2017

Estimating Landscape Quality And Genetic Structure Of Recovering American Marten Populations In The Northeastern United States

Cody Michael Aylward
University of Vermont

Recommended Citation

Aylward, Cody Michael, "Estimating Landscape Quality And Genetic Structure Of Recovering American Marten Populations In The Northeastern United States" (2017). *Graduate College Dissertations and Theses*. 784.
https://scholarworks.uvm.edu/graddis/784

ESTIMATING LANDSCAPE QUALITY AND GENETIC STRUCTURE OF RECOVERING AMERICAN MARTEN POPULATIONS IN THE NORTHEASTERN UNITED STATES

A Thesis Presented

by

Cody Michael Aylward

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Master of Science
Specializing in Natural Resources

October, 2017

Defense Date: July 7, 2017
Thesis Examination Committee:

James D. Murdoch, Ph.D., Advisor
C. William Kilpatrick, Ph.D., Chairperson
Therese M. Donovan, Ph.D.
Cynthia J. Forehand, Ph.D., Dean of the Graduate College

ABSTRACT

The American marten (*Martes americana*) is an endangered species in Vermont and a Regional Species of Greatest Conservation Need in the northeastern United States. Though historically widespread in northeastern forests, their range presumably contracted to northern Maine and the High Peaks region of the Adirondacks by the early 1900s. Regionally, populations appear to be in recovery. Natural recolonization is believed to have occurred in New Hampshire, northeastern Vermont and the western Adirondacks. A reintroduction effort in southern Vermont that was originally declared unsuccessful is now believed to be the source of a recently detected population in the area. However, our current knowledge of distribution, population history and population connectivity relies primarily on occurrence data from harvest records, which are limited in scope and resolution. In Vermont, where population size is estimated to be extremely low, more robust estimates of population status may be critical to continued recovery.

I genotyped individuals from Maine, New York, New Hampshire, northeastern Vermont and southern Vermont at ten microsatellite loci and amplified a 320 base pair segment of the control region of mtDNA to estimate the source(s) of the two Vermont populations using statistical tests of genetic differentiation. I also used Bayesian and stochastic genetic clustering methods to estimate population genetic structure in the northeastern United States. Genetic structure exists at multiple scales in the region as a result of natural barriers to gene flow, human-mediated gene flow, and lineage sorting in relic populations. My results suggest that New Hampshire is a major source of colonization of northeastern Vermont and the population in southern Vermont is either a remnant of the reintroduction or a pre-reintroduction relic that has experienced introgression from the reintroduction stock. I identified three regions where relic populations perceived to be extirpated in the 1900s may have persisted.

I also developed an occupancy model for American marten in the northeastern United States using mixed-effects logistic regression based on expert opinion data. Eighteen experts from Maine, New Hampshire, Vermont and New York with backgrounds in trapping, wildlife management, and wildlife science participated in the survey. Experts were asked to estimate the probability of marten occupancy at 30 sites in the northeastern United States. Three top models described the data. Habitat covariates in those models were 1) percent canopy cover, 2) percent spruce-fir forest cover, 3) winter temperature, 4) elevation, and 5) road density. An AIC-weighted average of these three models had significant predictive ability (area under an ROC curve = 0.88) with respect to occurrence records in the northeastern United States. In addition, the model predicted that high quality habitat existed patchily along the central and northern Green Mountain spine in Vermont – where no occurrence records exist for at least a century. Top-scoring movement corridors between southern Vermont and nearby populations in northeastern Vermont/New Hampshire and New York occurred in the northern and central Green Mountains and across high resistance movement barriers in the Champlain valley. Corridors to New York were considered strong movement barriers and are unlikely to facilitate gene flow.

ACKNOWLEDGMENTS

I thank the Vermont Fish and Wildlife Department, Northeastern States Research Cooperative, and USDA McIntire-Stennis Program for financial support of my thesis research. I also received a teaching assistantship from the University of Vermont Rubenstein School of Environment and Natural Resources. I thank my advisory committee: Drs. James Murdoch, Therese Donovan, and C. William Kilpatrick for their extensive support during my program. I also thank Chris Bernier, who was instrumental to both chapters of this thesis and provided logistical and data collection support; Jon Katz, who made a user-friendly survey interface possible with support from the Vermont Cooperative Fish and Wildlife Research Unit; Dr. Ruth Mickey, for her statistical support in analyzing expert opinion data; Dr. Paul Jensen, Jill Kilborn, Alexej Sirén, and Cory Mosby for providing samples and knowledge of population histories in New York, New Hampshire and Maine; the anonymous trappers and biologists who provided tissue samples from Maine; the many anonymous trappers, managers, and community members who participated as experts in the expert survey; and Kim Royar, Paul Hapeman, and Katy Crumley for their collaboration.

Finally, I am deeply grateful to have the loving support of my mother and father, my brother Westley and my sister Jenny, and Alana and Winnie.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENETIC STRUCTURE OF AMERICAN MARTEN POPULATIONS IN THE NORTHEASTERN UNITED STATES

1.1. Introduction

Efforts to combat species range contractions and restore extirpated populations commonly involve reintroductions (Seddon et al. 2007). At least 77 mammal translocations occurred over two decades following the establishment of the Endangered Species Act in 1973, 62 percent of which involved species of the Order Carnivora (Wolf et al. 1996). Reintroduction success has been variable; in particular, translocations of threatened or endangered species and reintroductions into the periphery of a species' distribution succeeded only 53% and 46% of the time, respectively (Wolf et al. 1996). Post-translocation monitoring efforts are rarely adequate however, and in many cases the outcomes remain unknown for decades (Schwartz 2005).

Restoring populations of wide ranging mesocarnivores is particularly important in the northeastern United States where large predators have been extirpated and mesocarnivores serve as a multi-species conservation umbrella (Lambeck 1997; Carroll 2007). The American marten (*Martes americana*) is one such species that historically ranged throughout most of the northeast (Hagmeier 1956). The southern periphery of marten distribution contracted significantly from the late 1800s through the mid 1900s due to unregulated harvest and deforestation (Mech and Rogers 1977; Distefano et al. 1990). By the mid 1900s, American marten populations were considered extirpated or non-viable in the northeastern United States with the exception of populations in northern

Maine and the High Peaks region of the Adirondack Mountains in New York (Mech and Rogers 1977; Clark et al. 1987). In New Hampshire and the mid-elevations of the Adirondacks, breeding populations were recently detected beginning in the 1980s and 1990s, respectively (Kelly et al. 2009; Paul Jensen in Lit.). While recovery is apparent in Vermont, population history is riddled with uncertainty and the long-term viability of contemporary populations remains questionable.

American marten were listed as an endangered species in Vermont in 1987, at which time only four confirmed 20th century detections existed in the state: 1910 in Chittenden (Kirk 1916), 1915 in Glastenbury (Kirk 1916), 1926 on Stratton Mountain in Windham County (Osgood 1938), and 1954 on Hogback Mountain in Windham County (Godin 1977). Subsequently, a recovery plan was developed to return a viable population of American martens to the state via translocation from nearby populations (Distefano et al. 1990; Royar 1992). The recovery plan called for the use of multiple source populations and a combination of slow- and quick-release methods to overcome common reintroduction challenges such as low genetic diversity in the reintroduced population and dispersal of translocated individuals (Trombulak and Royar 2001; Moruzzi et al. 2003). From 1989 to 1991, 104 individuals from Maine (77 males, 27 females) and 11 individuals from New York (11 males, 0 females) were released in two sites on the southern Green Mountain National Forest (Royar 1992; see Appendix I). Forty-eight individuals (35 males, 13 females) were released in White Rocks National Recreation Area (WRNRA), of which 12 were slow-released and 36 were quick-released. Sixty-seven individuals (53 males, 14 females) were released in Lye Brook Wilderness Area

(LBWA), of which 27 were slow-released and 40 were quick-released (Royar 1992; Appendix I).

Radio-telemetry in 1989 and 1990 suggested three males and four females had established home ranges occupying both release areas (Royar 1992). Estimates of female home range size ranged from 1 km^2 to 3 km^2, no male home range estimates were obtained (Royar 1992). Initial camera monitoring efforts began in winter 1994-1995, when remote cameras were deployed at 20 sites near the LBWA release sites. Martens were detected at only two sites (Brooks 1996). Further camera monitoring efforts near the LBWA and WRNRA release areas in 1997 and 1998 detected no martens, at which point monitoring was terminated under the assumption that a viable population had not been established in southern Vermont (Moruzzi et al. 2003).

Dispersal of translocated individuals is a common occurrence in mammals (Bright and Morris 1994; Moehrenschlager and MacDonald 2003; Russell et al. 2010; Lawes et al. 2013). Contrary to the animals that appeared to establish home ranges, five males and one female with radio-collars were never confirmed within 10 km of the release sites. Long distance dispersal following the reintroduction is evident by ear-tagged individuals reported by Moruzzi et al. (2003) that were incidentally trapped or road killed in Shrewsbury in 1990 and Winhall in 1991 (each ~15 km from release site), Candia, New Hampshire in 1990 (~145 km), Bakersville, Connecticut in 1992 (~160 km), and Rangeley, Maine in 1997 (~245 km). One unmarked marten was incidentally trapped in a fisher (*Pekania pennanti*) set near Barton in far northeastern Vermont (~180 km). Since 2005, martens have been regularly detected in the area east of Barton, and since 2010 occasional detections have occurred in the southern Green Mountain National Forest ~10 km south of the release sites (C. Bernier in Lit.). The population in northeastern Vermont may be part of an expanding population in northern New Hampshire (Kelly et al. 2009). The population in southern Vermont is hypothesized to be a remnant of the 1989-1991 reintroduction that went undetected in the 1997-1998 monitoring effort.

Molecular techniques can reveal the source of populations of unknown origin, and genetic monitoring programs are included in reintroduction efforts with increasing regularity (Drew et al. 2003; Schwartz 2005; Landguth et al. 2010; Mowry et al. 2015). We estimated genetic diversity and genetic structure of marten populations throughout the northeastern United States using mtDNA and microsatellite markers. We also tested hypotheses that the recently detect population in northeastern Vermont is colonized by dispersers from an expanding population in northern New Hampshire, and that the recently detected population in southern Vermont is a remnant of the 1989-1991 reintroduction program that went undetected in post-release monitoring.

1.2. Methods

1.2.1. Study area and sample collection

The study area (~183,575 km^2) consisted of Maine, New Hampshire, Vermont, and 12 counties in the Adirondack Mountain region of New York. Forests in this area have undergone significant historical conversion and species loss, but are now considered to be in recovery (Foster et al. 2008). Our study area spans a gradient of northern hardwood-dominated forests in the south to sub-boreal spruce-fir dominated forests in the north (Foster et al. 2008).

Tissue samples were obtained from state biologists and fur trappers in five geographic regions (populations) - southern Vermont, northern Vermont, northern New Hampshire, north-central Maine and the Adirondack Mountain region of New York (Fig. 1). Sample locations were either recorded via GPS or recorded to the township, in which case the town centroid was used as the sample locality for spatially explicit analyses (Appendix II).

1.2.2. Laboratory methods

DNA extraction was performed using Gentra DNA kits (Qiagen). D-loop sequences of mtDNA (320 bp) and 10 microsatellite loci (Ma-1, Ma-8, Ma-9, Tt-4, Mvi1341, Mvi 1354, Mvi2243, Mvis072, Mvis075, Mer041, and Gg443; Davis and Strobeck 1998; Fleming et al. 1999; Walker et al. 2001; Vincent et al. 2003) were amplified via polymerase chain reaction (PCR). These markers have regularly been used to examine population structure and reintroduction success of American marten and other mustelids such as fisher (*Pekania pennanti*) throughout North America (Kyle et al. 2000; Drew et al. 2003; Kyle and Strobeck 2003; Williams and Scribner 2010; Hapeman et al. 2011; Koen et al. 2012; Hapeman et al. 2014). Microsatellite PCR mixtures contained 75 ng DNA, 0.16 uM each primer, 120 uM dNTPs, 10X ThermoPol Reaction Buffer (New England BioLabs) and 0.5 units Taq DNA polymerase (New England BioLabs). Amplification conditions for microsatellite PCR were 94 °C for 1 minute, 35 cycles of 94 °C for 30 seconds, 54 °C for 20 seconds, and 72 °C for 5 seconds, and a final extension at 72 °C for 30 seconds (Ma-1, Ma-8, Ma-9, Tt-4, Mer041, Mvi1341, Mvi1354) or 94 °C for 5 minutes, 30 cycles of 94 °C for 30 seconds, 59 °C for 45 seconds, and 74 °C for 30 seconds, and a final extension at 65 °C for 45 minutes (Gg443, Mvis075, Mvi2243, Mvis 072). PCR mixtures for mtDNA contained 100 ng DNA, 0.4 uM primers L16022 (Shields and Kocher 1991) and H16498 (Woods et al. 1999), and PuReTaq Ready-To-Go PCR beads (GE Healthcare, UK). Conditions for mtDNA PCR were 35 cycles of 94 °C for 60 seconds, 50 °C for 60 seconds, and 72 °C for 70 seconds. Forward and reverse sequencing reactions using a BigDye^{TM} Terminator kit (Applied Biosystems) and purified with Sephadex spin-columns (Thermo Fisher Scientific). The Vermont Cancer Center (Burlington, Vermont, USA) performed capillary electrophoresis for sequencing and fragment size analysis.

1.2.3. Microsatellite data analysis

Microsatellite fragments were visualized and sized with GeneMapper5 (Applied Biosystems). Number of alleles (N_a), observed heterozygosity (H_o), expected heterozygosity (H_e) and unbiased heterozygosity (UH_e) for all loci and all populations were estimated in GenAlEx (Peakall and Smouse 2006). Paired t-tests of arcsine transformed diversity estimates were used to determine significance of differences in diversity between populations (Archie 1985; Schwartz et al. 2005). Tests for linkage disequilibrium and Hardy-Weinberg equilibrium were performed in GENEPOP (Raymond and Rousset 1995) with Bonferroni corrections (Rice 1989) to adjust for multiple independent loci. A Wilcoxon signed-rank test of heterozygosity excess (Cornuet and Luikart 1996) implemented in Bottleneck 1.2.02 (Piry et al. 1999) was used to test for recent population bottlenecks. Differentiation in allele and genotype frequencies among population pairs was estimated in GENEPOP. Population pairwise genetic distances (F_{st}) were estimated in Arlequin (Excoffier and Lischer 2010). Population assignment and exclusion of individuals from Vermont were implemented in GeneClass2 (Piry et al. 2004). In addition to geographically delimited populations, two potential source populations were simulated. One, representing the reintroduction stock, was created by simulating multi-locus genotype data for 104 individuals using allele frequencies from Maine and 11 individuals using allele frequencies from New York; a second, representing admixture between the reintroduction stock and New Hampshire, was created by combining the simulated reintroduction stock with simulated multi-locus genotype data for 115 individuals using allele frequencies from New Hampshire.

Non-spatial multi-locus genetic clustering was performed in STRUCTURE (Pritchard et al. 2000) and BAPS (Corander et al. 2008). Using STRUCTURE, the number of genetic clusters (K) was allowed to vary between 1 and 10 over 50 independent runs, and most likely K was determined by estimating Delta-K (Evanno et al. 2005) using Structure Harvester (Earl and vonHoldt 2012). In BAPS, K was allowed to vary from 1-10; most likely K was determined from the partitioning of individuals with the greatest log likelihood. Spatially explicit genetic clustering was performed in Geneland (Guillot et al. 2005), TESS (Chen et al. 2007), and BAPS. In Geneland, K was estimated under the D-model (uncorrelated allele frequencies; Pritchard et al. 2000) and the F-model (correlated allele frequencies; Falush et al. 2003). K was allowed to vary between 1 and 10 over 10 independent runs. Each run consisted 500,000 Markov Chain Monte Carlo (MCMC) iterations, storing every 50. Maximum rate of Poisson process was set to 100 and maximum number of Poisson-Voronoi tessellation nuclei set to 300. Sample coordinate uncertainty was allowed to vary between 0 and 14 km. In TESS, genetic clusters were estimated assuming a model of no admixture and two different admixture models (Durand et al. 2009). K was allowed to vary between 1 and 10 over 10 independent runs. Each run consisted of 50,000 sweeps with 10,000 burn-in sweeps. All other default parameters were kept and K was estimated from the run with minimal Deviance Information Criterion (DIC).

1.2.4. mtDNA data analysis

Sequence chromatograms were visualized in 4peaks (Griekspoor and Groothuis 2006) and aligned in ClustalW2 (Larkin et al. 2007). For statistical analyses, indels were treated as independent polymorphisms. Genetic diversity within geographic populations was examined with Arlequin (Schneider and Excoffier 1999; Excoffier 2004; Excoffier and Lischer 2010). Mismatch distributions within populations were examined for signs of sudden demographic and sudden spatial expansions. Arlequin was also used to examine genetic divergence (Fst) between geographic populations and Geneland was used to examine the genetic structuring of maternal lineages.

1.3. Results

1.3.1. mtDNA

Twelve D-loop haplotypes were identified in the study area (Table 1). Several populations were characterized by a single dominant haplotype. Eighty-three percent of individuals in southern Vermont were HapA and 63 percent of individuals in New Hampshire were HapB. Two haplotypes (HapA and HapI) accounted for 65 percent of the variation in New York, and each was associated with a distinct geographic region within New York. This pattern of substructure within New York was confirmed by genetic clustering in Geneland, and subsequent mtDNA and microsatellite analyses treat New York as two distinct populations, one in the High Peaks region (67 percent HapA) and one in the West Canada Lakes region (64 percent HapI). Private haplotypes were identified in West Canada Lakes (HapI and HapK), High Peaks (HapL), Maine (HapF and HapG) and northeastern Vermont/New Hampshire (HapE; Table 1). Number of haplotypes (N_a; range = 2.0-7.0), number of polymorphic sites (k; 3.0-11.0), haplotype diversity (h; 0.286-0.814), and nucleotide diversity (π; 0.0027-0.0102) were lowest in southern Vermont (Table 2). Watterson's estimator (θ; 1.1445-2.7432) was lowest in northeastern Vermont, though southern Vermont exhibited a similarly low estimate (θ = 1.2245).

Significant genetic divergence was detected for all population pairs with the exception of southern Vermont and High Peaks, northeastern Vermont and New Hampshire, and northeastern Vermont and Maine (Table 3). A generalized least squares test indicated mismatch distributions for Maine, southern Vermont, High Peaks and West Canada Lakes deviated from a model of no sudden demographic growth, though Harpending's Raggedness indicated the difference was not significant in southern Vermont or High Peaks (Table 4). Mismatch distributions for all populations fit a model of no spatial expansion (Table 4).

Spatially explicit genetic structuring of maternal lineages estimated in Geneland revealed K = 3 using an uncorrelated allele frequency model with 7 km of coordinate uncertainty. One cluster included southern Vermont, High Peaks, northwestern Maine, and the southernmost samples in northeastern Vermont and New Hampshire; a second included the majority of northeastern Vermont, northern New Hampshire, and central Maine; a third cluster was isolated to West Canada Lakes (Fig. 2). Use of an admixture model and removal of spatial uncertainty on sample coordinates identified additional substructure within the three clusters, but exhibited little additional spatial pattern.

1.3.2. Microsatellites

Number of alleles (N_a), observed heterozygosity (H_o), expected heterozygosity (H_e), and unbiased heterozygosity (UH_e) were similar for Maine, New Hampshire, West Canada Lakes, High Peaks and Northeastern Vermont (N_a = 4.3-5.0, H_o = 0.540-0.611, H_e = 0.549-0.605, UH_e = 0.567-0.620; Table 2). Estimates of genetic diversity in southern Vermont were notably lower than the other four populations (N_a = 3.3, H_o = 0.471, H_e = 0.478, UH_e = 0.514; Table 2). Statistically significant differences in observed heterozygosity relative to expectations were not detected in any populations, but heterozygosity excess was observed globally in the study area, suggesting underlying genetic structure was present. A Wilcoxon signed-rank test of heterozygosity excess implemented in Bottleneck found no evidence of recent genetic bottlenecks within populations.

No populations deviated from Hardy-Weinberg Equilibrium across all loci after Bonferroni correction. Linkage disequilibrium was observed in four pairs of loci in Maine, two pairs of loci in New Hampshire, and one pair of loci across all populations (Tt4 and Gg443). Linkage disequilibrium within Tt4 and Gg443 was not observed within New Hampshire, northeastern Vermont, southern Vermont, West Canada Lakes, or High

Peaks, therefore both loci were retained under the assumption linkage was caused by population structure within the study area.

All population pairs exhibited significant differentiation in allele and genotype frequencies except Maine and southern Vermont, New Hampshire and northeastern Vermont, and northeastern Vermont and southern Vermont (Table 5). All population pairs exhibited significant F_{st} except northeastern Vermont and New Hampshire (Table 3). Due to the detection of subdivision in New York, the simulated reintroduction source included only individuals from Maine and the High Peaks region of New York, as this was the area martens were taken for the reintroduction (Paul Jensen in Lit.). This population exhibited significant differentiation in allele and genotype frequencies and significant genetic divergence with respect to southern Vermont (Table 3; Table 5).

In northeastern Vermont, sixteen individuals (84%) were excluded from the High Peaks, fifteen individuals (79%) were excluded from West Canada Lakes, five individuals (26%) were excluded from Maine, three individuals (16%) were excluded from New Hampshire, 11 individuals (58%) were excluded from southern Vermont, seven individuals (37%) were excluded from the reintroduction sources, two individuals (11%) were excluded from the combination of reintroduction sources and New Hampshire, and one individual was excluded from all source populations (Table 6). Of the 19 individuals sampled from northeastern Vermont, assignment probabilities of greater than 50% were observed in seven individuals to Maine, seven individuals to New Hampshire, two individuals to West Canada Lakes, one individual to the High Peaks, one individual to southern Vermont, four individuals to the simulated reintroduction source and ten individuals to the reintroduction sources plus New Hampshire (Table 6). In southern Vermont, four individuals (57%) were excluded from West Canada Lakes, three individuals (43%) were excluded from the High Peaks, one individual (14%) was excluded from New Hampshire, and one individual (14%) was excluded from the simulated reintroduction source but no individuals could be excluded from Maine, northeastern Vermont, or a combination of the simulated reintroduction source and New Hampshire (Table 6). Of the seven individuals sampled from southern Vermont assignments probabilities of greater than 50% were observed for four individuals to Maine, one individual to New Hampshire, one individual to West Canada Lakes, three individuals to northeastern Vermont, two individuals to the simulated reintroduction source, and three individuals to the combination of reintroduction sources and New Hampshire (Table 6).

Results from STRUCTURE and Structure Harvester following methods of Evanno et al (2005) identified the most likely number of genetic clusters (K) was 2 (Fig. 3). K = 1, which cannot be evaluated using this method, was not accepted as an alternative due to low log likelihood scores (lnL = -2,911.84) relative to STRUCTURE runs of K = 2 (lnL = -2,739.98). Clustering largely followed a pattern of segregation between individuals from New York and New England, with some exceptions (Fig. 3).

Results from spatially explicit clustering in BAPS, TESS and using an uncorrelated allele frequency model in Geneland agreed that K = 2. The uncorrelated allele frequency model in Geneland estimated a complete division between New York and New England (Fig. 4). TESS and spatial BAPS demonstrated similar patterns, though both identified one individual from southern Vermont as sharing cluster membership with

New York (Fig. 5), and spatial BAPS identified one individual from New York that shared cluster membership with New England.

Implementing a correlated allele frequency model in Geneland identified further substructure, and resulted in an estimate of K = 5 (Fig. 6). Southern Vermont clustered distinctly from the remaining populations with the exception of one individual from central New Hampshire; northeastern Vermont and northern New Hampshire shared a single cluster; subdivision within Maine was identified by the presence of a northwestern cluster and a central cluster; New York was represented by a single cluster, although a slight drop in membership probability was identified between the High Peaks and West Canada Lakes regions (Fig. 6). Substructure was estimated in TESS by running separate clustering tests within each of the larger clusters (New York and New England). Two clusters were identified within New York and three clusters were identified within New England, for a total of K = 5 across the entire study area (Fig. 7). The two clusters identified within New York corresponded with the High Peaks and West Canada Lakes regions, in agreement with a division observed in the mtDNA data and the moderate drop in membership probability within the New York cluster in Geneland using the correlated allele frequency model. In New England, one cluster was restricted to northeastern Vermont and northern New Hampshire – also in agreement with the Geneland under the correlated allele frequency model (Fig. 7). Contrary to results from Geneland, TESS did not identify a division between Maine and southern Vermont. Instead, two clusters were spread throughout both Maine and southern Vermont – and in southern parts of the northeastern Vermont / northern New Hampshire geographic area – with no discrete pattern differentiating these two clusters (Fig. 7).

Multiple clustering techniques overestimated genetic structure such that results corresponded with noise rather than a spatial pattern of genetic structure. Estimates of genetic structure using the BYM admixture model in TESS estimated K = 10 with four ghost clusters for a true K = 6, with considerable noise. Non-spatial clustering in BAPS using a model of admixture and no model of admixture produced estimates of K = 5 and K = 9, respectively, with no discernable spatial pattern. Spatial and non-spatial clustering in BAPS was attempted within New York and New England separately, producing K = 2 and K = 4, respectively. No spatial pattern was observed.

1.4. Discussion

1.4.1. Genetic Diversity

Due to small sample size (n = 7) in southern Vermont, the most appropriate method for comparing microsatellite genetic diversity across populations was through estimates of unbiased heterozygosity (Pruett and Winker 2008). Unbiased heterozygosity estimates were relatively homogeneous among Maine, New Hampshire, New York and northeastern Vermont populations, and while southern Vermont demonstrated lower unbiased heterozygosity than other populations in the study area, arcsine transformed paired t-tests indicated this difference was not significant (p = 0.1211). Five loci from our study have previously been sampled in martens in Ontario (Koen et al 2012), which is considered within the core of the species' distribution. Within these five loci, global unbiased heterozygosity across our study area ($UH_e = 0.596$) was lower than in Ontario ($UH_e = 0.662$; p = 0.0297).

Only two D-loop haplotypes were observed in southern Vermont, and all mtDNA diversity measures were lowest in southern Vermont, with the exception of θ, which was lower in northeastern Vermont by a narrow margin (Table 2). Our results suggest that southern Vermont has experienced a significant reduction in genetic variation. Founder events or a significant bottleneck may be responsible for reduced genetic diversity in southern Vermont. We were unable to detect signs of a recent bottleneck in southern Vermont, although our estimates of diversity and ability to detect signs of such events may be biased by sample size.

1.4.2. Genetic Structure

Genetic structure in our study area appears to be caused by natural barriers to gene flow, human mediated gene flow, and lineage sorting in relic populations. At a broad scale, genetic clusters detected in microsatellite data were separated by a barrier consistent with Lake Champlain, Lake George, and the extensive agricultural land associated with these areas. This pattern is consistent with structure estimated from microsatellite data for fishers in the northeastern United States (Hapeman et al 2011). Clustering of mtDNA data at a broad scale did not identify a barrier to gene flow between New York and New England, which differs from genetic structure in mtDNA data of fishers in the region (Hapeman et al. 2014). This is most likely due to the shared predominance of HapA in marten populations in the High Peaks and southern Vermont. It is unlikely that the high frequency of HapA in these two populations is a result of natural gene flow, given the physical barriers on the landscape and genetic structure observed in microsatellite data. Furthermore, with the exception of possible sexing error during the reintroduction, it is unlikely that this similarity is due to human-mediated gene flow during the reintroduction, as no females were translocated from the High Peaks region to southern Vermont (Royar 1992). Most likely, HapA was relatively common in the ancestral population to Vermont and New York. When populations became fragmented, HapA was retained in high frequencies in southern Vermont and the High Peaks, but was lost or reduced to low frequencies in other populations in the study area.

Additional mtDNA structure due to lineage sorting was observed within New York. A sharp break in cluster membership probability was observed at the interface of the High Peaks and West Canada Lakes regions, corresponding with high frequencies of HapA and HapI, respectively (Fig. 2; Table 1). Due to the absence of a physical barrier to gene flow, this is an indication that two relic populations persisted through the 20th century in New York: one in the High Peaks region where martens were known to occur, and a second in the West Canada Lakes region where martens were believed to have been extirpated. Fine scale clustering of microsatellite data within the New York population estimated in TESS corroborated this pattern (Fig. 7).

Within New England, further substructure was observed in mtDNA and microsatellite data clustering, though results varied moderately depending on the data and analysis method. Clustering of microsatellite data using a correlated allele frequency model in Geneland and clustering within New England in TESS agreed that a genetic cluster within northeastern Vermont and New Hampshire was distinct from the rest of New England (Fig. 6; Fig. 7). This region was presumed to be extirpated in the 20th century and recolonized by dispersers from an expanding population in Maine (Hagmeier

1956; Kelly et al. 2009). However, this distinct cluster may be evidence of a relic population that persisted through the 1900s. In mtDNA clustering, this region shared cluster membership with individuals from central Maine (Fig. 2), which does not support the hypothesis of a relic isolated to northern New Hampshire. However, the high frequency of HapB in northeastern Vermont/New Hampshire and low frequency of HapB in central Maine provides support for historical isolation and lineage sorting. The restriction of HapE to northeastern Vermont and New Hampshire is another indication that this area was not colonized from Maine and may have maintained an isolated ancestral population.

With respect to other regions in New England, patterns of genetic structure varied depending on the data and clustering technique. Clustering of microsatellite data within New England in TESS revealed two similarly distributed clusters containing individuals from primarily from Maine and southern Vermont, but also the southernmost parts of northeastern Vermont and northern New Hampshire (Fig. 7). The division between these two clusters was unclear, and may have been a case of overestimated structure within a single true cluster, as has been reported in TESS (Latch et al. 2006). Clustering of mtDNA also revealed shared membership between individuals from southern Vermont, part of Maine, and the southernmost parts of northeastern Vermont and northern New Hampshire – though this cluster also included the High Peaks in New York (Fig. 2). Contrary, the correlated allele frequency model in Geneland did not estimate shared cluster membership between southern Vermont and Maine. One cluster included all members of southern Vermont and a single individual from central New Hampshire (Fig. 6). Two clusters were restricted to northwestern and central Maine, respectively (Fig. 6). While TESS microsatellite clustering and Geneland mtDNA clustering analyses suggest ancestry in the southern Vermont population from the reintroduction source in Maine, Geneland microsatellite clustering does not, and provides evidence that a native relic may have persisted in Vermont prior to the reintroduction. All estimates provide evidence of admixture from the southern Vermont population (reintroduced or relic) into northeastern Vermont and central New Hampshire.

1.4.3. Source of Martens in Northeastern Vermont

New Hampshire and northeastern Vermont were the only pair of populations that demonstrated non-significant allelic/genotypic differentiation and non-significant genetic divergence in both microsatellite and mtDNA markers (Table 5). Furthermore, these spatially contiguous populations shared cluster membership in all tests except non-spatial BAPS, which was considered invalid due to the inability to detect a spatial pattern of structure. Our results suggest that the barrier separating the northeastern Vermont and New Hampshire populations is purely geopolitical, and these contiguous regions function as a single population. There is also evidence that this population may not be an expansion of the population in Maine, as previously believed (Kelly et al. 2009). HapB was detected in high frequencies in this population relative to Maine, which would not be expected if the populations shared ancestry. In addition, the presence of a private haplotype (HapE) in New Hampshire and northeastern Vermont suggests that these populations are derived from a remnant that was isolated from other populations in the northeastern United States.

Although not statistically significant, northeastern Vermont was the only population exhibiting $H_o > H_e$ (Table 2), which can be an indication of admixture of two previously isolated populations (Hartl and Clark 1997). Given similar allele/genotype frequencies between northeastern Vermont and southern Vermont and shared genetic cluster membership between southern Vermont and the southern reaches of the northeastern Vermont/New Hampshire region, it is likely that dispersers from the reintroduction in southern Vermont contributed to the colonization of this region. A lack of mtDNA genetic divergence between northeastern Vermont and Maine – the source of reintroduced females in southern Vermont – suggests dispersers from the reintroduction may have had reproductive success in northeastern Vermont. A simulated source of the reintroduction stock combined with an equal number of individuals from New Hampshire obtained the highest assignment probabilities for 68 percent of individuals collected in northeastern Vermont, suggesting that dispersing translocated individuals may have admixed with individuals from New Hampshire to establish the population in northeastern Vermont. If this is the case, partial establishment of a population is attributable to a reintroduction effort ~180 km away, demonstrating the genetic consequences of reintroductions can occur far beyond the typical limit of dispersal distance of a species (80 km; Broquet et al. 2006).

1.4.4. Source of Martens in Southern Vermont

Results from tests of allelic/genotypic differentiation and genetic divergence of both microsatellite and mtDNA markers demonstrate that dispersers from New

Hampshire and New York can be rejected as a potential source of the population in southern Vermont (Table 3; Table 5). We obtained mixed results regarding the level of differentiation between Maine and southern Vermont. This leaves two possible scenarios that are supported by our results: 1) The population in southern Vermont is a remnant of the reintroduction that went undetected in post-release monitoring efforts, and biases in survival and reproduction or sampling have led to differentiation in our data, or 2) the population is an in situ recovery of an undetected relic population introgressed with an augmentation primarily from Maine. The translocation of individuals to southern Vermont included 77 males and 27 females from Maine, and 11 males from the High Peaks region of New York (Appendix I; Royar 1992). If the establishment of a previously extirpated population in southern Vermont were solely attributable to this translocation, we would expect microsatellite data from southern Vermont to be similar to one or both of Maine and the High Peaks, and mtDNA data from southern Vermont to be similar to Maine.

Genetic similarities between Maine and southern Vermont provide evidence that translocated individuals experienced reproductive success in southern Vermont. Genotype and allele frequencies demonstrate similarities between southern Vermont and Maine, and microsatellite clustering within New England in TESS and mtDNA clustering in Geneland demonstrates similarities between southern Vermont and at least part of Maine (Table 5; Fig. 2; Fig. 7). Furthermore, no individuals from southern Vermont could be excluded from Maine (Table 6). Despite population level differentiation in microsatellite data between southern Vermont and New York, TESS indicated that one individual from southern Vermont was more similar genetically to individuals from New

York. Due to the rapid mutation rate of microsatellite markers, this genetic similarity is more likely a result of the reintroduction than shared ancestry, and provides further support for reproductive success of translocated individuals in southern Vermont.

Contrary, signs of differentiation between southern Vermont and reintroduction sources suggest that a native relic may have persisted in southern Vermont prior to the reintroduction. F_{st} tests of microsatellite data suggested that Maine, the High Peaks, and the simulated reintroduction source population were genetically differentiated from southern Vermont (Table 3), and F_{st} tests of mtDNA also suggested significant differences between Maine and southern Vermont (Table 3). These results indicate genetic material in southern Vermont is derived from a source other than the reintroduction. In addition, assignment tests suggested that two individuals in southern Vermont were unlikely to have ancestry from Maine, New York and the simulated reintroduction source ($p < 0.13$; Table 6). Finally, clustering of microsatellite data using a correlated allele frequency model in Geneland suggested southern Vermont represented a genetic cluster distinct from the remainder of the study area, except for a single individual collected in central New Hampshire (Fig. 6). Differentiation between the reintroduction source and reintroduced population can result if a genetic bottleneck from a founding event occurred, but no such bottleneck was detected in southern Vermont using a test of heterozygosity excess (Cornuet and Luikart 1996).

The spatial distribution of HapA within New England suggests a relic population persisted in southern Vermont. If maternal lineages in southern Vermont were solely derived from the reintroduction, haplotype frequencies in southern Vermont would be similar to those in Maine – the only source of females in the reintroduction. Similarly, if maternal lineages in northeastern Vermont were derived from dispersers from New Hampshire and the reintroduction, haplotype frequencies in northeastern Vermont would be similar to those in New Hampshire and Maine. Under these scenarios, HapA is expected to be rare in both Vermont populations, as it is rare in both Maine and New Hampshire. However, it is the most frequent haplotype in both Vermont populations. Within New England, HapA frequencies occur along a southwestern gradient, increasing in frequency with proximity to southern Vermont (Fig. 8). This pattern would be unexpected under scenarios of colonization from Maine and New Hampshire, and is most parsimoniously explained by the presence of a native relic in southern Vermont with a high frequency of HapA. An alternative explanation for this gradient could be selective pressure leading to increased survival and reproductive success of HapA in southern latitudes. Under this scenario, HapA could have been introduced to southern Vermont in low frequency from Maine during the reintroduction, and become the dominant haplotype in southern Vermont as a result of greater reproductive success.

Reintroductions of fishers in the northeastern United States have resulted in strongly associated genetic markers in reintroduced populations and respective sources (Hapeman et al. 2011; Hapeman et al. 2014). Furthermore, marten reintroductions into the southern periphery of their historical distribution in the Midwest have resulted in populations that are strongly genetically associated with their respective sources (Williams and Scribner 2010). This was not the case with the marten reintroduction in southern Vermont. It is possible that this is due to the presence of a native relic competing with the reintroduced individuals, strong selective pressure imposed on reintroduced individuals, or sampling biases.

Our results suggest that presumably extirpated populations in West Canada Lakes and New Hampshire persisted undetected through much of the 20th century. It is therefore conceivable that a lack of occurrence records in Vermont between 1954 and 1989 was due to non-detection rather than extirpation. An alternative explanation for genetic divergence between southern Vermont and the reintroduction sources is founder effect. However, signs of a bottleneck were not detected in microsatellite data in southern Vermont, as would be expected if founder events were skewing the data. Another potential cause of source-introduced population divergence could be selective pressure driving biased survival and reproductive success in the reintroduced population. Potential selective forces facing the population in southern Vermont include differential habitat conditions (e.g. a higher proportion of deciduous forest cover than elsewhere in contemporary marten distribution), and mortality pressure from a flourishing fisher population during and shortly following the reintroduction (Moruzzi et al. 2003). If certain genetic markers are associated with greater survival and reproductive success in these conditions, our sampling would be biased towards these markers in southern Vermont.

Furthermore, biases in sample size or sample distribution may be the cause for our detection of differentiation between Maine and southern Vermont. Our sample size in southern Vermont was small, and perhaps the genetic material we detected in our southern Vermont sample was not completely representative of the relative frequencies of genetic markers in the population. In addition, localities of reintroduction source individuals were recorded at the state level, which may be too coarse for our objectives. Reintroduced individuals were sourced from Piscataquis and Aroostook Counties (Chris

Bernier in Lit.), where all of our Maine samples occurred; however there is no guarantee that the relative frequencies of individuals from specific localities within the two counties in our sample were representative of the reintroduction source. A historically robust population in this area of Maine and lack of physical barriers to gene flow should circumvent this potential sampling issue. However, genetic clustering results suggested a degree of subdivision within our Maine sample. If locality data for the origin of translocated individuals existed on a finer scale, we would have a stronger indication of whether differentiation between our southern Vermont and Maine sample populations is due to sampling bias.

The persistence of a native relic in southern Vermont would reclassify the true nature of the reintroduction as an augmentation. This has been observed in mustelids previously, as genetic data recently revealed an effort intended to be a reintroduction of fishers to the northern Rockies was in fact an augmentation (Vinkey et al. 2006). Augmentations can introduce non-native genetic material to a native population and lead to deleterious effects such as outbreeding depression. However, when population sizes are very small – as was presumably the case in southern Vermont given that a relic existed – augmentations can be used as a tool to bolster genetic diversity and provide rescue effects from genetic fixation and inbreeding depression (Weeks et al. 2011).

This case provides a compelling argument for intensive monitoring pre- and post-release for future reintroduction efforts. A lack of systematic monitoring and reliance on occurrence data in the 20th century may have led to an unintentional augmentation. Whether a pre-reintroduction relic or a remnant solely of the reintroduction, our results indicate that a population of martens persisted in southern Vermont during the monitoring efforts in the 1990s. These post-release monitoring efforts were insufficient spatially and temporally to detect the remnant population. We advocate that a robust post-reintroduction monitoring effort is an essential requirement for future reintroduction efforts. The population in southern Vermont was declared extirpated after three seasons of monitoring within seven years of the final releases (Moruzzi et al. 2003). Our results show that marten populations in the northeastern United States persisted in areas that lacked detections for decades. Therefore, monitoring efforts following reintroductions should be resilient to long term non-detection, and the criteria to declare a reintroduced population extirpated should include non-detection on the order of multiple decades. In addition, post-release monitoring efforts should consider spatial scales beyond the extent of release sites. In southern Vermont, the Lye Brook Wilderness was identified as the highest quality habitat and was therefore chosen as a release site (Trombulak and Royar 2001). Presumably under the assumption that these sites were the most probable areas to be colonized, post-release monitoring was restricted to these release areas, and the only detections from 1994-1995 monitoring efforts occurred on the southern periphery of the monitoring extent (Moruzzi et al. 2003). The current population exists in an area ~10 km south of the release sites, in the Glastenbury Wilderness (Chris Bernier in Lit.). Despite estimates that the Lye Brook Wilderness contained the highest quality habitat, it appears that the population that was present during the 1990s – whether established via reintroduction or a native relic – existed south of the release sites, and the monitoring effort detected the northernmost individuals from that population at the southernmost survey site. Future reintroduction attempts should consider that populations may be established outside of release areas, and buffering the survey effort beyond the release areas may be advantageous.

Finally, genotyping of source individuals prior to release should be an integral step for reintroductions to maximize the ability to confirm reintroduction success with post-release genetic monitoring. There are numerous sources of uncertainty in our sampling effort, especially considering the cryptic genetic structure we detected in the northeastern United States. Our estimates of the genetic relationship between southern Vermont and reintroduction sources rely on the assumption that our contemporary sampling of reintroduction sources is genetically representative of the stock collected for the reintroduction. This may not be the case, and could bias our results. Pre-release genotyping would eliminate this potential bias. When pre-release genotyping is not an option, locality records for reintroduction source individuals need to be precise. Locality records for individuals released in southern Vermont are at the state level. Given our detection of genetic structure at a scale finer than the state level, locality records at the state level are difficult to use. Finer scale records existed from personal communications, which allowed us to increase the confidence in our reintroduction source sampling to certain regions (High Peaks in New York) or counties (Piscataquis and Aroostook Counties in Maine), but even county- or region-level genetic structure can exist and bias efforts to create a representative sample of the reintroduction stock. In the absence of pre-release genotyping, locality records for reintroduction sources should be collected using precise GPS coordinates in order to increase the probability that a post-release genetic monitoring effort can obtain a representative genetic sample of the reintroduction stock.

1.5. References

Bright PW, Morris PA (1994) Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. Journal of Applied Ecology 31:699–708.

Brooks RT (1996) Assessment of two camera-based systems for monitoring arboreal wildlife. Wildlife Society Bulletin 24:298–300.

Broquet T, Johnson C, Petit E, Thompson I, Burel F, Fryxell JM (2006) Dispersal and genetic structure in the American marten, *Martes americana*. Molecular Ecology 15:1689–1697.

Carroll C (2007) Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and Lynx in the northern Appalachians. Conservation Biology 21:1092–1104.

Chen C, Durand E, Forbes F, François O (2007) Bayesian clustering algorithms ascertaining spatial population structure: A new computer program and a comparison study. Molecular Ecology Notes 7:747–756.

Clark TW, Anderson E, Douglas C, Strickland M (1987) *Martes americana*. Mammalian Species 289:1-8.

Corander J, Marttinen P, Sirén J, Tang J (2008) Enhanced Bayesian modelling in BAPS software for learning genetic structures of populations. BMC Bioinformatics 9:539.

Cornuet JM, Luikart G (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics 144:2001–2014.

Davis CS, Strobeck C (1998) Isolation, variability, and cross-species amplification of polymorphic microsatellite loci in the family Mustelidae. Molecular ecology

7:1776–1778.

Distefano JJ, Royar KJ, Pence DM, Denoncour JE (1990) Marten recovery plan for Vermont. Waterbury, Vermont, USA.

Drew RE, Hallett JG, Aubry KB, Cullings KW, Koepf SM, Zielinski WJ (2003) Conservation genetics of the fisher (*Martes pennanti*) based on mitochondrial DNA sequencing. Molecular Ecology 12:51–62.

Durand E, Jay F, Gaggiotti OE, François O (2009) Spatial inference of admixture proportions and secondary contact zones. Molecular Biology and Evolution 26:1963–1973.

Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources 4:359–361.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molecular Ecology 14:2611–2620.

Excoffier L (2004) Patterns of DNA sequence diversity and genetic structure after a range expansion: Lessons from the infinite-island model. Molecular Ecology 13:853–864.

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10:564–567.

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. Genetics

164:1567–1587.

Fleming MA, Ostrander EA, Cook JA (1999) Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). Molecular Ecology 8:1352–1354.

Foster DR, Donahue B, Kittredge DB, Motzkin G, Hall B, Turner BL, Chilton E (2008) New England's forest landscape: Ecological legacies and conservation patterns shaped by agrarian history. In: Redman, C.L., Foster, D.R., Agrarian landscapes in transition, Oxford University Press. New York, USA.

Godin AJ (1977) Wild Mammals of New England. Johns Hopkins University Press, Baltimore, Maryland, USA.

Griekspoor A, Groothuis T (2006) A high-tech infusion for science. In: 4Peaks. mekentosj.com. 10 Dec 2012.

Guillot G, Mortier F, Estoup A (2005) GENELAND: A computer package for landscape genetics. Molecular Ecology Notes 5:712–715.

Hagmeier EM (1956) Distribution of marten and fisher in North America. Canadian Field-Naturalist 70:149–168

Hapeman P, Latch EK, Fike JA, Rhodes OE, Kilpatrick CW (2011) Landscape genetics of fishers (*Martes pennanti*) in the Northeast: Dispersal barriers and historical influences. Journal of Heredity 102:251–259.

Hapeman P, Latch EK, Rhodes OE, Kilpatrick CW (2014) When recent and evolutionary histories meet: deciphering temporal events from contemporary patterns of mtDNA from fishers (*Martes pennanti*) in north-eastern North America. Journal of Zoological Systematics and Evolutionary Research 52: 331-337.

Hartl DL, Clark AG (1997) Principles of population genetics. Sinauer Associates, Sunderland, Massachusetts, USA.

Kelly JR, Fuller TK, Kanter JJ (2009) Records of recovering American marten, *Martes americana*, in New Hampshire. Canadian Field-Naturalist 123:1–6.

Kirk GL (1916) The mammals of Vermont. Joint Bulletin, Vermont Botanical and Bird Clubs 2:28–34.

Koen EL, Bowman J, Garroway CJ, Mills SC, Wilson PJ (2012) Landscape resistance and American marten gene flow. Landscape Ecology 27:29–43.

Kyle CJ, Davis CS, Strobeck C (2000) Microsatellite analysis of North American pine marten (*Martes americana*) populations from the Yukon and Northwest Territories. Canadian Journal of Zoology 78:1150–1157.

Kyle CJ, Strobeck C (2003) Genetic homogeneity of Canadian mainland marten populations underscores the distinctiveness of Newfoundland pine martens (*Martes americana atrata*). Canadian Journal of Zoology 66:57–66.

Lambeck RJ (1997) Focal species: A multi-species umbrella for nature conservation. Conservation Biology 11:849–856.

Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology 19:4179–4191.

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson, TJ Higgins DG (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23:2947–2948.

Latch EK, Dharmarajan G, Glaubitz JC, Rhodes OE (2006) Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of populations differentiation. Conservation Genetics 7:295–302.

Lawes TJ, Anthony RG, Robinson WD, Forbes JT, Lorton GA (2013) Movements and settlement site selection of pygmy rabbits after experimental translocation. Journal of Wildlife Management 77:1170–1181.

Mech LD, Rogers LL (1977) Status, distribution and movements of martens in northeastern Minnesota. Research Paper NC-143. St. Paul, Minnesota, USA: USDA, Forest Service, North Central Forest Experiment Station.

Moehrenschlager A, Macdonald DW (2003) Movement and survival parameters of translocated and resident swift foxes *Vulpes velox*. Animal Conservation 6:199–206.

Moruzzi TL, Royar KJ, Grove C, Brooks RT, Bernier C, Thompson FL, DeGraaf RM, Fuller TK (2003) Assessing an American marten, *Martes americana*, reintroduction in Vermont. Canadian Field-Naturalist 117:190–195.

Mowry RA, Schneider TM, Latch EK, Gompper ME, Beringer J, Eggert LS (2015) Genetics and the successful reintroduction of the Missouri river otter. Animal Conservation 18:196–206.

Osgood FL (1938) The mammals of Vermont. Journal of Mammalogy 19:435–441.

Peakall R, Smouse PE (2006) GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity 95:536–539.

Piry S, Luikart G, Cornuet J-M (1999) BOTTLENECK: a program for detecting recent effective population size reductions from allele data frequencies. Journal of Heredity 90:502–503.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–59.

Pruett CL, Winker K (2008) The effects of sample size on population genetic diversity estimates in song sparrows (*Melospiza melodia*). Journal of Avian Biology 39:252–256.

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Rice WER (1989) Analyzing tables of statistical tests. Evolution 43:223–225.

Royar KJ (1992) Monitoring reintroduced marten populations in Vermont. Vermont Fish and Wildlife Department. Waterbury, Vermont, USA.

Russell JC, McMorland AJC, MacKay JWB (2010) Exploratory behaviour of colonizing rats in novel environments. Animal Behaviour 79:159–164.

Schneider S, Excoffier L (1999) Estimation of past demographic parameters from the distribution of pairwise differences when the mutation rates vary among sites: Application to human mitochondrial DNA. Genetics 152:1079–1089.

Schwartz M (2005) Guidelines on the use of molecular genetics in reintroduction programs. In: The EU LIFE-Nature Projects to guidelines for the reintroduction of threatened species. Caramanico Terme, Italy, pp 51–58.

Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conservation Biology 21:303–312.

Shields GF, Kocher TD (1991) Phylogenetic relationships of north American ursids based on analyses of Mitochondrial DNA. Evolution 45:218–221.

Swanson BJ, Peters RL, Kyle CJ (2006) Demographic and genetic evaluation of an American marten reintroduction. Journal of Mammalogy 87:272–280.

Trombulak S., Royar KJ (2001) Restoring the wild: Species recovery and reintroductions. In: McGrory-Klyza C (ed) Wilderness Comes Home: Rewilding the Northeast. University Press of New England, Hanover, New Hampshire, USA, pp. 157–181.

Vincent IR, Farid A, Otieno CJ (2003) Variability of thirteen microsatellite markers in American mink (*Mustela vison*). Canadian Journal of Animal Science 83:597–599.

Vinkey RS, Schwartz MK, McKelvey KS, Foresman KR, Pilgrim KL, Giddings BJ, Lofroth EC (2006) When reintroductions are augmentations: the genetic legacy of the fisher (*Martes pennanti*) in Montana. Journal of Mammalogy 87:265-271.

Walker CW, Vilà C, Landa A, Linden M, Ellegren H (2001) Genetic variation and population structure in Scandinavian wolverine (*Gulo gulo*) populations. Molecular Ecology 10:53–63.

Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NH, Miller KA, Byrne M, Coates DJ, Eldridge MDB, Sunnucks P, Breek MF, James EA, Hoffmann AA (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4: 709-725.

Williams BW, Scribner KT (2010) Effects of multiple founder populations on spatial genetic structure of reintroduced American martens. Molecular Ecology 19:227–240.

Wolf CM, Griffith B, Reed C, Temple SA (1996) Avian and mammalian translocations: Update and reanalysis of 1987 survey data. Conservation Biology 10:1142-1154.

Woods JG, Paetkau D, Lewis D, McLellan BN, Proctor M, Strobeck C (1999) Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

1.6. Tables

Table 1. Haplotype counts of a 320 bp segment of the D-loop (control region) of mtDNA in American marten populations in the northeastern United States. Maine = ME, New Hampshire = NH, northeastern Vermont = VT-N, southern Vermont = VT-S, High Peaks region of New York = NY-HP, West Canada Lakes region of New York = NY-WCL.

	Population						
Haplotype	ME	NH	VT-N	VT-S	NY-HP	NY-WCL	Total
A	2	3	6	6	10	1	28
B	2	17	6	0	0	0	25
C	8	3	3	1	0	0	15
D	1	0	2	0	0	2	5
E	0	3	2	0	0	0	5
F	5	0	0	0	0	0	5
G	1	0	0	0	0	0	1
H	3	1	0	0	0	0	4
I	0	0	0	0	0	14	14
J	0	0	0	0	4	1	5
K	0	0	0	0	0	4	4
L	0	0	0	0	1	0	1
	n=22	n=27	n=19	n=7	n = 15	n=22	n =112

Table 2. Genetic diversity indices within populations of American martens in the northeastern United States: Number of alleles (Na), observed heterozygosity (Ho), expected heterozygosity (He) and unbiased heterozygosity (UHe) estimated from ten microsatellite loci, and number of haplotypes (Na), number of polymorphic sites (k), haplotype diversity (h), nucleotide diversity (π), and Watterson's estimator (θ) estimated from 320 bp segments of the D-loop (control region) of mtDNA. Maine = ME, New Hampshire = NH, northeastern Vermont = VT-N, southern Vermont = VT-S, High Peaks = NY-HP, and West Canada Lakes = NY-WCL, global values for the study area = NEUS, estimates from northern Ontario using five shared markers and five markers not used in this study (Koen et al. 2012) = ONT.

	Microsatellites				mtDNA				
	Na	Ho	He	UHe	Na	k	π	h	θ
ME	5	0.581	0.605	0.62	7	8	0.0085	0.8139	2.1946
NH	4.7	0.552	0.571	0.583	4	4	0.0045	0.5869	1.5567
VT-N	4.8	0.611	0.578	0.594	4	4	0.0053	0.7953	1.1445
VT-S	3.3	0.471	0.478	0.514	2	3	0.0027	0.2857	1.2245
NY-HP	4.3	0.563	0.549	0.567	3	6	0.0062	0.5143	1.5377
NY-WCL	4.8	0.54	0.583	0.595	5	11	0.0102	0.5758	2.7432
NEUS	6.2	0.561	0.618	0.621	12	14	0.0091	0.8510	2.4569
ONT	7.5	0.64	0.664	0.665	-	-	-	-	-

Table 3. Estimates of genetic divergence (F_{st}) between population pairs of American martens in the northeastern United States based on a 320 bp segment of the D-loop (control region) of mtDNA (above diagonal) and ten microsatellite loci (below diagonal). Maine = ME, New Hampshire = NH, New York = NY, northeastern Vermont = VT-N, southern Vermont = VT-S, High Peaks = NY-HP, West Canada Lakes = NY-WCL and simulated microsatellite data for a reintroduction stock of Maine and the High Peaks region of New York = RE.

Population	ME	NH	VT-N	VT-S	NY-HP	NY-WCL
ME	-	0.1885**	0.0460	0.1408*	0.1511**	0.3577**
NH	0.0576**	-	0.0617	0.4728**	0.4403**	0.4872**
VT-N	0.0314**	0.0023	-	0.2262*	0.2520**	0.3812**
VT-S	0.0342*	0.0596**	0.0303*	-	0.0605	0.2886**
NY-HP	0.1030**	0.0961**	0.0809**	0.1121**	-	0.3137**
NY-WCL	0.0842**	0.0760**	0.0600**	0.0958**	0.0363**	-
RE	0.0066	0.0467**	0.0249**	0.0368*	0.0219*	0.0374**

Table 4. Tests for sum of squared deviation (SSD) and Harpending's Raggedness from expected mismatch distributions of populations in equilibrium conditions under models of sudden demographic expansion and sudden spatial expansion in American marten populations in the northeastern United States. Maine = ME, New Hampshire = NH, northeastern Vermont = VT-N, southern Vermont = VT-S, High Peaks = NY-HP, West Canada Lakes = NY-WCL.

Mismatch Distribution for Demographic Expansion				
Population	SSD	p	Harpending's Raggedness	p
ME	0.08765993	0.023*	0.22284065	0.027*
NH	0.07882617	0.172	0.27898313	0.143
VT-N	0.02193533	0.166	0.10769126	0.295
VT-S	0.11195752	0.034*	0.67346939	0.723
NY	0.06820294	0.030*	0.17261856	0.017*
NYHP	0.42013585	<0.001**	0.44562358	1.000
NYWCL	0.16000067	0.042*	0.37019546	0.037*

Mismatch Distribution for Spatial Expansion				
Population	SSD	p	Harpending's Raggedness	p
ME	0.07546054	0.059	0.22284065	0.174
NH	0.03888322	0.336	0.27898313	0.430
VT-N	0.01853862	0.189	0.10769126	0.366
VT-S	0.05217191	0.253	0.67346939	0.801
NY	0.04098267	0.331	0.17261856	0.392
NYHP	0.08485041	0.251	0.44562358	0.569
NYWCL	0.05420816	0.359	0.37019546	0.600

Table 5. P-values for tests of differentiation in microsatellite allele frequencies (above diagonal) and genotype frequencies (below diagonal) between populations of American martens in the northeastern United States. Maine = ME, New Hampshire = NH, New York = NY, northeastern Vermont = VT-N, southern Vermont = VT-S. Significance values are Bonferroni corrected ($\alpha = 0.001$).

Population	ME	NH	VT-N	VT-S	NY-HP	NY-WCL	RE
ME	-	<0.0001**	<0.0001**	0.0108	<0.0001**	<0.0001**	0.9983
NH	<0.0001**	-	0.5968	0.0002**	<0.0001**	<0.0001**	<0.0001**
VT-N	0.0002**	0.6432	-	0.0153	<0.0001**	<0.0001**	<0.0001**
VT-S	0.0491	0.0007**	0.0395	-	<0.0001**	<0.0001**	<0.0001**
NY-HP	<0.0001**	<0.0001**	<0.0001**	<0.0001**	-	<0.0001**	<0.0001**
NY-WCL	<0.0001**	<0.0001**	<0.0001**	<0.0001**	<0.0001**	-	<0.0001**
RE	0.9994	<0.0001**	<0.0001**	<0.0001**	<0.0001**	<0.0001**	-

Table 6. Probability of American martens from Vermont having ancestry from other populations in the northeastern United States based on assignment/exclusion tests performed in GeneClass2 using data from ten microsatellite loci. Maine = ME, New Hampshire = NH, West Canada Lakes = NY-WCL, High Peaks = NY-HP, southern or northeastern Vermont (population from which assigned individual was not collected) = VT-S/N, simulated reintroduction stock = RE, the simulated reintroduction stock plus New Hampshire = RENH. Values in bold represent highest probability of assignment.

ID	Pop	ME	NH	NY-WCL	NY-HP	VT-S/N	RE	RENH
6224	VT-N	0.262	0.551	0.029*	0.011*	0.041*	0.237	**0.616**
25679	VT-N	0.107	0.396	0.033*	<0.001**	0.006**	0.026*	**0.526**
28783	VT-N	0.003**	**0.125**	<0.001**	<0.001**	0.008**	<0.001**	0.027*
34105	VT-N	0.013*	**0.402**	0.002**	<0.001**	0.008**	0.002**	0.195
34106	VT-N	0.377	**0.815**	0.003**	<0.001**	0.013*	0.197	0.775
34107	VT-N	0.511	0.172	0.001**	0.004**	0.037*	0.421	**0.621**
34108	VT-N	0.015*	**0.128**	0.003**	0.003**	0.007*	0.003**	0.118
34110	VT-N	0.646	0.695	0.079	0.009**	0.061	0.582	**0.895**
34112	VT-N	0.007**	0.016*	<0.001**	<0.001**	<0.001**	0.001**	**0.028***
34148	VT-N	0.044*	0.351	<0.001**	0.002**	0.021*	0.020*	**0.377**
34149	VT-N	0.097	**0.639**	<0.001**	<0.001**	0.019*	0.056	0.483
34150	VT-N	0.061	0.033*	<0.001**	<0.001**	0.006**	0.005**	**0.071**
35000	VT-N	0.441	0.043*	0.003**	<0.001**	0.153	0.406	**0.499**
35237	VT-N	0.335	0.369	0.007**	<0.001**	0.051	0.332	**0.661**
35556	VT-N	0.847	0.858	0.501	0.129	0.459	0.914	**0.974**
35557	VT-N	0.509	0.368	0.006**	0.002**	0.116	0.448	**0.648**
35608	VT-N	0.783	0.873	0.102	0.101	0.204	0.637	**0.936**
36454	VT-N	0.929	0.551	0.814	0.787	0.631	0.98	**0.979**
36944	VT-N	**0.581**	0.101	0.017*	0.011*	0.118	0.436	0.522
34100	VT-S	0.465	0.098	0.546	0.192	0.465	**0.499**	0.467
34102	VT-S	0.111	0.169	0.008**	<0.001**	0.101	0.032*	**0.303**
34111	VT-S	**0.931**	0.313	0.162	0.103	0.858	0.888	0.906
34981	VT-S	0.129	0.133	0.001**	<0.001**	0.122	0.061	**0.148**
34982	VT-S	0.996	0.363	0.028*	0.059	0.879	**0.998**	0.991
34983	VT-S	**0.701**	0.013*	<0.001**	<0.001**	0.232	0.452	0.355
36451	VT-S	0.511	**0.744**	0.486	0.051	0.654	0.315	0.743

1.7. Figures

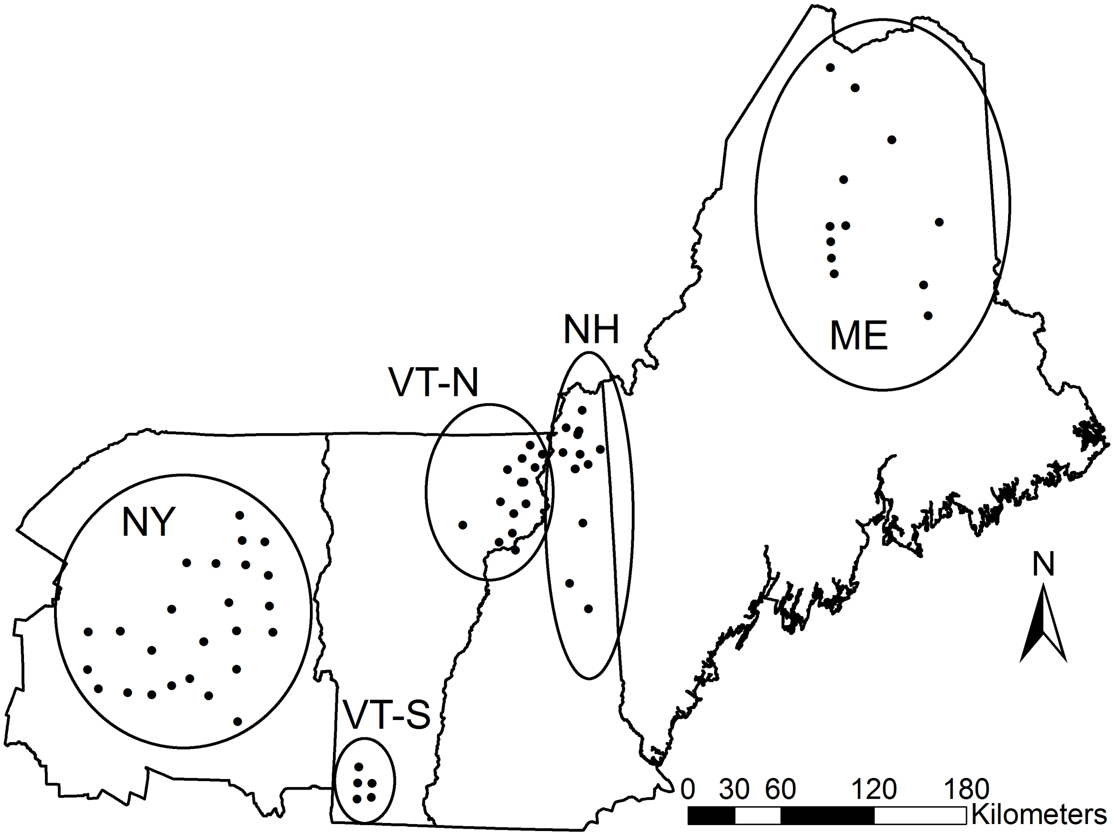


Figure 1. Study area and sample localities of individual martens (black dots) and geographic populations (hollow ovals). Maine = ME, New Hampshire = NH, New York = NY, northeastern Vermont = VT-N, southern Vermont = VT-S.

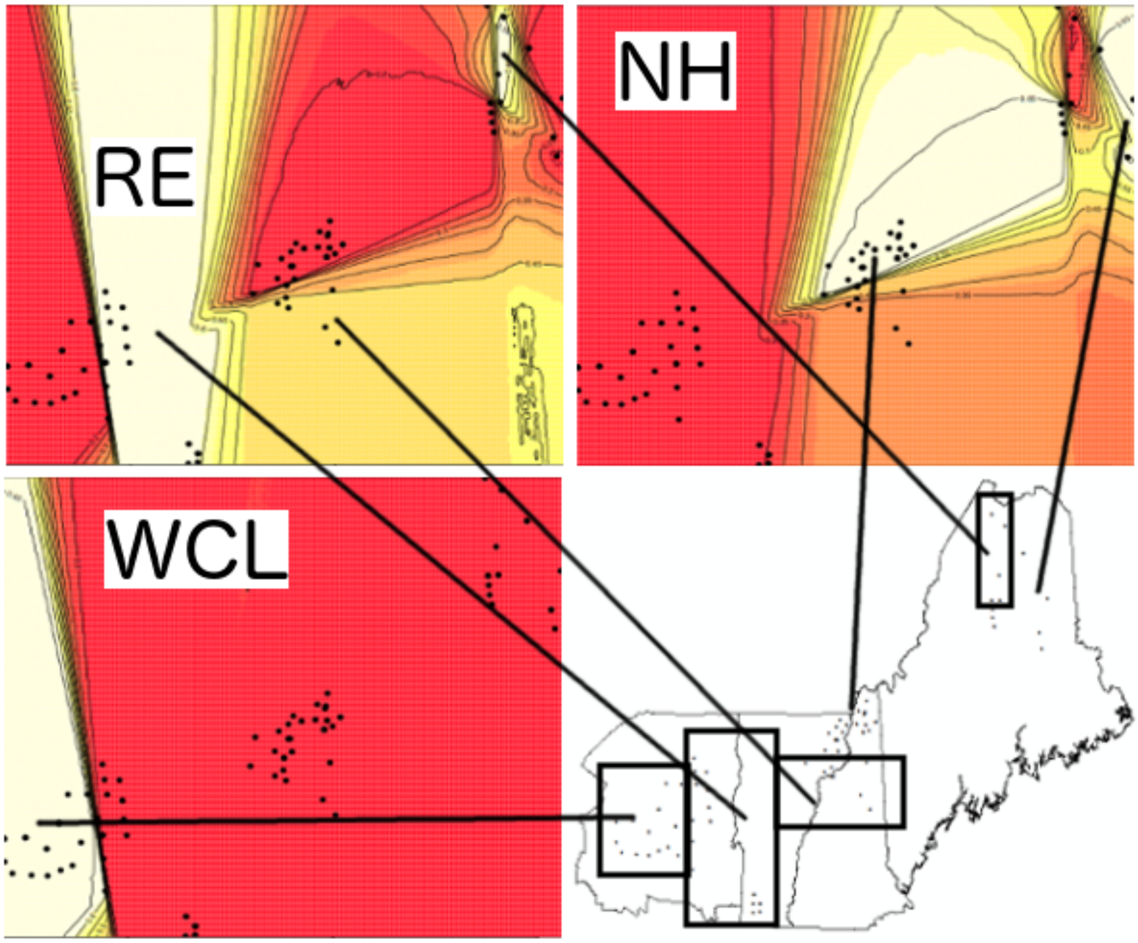


Figure 2. Estimated probability of genetic cluster membership for American martens in the northeastern United States estimated using an uncorrelated allele frequency model and 7 km spatial uncertainty in Geneland based on data from a 320 bp segment of the D-loop (control region) of mtDNA. One cluster is restricted to the West Canada Lakes (WCL), one cluster contains individuals from the High Peaks, southern Vermont, southern parts of northeastern Vermont and New Hampshire, and northwestern Maine (RE), and a third contains individuals from northern New Hampshire, northeastern Vermont and central Maine (NH).

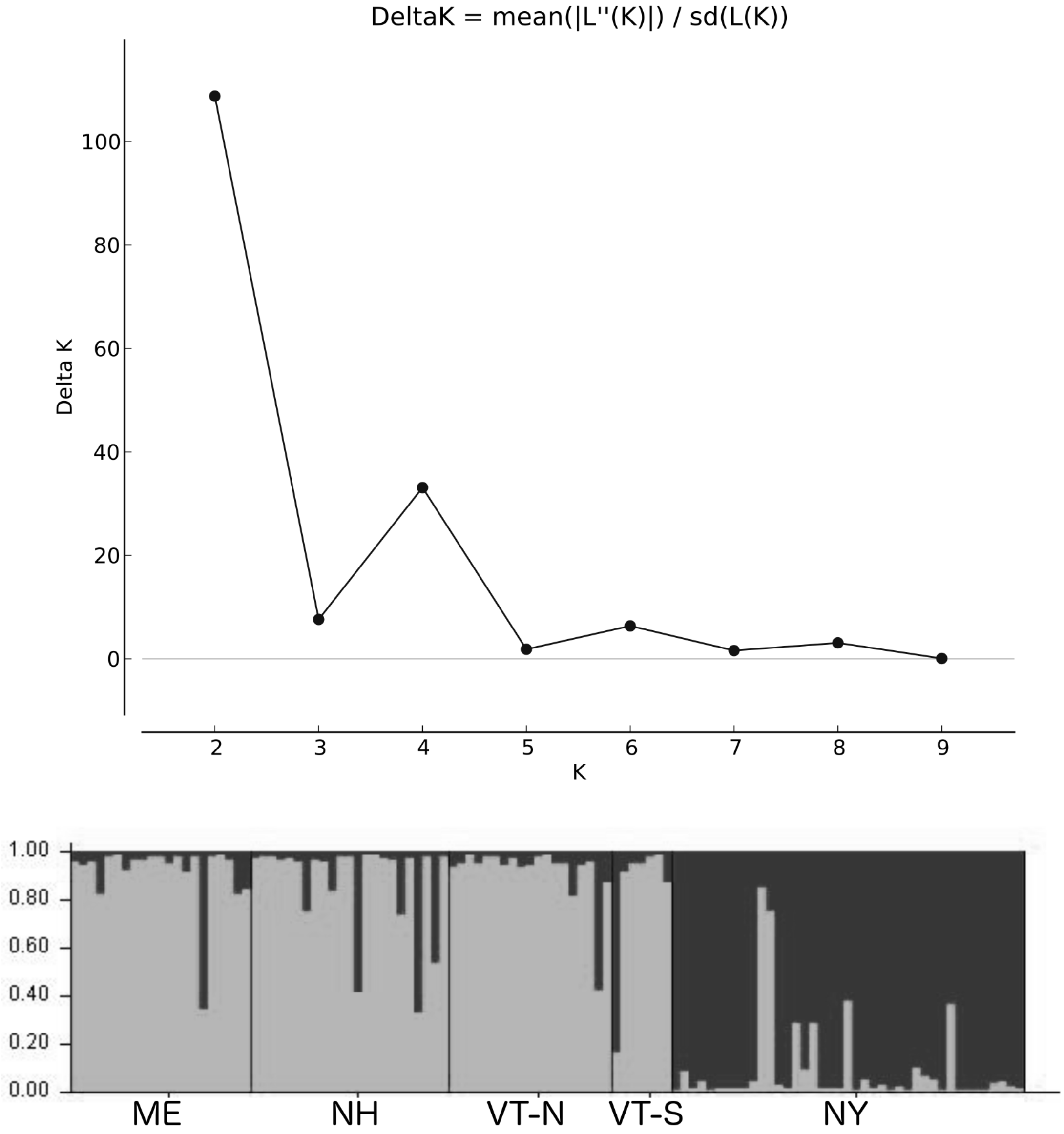


Figure 3. Delta-K estimates using data from ten microsatellite loci and methods of Evanno et al. (2005) in Structure Harvester shows the optimal number of genetic clusters (K) of American martens in the northeastern United States is K = 2. Bar plot of the probability of cluster membership for two genetic clusters estimated in STRUCTURE. Individuals are organized by geographic populations: Maine = ME, New Hampshire = NH, northeastern Vermont = VT-N, southern Vermont = VT-S, New York = NY.

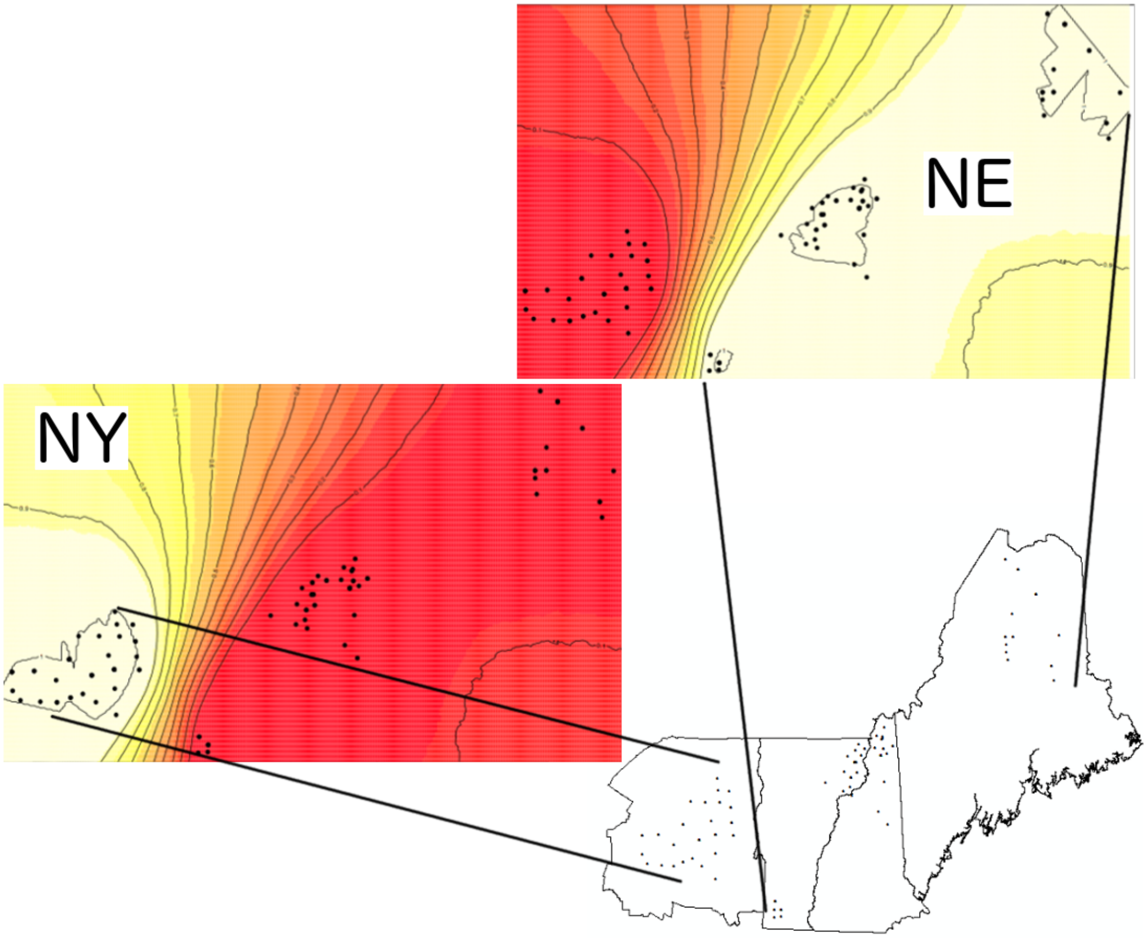


Figure 4. Estimated probability of genetic cluster membership for American martens in the northeastern United States estimated using an uncorrelated allele frequency model in Geneland based on data from ten microsatellite loci. Two clusters were identified demonstrating genetic divergence between New York (NY) and New England (NE).

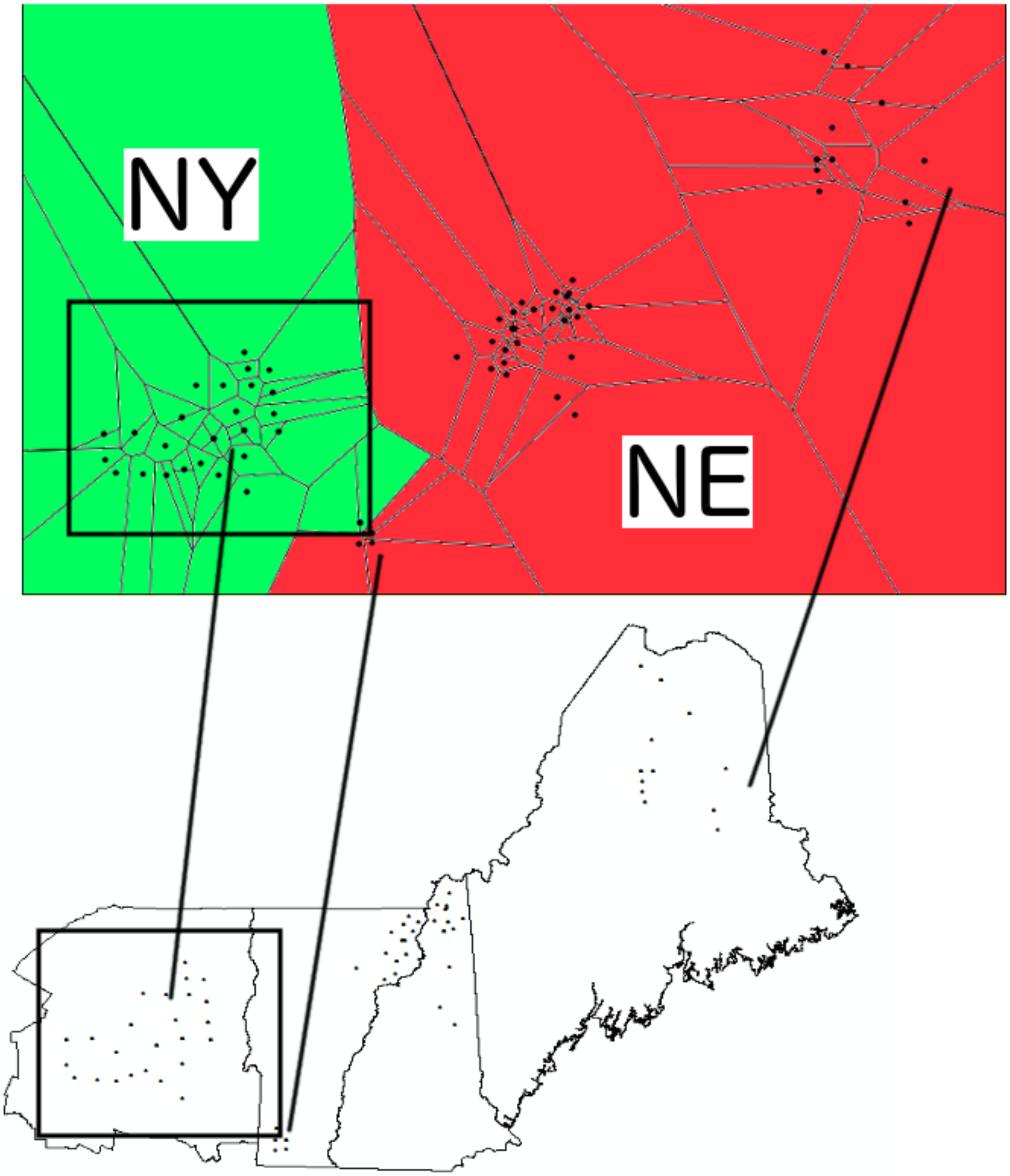


Figure 5. Estimated spatial distribution of genetic cluster membership for American martens in the northeastern United States estimated using no admixture model in TESS based on data from ten microsatellite loci. A pattern of division between New York (NY) and New England (NE) is present, with one individual from southern Vermont sharing membership with New York.

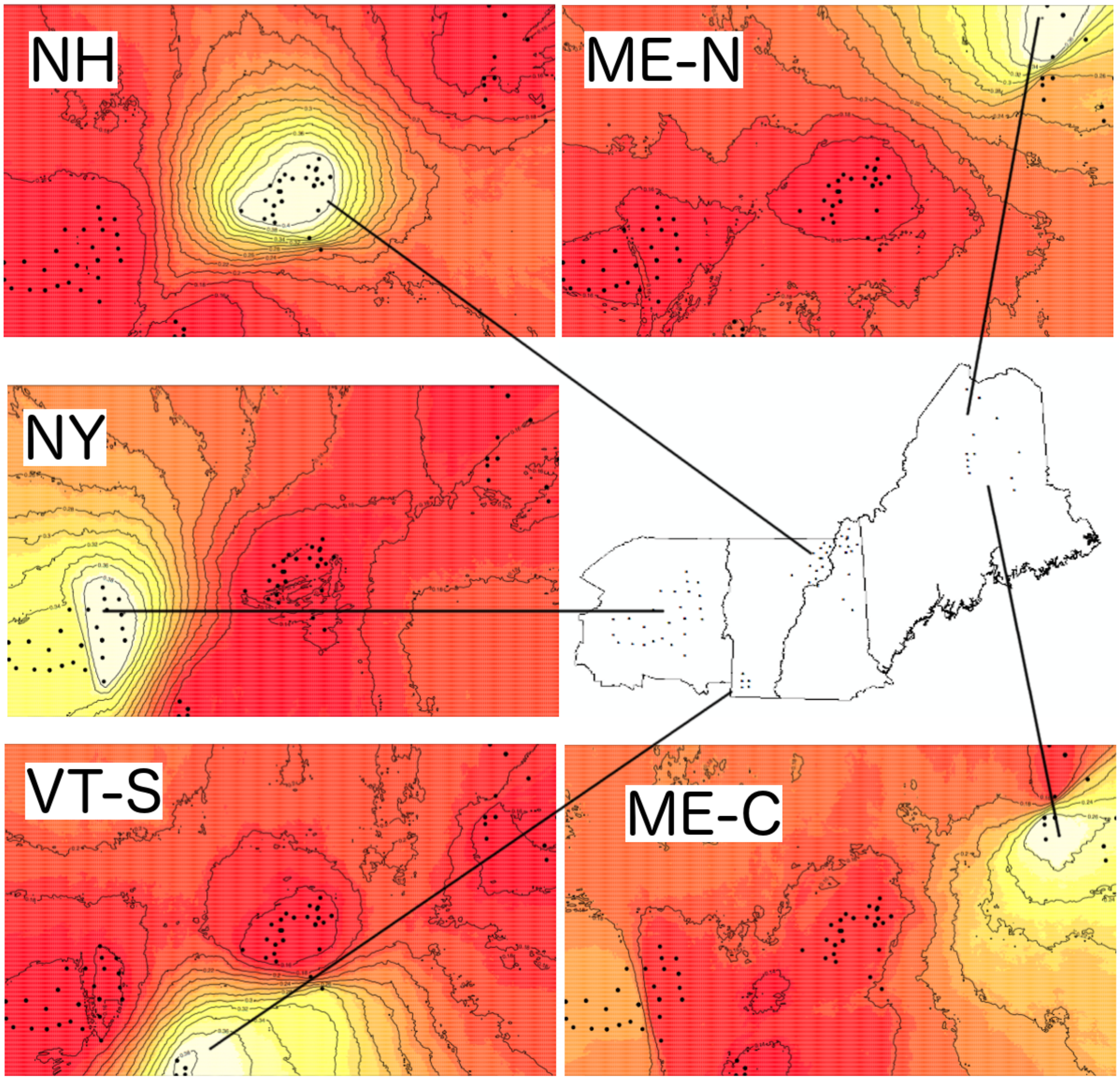


Figure 6. Estimated probability of genetic cluster membership for American martens in the northeastern United States estimated using a correlated allele frequency model in Geneland based on data from ten microsatellite loci. Northeastern Vermont and New Hampshire = NH, northwestern Maine = ME-N, central Maine = ME-C, southern Vermont = VT-S, New York = NY.

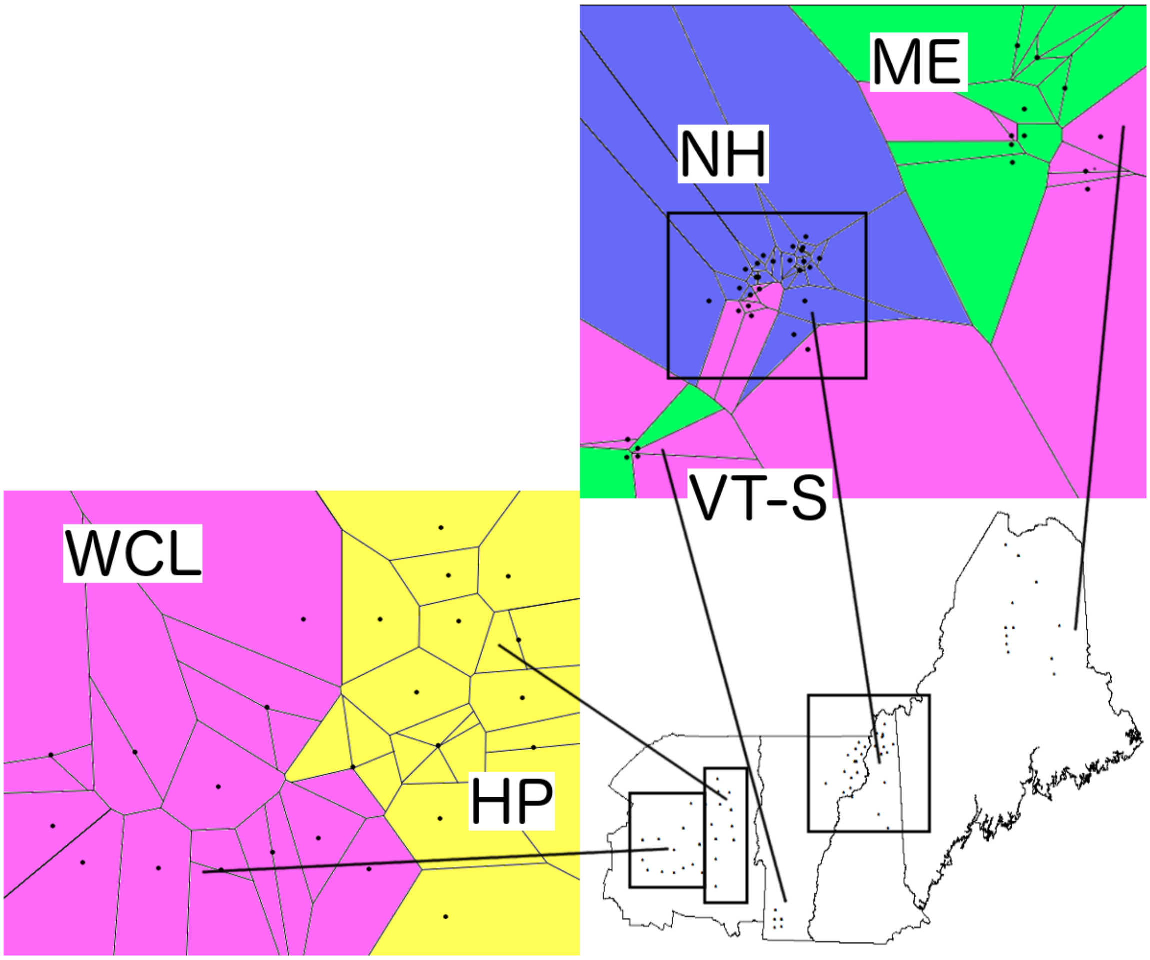


Figure 7. Estimated spatial distribution of American marten genetic substructure within broader genetic clusters in New York and New England estimated in TESS based on data from ten microsatellite loci. West Canada Lakes (NY) = WCL, High Peaks (NY) = HP, New Hampshire and northeastern Vermont = NH, Maine = ME, southern Vermont = VT-S.

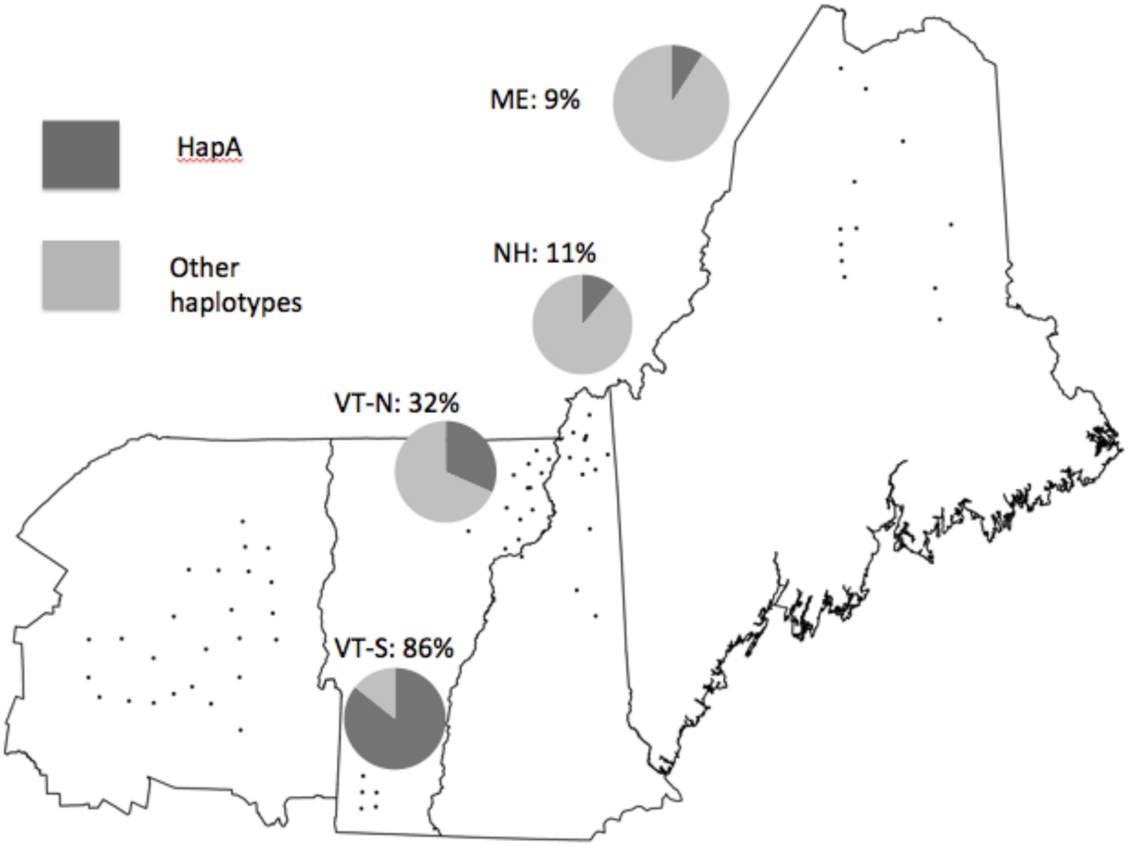


Figure 8. Relative frequencies of HapA within populations of American marten in New England increases along a southwestern gradient with proximity to the population in southern Vermont. Maine = ME, New Hampshire = NH, northeastern Vermont = VT-N, southern Vermont = VT-S.

CHAPTER 2: ESTIMATING LANDSCAPE QUALITY AND CONNECTIVITY FOR AMERICAN MARTEN IN THE NORTHEASTERN UNITED STATES BASED ON EXPERT ELICITATION DATA

2.1. Introduction

Numerous species of forest carnivores were extirpated from the northeastern United States during the past two centuries as a result of land development and unregulated harvest (Gibilisco 1994). As large tracts of mature forests returned to the region, some of these species have recolonized both naturally and through translocation (Foster et al. 2002). One such species, the American marten (*Martes americana*), is considered an indicator of late seral forest health and climate change, and acts as an umbrella species whose conservation supports habitat conditions for a suite of other species (Lambeck 1997; Carroll 2007). Martens historically ranged from Alaska to Newfoundland as far north as the tree line and as far south as West Virginia (Krohn 2012). Unregulated harvest and deforestation caused a significant range contraction in the northeastern United States during the early 1900s (Mech and Rogers 1977; Distefano 1990; Giblisco 1994; Krohn 2012). Population recovery is a priority for the northeastern United States and for New Hampshire and Vermont where martens are considered threatened and endangered, respectively (Vermont Wildlife Action Plan 2015; New Hampshire Wildlife Action Plan 2015).

Historically, estimates of marten distribution in the northeastern United States relied on occurrence records. These records suggest that by the 1930s marten were restricted to the mountainous regions of northern Maine and the High Peaks of the

Adirondack Mountains in New York (Mech and Rogers 1977; Clark et al. 1987). However, recent genetic data suggest that multiple undetected populations persisted throughout the 20th century in the western Adirondacks, New Hampshire and perhaps southern Vermont (Fig. 9; see Chapter 1). Furthermore, systematic surveys following a reintroduction effort in southern Vermont failed to detect a population that is now understood to have persisted at the time (see Chapter 1; Moruzzi et al. 2003). Populations appear to have expanded since the mid-20th century (Fig. 9; Kelly et al. 2009; Paul Jensen in Lit.). However, marten are not systematically surveyed in the northeastern United States and trapping localities may not be sufficient to provide accurate estimates of distribution. Models that estimate landscape quality may provide better estimates of distribution for this elusive forest-dependent carnivore.

Understanding how landscape quality influences species distribution, movements, and population parameters is essential to achieve recovery objectives. Identifying parcels of land that can potentially support viable populations helps prioritize recovery efforts (Early et al. 2008). When these areas are patchily distributed, increasing connectivity with movement corridors may facilitate dispersal and increase the probability of gene flow (Beier and Noss 1998; Hess and Fischer 2001; Hilty et al. 2006). Typically, models constructed from empirical data are used to describe habitat quality and connectivity across landscapes (MacKenzie et al. 2002). However, due to the uncertainties associated with historical empirical data, limited contemporary empirical data, and the high cost of obtaining such data, an alternative approach is needed to estimate landscape quality marten in the northeastern United States. Expert opinion can serve as a valuable alternative source of information when empirical data are lacking

(Murray et al. 2009). Recent advances in analytical techniques using expert opinion data allow for stand-alone models to be built, with the flexibility of combining expert opinion and empirical data to increase robustness of habitat quality estimates (James et al. 2010; Low Choy et al. 2012).

Our objectives were to 1) Administer a survey to allow for the elicitation of expert opinion regarding factors influencing American marten habitat quality; 2) Develop an expert-based occupancy model that describes habitat quality for American marten throughout the northeast, accounting for variation in expert opinions and individual expert biases; 3) Use the model to estimate probability of occurrence throughout the northeast; 4) Identify high-quality habitat parcels in Vermont and 5) Estimate connectivity between isolated core areas of marten occurrence.

2.2. Methods

Objective 1. Expert opinion survey. To elicit expert opinion, we used an online survey tool developed by the USGS Vermont Cooperative Fish and Wildlife Research Unit that is based on the Elicitator framework (James et al. 2010). The survey tool allowed experts to record their estimates of probability of marten occupancy at a set of randomly selected sites in the northeastern United States. Experts were identified from recent literature and from recommendations by state biologists or other experts. Surveys were conducted in-person or via tele- or videoconference and user guides were developed to aid experts during the survey (Appendix III).

The expert elicitation approach consisted of 4 main sections. In section 1, experts filled out a pre-survey questionnaire that captured basic information related to their background. In section 2, experts chose their geographic region(s) of expertise at the state level. States included New York, Vermont, New Hampshire, and Maine, which collectively defined the study area (~183,575 km^2). A set of 30 survey sites, spatially separated by a minimum of 3 km, was then generated in the expert's self-identified region of expertise. Sites were randomly selected from multivariate iterative-self organizing (ISO) clusters (ESRI 2012); each pixel (30 x 30 m) in the study area was assigned to one of 30 multivariate clusters, and one site was randomly selected within each cluster to maximize the variability of habitat conditions presented to the expert. A site was defined as a ~7 km^2 circular area (1.5 km radius) – a conservatively large estimate of a male home range in northeastern North America (Fuller and Harrison 2005; Broquet et al. 2006). In section 3, experts were presented with a Google satellite-view map (Google, Inc.) of each site (see Appendix III), along with data on twelve covariate values associated with the site (Table 7). Candidate covariates were identified from literature regarding marten habitat selection in the northeastern United States, and Quebec and Labrador, Canada. Covariates for which spatial data were available at the full extent of our study area and < 1 km resolution were used in the survey. For each site, experts indicated the mean probability of marten occupancy and a measure of uncertainty (sd), given the satellite image and covariate information. Section 4 consisted of a post-survey questionnaire to obtain feedback regarding the elicitation process.

Objective 2. Occupancy model. We used a model selection approach (Burnham and Anderson 2002) to identify the best model for estimating marten probability of occurrence, where the response variable was the expert defined probability of occurrence and the predictor variable(s) included one or more covariates (Table 8; we added elevation as an additional covariate *post hoc*). To develop the model set, we classified covariates into four categories: 1) Forest Characteristics, 2) Climate, 3) Human Impact, and 4) Competition (Table 8). Next, covariates that did not exhibit a moderate correlation ($r > 0.4$) with respect to mean estimates of occupancy were removed from the covariate set. Candidate models were developed for each individual category and for combinations of categories. Single category models were developed using an all subsets approach. Multi-category models were developed under the following conditions: 1) to avoid over parameterization, no more than one covariate from a single category was included in each candidate model, and 2) because martens are a forest obligate species, each multi-category model included a Forest Characteristic covariate (Appendix IV). All candidate models that included highly correlated covariates ($r > 0.6$) were discarded. A secondary model set was constructed using the same procedure with covariate values at a landscape scale (5 km radius) to incorporate the potential effect of spatial scale on occupancy estimates.

Each model in the full set (n = 39 models at each spatial scale) was fit using mixed-effects logistic regression in the R package lme4 (Bates et al. 2015). For model fitting, all covariates were normalized as z-scores with respect to mean and standard deviation values across the entire study area (Appendix V). In each candidate model, habitat covariates were considered fixed effects while random effects were estimated for each expert and site. Models were ranked using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). If multiple competing models had strong empirical support (ΔAIC < 2.0), we used model averaging based on respective AIC weights

(Buckland et al. 1997; Burnham and Anderson 2002) in the R package MuMIn (Barton 2016).

We evaluated performance of the final model using a receiver-operating-characteristic (ROC) curve (Fielding and Bell 1997, Eng 2014). A ROC curve, in the context of this study, estimated how frequently the model made a correct prediction (true positive) over a false prediction (false positive) of occupancy. The area under the curve (AUC) determines the predictive ability of the model. We used an AUC threshold of 80%, such that a model with AUC > 0.80 was considered to have strong predictive ability. Data points for the ROC curve were generated by creating a set of 1,000 "presence" points randomly within townships where martens have been detected since 2000, and a set of 1,000 "absence" points within townships where martens have not been detected since 2000 (see Fig. 9).

Objective 3. Distribution map. We used the parameter coefficients from the top model (or averaged model) to map distribution across the study area. We multiplied each covariate raster by the corresponding parameter coefficient, then summed resulting rasters to obtain a logit score fore each pixel. Logits were transformed to probabilities via the logit link function. We developed the map in ArcGIS (ESRI 2012).

Objective 4. High-quality habitat parcels in Vermont. We estimated habitat quality within Wildlife Management Areas, Wilderness Areas, and other public lands in Vermont by averaging pixel values from the occupancy map. Only parcels that were > 7 km^2 were considered, as smaller parcels may not be able to support a male marten home range.

Objective 5. Movement corridors. We estimated movement flow between core areas of marten occurrence using a circuit theory approach that treats animal movement across the landscape like movement of current through a circuit of varying resistances (McRae et al. 2008). Core areas were estimated as the "presence" townships from the ROC analysis. Due to geographic connectivity of core areas in Maine, New Hampshire and northeastern Vermont, and the unlikelihood of a corridor circumventing New Hampshire and northeastern Vermont to connect Maine with another core area, we limited the analysis to New York, Vermont, and New Hampshire. Resistance between areas was the inverse of squared-occupancy rescaled from 1 (least resistance, highest occupancy) to 100 (most resistance, lowest occupancy) in order to increase the relative effect of habitat quality over Euclidean corridor distance (McRae et al. 2008). We removed Lake George and Lake Champlain from the resistance raster as we considered them impenetrable to dispersal given their size. First, a current was connected between New York, southern Vermont, and northeastern Vermont/New Hampshire populations to map flow using Circuitscape 4.0 (McRae et al. 2008; McRae et al. 2016). We then estimated potential movement corridors between southern Vermont and neighboring populations by creating a cost-distance map using Linkage Mapper 1.1.0 (McRae et al. 2008; McRae et al. 2016). The final corridor map represented all cost-distance values < 1,000 km. We then used Barrier Mapper to identify areas that contributed the greatest cost to the overall cost-distance of the corridor (McRae et al. 2012). Barrier Mapper uses a moving window along each corridor to estimate the effect of habitat improvement at each pixel on cost-distance of the corridor. Pixels that obtain the highest "habitat improvement score" are areas where habitat improvement would provide the greatest increase in corridor quality, and are therefore assumed to currently represent barriers.

2.3. Results

Objective 1. Expert opinion survey. Eighteen experts participated in the survey and included seven state agency personnel, two federal agency personnel, three university researchers, and six furbearer trappers. Experts selected sites in Vermont (n = 5), Maine (n = 4), New York (n = 2), Vermont and New Hampshire (n = 4), New Hampshire and Maine (n = 1), and Vermont and New York (n = 2). Surveys took < 2 hours to complete for each expert.

Objective 2. Occupancy model. Seven covariates exhibited moderate correlation (r > 0.4) with expert-defined probability of occupancy and were included in the final model set: percent forest land cover (Forest), percent spruce-fir forest land cover (Spruce-Fir), percent canopy closure (Canopy), total basal area of tree stems (TBA), mean daily high temperature in winter (defined Nov to Mar; Temp), mean elevation (Elevation), and length of roads class 1-3 per km^2 (Roads; Table 8). These variables accounted for three of the four categories hypothesized to affect marten probability of occurrence. The fourth (Competition) was represented by a single covariate (estimated fisher, *Pekania pennanti*, occupancy) and removed due to limited covariate-mean correlation (r = 0.01) and experts' lack of confidence in the covariate's accuracy during site elicitation.

Of the 78 total models (39 at each scale) estimated, three models had strong empirical support (Table 9). All three models were at the 5 km scale and included covariates from all three categories: Canopy, Spruce-Fir, Temperature, Elevation, and

Roads (Table 9). The top scoring models accounted for 99.2 percent of the total weight of the model set (Table 9; Appendix VI). Individual covariate effects within each model were significantly different from 0 (Table 10; Fig. 10). Due to the similarity in AIC scores, we model averaged parameter estimates (Table 10). This averaged model was used for all occupancy and connectivity estimates. Model performance was strong for the averaged model. The ROC analysis resulted in an area under the curve of 88.1% (Fig. 11).

Objective 3. Distribution map. Occupancy in the study area ranged from 0.00 to 0.97, with a mean of 0.35. High-occupancy regions existed in northern Maine, northern New Hampshire and northeastern Vermont, throughout the Adirondack Mountains of New York, in the southern Green Mountain National Forest in Vermont, and patchily along the central and northern Green Mountain spine (Fig. 12).

Objective 4. High-quality habitat parcels in Vermont. Seven Wilderness Areas, seven WMAs, and 15 other public land parcels in Vermont were large enough to support a 7 km^2 home range had occupancy scores > 0.5 (Table 11).

Objective 5: Movement corridors. Circuit analysis estimated high current densities in areas adjacent to core populations, in the central Green Mountains in Vermont, and around Lake George in New York (Fig. 13A). The optimal dispersal corridor between southern Vermont and the Adirondacks was an approximately straight line due west (Fig. 13B; henceforth referred to as the Adirondack corridor). The optimal dispersal corridor between southern Vermont and New Hampshire/Northeastern Vermont traveled north through the central and northern Green Mountains, and then east to northeastern Vermont (Fig. 13B; henceforth referred to as the New Hampshire corridor). The optimal dispersal corridor between New Hampshire/Northeastern Vermont and New York also traveled through the northern and central Green Mountains, and crossed from the central Green Mountains to New York between Lake George and Lake Champlain (Fig. 13B; henceforth referred to as the NY-NH corridor; the section from the central Green Mountains to Lake George is henceforth referred to as the Lake George corridor). Cost-weighted distance of the New Hampshire corridor (5,448 km) was similar to that of the Adirondack corridor (5,621 km). The cost-weighted distance of the NY-NH corridor was much greater (9,263 km). The ratio of cost-weighted distance to Euclidean distance (CW/ED) between two core areas is representative of the corridor quality (McRae et al. 2008). Higher ratios are indicative of either travel through high resistance habitat or substantial deviation from straight line travel. The New Hampshire corridor exhibited the lowest CW/ED (44.47), followed by the NY-NH corridor (71.42) and finally the Adirondack corridor (84.56). The Adirondack and Lake George corridors were strong barriers (Fig. 13C). Moderate barriers were detected in small sections of the central and northern Green Mountains, and between the northern Green Mountains and northeastern Vermont (Fig. 13C)

2.4. Discussion

American martens are considered a forest obligate requiring deep snow to outcompete sympatric carnivores (Godbout and Ouellet 2010; Krohn 2012). Our expert-based model supports this. Five covariates were included in the top-ranking expert-opinion models: two forest covariates (canopy cover and Spruce-fir), two climatic covariates (temperature and elevation) and one covariate related to development (road density). Studies have also suggested high road densities limit marten distribution as they facilitate movements of larger competitors such as coyotes (*Canis latrans*) and red fox (*Vulpes vulpes*; Sirén 2009). Our attempt to quantify sympatric competition was through estimates of fisher occupancy, which is a limiting factor of marten distribution in New Hampshire (Kelly et al. 2009). However, the fisher model we chose was developed in Vermont (Long et al. 2011) and may not have extrapolated well to the rest of the study area, or may not have comprehensively captured negative effects of competition from other carnivores.

In the core of marten distribution, occupancy and abundance are strongly related to spruce fir cover (Bowman and Robitaille 1997; Godbout and Ouellet 2010). While one of the top models demonstrated this relationship to be the case in our study area, the association of occupancy with overall canopy cover (regardless of forest type) in other top models suggests that martens also use mixed and deciduous forest types in our study area. This may be due to availability, as the study area overlays the interface of sub-boreal and northern hardwood habitat types (Foster et al. 2008). Studies show that populations on the periphery of a species' distribution use irregular habitats, and their adaptations to such conditions may increase their conservation value (Hoffman and Blows 1994; Lesica and Allendorf 1993). For example, adaptations of martens in our study area to suboptimal habitat conditions, such as mixed northern hardwood forests, may increase the probability of persistence in areas that are anticipated to convert from the preferred spruce-fir habitat to mixed northern hardwood as a result of climate change.

We recognize that our modeling approach did not fully account for variation in experts' uncertainty when predicting occupancy at sites. While mixed-effects modeling accounts for relative over- or under-estimation of habitat quality among experts, it does not account for variations in confidence among site elicitations within an individual experts' survey (Low Choy et al. 2012). Plotting standard deviations of experts' site occupancy estimates as a function of estimated mean site occupancy shows that sites of moderate habitat quality resulted in higher levels of uncertainty than sites of extreme high or low quality, where experts were fairly certain about their estimate (Appendix VII). An important step for future studies seeking to model habitat quality from expert surveys is capturing the full range of uncertainty, both among experts and within an individual expert's survey. Furthermore, experts recommended that alternative response types (bar plots, numerical entries) would be advantageous for future expert elicitation surveys. Some experts felt distracted by the task of understanding their response as a probability density function, and expressed a preference for simply entering a point estimate with upper and lower bounds. Due to variations in expert preferences, either supplying surveys with multiple options or pre-screening experts for their preferred response type would streamline the site elicitation process and focus experts' attention to the task of estimating site habitat quality.

Our expert-opinion based occupancy model predicted marten distribution consistent with contemporary records of occurrence. Estimates of high occupancy from our model overlapped considerably with records of occurrence in Maine, New Hampshire, New York and southern Vermont (Fig. 9; Fig. 12). In addition, our model suggests that high quality habitat is dispersed throughout the Green Mountain spine.

However, no marten presence has been documented in the northern and central Green Mountains for a century. Anecdotal reports exist from the northern and central Green Mountains, though these are unconfirmed. It is possible the northern and central Green Mountains are occasionally occupied as dispersal habitat, or serve as a metapopulation – supporting temporary subpopulations for brief periods (Hanski 1998).

A true absence of breeding populations along the Green Mountains despite high habitat quality may be attributed to landscape configuration (Vergara and Armesto 2008; Hanski 2009). While high quality habitat does exist in quantity in the central and northern Green Mountains, it is primarily arranged in narrow north-south strips following a high elevation (up to 1,339 m) spine. In contrast, the occupied areas in southern and northeastern Vermont are plateaus, and habitat quality is not constricted on an axis like in the central and northern Green Mountains. Potential high density populations of competitors or predators may exist in close proximity to the west and east of high quality habitat in the northern and central Green Mountains, and therefore have to travel shorter distances to limit marten populations than in southern Vermont or northeastern Vermont, where competitors or predators would have to travel greater distances to reach the center of high quality habitat. Alternatively, a lack of detections in the central and northern Green Mountains may be a product of sampling bias rather than true absence – also as a result of landscape configuration. Most of the recent detection data is a result of incidental trapping, and reaching the high elevation spine of the central and northern Green Mountains requires more challenging foot travel than the plateaus in southern Vermont and northeastern. As a result, trapping effort may be less intense or non-existent in the high elevations of the central and northern Green Mountains compared to the plateaus.

Understanding the feasibility of a population persisting in the central Green Mountains is an important step in marten recovery in Vermont. Wilderness areas that are not currently known to support viable populations appear to be the best option for future population expansion. Namely, Peru Peak Wilderness, ~15 km north of the population in southern Vermont, has a similar mean occupancy to wilderness areas with documented occurrence, and contains enough land area to support a viable population (32 km^2). Additionally, Breadloaf Wilderness obtained a mean occupancy score similar to wilderness areas with documented occurrence and was identified as a high current density area within the New Hampshire corridor. Considering these indicators of high quality habitat, potential for dispersal facilitation, and its position in the central Greens, the Breadloaf Wilderness is an interesting area to monitor for empirical evidence of marten occurrence. In addition to large Wilderness Areas, several WMAs and public land parcels that are large enough to support a 7 km^2 home range had > 0.50 mean occupancy. While areas containing a single male home range may not support a long-term population in isolation, they may bolster the ability for Vermont to support metapopulations and dispersal corridors. Finally, the Bolton Mountain area exhibited the highest occupancy estimates in the state outside of areas of known occurrence, and falls only partially within Mount Mansfield State Forest. Furthermore, several unconfirmed reports exist from this area. Support from private landowners in this area is important to facilitate marten recovery in the northern Green Mountains.

Corridor analysis suggested that the central and northern Green Mountains were the path of least cost-weighted distance between core areas in Southern Vermont and New Hampshire/Northeastern Vermont. In the central Green Mountains our corridor overlaps with a corridor linking large forest habitat blocks between southern Vermont and northeastern Vermont (Sorensen and Osborne 2014). However, Sorensen and Osborne (2014) did not identify the northern Green Mountains as important corridor habitat, as our estimate does. The optimal dispersal corridor between New York and southern Vermont is a straight path that is largely considered a strong barrier. The estimated dispersal route travels through extensive low-occupancy agricultural land. Circumventing the high-resistance habitat by dispersing through more forested areas near Lake George is an unfavorable alternative, likely due to the increased travel distance and only limited reduction of travel through low-occupancy areas. In summation, the landscape between southern Vermont and New York is extensively low quality such that the optimal dispersal strategy is to minimize travel distance across a uniformly high-resistance matrix. Though these corridors represent the most cost-effective movements between core areas, the absolute feasibility of a dispersal event is not evident from these models. Genetic evidence suggests that contemporary gene flow is unlikely between New York and the New England populations, although the southern Vermont and northeastern Vermont/New Hampshire populations may exchange limited gene flow (see Chapter 1). It is possible that these corridor estimates – while the best currently available - are not adequate to functionally facilitate gene flow.

An important consideration to our corridor estimates is the assumption that dispersal habitat quality is directly related to home range habitat quality. While this general relationship probably exists, there is evidence that home range habitat selection and dispersal habitat selection are differentiated in other carnivore species (Palomares et al. 2000; Squires et al. 2013). Studies indicate that gene flow is influenced by factors that do not influence occupancy, such as slope or elevational gradients (Cushman et al. 2006; Cushman and Lewis 2010). Consideration should be given to alternative or additional dispersal costs such as total change in elevation, or slope, accumulated over the course of the corridor. In addition, we estimated dispersal habitat based on the top models – which estimated habitat characteristics at a 5 km scale. Corridor selection may occur at a finer scale. Testing hypotheses of dispersal habitat selection will help improve future estimates of movement corridors.

2.5. References

Bartoń K (2016) MuMIn: Multi-model inference R-package v.1156. URL https://cran.r-project.org/web/packages/MuMIn/index.html

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:51.

Beier P, Noss RF (1998) Do Habitat Corridors Provide Connectivity? Conservation Biology 12:1241–1252.

Bowman JC, Robitaille JF (1997) Winter habitat use of American martens Martes americana within second-growth forest in Ontario, Canada. Wildlife Biology 3:97–105.

Broquet T, Ray N, Petit E, Fryxell JM, Burel F (2006) Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*). Landscape Ecology 21:877–889.

Buckland ST, Burnham KP, Augustin NH (1997) Model selection: An integral part of inference. Biometrics 53:603-618.

Burnham K, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, USA.

Carroll C (2007) Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and Lynx in the northern Appalachians. Conservation Biology 21:1092–1104.

Clark TW, Anderson E, Douglas C, Strickland M (1987) *Martes americana*. Mammalian Species 289:1–8.

Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. Landscape Ecology 25:1613–1625.

Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. American Naturalist 168:486–99.

DiStefano JJ, Royar KJ, Pence DM, Denoncour JE (1990) Marten recovery plan for Vermont. Vermont Department of Fish and Wildlife, Waterbury, Vermont, USA.

Early R, Anderson B, Thomas CD (2008) Using habitat distribution models to evaluate large-scale landscape priorities for spatially dynamic species. Journal of Applied Ecology 45:228–238.

Eng J (2014) ROC analysis: web-based calculator for ROC curves. Johns Hopkins University. URL http://www.jrocfit.org. Accessed 03 June 2017.

ESRI, (2012) ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, California, USA.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38-49.

Foster DR, Motzkin G, Bernardos D, Cardoza JE (2002) Wildlife dynamics in the changing New England landscape. Journal of Biogeography 29:1337-1357.

Foster DR, Donahue B, Kittredge DB, Motzkin G, Hall B, Turner BL, Chilton E (2008) New England's forest landscape: Ecological legacies and conservation patterns shaped by agrarian history. In: Redman, C.L., Foster, D.R., Agrarian landscapes in transition, Oxford University Press. New York, USA.

Fuller AK, Harrison DJ (2005) Influence of partial timber harvesting on American martens in north-central Maine. Journal of Wildlife Management 69:710–722.

Fuller RW (1987) Proposed Endangered and Threatened Mammals, in: Laughlin, S. (Ed.), The Endangered and Threatened Species of Plants and Animals in Vermont. Vermont Agency of Environmental Conservation, Montpelier, Vermont, USA, pp. 42–54.

Gibilisco CJ (1994) Distributional dynamics of martens and fishers in North America. in: Buskirk, S.W., Harestad, A.S., Raphael, M.G., Powell, R.A. (Eds.), Martens, Sables, and Fishers: Biology and Conservation. Cornell University Press, Ithaca, New York, USA, pp. 59–71.

Godbout G, Ouellet JP (2010) Fine-scale habitat selection of American marten at the southern fringe of the boreal forest. Ecoscience 17:175–185.

Hagmeier EM (1956) Distribution of marten and fisher in North America. Canadian Field-Naturalist 70:149-168.

Hanski I (1998) Metapopulation dynamics. Nature 396:41-49.

Hanski I (2009) Incorporating the spatial configuration of the habitat into ecology and evolutionary biology, in: Cantrell, S., Cosner, C., Shitui, R.S., (Eds.), Spatial Ecology. Chapman and Hall, New York, USA, pp. 167-188.

Hess GR, Fischer RA (2001) Communicating clearly about conservation corridors. Landscape and Urban Planning 55:195–208.

Hilty JA, Lidicker Jr. WZ, Merenlender AM (2006) Corridor ecology: the science and practice of linking landscape for biodiversity conservation. Island Press, Washington D.C., USA

Hoffman AA, Blows MW (1994) Species borders: ecological and evolutionary perspectives. Trends in Ecology and Evolution 9:223–227.

James A, Low Choy S, Mengersen K, (2010) Elicitator: An expert elicitation tool for regression in ecology. Environmental Modelling and Software 25:129–145.

Kelly JR, Fuller TK, Kanter JJ (2009) Records of recovering American marten, *Martes americana*, in New Hampshire. Canadian Field-Naturalist 123:1–6.

Krohn WB (2012) Distribution Changes of American Martens and Fishers in Eastern North America, 1699-2001, in: Aubry, K.B., Zielinski, W.J., Raphael, M.G., Proulx, G., Buskirk, S.W. (Eds.), Biology and Conservation of Martens, Sables, and Fishers: A New Synthesis. Cornell University Press, Ithaca, New York, USA, pp. 58–73.

Lambeck RJ (1997) Focal species: A multi-species umbrella for nature conservation. Conservation Biology 11:849–856

Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? Conservation Biology 9:753–760.

Low Choy S, James A, Murray J, Mengersen K (2012) Elicitator: A user-friendly, interactive tool to support scenario-based elicitation of expert knowledge, in: Expert Knowledge and Its Application in Landscape Ecology. Springer, New York, USA. pp. 39–67.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle AA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

McRae BH, Dickson B, Keitt T, Shah V (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

McRae BH, Hall SA, Beier P, Theobald DM (2012) Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. PLoS ONE 7. doi:10.1371/journal.pone.0052604

McRae BH, Shah V, Edelman A (2016) Circuitscape: modeling landscape connectivity to promote conservation and human health. The Nature Conservancy, Fort Collins, Colorado, USA.

Mech LD, Rogers LL (1977) Status, distribution, and movements of martens in northeastern Minnesota. North Central Forest Experiment Station, St. Paul, Minnesota, USA.

Moruzzi TL, Royar KJ, Grove C, Brooks, RT, Bernier C, Thompson FL, DeGraaf RM, Fuller TK (2003) Assessing an American marten, *Martes americana*, reintroduction in Vermont. Canadian Field-Naturalist 117:190–195.

Murray JV, Goldizen AW, O'Leary R, McAlpine C, Possingham HP, Low Choy S (2009) How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. Journal of Applied Ecology 46:842–851.

New Hampshire Wildlife Action Plan Team (2015) New Hampshire Wildlife Action Plan 2015. Concord, New Hampshire, USA.

Palomares F, Delibes M, Ferreras P, Fedriani JM, Calzada J, Revilla E (2000) Iberian lynx in a fragmented landscape: Predispersal, dispersal and postdispersal habitats. Conservation Biology 14:809–818.

Royar KJ (1992) Monitoring Reintroduced Marten Populations In Vermont. Vermont Fish and Wildlife Department. Waterbury, Vermont, USA.

Sirén APK (2009) Population ecology of American marten in New Hampshire: Impact of wind farm development in high elevation habitat. M.S. Thesis, University of New Hampshire, Durham, New Hampshire, USA.

Sorenson E, Osborne J (2014) Vermont habitat blocks and habitat connectivity: An analysis using Geographic Information Systems. Vermont Department of Fish and Wildlife, Waterbury, Vermont, USA.

Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biological Conservation 157:187–195.

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

Vergara PM, Armesto JJ (2009) Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landscape Ecology 24:25–38.

Vermont Wildlife Action Plan Team (2015) Vermont Wildlife Action Plan 2015. Montpelier, Vermont, USA.

2.6. Tables

Table 7. Covariate descriptions, units, and range of values in the study area. Covariates were presented to experts during a survey to develop an occupancy model for American marten in the northeastern United States. An asterisk (*) denotes a covariate that was not presented to experts, but was used in model fitting.

			Range	
Covariate	Description and Source	Units	Min	Max
% Forest Cover	Amount of area in the site where the land cover is classified as coniferous forest, deciduous forest, or mixed forest. (NLCD 2011)	Percent	0	100
% Coniferous Forest Cover	Amount of area in a site classified as coniferous forest land cover. (NLCD 2011)	Percent	0	100
% Deciduous Forest Cover	Amount of area in a site classified as deciduous forest land cover. (NLCD 2011)	Percent	0	100
% Mixed Forest Cover	Amount of area in a site classified as mixed forest land cover. (NCLD 2011)	Percent	0	100
% Spruce-Fir Forest Cover	Amount of area in a site classified as spruce-fir forest or mixed spruce-fir/hardwood forest land cover. (USGS GAP Analysis)	Percent	0	100
% Canopy Cover	Amount of ground area in a site directly covered by tree crowns. (NLCD 2011)	Percent	0	92
Total Basal Area	Average cross-sectional area of tree stems at breast height per acre. (USDA 2012 National Insect and Disease Risk)	ft^2/ acre	0	295
Stand Age	Average time since previous disturbance of forest stand(s) within the site. (USDA FIA 2006)	Years	0	216
Mean Winter High Temperature	Average daily high temperature within the site during the months of November-March. (PRISM, Oregon State University 1980-2010 Normals)	Degrees (F)	20	41
Winter Precipitation	Average monthly precipitation from November-March. (PRISM, Oregon State University 1980-2010 Normals)	Approx. cm of snow (given freezing conditions)	41	163

Road Density	Total length of roads per unit area. (State Transportation Agencies)	Km/Km^2	0	20.21
Fisher Occupancy	Probability of fisher (*Pekania pennanti*) occupancy in the site. (Long et al. 2011)	Percent	0	99
Elevation*	Elevation above sea level (National Elevation Dataset)	Meters	0	1913

Table 8. Organizational structure of covariates into four categories for model sets describing American marten (*Martes americana*) occupancy. Models were developed from expert opinion data obtained using a web-based survey of experts in the northeastern United States. Model covariates were fixed effects in a mixed-effects logistic regression, where expert-specific and site-specific random effects were also assessed. Covariates were retained for the final model set if correlation with expert mean occupancy estimates (r) was > 0.4, denoted by an asterisk (*).

Category	Covariate	r
Forest Characteristics	Forest LC	0.506*
	Deciduous LC	0.109
	Conifer LC	0.295
	Mixed Forest LC	0.309
	Spruce-Fir LC	0.567*
	Canopy Cover	0.557*
	Total Basal Area	0.519*
	Stand Age	0.097
Climate	Winter Temperature	0.570*
	Elevation	0.626*
	Winter Precipitation	0.229
Human Impact	Road Density	0.539*
Competition	Fisher Occupancy	0.012

Table 9. Top ten candidate models for American marten occupancy in the northeastern United States and respective AIC, ΔAIC, and AIC weights. Models were developed from expert opinion data obtained using a web-based survey of experts in the northeastern United States. Model covariates were fixed effects in a mixed-effects logistic regression, where expert-specific and site-specific random effects were also assessed.

Model	Scale	AIC	ΔAIC	AIC weight
Canopy + Temp + Roads	5k	417.61	0	0.4491
Canopy + Elevation + Roads	5k	418.04	0.43	0.3622
SpruceFir + Elevation + Roads	5k	419.43	1.82	0.1808
Forest + Temp + Roads	5k	426.95	9.34	0.0042
TBA + Temp + Roads	5k	427.37	9.76	0.0034
Canopy + Roads	5k	432.53	14.92	0.0003
Forest + Roads	5k	437.30	19.69	<0.0001
Canopy + Temp	5k	445.08	27.47	<0.0001
TBA + Temp + Roads	1.5k	448.54	30.93	<0.0001
SpruceFir + Elevation + Roads	1.5k	449.53	31.92	<0.0001

Table 10. β estimates and corresponding 95% confidence intervals (CI) for covariate effects in three top models and an averaged model estimating American marten occupancy in the northeastern United States based on expert opinion data.

	Covariates	β	Lower 95% CI	Upper 95% CI
Model 1	Intercept	-1.5148	-2.0039	-1.0780
	Canopy	1.3531	0.8909	1.8638
	Temp	-0.7845	-1.1836	-0.4047
	Roads	-1.6544	-2.3132	-1.0376
Model 2	Intercept	-1.5169	-1.9923	-1.1002
	Canopy	0.6625	0.1549	1.2089
	Elevation	0.7389	0.3763	1.1268
	Roads	-2.0099	-2.6045	-1.4622
Model 3	Intercept	-1.4099	-1.8689	-0.9998
	Spruce-Fir	0.4225	0.0616	0.7990
	Elevation	0.9481	0.6417	1.2832
	Roads	-1.9300	-2.5474	-1.3602
Average	Intercept	-1.4965	-1.9432	-1.0500
	Canopy	1.0449	0.2040	1.8859
	Spruce-Fir	0.4225	0.0547	0.7903
	Temp	-0.7845	-1.1736	-0.3955
	Elevation	0.8086	0.4030	1.2141
	Roads	-1.8343	-2.5212	-1.1474

Table 11. Public land parcels, Wildlife Management Areas, and Wilderness Areas in Vermont larger than 7 km^2 exhibiting American marten occupancy estimates > 0.50 from a model developed using expert opinion data obtained from a web-based survey of experts in the northeastern United States. Asterisks (*) indicate parcels outside of areas with contemporary marten occurrence records. Double asterisks (**) indicate parcels outside the current distribution of occurrence records but nearby recent historical (1900s) occurrence localities.

Land type	Mean occupancy	Area (km^2)	Minimum	Maximum
Public land parcels				
Kingdom State Forest	0.79	88	0.51	0.91
Green Mountain Club*	0.78	12	0.59	0.86
Jay State Forest*	0.76	33	0.43	0.86
Victory State Forest	0.67	67	0.33	0.78
Granby Town Forest	0.64	7	0.60	0.69
Conte National Wildlife Refuge	0.64	109	0.04	0.90
Long Trail State Forest*	0.63	39	0.15	0.86
Camels Hump State Park*	0.62	86	0.02	0.87
Green Mountain National Forest	0.61	1587	0.01	0.94
Mt. Mansfield State Forest*	0.61	171	0.01	0.90
CC Putnam State Forest*	0.59	56	0.01	0.83
Lemington Town Forest	0.54	9	0.20	0.92
Groton State Forest*	0.53	111	0.16	0.80
Camels Hump State Forest*	0.52	10	0.03	0.73
Coolidge State Forest**	0.50	97	0.12	0.87
WMA				
Bill Sladyk WMA	0.74	37	0.42	0.81
Huntington Gap WMA*	0.72	7	0.65	0.80
Victory Basin WMA	0.70	20	0.58	0.77
Wenlock WMA	0.66	9	0.57	0.78
West Mountain WMA	0.65	91	0.27	0.88
Steam Mill Brook WMA	0.59	43	0.17	0.72
Plymsbury WMA**	0.51	8	0.40	0.63
Wilderness Area				
Peru Peak**	0.79	32	0.51	0.86
Breadloaf*	0.78	101	0.33	0.89
Aiken	0.77	19	0.70	0.82
Glastenbury	0.76	90	0.01	0.94
Battell*	0.74	50	0.43	0.82
Lye Brook	0.66	73	0.04	0.91
Big Branch**	0.64	27	0.37	0.80

2.7. Figures

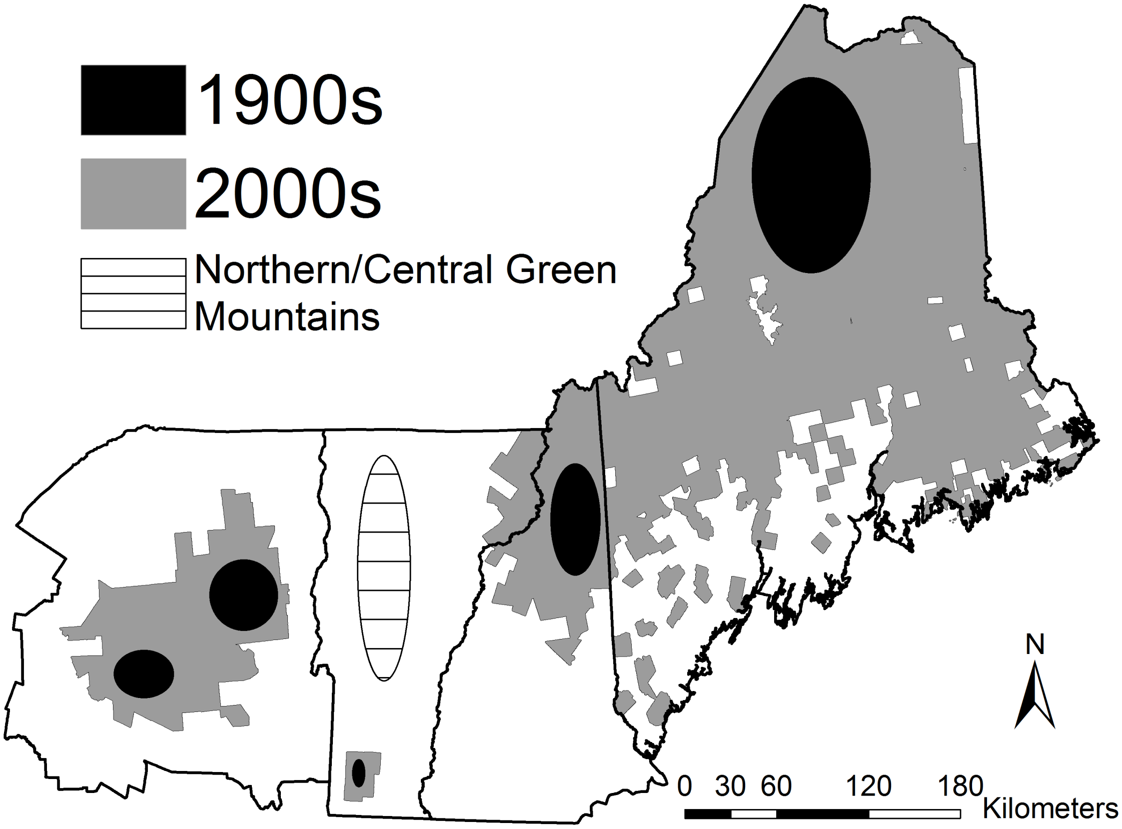


Figure 9. Distribution of American marten (*Martes americana*) in the northeastern United States since 2000 based on occurrence records and approximate location of contracted populations in the 1900s based on occurrence records (Hagmeier 1956) and inferences from genetic data (see Chapter 1).

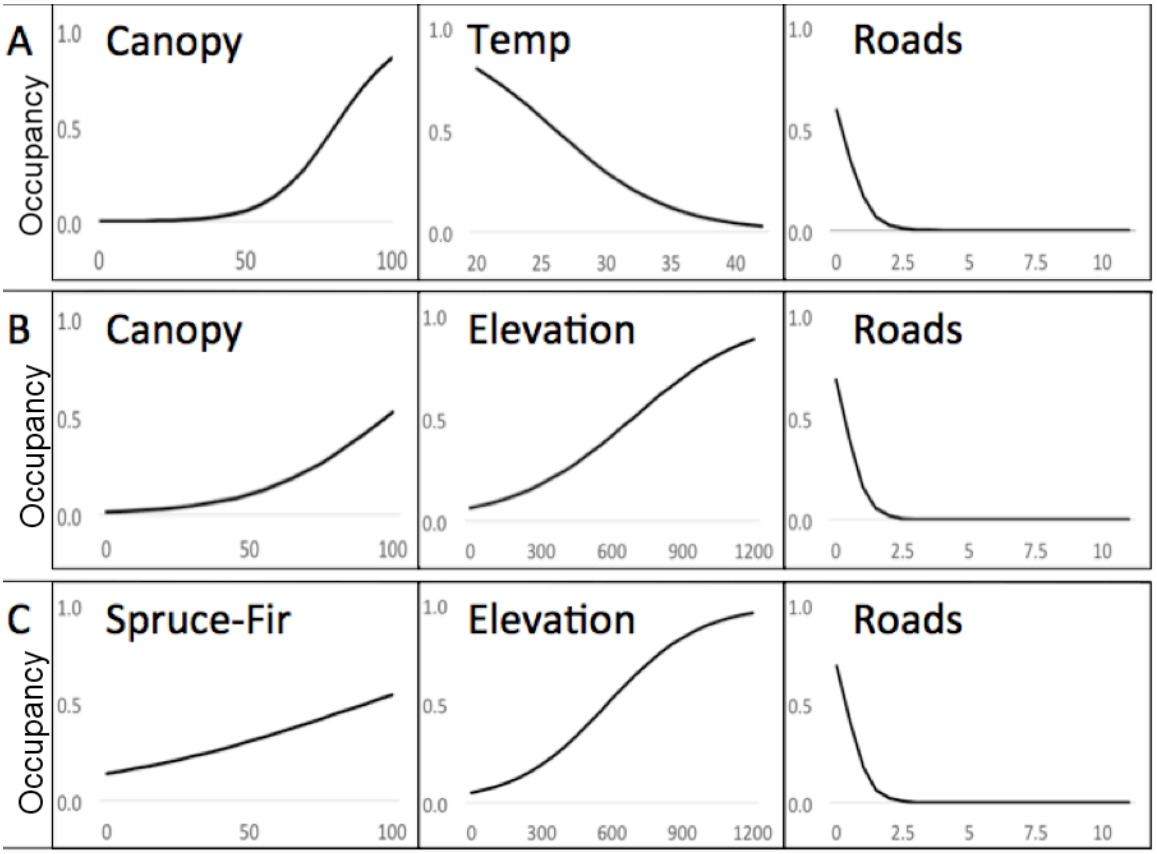


Figure 10. Effects of individual covariates in the top three models of American marten occupancy fitted by mixed-effects logistic regression based on expert opinion data from experts in the northeastern United States. X-axes on plots show the raw habitat covariate values back-converted from z-scores used in model fitting to units of percent cover (Canopy and Spruce-Fir), degrees Fahrenheit (Temp), km/km^2 (Roads), and meters (Elevation). Y-axes in plots show occupancy probability estimated from each model with only the effects of the intercept and individual model covariate. Each expert estimated occupancy at 30 sites in the northeastern US during a web-based survey, expert-specific and site-specific random effects were mixed with fixed habitat effects during model fitting.

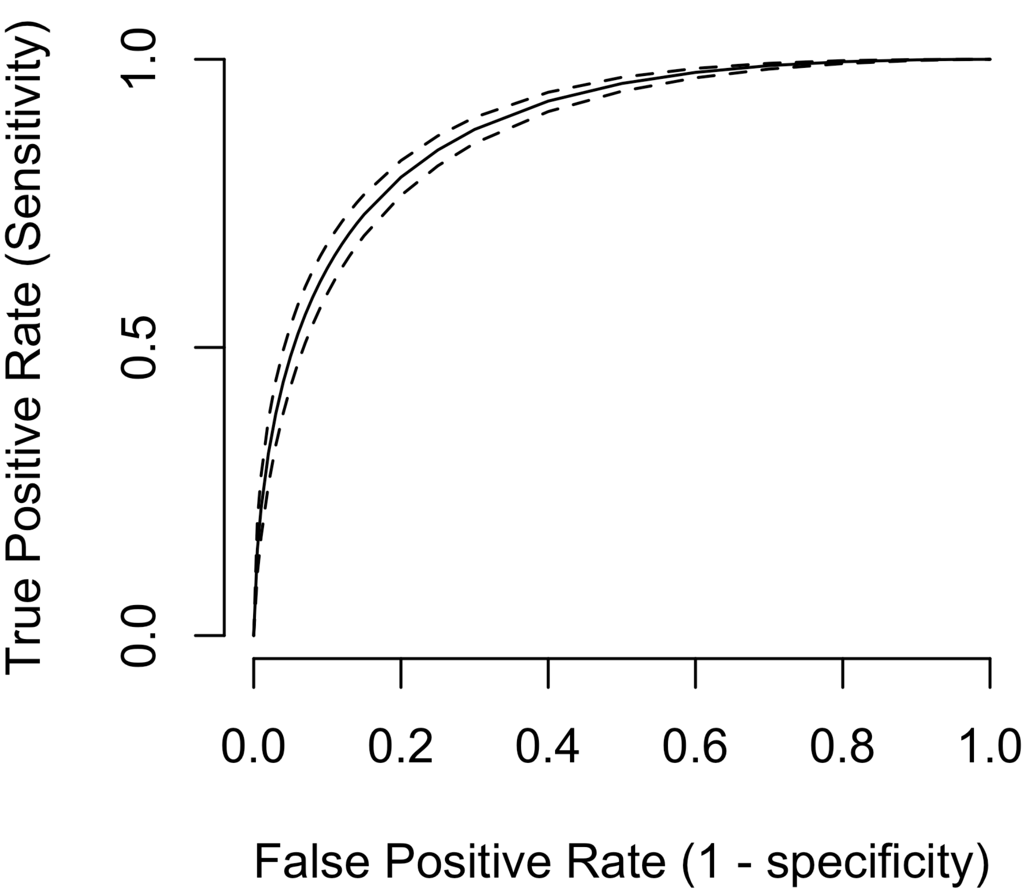


Figure 11. ROC curve obtained from occupancy estimates at 1000 random “presence” points in townships with recent marten detections and 1000 random “absence” points in townships lacking recent marten detections. The solid line represents the maximum likelihood estimate and dotted lines represent upper and lower 95% confidence limits.

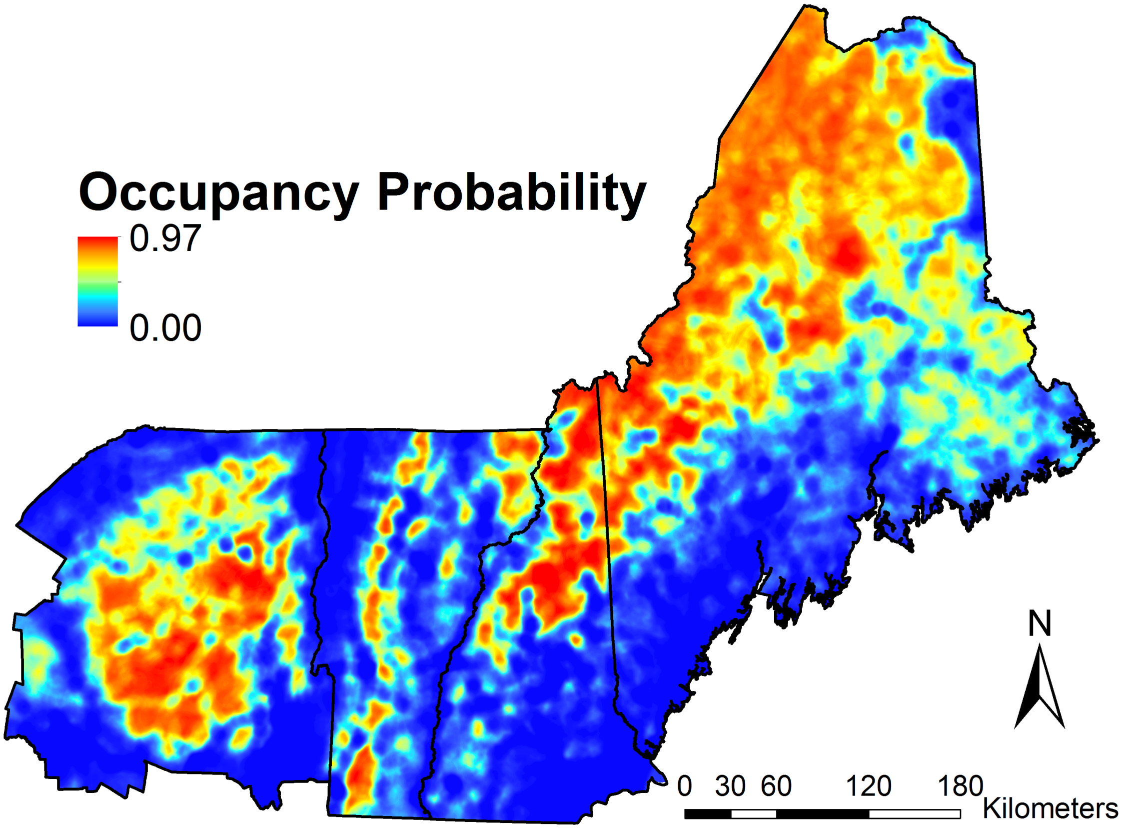


Figure 12. Estimated American marten occupancy in the northeastern United States based on combined estimates of three models weighted by their AIC weights. Models were fitted by mixed-effects logistic regression using expert opinion data from experts in the northeastern United States. Each expert estimated occupancy at 30 sites in the northeastern US using a web-based survey. Expert-specific and site-specific random effects were combined with fixed habitat effects in each model.

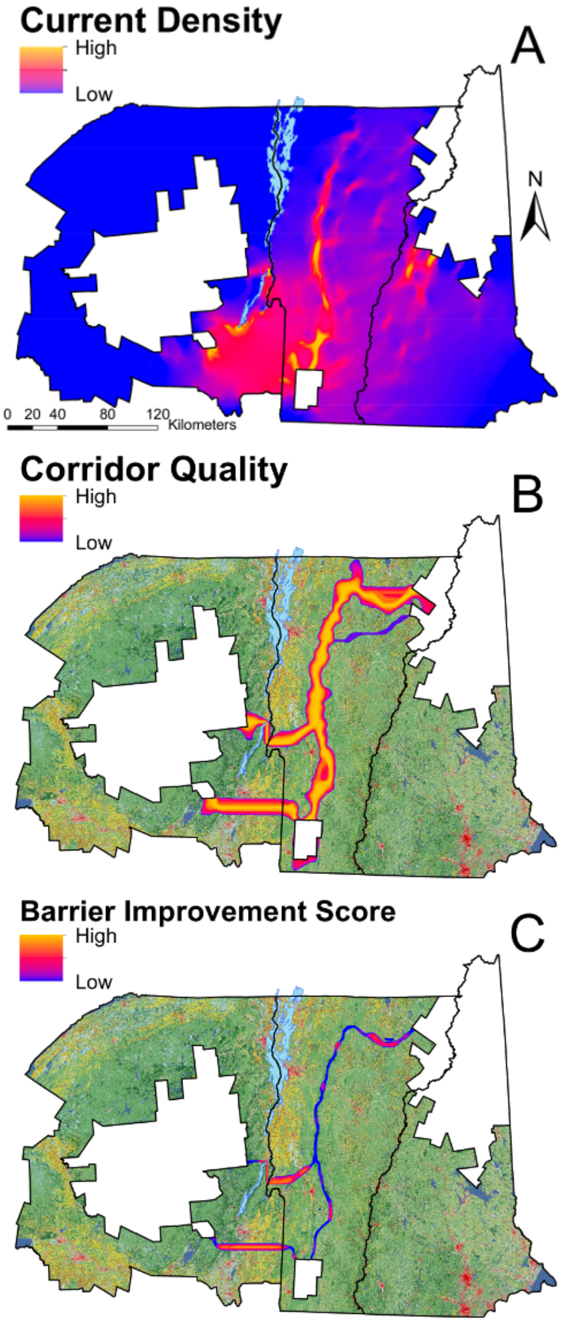


Figure 13. Circuit densities (A), dispersal corridors (B) and corridor barriers (C) estimated for American marten in southern Vermont and nearby populations based on circuit theory and a resistance surface derived from an occupancy model based on expert predictions of occupancy at offsets of 30 sites in the northeastern United States. The occupancy model combined three candidate models weighted by their AIC weights. Models were fit using mixed-effects logistic regression with expert- and site-specific random effects combined with fixed habitat covariate effects.

BIBLIOGRAPHY

Bartoń K (2016) MuMIn: Multi-model inference R-package v.1156. URL https://cran.r-project.org/web/packages/MuMIn/index.html

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-51.

Beier P, Noss RF (1998) Do Habitat Corridors Provide Connectivity? Conservation Biology 12:1241–1252.

Bright PW, Morris PA (1994) Animal translocation for conservation: performance of dormice in relation to release methods, origin and season. Journal of Applied Ecology 31:699–708.

Brooks RT (1996) Assessment of two camera-based systems for monitoring arboreal wildlife. Wildlife Society Bulletin 24:298-300.

Broquet T, Johnson C, Petit E, Thompson I, Burel F, Fryxell JM (2006) Dispersal and genetic structure in the American marten, *Martes americana*. Molecular Ecology 15:1689–1697.

Broquet T, Ray N, Petit E, Fryxell JM, Burel F, (2006) Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*). Landscape Ecology 21:877–889.

Buckland ST, Burnham KP, Augustin NH (1997) Model selection: An integral part of inference. Biometrics 53:603-618.

Burnham K, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, USA.

Carroll C (2007) Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: Marten and Lynx in the northern Appalachians. Conservation Biology 21:1092–1104.

Chen C, Durand E, Forbes F, François O (2007) Bayesian clustering algorithms ascertaining spatial population structure: A new computer program and a comparison study. Molecular Ecology Notes 7:747–756.

Clark TW, Anderson E, Douglas C, Strickland M (1987) *Martes americana*. Mammalian Species 289:1-8.

Corander J, Marttinen P, Sirén J, Tang J (2008) Enhanced Bayesian modelling in BAPS software for learning genetic structures of populations. BMC bioinformatics 9:539.

Cornuet JM, Luikart G (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics 144:2001–2014.

Cushman SA, Lewis JS, (2010) Movement behavior explains genetic differentiation in American black bears. Landscape Ecology 25:1613–1625.

Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. The American Naturalist 168:486–99.

Davis CS, Strobeck C (1998) Isolation, variability, and cross-species amplification of polymorphic microsatellite loci in the family Mustelidae. Molecular ecology 7:1776–1778.

Distefano JJ, Royar KJ, Pence DM, Denoncour JE (1990) Marten recovery plan for Vermont. Waterbury, Vermont, USA.

Drew RE, Hallett JG, Aubry KB, Cullings KW, Koepf SM, Zielinski WJ (2003) Conservation genetics of the fisher (*Martes pennanti*) based on mitochondrial DNA sequencing. Molecular Ecology 12:51–62.

Durand E, Jay F, Gaggiotti OE, François O (2009) Spatial inference of admixture proportions and secondary contact zones. Molecular Biology and Evolution 26:1963–1973.

Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources 4:359–361.

Early R, Anderson B, Thomas CD (2008) Using habitat distribution models to evaluate large-scale landscape priorities for spatially dynamic species. Journal of Applied Ecology 45:228–238.

Eng J (2014) ROC analysis: web-based calculator for ROC curves. Johns Hopkins University. URL http://www.jrocfit.org. Accessed 03 June 2017.

ESRI (2012) ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, California, USA.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molecular Ecology 14:2611–2620.

Excoffier L (2004) Patterns of DNA sequence diversity and genetic structure after a range expansion: Lessons from the infinite-island model. Molecular Ecology 13:853–864.

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources 10:564–567.

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. Genetics 164:1567–1587.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38-49.

Fleming MA, Ostrander EA, Cook JA (1999) Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). Molecular ecology 8:1352–1354.

Foster DR, Motzkin G, Bernardos D, Cardoza JE, (2002) Wildlife dynamics in the changing New England landscape. Journal of Biogeography 29:1337-1357.

Fuller AK, Harrison DJ (2005) Influence of partial timber harvesting on American martens in north-central Maine. The Journal of Wildlife Management 69:710–722.

Gibilisco CJ (1994) Distributional dynamics of martens and fishers in North America., in: Buskirk, S.W., Harestad, A.S., Raphael, M.G., Powell, R.A. (Eds.), Martens, Sables, and Fishers: Biology and Conservation. Cornell University Press, Ithaca, NY, USA. pp. 59–71.

Godbout G, Ouellet JP (2010) Fine-scale habitat selection of American marten at the southern fringe of the boreal forest. Ecoscience 17:175–185.

Godin AJ (1977) Wild Mammals of New England. Johns Hopkins University Press, Baltimore, Maryland, USA.

Griekspoor A, Groothuis T (2006) A high-tech infusion for science. In: 4Peaks. URL mekentosj.com.

Guillot G, Mortier F, Estoup A (2005) GENELAND: A computer package for landscape genetics. Molecular Ecology Notes 5:712–715.

Hagmeier EM (1956) Distribution of marten and fisher in North America. Canadian Field-Naturalist 70:149–168.

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49.

Hanski I (2009) Incorporating the spatial configuration of the habitat into ecology and evolutionary biology, in: Cantrell, S., Cosner, C., Shitui, R.S., (Eds.), Spatial Ecology. Chapman and Hall, New York, NY, USA. pp. 167–188.

Hapeman P, Latch EK, Fike JA, Rhodes OE, Kilpatrick CW (2011) Landscape genetics of fishers (*Martes pennanti*) in the Northeast: Dispersal barriers and historical influences. Journal of Heredity 102:251–259.

Hapeman P, Latch EK, Rhodes OE, Kilpatrick CW (2014) When recent and evolutionary histories meet: deciphering temporal events from contemporary patterns of mtDNA from fishers (*Martes pennanti*) in north-eastern North America. Journal of Zoological Systematics and Evolutionary Research 52: 331–337.

Hartl DL, Clark AG (1997) Principles of population genetics. Sinauer Associates, Sunderland, Massachusetts, USA.

Hess GR, Fischer RA (2001) Communicating clearly about conservation corridors. Landscape and Urban Planning 55:195–208.

Hilty JA, Lidicker WZ, Merenlender AM (2006) Corridor ecology: the science and practice of linking landscape for biodiversity conservation. Island Press, Washington D.C., USA.

Hoffman AA, Blows MW (1994) Species borders: ecological and evolutionary perspectives. Trends in Ecology and Evolution 9:223–227.

James A, Low Choy S, Mengersen K (2010) Elicitator: An expert elicitation tool for regression in ecology. Environmental Modelling and Software 25:129–145.

Kelly JR, Fuller TK, Kanter JJ (2009) Records of recovering American marten, *Martes americana*, in New Hampshire. Canadian Field-Naturalist 123:1–6.

Kirk GL (1916) The mammals of Vermont. Joint Bulletin, Vermont Botanical and Bird Clubs 2:28-34.

Koen EL, Bowman J, Garroway CJ, Mills SC, Wilson PJ (2012) Landscape resistance and American marten gene flow. Landscape Ecology 27:29–43.

Krohn WB (2012) Distribution Changes of American Martens and Fishers in Eastern North America, 1699-2001, in: Aubry, K.B., Zielinski, W.J., Raphael, M.G., Proulx, G., Buskirk, S.W. (Eds.), Biology and Conservation of Martens, Sables, and Fishers: A New Synthesis. Cornell University Press, Ithaca, NY, USA. pp. 58–73.

Kyle CJ, Davis CS, Strobeck C (2000) Microsatellite analysis of North American pine marten (*Martes americana*) populations from the Yukon and Northwest Territories. Canadian Journal of Zoology 78:1150–1157.

Kyle CJ, Strobeck C (2003) Genetic homogeneity of Canadian mainland marten populations underscores the distinctiveness of Newfoundland pine martens (*Martes americana atrata*). Canadian Journal of Zoology 66:57–66.

Lambeck RJ (1997) Focal species: A multi-species umbrella for nature conservation. Conservation Biology 11:849–856.

Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology 19:4179–4191.

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23:2947–2948.

Latch EK, Dharmarajan G, Glaubitz JC, Rhodes OE (2006) Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. Conservation Genetics 7:295–302.

Lawes TJ, Anthony RG, Robinson WD, Forbes JT, Lorton GA (2013) Movements and settlement site selection of pygmy rabbits after experimental translocation. Journal of Wildlife Management 77:1170–1181.

Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? Conservation Biology 9:753–760.

Low Choy S, James A, Murray J, Mengersen K (2012) Elicitator: A user-friendly, interactive tool to support scenario-based elicitation of expert knowledge, in: Expert Knowledge and Its Application in Landscape Ecology. pp. 39–67.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle AA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

McRae BH, Dickson B, Keitt T, Shah V (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

McRae BH, Hall SA, Beier P, Theobald DM (2012) Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits. PLoS ONE 7. doi:10.1371/journal.pone.0052604

McRae BH, Shah V, Edelman A (2016) Circuitscape: modeling landscape connectivity to promote conservation and human health. The Nature Conservancy 1–14.

Mech LD, Rogers LL (1977) Status, distribution and movements of martens in northeastern Minnesota. Research Paper NC-143. St. Paul, MN: USDA, Forest Service, North Central Forest Experiment Station.

Moehrenschlager A, Macdonald DW (2003) Movement and survival parameters of translocated and resident swift foxes *Vulpes velox*. Animal Conservation 6:199–206.

Moruzzi TL, Royar KJ, Grove C, Brooks RT, Bernier C, Thompson FL, DeGraaf RM, Fuller TK (2003) Assessing an American marten, *Martes americana*, reintroduction in Vermont. Canadian Field-Naturalist 117:190–195.

Mowry RA, Schneider TM, Latch EK, Gompper ME, Beringer J, Eggert LS (2015) Genetics and the successful reintroduction of the Missouri river otter. Animal Conservation 18:196–206.

Murray JV, Goldizen AW, O'Leary R, McAlpine C, Possingham HP, Low Choy S (2009) How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. Journal of Applied Ecology 46:842–851.

New Hampshire Wildlife Action Plan Team (2015) New Hampshire Wildlife Action Plan 2015. Concord, New Hampshire, USA.

Osgood FL (1938) The mammals of Vermont. Journal of Mammalogy 19:435–441.

Palomares F, Delibes M, Ferreras P, Fedriani JM, Calzada J, Revilla E (2000) Iberian lynx in a fragmented landscape: Predispersal, dispersal and postdispersal habitats. Conservation Biology 14:809–818.

Peakall R, Smouse PE (2006) GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity 95:536–539.

Piry S, Luikart G, Cornuet J-M (1999) BOTTLENECK: a program for detecting recent effective population size reductions from allele data frequencies. Journal of Heredity 90:502–503.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–59.

Pruett CL, Winker K (2008) The effects of sample size on population genetic diversity estimates in song sparrows (*Melospiza melodia*). Journal of Avian Biology 39:252–256.

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Rice WER (1989) Analyzing tables of statistical tests. Evolution 43:223–225.

Royar KJ (1992) Monitoring reintroduced marten populations in Vermont. Vermont Fish and Wildlife Department. Waterbury, Vermont, USA.

Russell JC, McMorland AJC, MacKay JWB (2010) Exploratory behaviour of colonizing rats in novel environments. Animal Behaviour 79:159–164.

Schneider S, Excoffier L (1999) Estimation of past demographic parameters from the distribution of pairwise differences when the mutation rates vary among sites: Application to human mitochondrial DNA. Genetics 152:1079–1089.

Schwartz M (2005) Guidelines on the use of molecular genetics in reintroduction programs. In: The EU LIFE-Nature Projects to guidelines for the reintroduction of threatened species. Caramanico Terme, Italy, pp 51–58

Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conservation Biology 21:303–312.

Shields GF, Kocher TD (1991) Phylogenetic relationships of north American ursids based on analyses of Mitochondrial DNA. Evolution 45:218–221.

Sirén APK, (2009) Population ecology of American marten in New Hampshire: Impact of wind farm development in high elevation habitat. M.S. Thesis, University of New Hampshire, Durham, New Hampshire, USA.

Sorenson E, Osborne J (2014) Vermont habitat blocks and habitat connectivity: An analysis using Geographic Information Systems. Vermont Department of Fish and Wildlife, Montpelier, Vermont, USA.

Swanson BJ, Peters RL, Kyle CJ (2006) Demographic and genetic evaluation of an American marten reintroduction. Journal of Mammalogy 87:272–280.

Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biological Conservation 157:87–195.

Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

Trombulak S., Royar KJ (2001) Restoring the wild: Species recovery and reintroductions. In: McGrory-Klyza C (ed) Wilderness Comes Home: Rewilding the Northeast. University Press of New England, Hanover, New Hampshire, pp 157–181.

Vergara PM, Armesto JJ (2009) Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landscape Ecology 24:25–38.

Vermont Wildlife Action Plan Team (2015) Vermont Wildlife Action Plan 2015. Montpelier, Vermont, USA.

Vincent IR, Farid A, Otieno CJ (2003) Variability of thirteen microsatellite markers in American mink (*Mustela vison*). Canadian Journal of Animal Science 83:597–599.

Vinkey RS, Schwartz MK, McKelvey KS, Foresman KR, Pilgrim KL, Giddings BJ, Lofroth EC (2006) When reintroductions are augmentations: the genetic legacy of the fisher (*Martes pennanti*) in Montana. Journal of Mammalogy 87:265–271.

Walker CW, Vilà C, Landa A, Linden M, Ellegren H (2001) Genetic variation and population structure in Scandinavian wolverine (*Gulo gulo*) populations. Molecular Ecology 10:53–63.

Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NH, Miller KA, Byrne M, Coates DJ, Eldridge MDB, Sunnucks P, Breek MF, James EA, Hoffmann AA (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4: 709–725.

Williams BW, Scribner KT (2010) Effects of multiple founder populations on spatial genetic structure of reintroduced American martens. Molecular Ecology 19:227–240.

Wolf CM, Griffith B, Reed C, Temple SA (1996) Avian and mammalian translocations: Update and reanalysis of 1987 survey data. Conservation Biology 10:1142–1154.

Woods JG, Paetkau D, Lewis D, et al (1999) Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

APPENDICES

Appendix I. American martens (*Martes americana*) released in southern Green Mountain National Forest during a reintroduction attempt from 1989 to 1991 (from Royar 1992).

	1989	1990	1991	Total
Quick Release	28	24	24	76
Slow Release	12	7	20	39
Male	29	25	34	89
Female	11	6	10	27
New York	6	5	0	11
Maine	34	26	44	104
White Rocks	40	0	8 (2F, 6M)	48
Lye Brook	0	31	36 (8F, 28M)	67
Collared	6	7	0	13

Appendix II. Locality data for American marten (*Martes americana*) samples in this study. Locations recorded by GPS are marked by an asterisk (*); otherwise, longitude and latitude were estimated by the township centroid. ME = Maine, NH = New Hampshire, NY = New York, and VT-N = northern Vermont.

Sample	State	Location	Longitude	Latitude
1511	ME	Benedicta, Aroostook Co.	-68.5989	46.6588
1520	ME	Molunkus, Aroostook Co.	-68.8873	46.9700
1521	ME	Allagash, Aroostook Co.	-68.5989	46.6588
1525	ME	Allagash, Aroostook Co.	-68.5989	46.6588
1528	ME	Benedicta, Aroostook Co.	-68.3945	45.8057
1530	ME	T9R10, Piscatiquis Co.	-68.8873	46.9700
1532	ME	T6R11, Piscatiquis Co.	-68.8873	46.9700
1533	ME	T6R11, Piscatiquis Co.	-68.8873	46.9700
1536	ME	T6R10, Piscatiquis Co.	-68.8873	46.9700
1545	ME	Merrill, Aroostook Co.	-68.3684	45.6246
1546	ME	T6R10, Piscatiquis Co.	-69.0902	47.0937
1547	ME	T5R11, Piscatiquis Co.	-69.0902	47.0937
1503	ME	Aroostook Co.	-68.3945	45.8057
1507	ME	T15R9, Aroostook Co.	-69.0183	46.4393
1508	ME	Aroostook Co.	-69.1510	46.1708
1509	ME	Aroostook Co.	-69.1510	46.1708
1512	ME	T15R9, Aroostook Co.	-69.0191	46.1712
1513	ME	T15R9, Aroostook Co.	-68.2351	46.1654
1514	ME	T15R9, Aroostook Co.	-69.0191	46.1712
1515	ME	T15R9, Aroostook Co.	-69.1507	46.0817
1615	ME	T4R11, Piscataquis Co.	-69.1510	45.9875
1618	ME	T3R11, Piscataquis Co.	-69.1332	45.8949
1619	ME	T3R11, Piscataquis Co.	-69.1332	45.8949
1620	ME	T6R11, Piscatiquis Co.	-69.1510	46.1708
F12	NH	Mt. Kelsey, Coos Co.	-71.2089	44.8280
F16	NH	Mt. Kelsey, Coos Co.	-71.2876	45.0080
F2	NH	Mt. Kelsey, Coos Co.	-71.2793	45.0236
F5	NH	Mt. Kelsey, Coos Co.	-71.3844	45.0432
F5K1	NH	Mt. Kelsey, Coos Co.	-71.2918	45.0004
F5K2	NH	Mt. Kelsey, Coos Co.	-71.3137	44.8012
F6	NH	Mt. Kelsey, Coos Co.	-71.3137	44.8012
F8	NH	Mt. Kelsey, Coos Co.	-71.3137	44.8012
F9	NH	Mt. Kelsey, Coos Co.	-71.3137	44.8012
M10	NH	Mt. Kelsey, Coos Co.	-71.3137	44.8012
M3	NH	Mt. Kelsey, Coos Co.	-71.3137	44.8012

M8	NH	Mt. Kelsey, Coos Co.	-71.3137	44.8012
MINC2013A	NH	Littleton, Grafton Co.	-71.3137	44.8012
MINC2013B	NH	Pittsburg, Coos Co.	-71.3137	44.8012
MINC2013C	NH	Berlin, Coos Co.	-71.3137	44.8012
MINC2013D	NH	Hart's Location, Carroll Co.	-71.2255	43.9860
MINC2013E	NH	Dixville, Coos Co.	-71.3137	44.8012
MINC2013F	NH	Colebrook, Coos Co.	-71.3137	44.8012
MINC2013G	NH	Second Coll, Coos Co.	-71.3137	44.8012
MINC2013H	NH	Second Coll, Coos Co.	-71.3137	44.8012
MINC2013J	NH	Dixville, Coos Co.	-71.8095	44.3323
M13	NH	Mt. Kelsey, Coos Co.	-71.2508	45.1431
F3	NH	Mt. Kelsey, Coos Co.	-71.2602	44.4871
454	NH	*Errol, Coos Co.	-71.3725	44.1366
455	NH	*Clarksville, Coos Co.	-71.2728	44.8867
456	NH	*Clarksville, Coos Co.	-71.4145	44.8990
457	NH	*Clarksville, Coos Co.	-71.1073	44.9131
458	NH	*Clarksville, Coos Co.	-71.1073	44.9131
HB16	NH	*Albany, Carroll Co.	-71.2728	44.8867
0006039	NY	Arietta, Hamilton Co.	-74.5697	43.5266
0006040	NY	Wells, Hamilton Co.	-74.2733	43.4738
0006042	NY	Indian Lake, Hamilton Co.	-74.3219	43.7874
0006218	NY	Ohio, Herkimer Co.	-74.9211	43.4783
0006224	NY	Day, Saratoga Co.	-74.0364	43.3263
0006236	NY	Schroon, Essex Co.	-73.7661	43.8499
0030078	NY	Minerva, Essex Co.	-74.0589	43.8538
0030080	NY	Minerva, Essex Co.	-74.0589	43.8538
0030083	NY	Minerva, Essex Co.	-74.0589	43.8538
0030085	NY	Minerva, Essex Co.	-74.0589	43.8538
0030131	NY	Long Lake, Hamilton Co.	-74.5861	43.9718
0030136	NY	Long Lake, Hamilton Co.	-74.5861	43.9718
0030284	NY	Morehouse, Hamilton Co.	-74.7272	43.4712
0030384	NY	Tupper Lake, Franklin Co.	-74.4747	44.2431
0030396	NY	Harrietstown, Franklin Co.	-74.2363	44.2431
0030397	NY	Harrietstown, Franklin Co.	-74.2363	44.2431
0030409	NY	La. Pleasant, Hamilton Co.	-74.4265	43.5692
0030426	NY	Schroon, Essex Co.	-73.7661	43.8499
0030428	NY	Schroon, Essex Co.	-73.7661	43.8499
0030439	NY	Webb, Herkimer Co.	-74.9937	43.8355
0030440	NY	Long Lake, Hamilton Co.	-74.5861	43.9718
0030441	NY	Webb, Herkimer Co.	-74.9937	43.8355
0030444	NY	Webb, Herkimer Co.	-74.9937	43.8355
0030702	NY	Morehouse, Hamilton Co.	-74.7272	43.4712

0030705	NY	Inlet, Hamilton Co.	-74.7375	43.7287
0030707	NY	Inlet, Hamilton Co.	-74.7375	43.7287
0030714	NY	Indian Lake, Hamilton Co.	-74.3219	43.7874
0030766	NY	Keene, Essex Co.	-73.8119	44.1805
0030767	NY	Keene, Essex Co.	-73.8119	44.1805
0030856	NY	Johnsburg, Warren Co.	-74.0531	43.6303
0030881	NY	North Elba, Essex Co.	-73.9969	44.2396
0053013	NY	North Hudson, Essex Co.	-73.7980	44.0015
0058097	NY	North Hudson, Essex Co.	-73.7980	44.0015
0073794	NY	Minerva, Essex Co.	-74.0589	43.8538
0073811	NY	Lyonsdale, Oneida Co.	-75.2466	43.6062
0073816	NY	Forestport, Oneida Co.	-75.1547	43.4956
0080435	NY	North Elba, Essex Co.	-73.9969	44.2396
0080436	NY	North Elba, Essex Co.	-73.9969	44.2396
0081270	NY	Indian Lake, Hamilton Co.	-74.3219	43.7874
0081271	NY	Arietta, Hamilton Co.	-74.5697	43.5266
0081272	NY	Indian Lake, Hamilton Co.	-74.3219	43.7874
0084164	NY	Franklin, Clinton Co.	-74.0506	44.5274
0084166	NY	Wilmington, Essex Co.	-73.8430	44.3756
0084176	NY	St Armand, Essex Co.	-74.0280	44.3803
0087281	NY	Newcomb, Essex Co.	-74.1256	44.0178
0106032	NY	Indian Lake, Hamilton Co.	-74.3219	43.7874
0106036	NY	Indian Lake, Hamilton Co.	-74.3219	43.7874
0106157	NY	Watson, Lewis Co.	-75.2535	43.8246
0106158	NY	Watson, Lewis Co.	-75.2535	43.8246
0106159	NY	Watson, Lewis Co.	-75.2535	43.8246
6224	VT-N	Averill, Essex Co.	-71.6820	44.9432
25679	VT-N	Essex Co.	-71.7362	44.7279
28783	VT-N	Granby, Essex Co.	-71.7207	44.6024
34105	VT-N	Ferdinand, Essex Co.	-72.1652	44.7547
34106	VT-N	Walden, Caledonia Co.	-71.7564	44.7275
34107	VT-N	Burke, Caledonia Co.	-72.2363	44.4813
34108	VT-N	Waterford, Caledonia Co.	-71.9288	44.6146
34109	VT-N	Victory, Essex Co.	-71.9404	44.3791
34110	VT-N	Victory, Essex Co.	-71.8197	44.5467
34112	VT-N	Concord, Essex Co.	-71.8197	44.5467
34148	VT-N	Victory, Essex Co.	-71.8337	44.4315
34149	VT-N	Lemington, Essex Co.	-71.8197	44.5467
34150	VT-N	Lemington, Essex Co.	-71.5834	44.8906
35000	VT-N	Lewis, Essex Co.	-71.5834	44.8906
35237	VT-N	Granby, Essex Co.	-71.7486	44.8662
36453	VT-N	Bloomfield, Essex Co.	-71.7207	44.6024

35556	VT-N	Lewis, Essex Co.	-71.7486	44.8662
35557	VT-N	Ferdinand, Essex Co.	-71.7564	44.7275
35608	VT-N	Ferdinand, Essex Co.	-71.7564	44.7275
36454	VT-N	Essex Co.	-71.6447	44.8121
36944	VT-N	Brighton, Essex Co.	-71.7362	44.7279
34100	VT-S	Sunderland, Bennington Co.	-71.8695	44.8027
34102	VT-S	Woodford, Bennington Co.	-73.0690	43.0709
34111	VT-S	Sunderland, Bennington Co.	-73.0800	42.8828
34981	VT-S	Searsburg, Bennington Co.	-73.0690	43.0709
34982	VT-S	Somerset, Windham Co.	-72.9673	42.8933
34983	VT-S	Somerset, Windham Co.	-72.9635	42.9756
36451	VT-S	Somerset, Windham Co.	-72.9635	42.9756

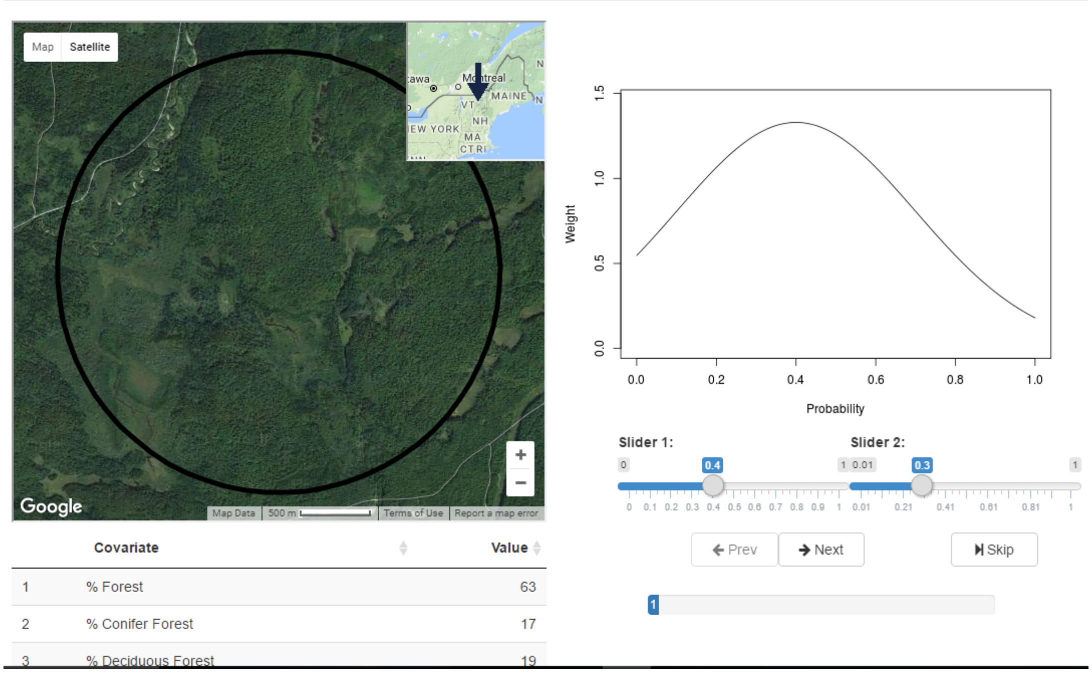
Appendix III. User guides given to experts to assist their interpretation of a survey to estimate American marten (*Martes americana*) occupancy at sites in the northeastern United States.

Marten Survey User Guide

Site Evaluation

Each site in this survey is a 7 km^2 circular area, representative of a typical male marten home range in the northeastern United States. Given a satellite view of the site and values for twelve habitat variables (see table below), you will be asked to estimate the probability of marten occupancy on a scale from 0.0 to 1.0, with 0.0 indicating that the species does not occur at the site and 1.0 indicating that there is a 100% chance that the species occurs there. Values along the scale are like percents, so 0.7 would indicate a 70% chance of the species occurring at the site. You will also be asked to specify a measure of your confidence in your estimate using a standard deviation. The larger the standard deviation of your estimate, the less confidence you are expressing in your estimate.

Let's walk through a quick example. The photo below displays the interface you will see for a site.



	Covariate	Value
1	% Forest	63
2	% Conifer Forest	17
3	% Deciduous Forest	19

The left side of the screen displays the site information. A Google map is on top and shows the entire site, which is the area within the circle. You can zoom in and out using the + and – buttons to see the site at different scales. Below the map, you will find a table of twelve variables (called covariates) and their values within the site (only three variables are visible in this screenshot). These variables include habitat amounts and other landscape conditions (see descriptions in the table below). You should use the information from the map and the variable data to estimate occupancy probability. To make your estimate, use the graph on the right side of the screen. This graph shows a curve of probability. The peak of the curve corresponds to your estimate of occupancy probability and the width of the curve corresponds to your confidence in that estimate. You set the peak and width using two sliders that are below the graph. In the graph shown, the expert used Slider 1 to indicate that their occupancy estimate was 0.4 (or 40%) at the site. Slider 2 was then adjusted to set the width of the curve and reflect confidence in that estimate. The width in this example is fairly wide meaning that there is a reasonable chance that occupancy could be higher or lower than the estimate. If the width was set to be very narrow, then this would indicate that the expert is feels that the estimate is highly precise. Below the sliders are options to proceed to the next site or return to a previous site. You also have the option to skip a site if you are unable to make an estimate. A progress bar is shown that displays which site number you are currently evaluating. As you progress through the survey, your responses to individual sites will be saved automatically. If you decide to take a break and resume at a later time, you will start where you left off and your previous responses will be saved. You may revisit any previously completed site and revise your response at any time. After finishing all sites, you will then be given the Post-Survey Questionnaire.

Site variables

We identified twelve variables that are thought to be associated with marten occurrence in the northeast. Variable descriptions are provided in the table on the following page, and for some variables we have provided visual guides with photographs or example regions. If there are other variables not included in the table that you believe influence marten occupancy, please share them in the Pre-Survey Questionnaire.

There are two habitat variable guides available to help translate your personal understanding of habitat conditions into the measurements and units used in our survey. For visual representations of a forest stand at different ages and with different values of Total Basal Area, see the “Total Basal Area and Stand Age Guide”. For distinguishing between forest land cover percentages and canopy cover percentages using example sites from our survey, see the “Forest Cover vs. Canopy Cover Guide”.

Basal Area and Stand Age Guide

Total basal area and stand age are two variables used to describe the conditions of a survey site. We estimated basal area as the average cross-sectional area of tree stems at breast height per acre (unit of measure: ft^2/acre) and stand age as the average time since previous disturbance of a forest stand (unit of measure: years). Below are some examples of different basal area and stand ages that may help you better visualize these variables when estimating marten occupancy.

Source: http://www.nrs.fs.fed.us/units/sustainingforests/focus/ltr/arnot/

Basal Area: 3.1 ft^2/acre, Stand Age: 0 years

Basal area: 8.1 ft^2/acre, Stand Age: 10 years

Basal Area: 34.4 ft^2/acre, Stand Age: 20 years

Basal Area: 107.6 ft^2/acre, Stand Age: 31 years

Basal Area: 120.4 ft^2/acre, Stand Age: 45 years

Basal Area: 125.8 ft²/acre, Stand Age: 51 years

Basal Area: 149.8 ft²/acre, Stand Age: 62 years

Basal Area: 158.0 ft^2/acre, Stand Age: 71 years

Appendix IV. Complete set of candidate models to describe American marten (*Martes americana*) occupancy in the northeastern United States. Models were developed from expert opinion data obtained using a web-based survey of experts in the northeastern United States. Model covariates were fixed effects in a mixed-effects logistic regression, where expert-specific and site-specific random effects were also assessed. Models with an asterisk (*) contain variables that are highly correlated (r > 0.6) and were removed from the model fitting process.

Forest Models
Forest
SpruceFir
Canopy
TBA
Forest + SpruceFir
Forest + Canopy *
Forest + TBA *
SpruceFir + Canopy
SpruceFir + TBA
Canopy + TBA *
Forest + SpruceFir + Canopy
Forest + SpruceFir + TBA
Forest + Canopy + TBA
SpruceFir + Canopy + TBA
Forest + SpruceFir + Canopy + TBA
Climate Models
Temp
Elevation
Temp + Elevation *
Human Impact Models
Roads
Forest + Climate Models
Forest + Temp
Forest + Elevation *
SpruceFir + Temp *
SpruceFir + Elevation
Canopy + Temp
Canopy + Elevation
TBA + Temp
TBA + Elevation *
Forest + Human Impact Models
Forest + Roads
SpruceFir + Roads
Canopy + Roads

TBA + Roads
Forest + Climate + Human Impact Models
Forest + Temp + Roads
Forest + Elevation + Roads
SpruceFir + Temp + Roads
SpruceFir + Elevation + Roads
Canopy + Temp + Roads
Canopy + Elevation + Roads
TBA + Temp + Roads
TBA + Elevation + Roads

Appendix V. Statistics used to calculate covariate z-scores for fitting models of American marten (*Martes americana*) occupancy using mixed-effects logistic regression based on expert opinion data obtained in the northeastern United States.

Scale	1.5 km		5 km	
Covariate	Mean	Std	Mean	Std
Forest	65.13	25.27	67.85	18.21
SpruceFir	20.60	23.24	21.03	21.10
Canopy	62.33	20.32	64.05	14.74
TBA	75.70	35.05	73.62	31.39
Temp	32.95	3.47	32.77	3.47
Elevation	287.19	207.82	301.15	187.71
Roads	0.90	1.04	0.95	0.83

Appendix VI. AIC, ΔAIC, and AIC weights for all candidate models for American marten (*Martes americana*) occupancy in the northeastern United States. Models were developed from expert opinion data obtained using a web-based survey of experts. Model covariates were fixed effects in a mixed-effects logistic regression, in which expert-specific and site-specific random effects were also assessed.

Model	Scale	AIC	ΔAIC	AIC weight
Canopy + Temp + Roads	5k	417.61	0.00	0.4491
Canopy + Elevation + Roads	5k	418.04	0.43	0.3622
SpruceFir + Elevation + Roads	5k	419.43	1.82	0.1808
Forest + Temp + Roads	5k	426.95	9.34	0.0042
TBA + Temp + Roads	5k	427.37	9.76	0.0034
Canopy + Roads	5k	432.53	14.92	0.0003
Forest + Roads	5k	437.30	19.69	<0.0001
Canopy + Temp	5k	445.08	27.47	<0.0001
TBA + Temp + Roads	1.5k	448.54	30.93	<0.0001
SpruceFir + Elevation + Roads	1.5k	449.53	31.92	<0.0001
TBA + Roads	5k	454.09	36.48	<0.0001
SpruceFir + Canopy	5k	454.27	36.66	<0.0001
SpruceFir + Roads	5k	455.19	37.58	<0.0001
Canopy + Temp + Roads	1.5k	458.74	41.13	<0.0001
Canopy + Elevation + Roads	1.5k	462.17	44.56	<0.0001
SpruceFir + Canopy	1.5k	462.67	45.06	<0.0001
SpruceFir + Elevation	5k	467.48	49.87	<0.0001
TBA + Temp	5k	469.00	51.39	<0.0001
Roads	5k	469.63	52.02	<0.0001
TBA + Temp	1.5k	470.31	52.70	<0.0001
Forest + SpruceFir	5k	473.31	55.70	<0.0001
Canopy + Elevation	5k	474.12	56.51	<0.0001
Forest + Temp	5k	475.91	58.30	<0.0001
Canopy + Temp	1.5k	477.41	59.80	<0.0001
SpruceFir + Elevation	1.5k	481.96	64.35	<0.0001
SpruceFir + Roads	1.5k	483.44	65.83	<0.0001
Forest + Temp + Roads	1.5k	483.99	66.38	<0.0001
Canopy + Roads	1.5k	484.82	67.21	<0.0001
SpruceFir + TBA	1.5k	486.14	68.53	<0.0001
Canopy + Elevation	1.5k	489.89	72.28	<0.0001
TBA + Roads	1.5k	490.30	72.69	<0.0001
Elevation	5k	490.47	72.86	<0.0001
SpruceFir + TBA	5k	503.75	86.14	<0.0001
Forest + Roads	1.5k	504.08	86.47	<0.0001

Forest + SpruceFir	1.5k	510.58	92.97	<0.0001
Canopy	5k	512.16	94.55	<0.0001
Elevation	1.5k	512.90	95.29	<0.0001
Canopy	1.5k	522.56	104.95	<0.0001
Forest + Temp	1.5k	523.15	105.54	<0.0001
Roads	1.5k	524.03	106.42	<0.0001
Forest	5k	532.37	114.76	<0.0001
Temp	5k	542.70	125.09	<0.0001
SpruceFir	5k	545.25	127.64	<0.0001
Temp	1.5k	547.08	129.47	<0.0001
SpruceFir	1.5k	547.27	129.66	<0.0001
TBA	1.5k	553.86	136.25	<0.0001
Forest	1.5k	566.16	148.55	<0.0001
TBA	5k	575.08	157.47	<0.0001

Appendix VII. Mean and standard deviation (SD) of experts' occupancy estimates of sites from a web-based survey for American marten (*Martes americana*) occupancy in the northeastern United States. Standard deviation is maximized at moderate mean values and minimized at extreme mean values, demonstrating that perceived habitat quality affects experts' certainty in their estimates.