.125$ ), 20 and 29 (0.121), 20 and 14 (0.114), and 26 and 14 (0.122) (Fig. 1). We found evidence for isolation by distance ( $D_{est}$  and the log of Euclidean distance between sites; Mantel  $r = 0.245$ ,  $P = 0.003$ ). The mean (SD)  $D_{est}$  across all pairs of sites was 0.019 (0.021).

#### Population graphs

Our population graph contained 160 edges connecting 29 nodes (Fig. 3). The distribution of  $cGD$  values was not different than normal (Kolmogorov–Smirnov test;  $D = 0.057$ ,  $P = 0.143$ ; mean = 6.16, SD = 1.94, range = 2.31–11.03). There was a significant, positive relationship between  $cGD$  and  $D_{est}$  (Mantel  $r = 0.335$ ,  $P < 0.001$ ).

#### Spatial principal component analysis

We detected at least one significant global pattern with our sPCA ( $\max(t) = 0.084$ ,  $P = 0.016$ ). We did not detect a local pattern ( $\max(t) = 0.045$ ,  $P = 0.991$ ). We retained the first two global axes because the decomposition of each eigenvalue into its spatial autocorrelation and variance components (Fig. 4c) showed that the first ( $\lambda_1$ ) and second ( $\lambda_2$ ) eigenvalues contained more variability and spatial structure relative to the other eigenvalues. The first and second global scores revealed a cline of genetic differentiation across space (Fig. 4a, b), in particular near the Chapleau Game Preserve (CGP; Fig. 4b).

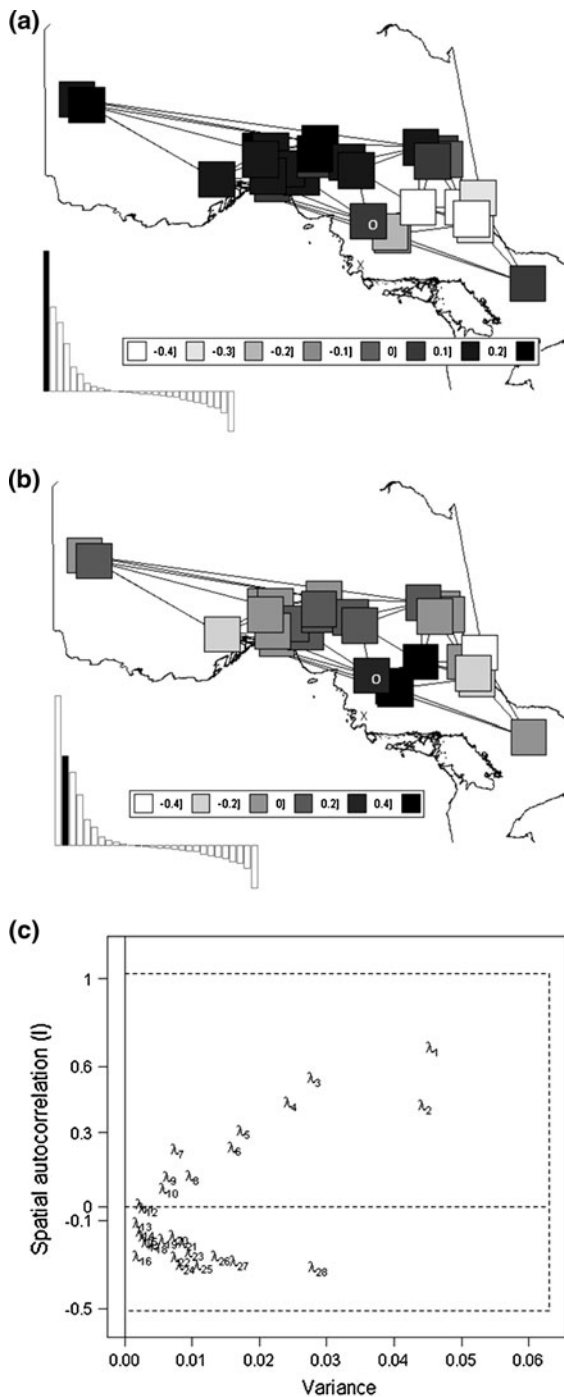


**Fig. 3** A population graph representing the genetic relatedness among populations of martens sampled at 29 sites across Ontario, Canada, profiled at 12 microsatellite loci. Edge length is proportional to the multivariate genetic covariance between sites, and node size is proportional to the allelic diversity at each site. Conditional genetic distance is calculated as the shortest path between pairs of sites on the network

#### Landscape resistance and gene flow

The resistance surface for martens in Ontario consisted of 1,777,353 cells (65% low quality, 25% medium quality, and 10% high quality) with a pixel size of 0.25 km<sup>2</sup>. When we added a 100-km wide buffer, the resistance surface consisted of 3,272,207 cells (66% low quality, 25% medium quality, and 9% high quality; Fig. 2).

We modeled marten gene flow across our resistance surface between all pairs of sites. When we compared  $cGD$  to different iterations of landscape conductance, Mantel test statistics became progressively smaller and less significant as we increased the range of values assigned to low, medium, and high quality cells (Table 3). Mean effective resistance values across all pairs of sites decreased as we increased the contrast of conductance values (Table 3). We varied the high quality habitat by multiples of 4 to assess the effect of the relative difference between medium and high quality classes; we did not show these results because the pattern was similar to when high quality habitat varied by multiples of 3. Effective resistance estimates that correlated most strongly with  $cGD$  were based on the resistance surface with low quality cells scored as 1, medium quality as 2, and high quality as 3 (Mantel



**Fig. 4** The **a**) first and **b**) second global scores from the spatial principal component analysis, representing positive spatial autocorrelation of allele frequencies. Data are from 653 martens sampled at 29 sites and genotyped at 12 microsatellite loci. Scores are plotted on a map of Ontario depicting the location of the sampling site. Edges between sites indicate which sites were considered neighbours for the calculation of Moran's  $I$ , based on a Delaunay triangulation. *Squares* represent the score of the individuals at that site; *white squares* are negative scores, *black squares* are positive scores, and *grey squares* represent less extreme scores. The eigenvalue of the displayed global score is depicted in *black* on the bar graph of eigenvalues. The location of Sault Ste. Marie is indicated with "X" and Chapleau Game Preserve is indicated with "O". The spatial autocorrelation (Moran's  $I$ ) and variance components of the  $n$  eigenvalues ( $\lambda_i$ ,  $i = 1 \dots n - 1$ ) are decomposed in **c**, where  $\lambda_1$  is the strongest global eigenvalue and  $\lambda_{28}$  is the strongest local eigenvalue

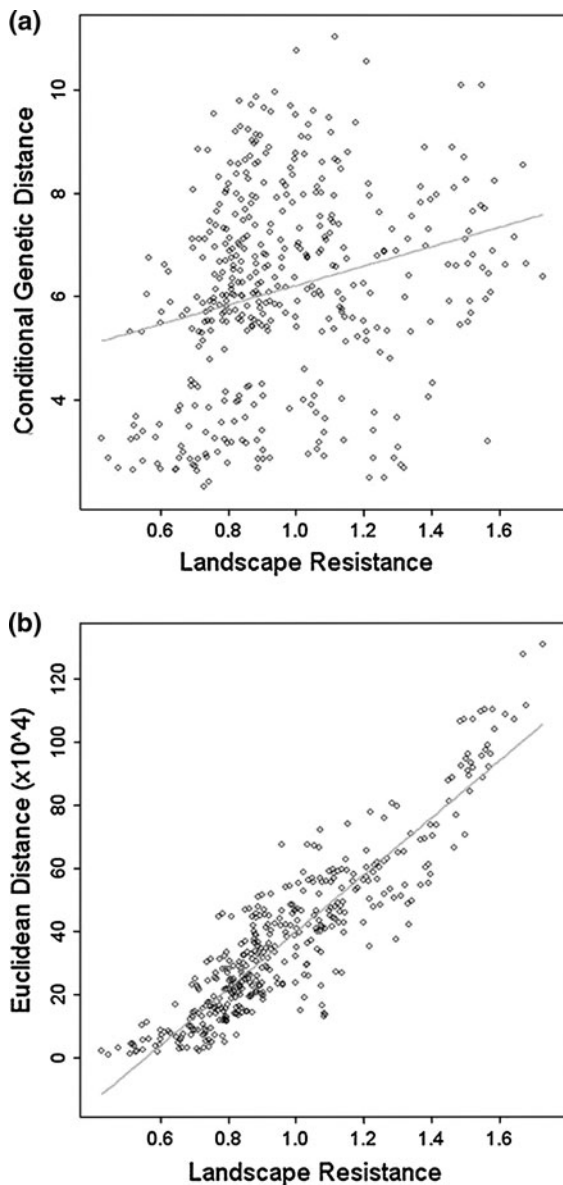
Mantel  $r = 0.410$ ,  $P < 0.001$ ). There was also a strong, positive relationship between the log of Euclidean distance and effective resistance between sites (Mantel  $r = 0.908$ ,  $P < 0.001$ ; Fig. 5b). We used partial Mantel tests to discriminate between our hypotheses of isolation by distance and isolation by resistance. When we partialled out the effect of log Euclidean distance we found no relationship between effective resistance and  $cGD$  (Mantel  $r = -0.166$ ,  $P = 0.986$ ). Conversely, when we partialled out effective resistance, we found a significant relationship between log Euclidean distance and  $cGD$  (Mantel  $r = 0.371$ ,  $P < 0.001$ ).

## Discussion

Forest management has caused a decrease in the quantity of mature and old-growth coniferous forests across Ontario compared to pre-settlement conditions (Perera and Baldwin 2001). Because American martens are considered specialists of late-seral coniferous forests, we expected that the loss and fragmentation of suitable habitat would limit the ability of martens to disperse, resulting in the population as a whole being genetically fragmented due to limited gene flow, founder effects, and genetic drift. Instead however, we detected a positive relationship between genetic and Euclidean distances when we partialled out effective resistance, suggesting a pattern of isolation-by-distance. Although we did find a significant relationship between effective resistance and genetic distance, this appeared to be largely attributable to isolation-by-distance, since effective resistance and Euclidean

$r = 0.249$ ,  $P < 0.001$ , Table 3, Fig. 5a). We used this surface to represent both effective resistance and our isolation by resistance hypothesis.

We detected a significant pattern of isolation by distance ( $cGD$  and the log of Euclidean distance;



**Fig. 5** The relationship between a) effective resistance and conditional genetic distance, and b) effective resistance and log Euclidean distance (m) between sites

distance were closely correlated, and when we removed the effect of Euclidean distance, we found no relationship between effective resistance and genetic distance. Thus, we conclude that gene flow of martens in Ontario was not affected by forest-management induced landscape structure, but instead was better characterized by an isolation-by-distance pattern, likely arising from neighbour mating.

The costs we employed in the Ontario marten habitat models were arbitrary, and thus, we sought to avoid idiosyncratic conclusions arising from using these arbitrary costs in our landscape resistance surface. We accomplished this by varying the conductance values of the habitat quality categories and reassessing relationships among effective resistance, Euclidean distance, and gene flow. Increasing the relative contrast of conductance values in our resistance surface had the effect of reducing the mean effective resistance. The resistance surface that was most closely correlated with genetic distance was the surface with the highest mean effective resistance. This same resistance surface was also the most strongly correlated to Euclidean distance of all the resistance surfaces. Thus, the mosaic of habitat appeared configured such that it did not impede marten gene flow. We draw this conclusion in concordance with our  $D_{est}$  and Bayesian clustering results: both indicated that there was little genetic differentiation among sample sites. We note also that although we did not find an effect of forest-management induced landscape structure on gene flow, we recognize that forest management may still influence marten gene flow in other regions, especially where management produces landscapes that are more heterogeneous or fragmented than our study area (e.g., Short Bull et al. 2011). Similarly, it is plausible that genetic differentiation of martens could increase in Ontario if available habitat decreases from current levels.

Our results differ from the genetic pattern described by Broquet et al. (2006b), who concluded that marten dispersal in Ontario is impeded by the loss and fragmentation of suitable habitat. They found that in logged habitats, the genetic relatedness of individual martens correlated with the least-cost path between individuals, whereas in unlogged habitats marten movement correlated with the Euclidean distance between individuals (Broquet et al. 2006b). The studies by Broquet et al. (2006a, b) were conducted at a smaller spatial scale than our study (two sites of approximately 500 and 800 km<sup>2</sup>). Cushman et al. (2011) also found that marten movement in Wyoming, USA, was influenced by habitat loss and fragmentation due to logging. It is possible that the factors that influence marten movements at small scales are not influential enough to cause province-wide disruption in gene flow. Accordingly, Kyle and Strobeck (2003)

showed that at very large spatial scales (i.e., across the continent of North America), marten populations exhibit relatively little genetic structure. We speculate that Kyle and Strobeck (2003) might have detected isolation-by-distance had they measured  $cGD$ , which has greater power than pairwise measures such as  $F_{ST}$  (Dyer et al. 2010).

Our results also differ from those of Wasserman et al. (2010) for martens in northern Idaho, USA. Wasserman et al. (2010) found that marten gene flow was related to elevation, which they considered a proxy for climate, and they found no relationship between gene flow and roads, barriers, canopy closure, seral stage, Euclidean distance, or habitat suitability. We consider it unlikely that elevation and climate had a similar effect on marten gene flow in Ontario as they do in Idaho, because the topography of our Ontario study area was relatively homogeneous, as was the climate with respect to marten requirements (e.g., Krohn et al. 1995). This may be an interesting area of future research in Ontario however, as climate change trends may serve to introduce more spatial variability in snow cover in the boreal forest.

There may be other landscape features that we did not measure that influence marten gene flow in Ontario. For example, Garroway et al. (2011b) found that road density, snow depth, and river density impeded fisher (*Martes pennanti*) gene flow during a range expansion in the temperate forest south of our marten study area. Similarly, there may have been effects that we did not detect arising from our use of a 3-class resistance surface (Cushman and Landguth 2010a). We did not test a variety of other hypotheses or resistance surfaces because our goal was to assess the effect of recent forest management plans on the gene flow of martens, so we restricted our analyses to forest inventories, and the relevant marten habitat management models. Although there are many landscape features that we did not measure that may impede marten gene flow, we underscore the point that we detected very little genetic differentiation among sites (i.e.,  $K = 1$  and mean  $D_{est} = 0.019$ ). Thus, we suspect that the effect of unmeasured features on genetic distance was relatively small. Future work could assess whether alternate landscape features and structures affect marten gene flow, particularly if subsequent genetic studies show more genetic differentiation between marten populations than the subtle differentiation we found here.

The first and second axes of our sPCA suggest a subtle cline of genetic differentiation across Ontario. In particular, the second axis suggests subtle genetic differentiation between sites close to CGP and neighbouring sites. We propose two hypotheses that may explain this pattern. First, we speculate that marten population expansion from a refuge may explain this genetic pattern. Marten populations have declined in Ontario since the late 1800s (de Vos 1951; Hagmeier 1956), and by 1948 the marten fur harvest in the province was closed (de Vos 1951). During the 1940s, there were two known refuges for martens in Ontario: CGP (Peterson and Crichton 1949; de Vos 1951) and Algonquin Provincial Park (APP) (Ontario Ministry of Natural Resources, unpublished data; Fig. 1). Marten harvest records from the Chapleau district in the 1940s suggest that CGP acted as a source, leading to an expansion of the marten range from this remnant population (de Vos 1951). If martens expanded from this refuge, then we might expect allelic diversity to be higher at the source, and decline at greater distances from the source because of founder effects (Garroway et al. 2011a); this might account for the genetic pattern we detected around CGP with sPCA. Alternatively, we speculate that there may be natural gene flow between the Upper Peninsula of Michigan (UP), USA, and Ontario, across the narrows near Sault Ste. Marie, Ontario (Fig. 1). Martens were extirpated in Michigan and Wisconsin (Williams et al. 2007), and have since been reintroduced to these states with animals originating from several regions of Ontario (CGP, APP, Nipigon area), Minnesota, British Columbia, and Colorado (Williams et al. 2007). These reintroductions have resulted in three genetic clusters in UP (Williams and Scribner 2010). Potential immigration from UP into Ontario may account for the genetic pattern we detected with sPCA. Future studies could explicitly address these two alternative hypotheses.

In conclusion, based on our analysis, marten dispersal across Ontario can best be described as neighbour-mating with no directional bias caused by forest-management induced landscape structure, resulting in a pattern of isolation by distance. Martens are thought to be sensitive to habitat fragmentation, and our results do not suggest otherwise. Rather, our results suggest that the Ontario landscape is well connected with respect to suitable marten habitat and does not impede gene flow. In recent years, forest management plans for the province of Ontario have



been required to adhere to guidelines that maintain an adequate quality and quantity of habitat for martens (Watt et al. 1996), and these guidelines have been based on the same habitat-suitability models that we used to build our resistance surface. We found positive correlations between Euclidean distance, effective resistance, and genetic distance, as well as evidence of high gene flow among martens in the province. Overall, our analyses suggest that the marten models by which forest managers have planned future forestry operations are adequate for maintaining landscape-wide marten gene flow.

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## References

- Berg WE (1982) Reintroduction of fisher, pine marten, and river otter. In: Sanderson GC (ed) Midwest furbearer management. Proceedings of the 43rd midwest fish and wildlife conference, Wichita, Kansas, 1981
- Bowman JC, Robitaille J-F (1997) Winter habitat use of American martens *Martes americana* within second-growth forest in Ontario, Canada. *Wildl Biol* 3:97–105
- Bowman J, Robitaille J-F (2005) An assessment of expert-based marten habitat models used for forest management in Ontario. *For Chron* 81:801–807
- Broquet T, Johnson CA, Petit E et al (2006a) Dispersal and genetic structure in the American marten, *Martes americana*. *Mol Ecol* 15:1689–1697
- Broquet T, Ray N, Petit E et al (2006b) Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*). *Landscape Ecol* 21:877–889
- Buskirk SW, Powell RA (1994) Habitat ecology of fishers and American martens. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds) Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, pp 283–296
- Chapin TG, Harrison DJ, Katnik DD (1998) Influence of landscape pattern on habitat use by American marten in an industrial forest. *Conserv Biol* 12:1327–1337
- Crawford NG (2010) SMOGD: software for the measurement of genetic diversity. *Mol Ecol Resour* 10:556–557
- Cushman SA, Landguth EL (2010a) Scale dependent inference in landscape genetics. *Landscape Ecol* 25:967–979
- Cushman SA, Landguth EL (2010b) Spurious correlations and inference in landscape genetics. *Mol Ecol* 19:3592–3602
- Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. *Landscape Ecol* 25:1613–1625
- Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *Am Nat* 168:486–499
- Cushman SA, Raphael MG, Ruggiero LF et al (2011) Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. *Landscape Ecol* 26:1137–1149
- Dallas JF, Piertney SB (1998) Microsatellite primers for the Eurasian otter. *Mol Ecol* 7:1248–1251
- Davis CS, Strobeck C (1998) Isolation, variability, and cross-species amplification of polymorphic microsatellite loci in the family Mustelidae. *Mol Ecol* 7:1776–1778
- de Vos A (1951) Overflow and dispersal of marten and fisher from wildlife refuges. *J Wildl Manag* 15:164–175
- Driezen K, Adriaansen F, Rondinini C et al (2007) Evaluating least-cost model predictions with empirical dispersal data: a case study using radio tracking data of hedgehogs (*Erinaceus europaeus*). *Ecol Model* 209:314–322
- Duffy AJ, Landa A, O’Connell M et al (1998) Four polymorphic microsatellites in wolverine, *Gulo gulo*. *Anim Genet* 29:63
- Dyer RJ (2009) GeneticStudio: a suite of programs for spatial analysis of genetic-marker data. *Mol Ecol Resour* 9:110–113
- Dyer RJ, Nason JD (2004) Population Graphs: the graph theoretic shape of genetic structure. *Mol Ecol* 13:1713–1727
- Dyer RJ, Nason JD, Garrick RC (2010) Landscape modelling of gene flow: improved power using conditional genetic distance derived from the topology of population networks. *Mol Ecol* 19:3746–3759
- Elkie PC, Hooper G, Carr AP, Rempel RS (1999) Ontario marten analyst and marten1 models: Directions for applying the forest management guidelines for the provision of marten habitat in the northwest region. Ontario Ministry of Natural Resources Northwest Science and Technology, Thunder Bay, Ontario, NWST TM-004
- Elkie PC, Gluck M, Boos J, et al. (2009) Science and information in support of the forest management guide for landscapes: package “A” simulations, rationale, and inputs. Ontario Ministry of Natural Resources, Forest Policy Section
- Fleming MA, Ostrander EA, Cook JA (1999) Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). *Mol Ecol* 8:1352–1354
- Fuller AK, Harrison DJ (2005) Influence of partial timber harvesting on American martens in north-central Maine. *J Wildl Manag* 69:710–722
- Garroway CJ, Bowman J, Carr D, Wilson PJ (2008) Applications of graph theory to landscape genetics. *Evol Appl* 1:620–630
- Garroway CJ, Bowman J, Holloway GL et al (2011a) The genetic signature of rapid range expansion by flying squirrels in response to contemporary climate warming. *Glob Change Biol* 17:1760–1769
- Garroway CJ, Bowman J, Wilson PJ (2011b) Using a genetic network to parameterize a landscape resistance surface. *Mol Ecol* 20:3978–3988
- Hagmeier EM (1956) Distribution of marten and fisher in North America. *Can Field Nat* 70:101–148

- Hargis CD, Bissonette JA (1997) Effects of forest fragmentation on populations of American marten in the intermountain west. In: Proulx G, Bryant HN, Woodard PM (eds) *Martes: taxonomy, ecology, techniques, and management*. Provincial Museum of Alberta, Edmonton, Alberta, pp 437–451
- Hargis CD, Bissonette JA, Turner DL (1999) The influence of forest fragmentation and landscape pattern on American martens. *J Appl Ecol* 36:157–172
- Holloway GL, Naylor BJ, Watt WR (2004) Habitat relationships of wildlife in Ontario. Revised habitat suitability models for the Great Lakes-St. Lawrence and Boreal East forests. Ontario Ministry of Natural Resources, Science and Information Branch, Southern Science and Information and Northeast Science and Information Joint Technical Report #1
- Johnson CA (2008) Mammalian dispersal behaviour and its fitness correlates. Dissertation, University of Guelph
- Johnson CA, Fryxell JM, Thompson ID, Baker JA (2009) Mortality risk increases with natal dispersal distance in American martens. *Proc R Soc B* 276:3361–3367
- Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24:1403–1405
- Jombart T, Devillard S, Dufour AB, Pontier D (2008) Revealing cryptic spatial patterns in genetic variability by a new multivariate method. *Heredity* 101:92–103
- Jost L (2008)  $G_{ST}$  and its relatives do not measure differentiation. *Mol Ecol* 17:4015–4026
- Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The effect of map boundary on estimates of landscape resistance to animal movement. *PLoS One* 5(7):e11785
- Krohn WB, Elowe KD, Boone RB (1995) Relations among fishers, snow, and martens: development and evaluation of two hypotheses. *For Chron* 71:97–105
- Kyle CJ, Strobeck C (2003) Genetic homogeneity of Canadian mainland marten populations underscores the distinctiveness of Newfoundland pine martens (*Martes americana atrata*). *Can J Zool* 81:57–66
- Legendre P, Fortin M-J (2010) Comparison of the Mantel test and alternative approaches for detecting complex multivariate relationships in the spatial analysis of genetic data. *Mol Ecol Resour* 10:831–844
- Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol Evol* 18:189–197
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* 27:209–220
- McLaren MA, Thompson ID, Baker JA (1998) Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. *For Chron* 74:241–248
- McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. *Proc Natl Acad Sci USA* 104:19885–19890
- McRae BH, Shah VB (2009) Circuitscape user's guide. <http://www.circuitscape.org>. Accessed Jan 2011
- McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712–2724
- Moran P (1948) The interpretation of statistical maps. *J R Stat Soc B* 10:243–251
- Moran P (1950) Notes on continuous stochastic phenomena. *Biometrika* 37:17–23
- Naylor B, Kaminski D, Bridge S, et al. (1999) User's guide for OWHAM99 and OWHAMTool (Ver. 4.0). Ontario Ministry of Natural Resources, SCSS Technical Report. no. 54
- O'Grady JJ, Brook BW, Reed DH et al (2006) Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biol Conserv* 133:42–51
- Oksanen J, Kindt R, Legendre P et al (2009) Vegan: community ecology package. R package version 1.15-3. <http://vegan.r-forge.r-project.org/>. Accessed June 2009
- Payer DC, Harrison DJ (2003) Influence of forest structure on habitat use by American marten in an industrial forest. *For Ecol Manag* 179:145–156
- Perera AJ, Baldwin DJB (2001) Spatial patterns in the managed forest landscape of Ontario. In: Perera AH, Euler DL, Thompson ID (eds) *Ecology of a managed terrestrial landscape: patterns and processes of forest landscapes in Ontario*. Ontario Ministry of Natural Resources and UBC Press, Vancouver, British Columbia, pp 74–99
- Perez-Espona S, Perez-Barberia FJ, McLeod JE et al (2008) Landscape features affect gene flow of Scottish Highland red deer (*Cervus elaphus*). *Mol Ecol* 17:981–996
- Peterson RL, Crichton V (1949) The fur resources of Chapleau District, Ontario. *Can J Res* 27:68–84
- Potvin F, Belanger L, Lowell K (2000) Marten habitat selection in a clearcut boreal landscape. *Conserv Biol* 14:844–857
- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* 155:945–959
- R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed Jan 2011
- Raufaste N, Rousset F (2001) Are partial Mantel tests adequate? *Evolution* 55:1703–1705
- Rousset F (2008) GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Mol Ecol Resour* 8:103–106
- Schwartz MK, Copeland JP, Anderson NJ et al (2009) Wolverine gene flow across a narrow climatic niche. *Ecology* 90:3222–3232
- Shirk AJ, Wallin DO, Cushman SA et al (2010) Inferring landscape effects on gene flow: a new model selection framework. *Mol Ecol* 19:3603–3619
- Short Bull RA, Cushman SA, Mace R et al (2011) Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Mol Ecol* 20:1092–1107
- Spear SF, Balkenhol N, Fortin MJ et al (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Mol Ecol* 19:3576–3591
- Storfer A, Murphy MA, Evans JS et al (2007) Putting the 'landscape' in landscape genetics. *Heredity* 98:128–142
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 68:571–573
- Ter-Mikaelian MT, Columbo SJ, Chen J (2009) Estimating natural forest fire return interval in northeastern Ontario, Canada. *For Ecol Manag* 258:2037–2045
- Thompson ID (2000) Forest vegetation of Ontario: factors influencing landscape change. In: Perera AH, Euler DL, Thompson ID (eds) *Ecology of a managed terrestrial landscape: patterns and processes of forest landscapes in*



- Ontario. Ontario Ministry of Natural Resources and UBC Press, Vancouver, British Columbia, pp 30–53
- Thompson ID, Colgan PW (1987) Numerical responses of martens to a food shortage in northcentral Ontario. *J Wildl Manag* 51:824–835
- Tully SM (2006) Habitat selection of fishers (*Martes pennanti*) in an untrapped refugium: Algonquin Provincial Park. Thesis, Trent University, Ontario, Canada
- Vincent IR, Farid A, Otieno CJ (2003) Variability of thirteen microsatellite markers in American mink (*Mustela vison*). *Can J Anim Sci* 83:597–599
- Voigt DR, Baker JA, Rempel RS, Thompson ID (2000) Forest vertebrate responses to landscape-level changes in Ontario. In: Perera AH, Euler DL, Thompson ID (eds) *Ecology of a managed terrestrial landscape: patterns and processes of forest landscapes in Ontario*. Ontario Ministry of Natural Resources and UBC Press, Vancouver, British Columbia, pp 198–233
- Walker CW, Vila C, Landa A et al (2001) Genetic variation and population structure in Scandinavian wolverine (*Gulo gulo*) populations. *Mol Ecol* 10:53–63
- Wasserman TN, Cushman SA, Schwartz MK, Wallin DO (2010) Spatial scaling and multi-modal inference in landscape genetics: *Martes Americana* in northern Idaho. *Landscape Ecol* 25:1601–1612
- Watt WR, Baker JA, Hogg DM, et al. (1996) Forest management guidelines for the provision of marten habitat, version 1.0. Ontario Ministry of Natural Resources Forest Management Branch MNR#50908, Queens Printer for Ontario
- Williams BW, Scribner KT (2010) Effects of multiple founder populations on spatial genetic structure of reintroduced American martens. *Mol Ecol* 19:227–240
- Williams BW, Gilbert JH, Zollner PA (2007) Historical perspective on the reintroduction of the fisher and American marten in Michigan and Wisconsin. General Technical Report NRS-5. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station