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Historical biogeography sets the foundation for contemporary conservation of martens (genus *Martes*) in northwestern North America

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Effective conservation of insular populations requires careful consideration of biogeography, including colonization histories and patterns of endemism. Across the Pacific Northwest of North America, Pacific martens (*Martes caurina*) and American pine martens (*Martes americana*) are parapatric sister species with distinctive postglacial histories. Using mitochondrial DNA and 12 nuclear microsatellite loci, we examine processes of island colonization and anthropogenic introductions across 25 populations of martens. Along the North Pacific Coast (NPC), *M. caurina* is now found on only 2 islands, whereas *M. americana* occurs on mainland Alaska and British Columbia and multiple associated islands. Island populations of *M. caurina* have a longer history of isolation reflected in divergent haplotypes, private microsatellite alleles, and relatively low within-population diversity. In contrast, insular *M. americana* have lower among-population divergence and higher metrics of within-population diversity. On some NPC islands, introductions of *M. americana* may be related to decline of *M. caurina*. Long-term persistence of these species likely has been influenced by anthropogenic manipulations, including wildlife translocations and industrial-scale deforestation, yet, the distinctive histories of these martens have not been incorporated into natural resource policies.

Key words: carnivore, endemic, introductions, islands, marten

Genetic parameters provide key indicators of the vulnerability of natural populations to extinction (Frankham 2005). Island populations, because they are typically small and isolated, often exhibit reduced genetic variability and elevated levels of inbreeding when juxtaposed against conspecific mainland (continental) populations (Frankham 1997; Bidlack and Cook 2001). Cold saltwater and strong currents are effective barriers to gene flow in many terrestrial vertebrate species (Williamson 1981; Baker et al. 1990), so populations on archipelagos often are differentiated from mainland populations. Although the relationship between genetic variability and extinction is complex (Aguilar et al. 2004), reduced variability and low levels of immigration may increase the probability of extirpation for isolated populations (MacArthur and Wilson 1967; Frankham 2005). Although island populations typically contain low levels of genetic variation (Frankham 1997), they may be essential to long-term persistence of the species and to the origin of new lineages because of their tendency to accumulate novel variation (Wilson et al. 2009). Isolation, therefore, increases the potential for divergence, while also increasing the risk of extinction (MacArthur and Wilson 1967), and these 2 factors have made island populations the focus of research and conservation efforts worldwide (Losos and Ricklefs 2009). Understanding how historical biogeography influences the contemporary distribution of genetic diversity within natural populations is a critical first step towards effective management of island biodiversity.

Early scientific surveys along the northern North Pacific Coast (NPC) of North America identified high numbers of endemic or regionally distinct organisms (Swarth 1936; Hall 1944) and subsequent investigations of the region's fauna (e.g., Reid et al. 1999), combined with advances in molecular techniques, uncovered a suite of genetically distinct populations and species of conservation concern (Cook et al. 2006). Recent investigations are providing more detailed views of these endemics (Topp and Winker 2008; Sawyer and Cook 2016) and revealing new areas supporting high genetic diversity along the NPC (Latch et al. 2008). This region includes 2 large, north-south oriented archipelagos: the Alexander Archipelago in southeastern Alaska (> 2,000 islands) and to the south, the Haida Gwaii Archipelago along coastal British Columbia (> 150 islands). These archipelagos, and the nearby narrow mainland bounded to the east by the Coast Range, support the largest remaining tract of old-growth temperate rainforest in the world (Alaback 1988). Potential Late Quaternary glacial refugia in this region have been proposed (Byun et al. 1997) and have been explored from geological (Carrara et al. 2003, 2007), paleontological (Heaton and Grady 2003; Ramsey et al. 2004), anthropological (Carlson and Baichtal 2015), and phylogeographical perspectives (Cook et al. 2006; Dawson et al. 2014).

Pacific martens (*Martes caurina* Merriam 1890) are distributed along the northern NPC of North America with disjunct populations found southward into California and the southern Rocky Mountains (Fig. 1). More widespread American pine martens (*M. americana* Turton 1806) have a parapatric northern distribution across North America. Originally described as distinct species, *M. caurina* was later subsumed within *M. americana* on the basis of a hypothesized zone of introgression in Montana (Wright 1953). We use the original 2-species taxonomic classification of Merriam (1890), which has been supported by molecular (Carr and Hicks 1997; Dawson and Cook 2012) and parasitological (Koehler et al. 2009; Hoberg et al. 2012) evidence. Reassessment of genetic diversity and conservation status of these 2 species provides a foundation for effective wildlife management prescriptions within the archipelagos and elsewhere. Further, 3 populations (Kuiu Island, northern and southern Montana) include areas of sympatry for

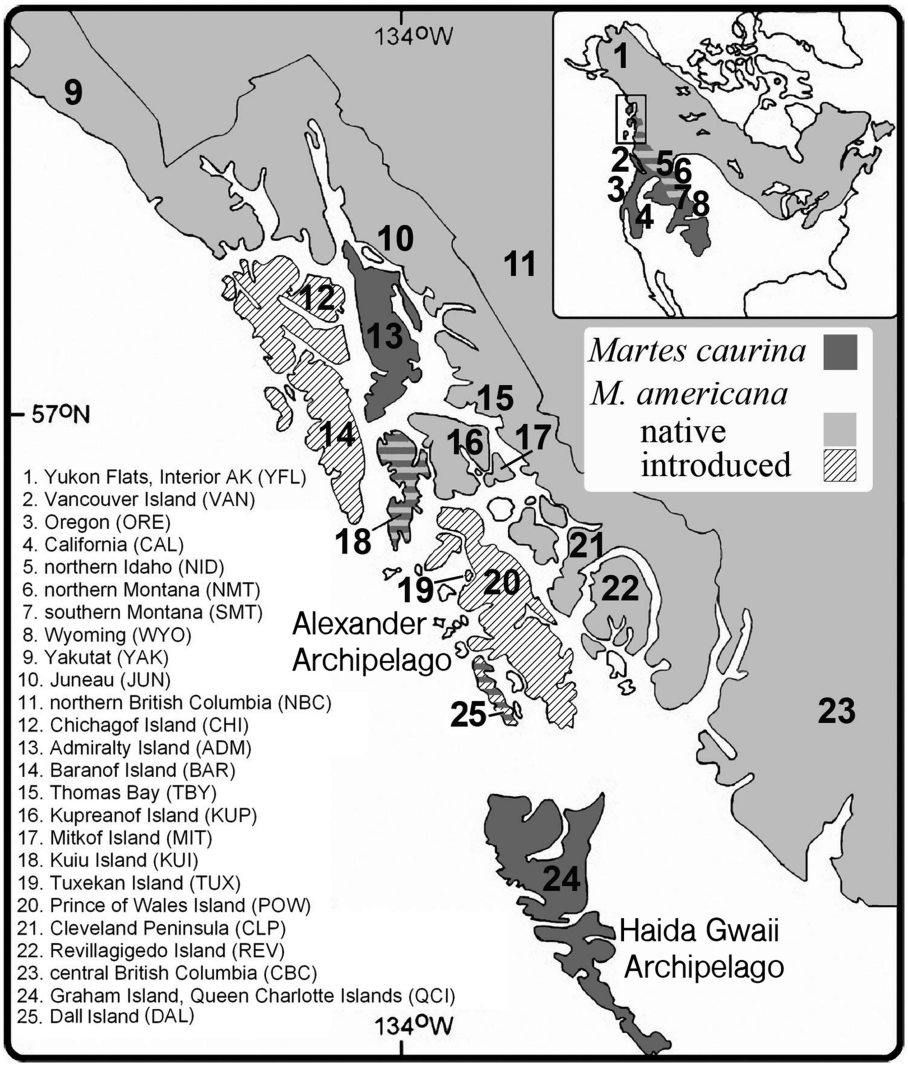

Fig. 1.—Map of localities for all *Martes americana* (light gray) and *M. caurina* (dark gray) populations. Bold hatched lines indicate hybrid zones between the 2 species, light hatching indicates islands that received *M. americana* introductions.

the 2 species and represent documented hybrid zones (morphological intergradation—Wright 1953; intermixed microsatellite alleles—Small et al. 2003).

A series of wildlife translocations conducted from 1930 to 1950 by the Alaska Game Commission from the coastal mainland and elsewhere into multiple islands of the Alexander Archipelago (Chichagof, Baranof, and Prince of Wales islands) further complicates our understanding of the distribution of these species (Paul 2009). We deliberately include introduced populations in our analysis to facilitate exploration of the dynamics of natural versus human-mediated colonization, an aspect unaddressed by previous phylogenetic studies in this system. We expand upon previous genetic studies of North American martens (Stone and Cook 2000; Stone et al. 2002; Small et al. 2003) in an effort to refine contact zone geography and reconstruct historical biogeographic patterns relevant to conservation. We add key locations, including new insular (Dall Island, Tuxekan Island) and continental (southern Montana, northern Idaho, California) populations, and an additional mitochondrial gene (control region) to fully characterize variation in these species. By placing our new analyses into the context of past studies (Stone et al. 2002; Small et al. 2003), we evaluate historical demographics relevant to conservation of insular and continental populations. We hypothesize that *M. caurina* exhibits a characteristic signature of long-term persistence and diversification in island populations (Stone et al. 2002). Persistence would be consistent with extensive geographic structure uncovered in an associated endoparasitic nematode across island populations of the northern NPC (Koehler et al. 2009). In contrast, we expect *M. americana* will exhibit minimal geographic structure among populations in the Pacific Northwest as a result of recent expansion into the region (Stone et al. 2002). In this paper, we seek to: 1) describe diversity within and among insular populations of 2 species with distinct biogeographic histories; 2) compare genetic structure of both indigenous and introduced insular populations with mainland populations; 3) identify vulnerable island populations based on genetic variability; and 4) discuss these results within the context of future management considerations for this complex coastal island ecosystem.

Materials and Methods

Sampling.—Marten samples were obtained from furbearer trappers through cooperative efforts with state, federal, or provincial natural resource agencies for disposition in the University Alaska Museum of the North at the University of Alaska in Fairbanks, Alaska and Museum of Southwestern Biology at the University of New Mexico in Albuquerque, New Mexico. Other specimens were obtained from the Museum of Vertebrate Zoology at the University of California in Berkeley, California. Samples represent 268 individuals (Supplementary Data SD1) and 25 populations (Fig. 1; Table 1). Populations were defined based on their locations (e.g., islands). The use of vertebrate specimens conforms to American Society of Mammalogists guidelines (Sikes et al. 2016) and institutional requirements. Sampling effort focused on the western region of North America and most intensively on the northern NPC. Of the 6 "pure" *M. caurina* populations (Stone et al. 2002; Small et al. 2003), 3 are restricted to islands and 3 are on the mainland (Fig. 1). *Martes americana* is represented by 16 "pure" populations, including 8 island populations (2 naturally colonized recently, 3 documented deliberate human introductions within the last 80 years, and 1 probable introduction [Tuxekan], and 2 populations of unclear origin [Dall and Revillagigedo]; Table 1—Stone et al. 2002; Small et al. 2003; Paul 2009). The remaining 8 mainland populations are either coastal (west of the Coast Range) or continental (east of the Coast Range).

Laboratory procedures.—DNA was extracted following methods in Fleming and Cook (2002) and Slauson et al. (2008). PCR amplifications were in 50 µl volumes with the following reagents: 1.5 mM $MgCl_2$, 1× dNTPs, 1.0 µM of each primer, 0.05 µl of AmpliTaq polymerase, and 10× polymerase PCR buffer with approximately 1–100 µg of DNA. Control region PCR was completed with a PTC-0200 (MJ Research, Inc., Waltham, Massachusetts) thermocycler with the following conditions: 1 cycle of 94°C for 45 s, followed by 35 denaturation cycles at 94°C for 10 s, annealing at 45°C for 15 s, and an extension at 72°C for 45 s, followed by a final extension at 72°C for 3 min (Stone et al. 2002). Negative and positive controls were included in all experiments. PCR products were cleaned with a PEG (30%) cleanup procedure. The following primer pair was used to amplify 304 bp of the control region: TDKD (5′-CCT GAA GTA GGA ACC AGA TG—Kocher et al. 1993) and CTRL-L (5′-CAC YWT YAACWC CCA AAG CT—Bidlack and Cook 2001). Both forward and reverse strands were sequenced for each individual using either an ABI 377 or ABI 3100 (Wyoming sequences) automated sequencer. Big Dye 1.0 and 3.1 Terminators (Applied Biosystems, Foster City, California) were used in DNA sequencing. Dall Island sequences (n = 5) were generated using an Illumina MiSeq small genome analyzer.

Sequencher v4.6 (Gene Codes Corporation, Ann Arbor, Michigan) was used to navigate sequences, in both forward and reverse directions. Two programs, MacClade v4.0 (Maddison and Maddison 1992) and ClustalX v1.8 (Thompson et al. 1997), were used to align sequences and identify insertions and deletions (indels). We analyzed control region sequences separately and in a second analysis we concatenated control region sequences with cytochrome *b* sequences from Stone et al. (2002) to accommodate linked mitochondrial (mtDNA) inheritance. Genetic diversity and differentiation metrics generated from mtDNA data were compared to data generated from 12 nuclear microsatellite loci (Small et al. 2003). Microsatellite locus Mvis20 of Small et al. (2003) was not included in the current analysis, as Dawson (2008) found that the locus was X-linked. Sequences (n = 268) were deposited in GenBank (KX807723–KX807981).

Evolutionary relationships.—For 304 bp of the mtDNA control region (n = 268), we used jModelTest v2.1.7 (Guindon and Gascuel 2003; Darriba et al. 2012) to find the best model of evolution to fit the data. Akaike information criteria, Bayesian

Table 1.—Summary statistics from nucleotide sequences of the mtDNA cytochrome *b* (Stone et al. 2002 and this study) and control region (this study) for *Martes americana* and *M. caurina* from northwestern North America, and fragment data from 12 nuclear microsatellites (Small et al. 2003). Bold F_{IS} values denote significant inbreeding (Bonferroni correction applied). BC = British Columbia; SE AK = Southeast Alaska.

Populations	Abbreviation	Cytochrome *b*			Control region			Nuclear microsatellites (12 loci)					
		n	Haplotypes	Haplotype richness	*n*	Haplotypes	Haplotype richness	*n*	Alleles	Allelic richness	H_E	H_O	F_{IS}
Martes americana													
Mainland													
Northern Idaho	NID				19	7	0.37						
Central British Columbia	CBC	6	2	0.33	10	6	0.60	17	5.46	4.13	0.70	0.61	0.12
Yukon Flats, interior AK	YFL	10	3	0.30	9	6	0.67	25	5.69	3.63	0.23	0.55	**0.13**
Thomas Bay, SE AK	TBY	5	3	0.60	10	5	0.50	20	4.23	3.34	0.62	0.50	**0.21**
Northern British Columbia	NBC	5	3	0.60	5	4	0.80	5	4.00	4.00	0.67	0.66	0.02
Juneau, SE AK	JUN	5	2	0.40	12	4	0.33	25	5.08	3.46	0.61	0.61	**0.17**
Cleveland Peninsula, SE AK	CLP	5	3	0.60	10	3	0.30	25	5.31	3.66	0.63	0.56	0.12
Yakutat, SE AK	YAK	5	1	0.20	10	3	0.30	22	4.00	2.91	0.54	0.47	0.13
Island, non-introduced													
Dall Island, SE AK[a]	DAL	6	2	0.33	5	2	0.40						
Mitkof Island, SE AK	MIT	5	2	0.40	10	4	0.40	25	4.69	3.39	0.59	0.48	**0.18**
Kupreanof Island, SE AK	KUP	2	1	0.50	11	3	0.27	25	4.45	3.10	0.56	0.49	**0.13**
Revillagigedo Island, SE AK[a]	REV	5	1	0.20	10	2	0.20	25	3.54	2.74	0.48	0.40	0.26
Island, introduced													
Chichagof Island, SE AK	CHI	15	3	0.20	14	6	0.43	25	4.23	3.24	0.57	0.50	0.11
Prince of Wales Island, SE AK	POW	10	2	0.20	11	3	0.30	25	4.38	3.29	0.62	0.47	**0.24**
Baranof Island, SE AK	BAR	10	1	0.10	11	1	0.09	26	3.54	2.46	0.45	0.36	**0.20**
Tuxekan Island, SE AK	TUX				4	1	0.25						
Hybrid *M. americana*/*caurina*													
Northern Montana	NMT	2	2	1.00	9/1	7	0.70	11	4.54	3.72	0.63	0.55	0.14
Southern Montana	SMT	2	1/1	1.00	9/1	7	0.70	11	5.31	4.20	0.68	0.48	**0.31**
Kuiu Island, SE AK	KUI	23	3/1	0.17	1/9	6	0.50	25	4.85	3.20	0.54	0.45	**0.18**
Martes caurina													
Mainland													
California	CAL				20	5	0.25						
Wyoming	WYO	5	1	0.20	5	3	0.60						
Oregon	ORE	6	1	0.17	15	1	0.07	16	3.31	2.73	0.50	0.53	-0.04
Island													
Vancouver Island, BC	VAN	2	1	0.50	14	3	0.21	23	2.92	2.08	0.31	0.29	0.07
Admiralty Island, SE AK	ADM	21	1	0.05	12	1	0.08	25	1.31	1.23	0.09	0.08	**0.09**
Queen Charlotte Islands, BC	QCI	5	1	0.20	9	1	0.10	11	2.00	1.87	0.30	0.28	0.05
Totals													
Martes americana		96			178			301					
Martes caurina		64			90			112					

[a]Populations of uncertain origin.

information criteria, and decision theory all selected the HKY (Hasegawa, Kishino, and Yano 1985) model of evolution (Yang et al. 1994). We included nucleotide sequence data from portions of mtDNA control region and cytochrome *b* from 1 European pine marten (*M. martes*; GenBank AF336969 and AF154975, respectively) and 1 sable (*M. zibellina*; GenBank AF336970 and JQ343004, respectively) as outgroups for phylogenetic reconstruction. Phylogenetic trees were constructed using MrBayes (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) and RAxML (Stamatakis 2014). In this case, we constructed trees using control region and cytochrome *b* independently and then by concatenating the 2 loci. We ran HKY and GTR (general time reversible) reverse-jump models of evolution as a comparative framework. We completed 6 runs over 5,000,000 generations with a burn-in period of 1,250,000 (25%) at which point the log-likelihood values became stationary. Consensus phylogenies were visualized in FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/). For network construction, we employed the Median-Joining Network (MJN—Bandelt et al. 1999), a method that yields the best genealogies under strict parsimony conditions (Cassens et al. 2003). Networks are often employed for large datasets based on closely related species or for population-level studies (Posada and Crandall 2001) as they show the number of base-pair differences between each haplotype. We used the R{Pegas} package (Paradis 2010) to construct the shortest network separating *M. americana* from *M. caurina* based on control region variation. Arlequin v3.01 (Excoffier et al. 2005) was used to calculate haplotype (h) and nucleotide diversity (π) for each population.

Population structure.—All population-level analyses were carried out using the 304 bp segment of the mitochondrial control region and then compared across the cytochrome *b* and microsatellite data (Stone et al. 2002; Small et al. 2003) for

corresponding specimens (n = 209). We conducted a hierarchical analysis of molecular variance (AMOVA) to examine population structure within and between species using Arlequin. Significance was assessed using nonparametric permutations, followed by recalculation of all statistics to form a null distribution ($\alpha < 0.05$—Excoffier et al. 1992). An AMOVA was conducted independently for both species to determine the relative partitioning of variance among individuals within populations and among island and mainland populations. Introduced populations (Table 1) were excluded from the AMOVAs to ensure that the tests summarized genetic variation within and among groups with no a priori assumptions (Araya-Anchetta et al. 2013). We generated pairwise F_{ST} statistics (Weir and Cockerham 1984) in Arlequin to assess interpopulation differentiation and compared the results to independent values generated from 12 microsatellite loci for a subset of the populations, as reported elsewhere (Small et al. 2003).

Population expansion.—We tested for signals of expansion in each population using DNAsp v5 (Librado and Rozas 2009) for mismatch analysis, Lamarc v2.1.10 (Kuhner 2006) for g-statistics, and Arlequin for Tajima's D and Fu's F_S ($\alpha < 0.05$—Fu 1997). All analyses were run with 10,000 iterations unless otherwise noted. The mismatch distribution test measures population expansion based on pairwise differences between haplotypes (Rogers and Harpending 1992) and assumes that the taxa are related, the differences are mutations, and the mutations occur at a constant rate through time. Fu's F statistics (F_S—Fu 1997) and Tajima's D (Tajima 1989) allow for additional, independent tests of expansion by examining deviations from neutrality. Fu's F_S uses pairwise differences and D compares theta ($\theta = 2N_f\mu$) values based on nucleotide site differences (Excoffier et al. 2005). Significantly negative values of F_S or D indicate an excess of low-frequency mutations over that expected under a standard model of neutrality for populations. Fu's F_S and Tajima's D are used widely in tests for signals of expansion and are more conservative and arguably have greater statistical power than other tests, such as mismatch distributions (Ramos-Onsins and Rozas 2002). Although most demographic analyses are prone to overestimation, especially in closely related populations, they can still provide a relative measure of growth or contraction for species at similar levels of divergence (Grant 2015).

We used g-statistics as an additional test for expansion in each population, excluding all invariable populations (Admiralty Island, Baranof Island, Tuxekan Island, Haida Gwaii, and Oregon). The g-statistic measures exponential population growth using estimates of θ ($2N_f\mu$). The g-statistic measures growth in populations and θ measures effective population size relative to mutation rate, $\theta = 2N_f\mu$, where μ is the mutation rate of the control region and N_f the female effective population size (Domingues et al. 2006) when based on mtDNA. Negative values of g indicate that a population is in decline, while positive values indicate population growth. In this analysis, θ indicates time to coalescence for genealogies of a specific population. When compared to unbiased estimates such as number of pairwise differences or nucleotide diversity, a larger θ reflects a longer time to coalescence across population genealogies given the observed population growth (Delport et al. 2007). The g-statistic has an upward bias (Kuhner et al. 1998), so we used 3 *SD*s as our test of significance (Lessa et al. 2003).

Lastly, we generated control region Extended Bayesian Skyline Plots (EBSPs; Supplementary Data SD2) for each putative species with admixed localities excluded. Analyses were run in Beast v2.4.3 (Bouckaert et al. 2014) with a chain length of 500 million generations, a strict clock, and sampling every 5,000 generations with a burn-in of 25% resulting in 10,000 final trees. General set up followed the online Beast2 EBSP tutorial (Heled and Vaughan: beast2.org/tutorials). Convergence (effective sample size > 300) was evaluated in Tracer v1.6 (Rambaut et al. 2014) and plots were visualized in R.

Results

Control region.—Control region sequences were variable in both *M. americana* and *M. caurina* populations with a total of 49 haplotypes identified with 38 variable sites, 33 substitutions (28 transitions, 6 transversions), and 6 indels. There were 7 sites with fixed differences between *M. americana* and *M. caurina* (Fig. 2). Across 178 *M. americana*, 29 distinct haplotypes (Table 2a) were identified, whereas 92 *M. caurina* had 20 haplotypes (Table 2b). Admiralty, Baranof, Tuxekan, and Haida Gwaii islands, and Oregon were invariable; these populations were excluded from population-level analyses but included in phylogenetic analyses. Sixteen of 29 (55%) *M. americana* haplotypes were unique to single populations,

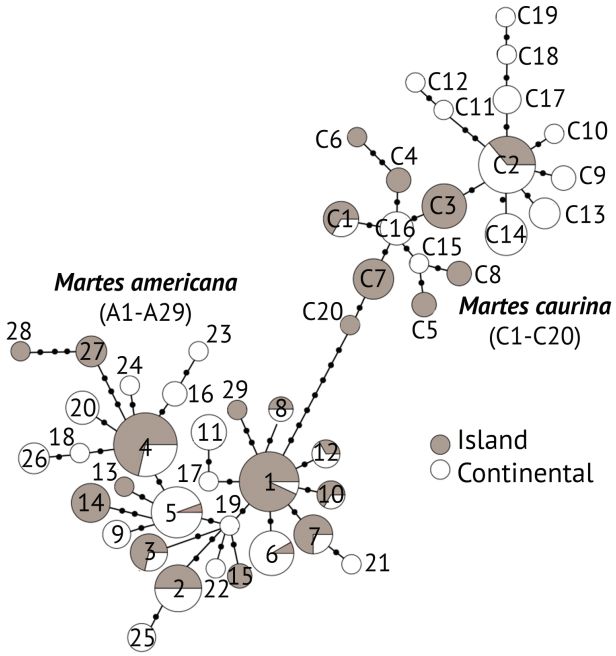

Fig. 2.—Haplotype network for *Martes americana* and *M. caurina* mitochondrial control region sequences. Circle size is proportional to the number of individuals with each haplotype; the number of mutations separating haplotypes is indicated by dots along the links. Pie colors indicate mainland haplotypes (white) and island haplotypes (gray).

Table 2.—Control region haplotypes by locality for populations of a) *M. americana* and b) *M. caurina*. Bold populations are recognized hybrid populations.

a) *M. americana*

Population	Haplotype																											
	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19	A20	A21	A22	A23	A24	A25	A26	A27	A28	A29
BAR	11																												
CHI	4	2	5	1	1	1																							
DAL																											4	1	
KUI	3			3									1																
KUP	5			4			2																						
MIT	1	3		2			4																						
POW		1		8				1																					1
REV														8	2														
TUX				4																									
CBC	1				4											2	1	1	1										
NBC		1		1					2	1																			
NID		3		5			2					2								5	1	1							
NMT		1	2	2		2			1		1																		
SMT											1																		
YFL					2	2		1			2												1	1					
CLP		2		2	6																								
JUN	1				5	3																			3				
TBY	3	1		3						2		1																	
YAK						4					2															4			
Total	29	14	7	35	18	12	8	2	3	3	6	3	1	8	2	2	1	1	1	5	1	1	1	1	3	4	4	1	1

b) *M. caurina*

Population	Haplotype																			
	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19	C20
ADM			12																	
KUI				2	2	1														
QCI							9													
VAN	4	8						2												
NMT																				1
SMT	2	2							2	1	1	1								
ORE		15																		
CAL													4	10	1	5				
WYO																	3	1	1	
Total	6	25	12	2	2	1	9	2	2	1	1	1	4	10	1	5	3	1	1	1

and 17 of 20 (85%) *M. caurina* haplotypes were unique to single populations. Sequences in 6 populations exhibited transversions (1 *M. caurina*: Wyoming; *2 M. americana*: Dall Island and Prince of Wales Island; 3 hybrid populations: northern and southern Montana and Kuiu Island).

We calculated haplotype richness (Table 1) for each population by dividing the number of control region haplotypes within a population by the total number of haplotypes and correcting for sample size. Haplotype richness is an analogue to allelic richness (Kawamoto et al. 2008) and was higher for the control region compared to cytochrome *b* in 7 of the 14 *M. americana* populations that had both sequences. Three island populations of *M. americana* had equivalent richness across both loci, while 4 localities (1 island, 3 mainland) had lower haplotype richness for control region over cytochrome *b*. In contrast, only the Wyoming population of *M. caurina* showed greater haplotype richness for control region compared to cytochrome *b*. The remaining 4 *M. caurina* populations had elevated cytochrome *b* richness. Populations demonstrating the highest haplotype and nucleotide diversity occurred in recognized hybrid populations. Haplotype diversity was highest in southern and northern Montana, and nucleotide diversity was highest in Kuiu Island and northern Montana where haplotypes characteristic of both species were present (Table 3).

Phylogenetic relationships.—For the Bayesian consensus tree (Fig. 3), control region sequences were concatenated with cytochrome *b* sequences only for the 23 individuals with complete cytochrome *b* sequences (1,140 bp) described in Stone et al. (2002). Some localities are not represented because corresponding cytochrome *b* sequences were unavailable. The 50% majority rule consensus tree consistently separated *M. caurina* from *M. americana* populations.

Comparatively, cytochrome *b* analyses identified 9 mutations separating these 2 species. Network analyses also highlight differences in haplotype diversity within each group. Whereas common *M. americana* haplotypes are widely dispersed across both continental and island locations for this species (i.e., Haps A1, A3, A4, A5, A6; Fig. 2), *M. caurina* haplotypes tend to be more limited in geographic distribution (i.e., haplotypes C4–C8; Fig. 2). Approximately 32% of *M. caurina* haplotypes are endemic to a single island, whereas only 10% of *M. americana* haplotypes are endemic to an island.

Population structure.—Overall, AMOVA values across all *M. americana* and all *M. caurina* populations (Table 4) indicate greater percent haplotypic variation within populations compared to among populations; however, there are differences between species when island and mainland populations are compared. Across insular *M. caurina* populations, there is significantly greater genetic variation among populations and relatively little variation within populations ($\alpha = 0.05$ level; Table 4). In contrast, island *M. americana* populations have haplotypic variation more evenly partitioned among and within populations. For mainland populations of *M. caurina*, there is nearly twice as much variation partitioned among individuals within populations as there is among populations and this pattern is amplified in mainland *M. americana* which harbor substantially more haplotypic variation within populations than among populations.

Across all *M. americana* populations except Dall and Revillagigedo islands, pairwise F_{ST} values were rarely higher than 0.2 (Table 5) and lower than all pairwise F_{ST} values among *M. caurina* populations. Pairwise F_{ST} values among *M. americana* populations were within the range of pairwise

Table 3.—Results of demographic tests for 2 species of *Martes* from northwestern North America. *SD*s are provided for nucleotide diversity (π) and haplotype diversity (h). Tests of expansion (Fu's F_S, Tajima's *D*, *g*-statistics) are reported for all variable populations of *M. americana* and *M. caurina.* All *g*-statistics are nonsignificant (within 3 *SD*s of zero) and their associated θ ($2N_f\mu$) values are reported.

Species	Population	π	h	*D*	F_S	*g*	θ
M. americana							
	NID	0.007 ± 0.005	0.854 ± 0.047	0.95	–0.99	161.56	0.0106
	CBC	0.007 ± 0.005	0.844 ± 0.103	0.53	–1.58	675.05	0.0293
	YFL	0.008 ± 0.005	0.911 ± 0.062	1.29	–1.72	383.86	0.0138
	TBY	0.007 ± 0.005	0.844 ± 0.080	1.47	–0.65	253.08	0.0093
	NBC	0.009 ± 0.006	0.833 ± 0.222	1.09	0.01	380.53	0.0105
	JUN	0.008 ± 0.005	0.758 ± 0.081	0.60	1.31	5.26	0.0051
	CLP	0.003 ± 0.003	0.622 ± 0.138	0.83	0.46	236.30	0.0029
	YAK	0.004 ± 0.003	0.711 ± 0.086	1.64	0.6	100.23	0.0026
	DAL	0.004 ± 0.004	0.400 ± 0.237	–1.05	1.69	–37.25	0.0038
	MIT	0.007 ± 0.005	0.778 ± 0.091	1.59	0.59	58.00	0.0049
	REV	0.005 ± 0.004	0.356 ± 0.159	0.02	3.03	–173.92	0.0026
	KUP	0.006 ± 0.004	0.691 ± 0.086	1.31	1.96	–79.15	0.0061
	CHI	0.006 ± 0.004	0.833 ± 0.071	1.03	–1.51	512.17	0.0081
	POW	0.006 ± 0.004	0.491 ± 0.175	–0.89	0.36	43.32	0.0062
Hybrid populations							
	KUI	0.023 ± 0.013	0.879 ± 0.060	1.70	1.98	–0.26	0.0151
	NMT	0.012 ± 0.007	0.933 ± 0.062	–1.04	–1.61	11.49	0.0136
	SMT	0.006 ± 0.004	0.933 ± 0.062	–1.14	–1.53	42.94	0.0201
M. caurina							
	CAL	0.006 ± 0.004	0.679 ± 0.074	0.95	1.55	–21.29	0.0043
	VAN	0.003 ± 0.002	0.615 ± 0.102	0.70	0.38	161.32	0.0024
	WYO	0.003 ± 0.003	0.700 ± 0.218	0.24	–0.48	911.12	0.0092

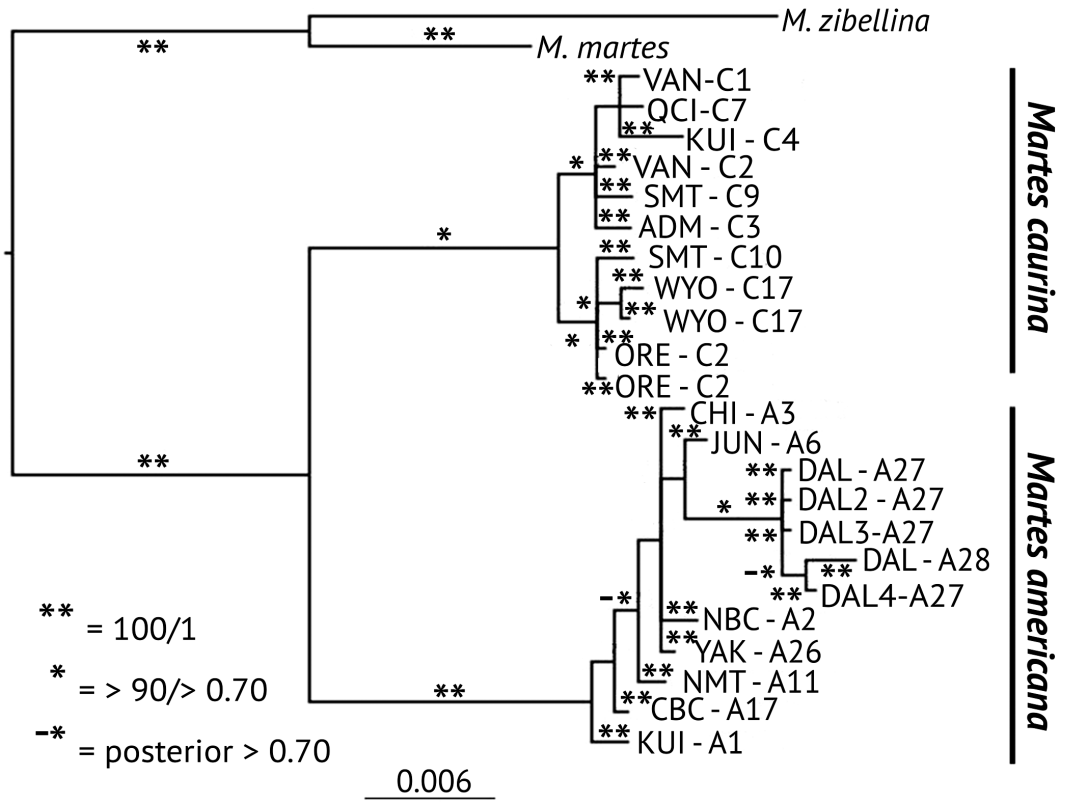

Fig. 3.—Phylogeny of *Martes americana* and *M. caurina* based on maximum likelihood (ML) and Bayesian inference (rooted). Analyses are based on mtDNA from the control region (this study: 304 bp) and cytochrome *b* (Stone et al. 2002) using an HKY + I evolutionary model. ML bootstrap and Bayesian posterior probabilities are displayed at each node (bootstrap support value/posterior probability).

F_{ST} values measured in other mammal species with moderate gene flow between populations (Hellborg et al. 2002). The highest pairwise F_{ST} values between *M. americana* populations are between Dall and Revillagigedo Islands when compared to other populations. These 2 islands were also the only *M. americana* populations that were significantly different from all other *M. americana* populations. Dall Island, in particular, harbors 2 endemic haplotypes (Fig. 2: A27, A28), separated from the nearest *M. americana* haplotype by multiple mutations.

Although average pairwise F_{ST} values for the mtDNA control region for *M. caurina* was more than double that of *M. americana* populations (0.69 and 0.33, respectively), these values were not significantly different (2 tailed students *t*-test $\alpha > 0.01$; Table 5). Microsatellite F_{ST} values (0.54 and 0.13, $\alpha < 0.01$, for *M. caurina* and *M. americana*, respectively) were significantly different and support greater population structure and lower gene flow among populations of *M. caurina* compared to *M. americana.* The highest pairwise F_{ST} value, other than between the invariable populations (Admiralty, Baranof, and Haida Gwaii islands and Oregon), was between Wyoming and other *M. caurina* populations.

Population expansion.—Mismatch distributions (Supplementary Data SD3) show weak support for recent expansion in *M. americana* and *M. caurina* populations. However, mismatch distributions have low statistical power (Ramos-Onsins and Rozas 2002) and are sensitive to recently bottlenecked populations (Roques and Negro 2005). A recent bottleneck is a distinct possibility for several insular populations including Admiralty and Haida Gwaii islands (populations with extremely low variation), and Baranof, Prince of Wales, and Chichagof islands, which received recent introductions of few individuals. The mismatch distributions for Yukon Flats, Yakutat, Idaho, central British Columbia, Prince of Wales Island, and northern and southern Montana show strict, unimodal distributions, corroborating the hypothesis of recent (Holocene) expansion (Rogers and Harpending 1992). We can reject a model of demographic expansion (sum of squared deviation [SSD]; $\alpha < 0.05$) for central British Columbia, Wyoming, Yakutat, Northern Idaho, and Revillagigedo Island populations, suggesting demographic stability for these localities. Significantly bimodal or "ragged" distributions ($\alpha < 0.05$) further support demographic equilibrium of central British Columbia and Yakutat populations.

For each population, we used Fu's *F* statistic (F_S), Tajima's *D* (*D*), the *g* parameter (*g*), and theta (θ; Fluctuate—Kuhner et al. 1998) as tests of demographic expansion for the mtDNA (Table 3). Fu's F_S showed significant signals of expansion averaged over all populations for both *M. caurina* (−7.98; $\alpha < 0.005$) and *M. americana* (−15.55; $\alpha < 0.001$), but no single population was significant. Tajima's *D* was not significant for any population of either species. All populations were nonsignificant for recent demographic expansion (e.g., zero was within the 95% confidence intervals or within 3 *SD*s [values not shown] for *g*-statistics for all populations). EBSPs were

Table 4.—Analysis of molecular variance (AMOVA) results reported for populations of *Martes americana* and *M. caurina* in this study. We compared across each species, as well as each species group of island or mainland populations. Overall F_{ST} values for each group are reported in the last column.

AMOVA	Source of variation	Sum of squares	Variance components	% Haplotype variation	Overall F_{ST}
All *M. americana*	Among	18.10	0.13	27.88	0.12
	Within	81.09	0.95	72.12	
All *M. caurina*	Among	8.24	0.31	33.58	0.34
	Within	21.71	0.60	66.42	
All *M. caurina* islands	Among	28.86	1.20	88.51	0.89
	Within	5.14	0.16	11.49	
All *M. caurina* mainland	Among	8.45	0.32	37.27	0.37
	Within	19.35	0.54	62.73	
All *M. americana* islands	Among	15.33	0.66	42.72	0.43
	Within	24.67	0.88	57.28	
All *M. americana* mainland	Among	18.10	0.13	11.76	0.12
	Within	81.09	0.95	88.24	

Table 5.—Weir and Cockerham's (1984) pairwise F_{ST} values for a) *M. americana* and b) *M. caurina* for 13 and 12 microsatellite loci[a], respectively (above diagonal; microsatellite data from Small et al. 2003) and mtDNA control region (below diagonal; this study). Bold values are significantly different from zero (α = 0.05, Bonferroni correction applied to microsatellite data). n/a = not available.

a) *M. americana*

	BAR	CBC	CHI	CLP	DAL	JUN	KUP	MIT	NBC	NID	POW	REV	TBY	TUX	YAK	YFL
BAR		0.16	0.25	0.21	n/a	0.23	0.22	0.21	0.21	n/a	n/a	0.31	0.15	n/a	0.27	0.21
CBC	**0.54**		0.08	**0.05**	n/a	**0.03**	**0.11**	**0.06**	0.00	n/a	n/a	**0.15**	**0.07**	n/a	**0.11**	**0.03**
CHI	**0.46**	**0.14**		0.09	n/a	0.13	0.13	0.16	0.09	n/a	n/a	0.19	0.12	n/a	0.24	0.08
CLP	**0.81**	0.00	**0.27**		n/a	**0.05**	**0.12**	**0.08**	0.04	n/a	n/a	**0.12**	**0.09**	n/a	**0.17**	**0.07**
DAL	**0.96**	**0.73**	**0.78**	**0.83**		n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
JUN	**0.49**	0.05	0.08	0.11	**0.73**		**0.15**	**0.12**	0.03	n/a	n/a	**0.19**	**0.12**	n/a	**0.14**	0.02
KUP	**0.27**	0.11	0.08	**0.26**	**0.77**	**0.15**		**0.06**	**0.06**	n/a	n/a	**0.24**	**0.14**	n/a	**0.19**	**0.10**
MIT	**0.39**	**0.17**	0.07	**0.31**	**0.77**	**0.16**	–0.04		0.01	n/a	n/a	**0.27**	**0.10**	n/a	**0.21**	**0.07**
NBC	**0.82**	–0.07	**0.22**	0.06	**0.77**	0.10	0.23	0.24		n/a	n/a	**0.21**	0.05	n/a	**0.08**	–0.01
NID	**0.50**	0.08	**0.14**	0.08	**0.71**	**0.16**	0.10	0.09	0.07		n/a	n/a	n/a	n/a	n/a	n/a
POW	**0.70**	**0.14**	**0.21**	**0.14**	**0.74**	**0.22**	**0.24**	**0.24**	0.10	0.03		n/a	n/a	n/a	n/a	n/a
REV	**0.81**	**0.43**	**0.56**	**0.54**	**0.84**	**0.45**	**0.54**	**0.56**	**0.50**	**0.42**	**0.57**		0.20	n/a	0.27	**0.21**
TBY	**0.32**	**0.08**	**0.07**	**0.23**	**0.76**	0.13	–0.06	0.03	0.19	0.10	**0.20**	**0.53**		n/a	0.21	**0.12**
TUX	**1.00**	0.20	**0.39**	**0.30**	**0.87**	**0.30**	0.41	**0.41**	0.27	0.07	–0.06	**0.67**	0.37		n/a	n/a
YAK	**0.74**	**0.26**	**0.24**	**0.48**	**0.85**	**0.25**	**0.35**	**0.30**	0.22	**0.33**	**0.44**	**0.65**	**0.34**	**0.66**		**0.11**
YFL	**0.44**	–0.03	0.01	0.09	**0.75**	0.03	0.01	0.04	–0.02	0.06	**0.13**	**0.48**	–0.01	**0.27**	0.14	

b) *M. caurina*

	CAL	ADM	ORE	QCI	VAN	WYO
CAL		n/a	n/a	n/a	n/a	n/a
ADM	**0.70**		**0.58**	**0.75**	**0.65**	n/a
ORE	**0.27**	**1.00**		**0.39**	**0.35**	n/a
QCI	**0.58**	**1.00**	**1.00**		**0.51**	n/a
VAN	**0.18**	**0.88**	**0.31**	**0.73**		n/a
WYO	**0.46**	**0.94**	**0.83**	**0.90**	**0.61**	

[a]Microsatellite locus Mvis20 originally included in Small et al. (2003) was found to be X-linked (Dawson 2008) and not included in the current analysis for both species. MA15 was monomorphic in *M. caurina* and removed from F_{ST} analyses of *M. caurina*.

uninformative (Supplementary Data SD2), suggesting either an extreme historic bottleneck event in both populations that effectively prevented interpretation of N_f or that additional loci are required.

Discussion

Within the archipelagos of North America's northern NPC, contemporary genetic diversity and patterns of endemism result from complex geologic processes, natural fragmentation of the temperate rainforests, long-term population isolation, and more recently, human-mediated disturbances (Murie 1959; Bailey 1993; Paul 2009; Cook and MacDonald 2013). Thus, parsing signatures of demographic change in martens potentially illustrates the impact of both evolutionary processes and anthropogenic manipulation on island diversity. As a federally designated Management Indicator Species, martens function as a proxy for forest health (Simon 1980; Hargis and McCullough 1984;

Flynn and Schumacher 1997). Because negative responses to insularity are evident in specialized, higher trophic taxa (Holt et al. 1999; Krauss et al. 2003), these mesocarnivores have an increased risk of extirpation. Taxonomy, biogeographic history, introductions, pathogens, hybridization, and the consequences of isolation on islands are all critical factors to consider in management, particularly within the context of accelerating environmental change (Ruesink et al. 1995; Pyšek and Richardson 2010; Malaney and Cook 2013; Robertson et al. 2014).

History highlights diversity.—Understanding Pleistocene refugial distributions and subsequent colonization histories enables rigorous interpretation of contemporary genetic diversity (Waltari et al. 2007). Along the NPC, significant variability between island and continental sister species or lineages reflects the consequences of historical processes on contemporary species assemblages (e.g., Dawson et al. 2014; Sawyer et al. 2017). Following the Last Glacial Maximum (LGM), *M. americana* tracked boreal forest expansion northwestward from a refugium in eastern North America (Graham and Graham 1994). This species arrived recently (late Holocene) along the NPC (Fig. 1) via river corridors through the Coast Range (Stone et al. 2002) and subsequently colonized or was translocated to several islands. In contrast, *M. caurina* was thought to be isolated in 1 or more southern LGM refugia along the west coast, spreading northward along the Pacific Coast (early Holocene—Stone et al. 2002) or eastward to the southern Rocky Mountains (Graham and Graham 1994). Haplotype networks (Fig. 2) and phylogenetic reconstructions (Fig. 3) illustrate the historical divergence within each species and each population's contribution to geographic structure and overall genetic diversity. Unique haplotypes and elevated differentiation (F_{ST}) on Revillagigedo and Dall islands suggest that geographic proximity does not necessarily translate to higher genetic similarity (Fig. 2; Tables 2a and 4). This curious result, also seen in red squirrels (*Tamiasciurus hudsonicus*) on Revillagigedo Island (Hope et al. 2016), requires additional investigation in other forest-associated species. The history of the Dall Island population, which plausibly received migrants from the neighboring introduced population on Prince of Wales Island, also needs more detailed sampling and assessment. Whether the 2 endemic haplotypes, separated from other *M. americana* haplotypes by multiple mutations, reflect earlier colonization event of martens on this remote western island is unclear.

Overall low F_{ST} values within *M. americana* suggests less population structure compared to *M. caurina* populations. The degree of divergence among private mtDNA haplotypes in Southeast Alaskan *M. americana* populations and other *M. americana* haplotypes is less than that between the private insular haplotypes among *M. caurina* populations (e.g., Admiralty, Haida Gwaii, Kuiu islands). Greater divergence among insular *M. caurina* populations reflects longer persistence and isolation in the region and possibly smaller population sizes, despite apparently viable densities for Kuiu and Admiralty islands (R. Flynn, Alaska Department of Fish and Game, pers. comm.). In addition, several mitochondrial and microsatellite alleles are shared widely across *M. americana* populations. One widespread *M. americana* haplotype (A4) is found from northern Montana to Kuiu Island. These sites, largely covered by ice during the LGM, were recently colonized by *M. americana*. *Martes caurina* on average has more private alleles (both control region and microsatellite) per population (2.33 and 0.78, respectively) compared to *M. americana* (1.67 and 0.69, respectively). High within-population diversity (and heterozygosity) and fewer private alleles in *M. americana* suggest higher historic or contemporary connectivity among populations, consistent with recent (late Holocene) expansion across North America. This general pattern is mirrored in other forest-associated organisms that colonized deglaciated areas at the end of the Pleistocene (Lessa et al. 2003; Hope et al. 2012; Chavez et al. 2014; Kerhoulas et al. 2015).

Many of the patterns we document are also found in genetic signatures of some marten parasites. Genetic structure in *Soboliphyme baturini*, a parasitic nematode (Koehler et al. 2009) of northern mustelids, mirrors host patterns, including long-term separation of *M. caurina* nematodes endemic to Admiralty Island and Haida Gwaii, recent westward expansion of *M. americana* into Southeast Alaska with subsequent colonization by the nematode, and also multiple, independent anthropogenic transplants of *M. americana* to Chichagof Island (Koehler et al. 2009; Hoberg et al. 2012).

Introduced populations.—Species introductions can facilitate mixing of previously distinct populations of a single species (Peacock et al. 2009) or may introduce novel parasites or invasive species. The Alexander Archipelago has experienced a series of introductions ranging from amphibians (Pauly et al. 2008) to ungulates (Cook et al. 2006; MacDonald and Cook 2007), yet the consequences are poorly understood. Because martens are a commercially important component of the furbearer industry (MacDonald and Cook 2007; Alaska Department of Fish and Game 2010), the Alaska Game Commission established "new" populations or supplemented existing populations during the 1930–1950s on Baranof, Chichagof, and Prince of Wales islands (Elkins and Nelson 1954; Burris and McKnight 1973; Alaska Department of Fish and Game 2010) from several mainland *M. americana* sources. Molecular signatures largely corresponded with the written records of introductions (Stone et al. 2002; Small et al. 2003), although the possibility of prior occupation by *M. caurina* on islands such as Prince of Wales (Pauli et al. 2015) should be more rigorously explored using genome-level analyses aimed at detecting admixture.

Some introduced *M. americana* populations exhibit relatively high genetic diversity (Prince of Wales, Chichagof islands) while others have lower diversity (Baranof Island) when compared to naturally colonized islands (Table 1). Introductions from multiple source populations, as recorded for martens on Prince of Wales and Chichagof islands, may lessen the impact of founder effects (i.e., loss of variation) that typify many introduced populations (Dlugosch and Parker 2007). Chichagof Island martens are derived from populations from Baranof Island, Revillagigedo Island, the Stikine River area, Wrangell Island, Mitkof Island, and a site near Anchorage, Alaska (Elkins and Nelson 1954; Burris and McKnight 1973). Baranof

and Prince of Wales islands martens were from coastal mainland populations taken near Behm Canal and Thomas Bay. The different levels of variation in these translocated populations may reflect severe founder events, subsequent bottlenecks, or simply differing histories of colonization and introduction (Nei et al. 1975). Other island populations of *M. americana* in Southeast Alaska (MacDonald and Cook 2007) may have originated through colonization from nearby island source populations (e.g., Dall from Prince of Wales). Future investigations could monitor the effects of colonization on the genetic structure of these introduced populations if specimen archives were augmented annually. Because these islands function as independent tests of the impact of translocations, they have the potential to provide key insight into changing conditions.

Additional layers of genetic complexity in North American martens include 2 natural hybrid zones previously hypothesized in Montana and on Kuiu Island (Small et al. 2003). Both hybrid zones are characterized by admixed microsatellite alleles and mtDNA haplotypes characteristic of both species (Table 1, 2), producing higher haplotype or nucleotide diversity in hybrid populations relative to parental populations (Hewitt 2004; Swenson and Howard 2005). Of the 11 control region sequences from Kuiu Island, 2 haplotypes are shared throughout the range of *M. americana* including island and continental populations. Four new haplotypes were identified on Kuiu, among which 1 is *americana*-like (A13) and 3 are *caurina*-like (C4, C5, C6). Elevated and novel haplotypic diversity in this contact zone is consistent with patterns in other hybrid zones (e.g., Bradley et al. 1993). Hybridization can lead to decreased hybrid fitness (Muhlfeld et al. 2009), extinction of parental species (Rhymer and Simberloff 1996), prevention of adaptation (Eroukhmanoff et al. 2013), an increase in invasive success (Blumler 2003; Rieseberg et al. 2007), and outbreeding depression due to the disruption of co-adapted gene complexes (Shields 1987). Hybridization also may enhance the fitness of colonizing lineages via the capture of local adaptation (Racimo et al. 2015) and may promulgate speciation (Rheindt and Edwards 2011).

Conservation implications for insular populations.—Populations on islands, especially small islands, often contain less genetic variation than mainland populations (Bidlack and Cook 2001; Hayaishi and Kawamoto 2006). Decreased variation can lower fitness and evolutionary potential, ultimately leading to extinction in extreme cases (e.g., an extinction vortex—Gilpin and Soulé 1986; Newman and Pilson 1997; Frankham 1998, 2005; Alsos et al. 2012).

Martens provide a case study in conservation biology at multiple temporal and spatial scales (Cook et al. 2006; Dawson et al. 2007). Although they are tightly associated with high-volume old-growth forests (Potvin et al. 1999; Flynn and Schumacher 2016), federal timber harvest standards in the Tongass National Forest were adopted (United States Department of Agriculture, Forest Service, Alaska Region 1997; United States Department of Agriculture, Forest Service 2016) without a clear understanding of the complexity of insular marten populations and without the knowledge of 2 species in the region. This lack of clarity resulted in uneven application of timber harvest rules (Cook et al. 2006; United States Department of Agriculture, Forest Service 2016). For example, Kuiu Island is currently scheduled for significant habitat modification in old-growth reserves originally identified as central for martens' persistence (Stewart 2016). Kuiu Island supported an endemic population of *M. caurina*, but this population is now apparently being introgressed by *M. americana* (Small et al. 2003). Furthermore, the low genetic variability of the other *M. caurina* population potentially portends an increased risk of extinction (Frankham 2005; Whittaker and Fernández-Palacios 2007). Given their federal status related to old-growth forests and our growing understanding of how fundamental principles of island biology (insularity, distribution of genetic diversity, species assemblages—MacArthur and Wilson 1967; Whittaker and Fernandez-Palacios 2007) are impacting martens, we encourage the incorporation of new scientific information into management prescriptions for this vast and dynamic archipelago.

We note that declining populations of the Alexander Archipelago wolf (*Canis lupus ligoni*) did not figure into recent policy decisions (United States Fish and Wildlife Service 2016), despite documented genetic discreteness of populations at island and regional scales (Weckworth et al. 2005, 2015; Muñoz-Fuentes et al. 2009, 2010; Stronen et al. 2014; Cronin et al. 2015; Fredrickson et al. 2015). The Alexander Archipelago continues to be identified as a center of endemism in the northern latitudes due to its distinct biological diversity (Smith 2016). Unfortunately, the maintenance of endemism is only tangentially incorporated into contemporary forest conservation practices.

Wildlife management in the region may benefit from an island-by-island approach (MacDonald and Cook 2007). Understanding the historical framework that contributed to the evolutionary distinction of insular populations, in particular, is critical to the maintenance of contemporary biodiversity. Only within the last several decades have modern molecular tools demonstrated the hidden diversity of this coastal biome, long suspected by early 20th century naturalists (e.g. Swarth 1911, 1936). Still, significant human-induced change has already impacted islands (Cook and MacDonald 2013). For *M. caurina*, control region haplotypes on 3 NPC islands represent over one-third of documented mtDNA diversity (Table 1). Other old-growth obligates sharing similar patterns of endemism and evolutionary histories (flying squirrels, *Glaucomys sabrinus*—Bidlack and Cook 2002; ermines, *Mustela erminea*— Fleming and Cook 2002; Alexander Archipelago wolves—Weckworth et al. 2015) may be impacted by decreased volume of old-growth forests. In a period of accelerating change, understanding the evolutionary history of the Alexander Archipelago's biota could provide resource managers with key perspectives to build effective management prescriptions (Smith 2016). This pair of species, in particular, represents the results of 1 of several intriguing evolutionary experiments that played out along the NPC producing unique variability and complex interactions. This natural experiment, however, has been impacted by a series of anthropogenic manipulations that deserve further scrutiny and debate.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Appendix of all samples used, listed by museum identification number (UAM numbers, unless otherwise noted), with haplotype assignment and frequencies (N). "A" haplotypes indicate those belonging to *M. americana* and "C" haplotypes, to *M. caurina*.

Supplementary Data SD2. Extended Bayesian Skyline Plots and associated histograms for *M. americana* and *M. caurina* control region samples, with hybrid localities removed. Plots show a relatively constant N_f through time for both species, however histogram results indicate there is not enough information in a single mitochondrial locus to accurately infer N_f through time and these distributions likely reflect the priors.

Supplementary Data SD3. Mismatch distribution α values ($\alpha < 0.05$*, $\alpha < 0.01$**, $\alpha < 0.001$***) for mitochondrial control region sequences from each sampled locality.

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