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RESEARCH ARTICLE

Ice age land bridges to continental islands: Repeated migration of the forest-dwelling sable in northeastern Asia

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Abstract

Aim: The continental island system comprising Sakhalin, Hokkaido and the southern Kuril Islands (SHSK) in northeastern Asia serves as one of the southernmost habitats for many boreal and arctic organisms, with colonization via land bridges formed during glacial periods. To understand the impacts of past land-bridge formation under Quaternary climate changes across SHSK, we investigated the demographic history of forest-dwelling marten species.

Location: Sakhalin, Hokkaido and the southern Kuril Islands in northeastern Asia.

Taxon: Sable, *Martes zibellina* (Carnivora, Mustelidae).

Methods: We employed multiplexed inter-simple sequence repeat genotyping by sequencing (MIG-seq) to obtain genome-wide single nucleotide polymorphisms (SNPs). We tested possible scenarios of colonization and diversification for SHSK sables using several population genetics approaches including clustering analysis, population tree estimation and approximate Bayesian computation modelling. We also examined haplotype diversity for the mitochondrial *ND2* gene.

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Results: The genetic diversity of the island populations and their affinity for continental populations were found to be higher in the order Sakhalin > Hokkaido > Iturup in both nuclear SNP and mitochondrial DNA analyses. Demographic analyses indicated that the sable migrated repeatedly from the continent, particularly to the neighbouring Sakhalin Island. However, only an earlier colonized lineage has persisted on marginal Iturup Island since the Middle Pleistocene. The stronger effects of repeated migrations and/or isolation influenced by the distance to the continent have shaped the contemporary genetic diversity and differentiation of sable populations in SHSK.

Main Conclusions: Genome-wide and comprehensive sampling approaches demonstrated that the forest-dwelling sable had long-term persistence with partial admixture of multiple lineages in SHSK, suggesting the existence of forest corridors and refugia on the islands during the last several glacial periods. The SHSK system of continental islands is valuable for understanding the impacts of Quaternary climate changes on the genetic diversity and evolutionary histories of boreal organisms.

KEYWORDS

continental islands, demographic modelling, forest-dwelling mammal, land bridge, MIG-seq, northeastern Asia, phylogeography, Quaternary climate change

1 | INTRODUCTION

Islands are excellent natural laboratories for the study of biogeography and evolution of organisms. In recent island biology, it is a key challenge to understand the role of past climate changes in divergence and extinction of organisms (Patiño et al., 2017). Quaternary sea-level oscillations altered island sizes, distances and connectivity between neighbouring islands and the mainland, influencing current insular biodiversity and endemism (Fernández-Palacios et al., 2016; Lourenço et al., 2018; Papadopoulou & Knowles, 2017; Rijsdijk et al., 2014; Simaiakis et al., 2017; Weigelt et al., 2016). Unlike oceanic islands, continental islands that were repeatedly connected to the adjacent continental landmass, by sea level drop, during glacial periods received migration waves from the continent through land bridges (Jiang et al., 2019; Patiño et al., 2017; Shao et al., 2019). Massive and recurrent gene flows from the continent are likely to impede genetic differentiation of populations on continental islands, causing low endemism, whereas infrequent gene flows facilitate genetic divergence and speciation (Cao et al., 2018; Faria et al., 2016; Warren et al., 2015). Clarifying the timing and scale of migration events from a mainland to islands is, therefore, important for understanding how past distribution dynamics under climate changes affected the genetic diversity and evolution of organisms.

The Japanese Archipelago, Sakhalin and the southern Kuril Islands constitute a large continental island system (latitude N30–N54) surrounded by the Pacific Ocean, the Sea of Japan and the Sea of Okhotsk (Figure 1). The depth of the straits around the island chain varies and is likely to have contributed to the complex biodiversity on these islands (McKay, 2012; Qiu et al., 2011; Sato, 2017). This continental island system can be divided into two major parts: Honshu, Shikoku and Kyushu (HSK) in the south, and Sakhalin, Hokkaido and the southern Kuril Islands (SHSK) in the north. The depth of the Tsugaru Strait and the Korea (Tsushima) Strait (Figure 1) is so considerable that these straits functioned as channels even during the last glacial maximum (LGM), providing stronger isolation effects that facilitated the HSK to retain a rich assemblage of endemic species (Sato, 2017). In contrast, the northern straits separating the SHSK islands and continent are much shallower, which facilitated the development of the paleo-SHSK Peninsula during glacial periods in the Pleistocene. The SHSK islands are mainly inhabited by boreal species, common to the continent throughout the paleo-peninsula (I–III in Figure 1) and provide the southernmost distribution areas for these species. Thus, terrestrial organisms on the SHSK islands may have experienced repeated migrations and isolation during the last several glacial–interglacial periods; this context offers a good opportunity for investigation of processes of genetic divergence and admixture. In fact, previous phylogenetic studies mainly based on mitochondrial DNA (mtDNA) suggest variable colonization timing among terrestrial mammals in the SHSK (McKay, 2012; Sato, 2017) and repeated migrations by multiple lineages in some species (brown bears, Korsten et al., 2009; mountain hares, Kinoshita et al., 2012; sables, Kinoshita et al., 2015; red foxes, Kutschera et al., 2013).

The sable, *Martes zibellina* (Carnivora, Mustelidae) is a suitable model species for assessing colonization processes through straits that were exposed during glacial periods and diversification under climate changes across SHSK. This marten is ecologically associated with boreal forests and is distributed across the northern Eurasia from around the Ural Mountains to the Kamchatka Peninsula, as well as in SHSK (Monakhov, 2011). Several phylogeographic studies using mtDNA markers suggested that continental populations experienced retreat to multiple refugia during glacial periods, with post-glacial expansion and admixture among intra-specific lineages associated

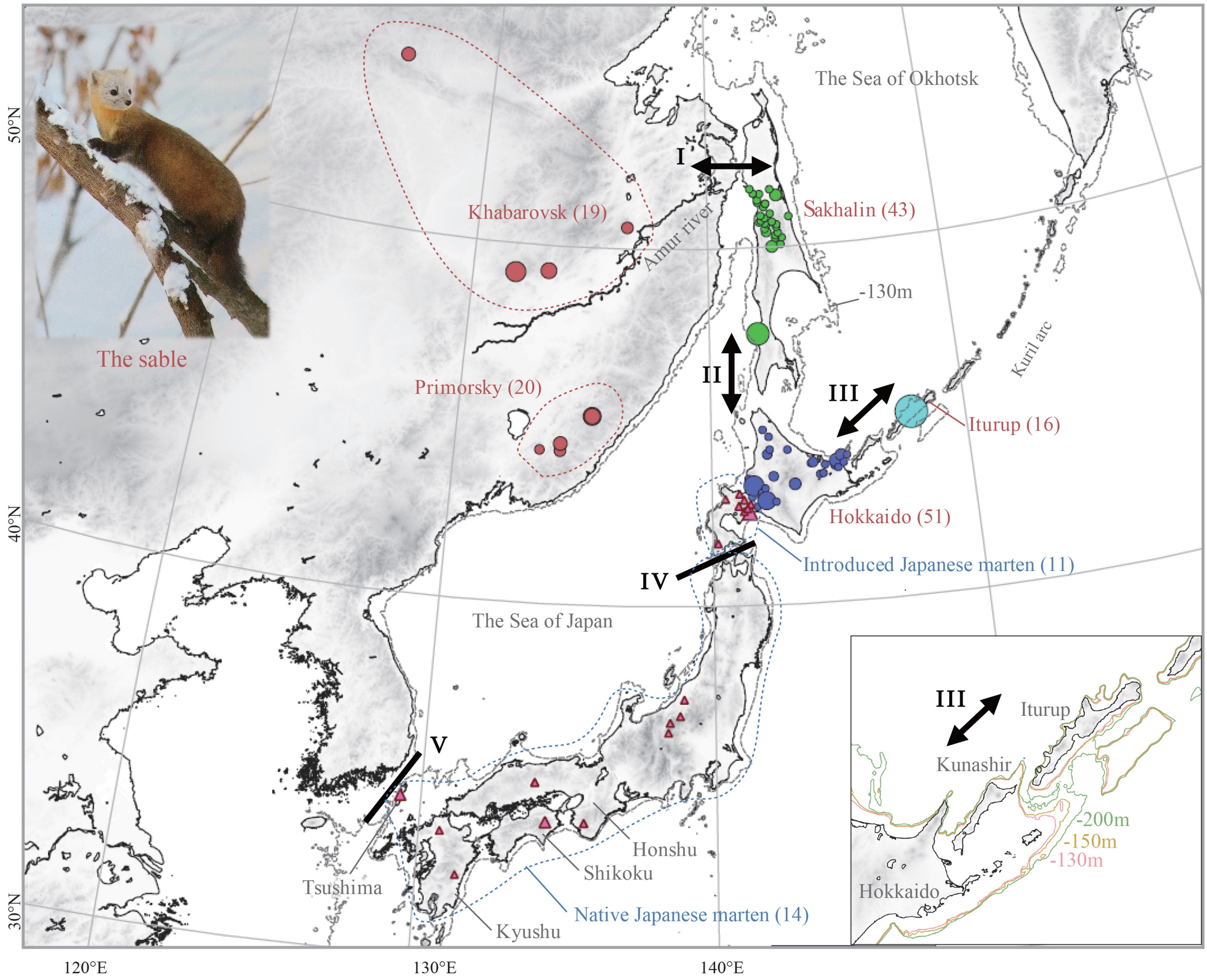

FIGURE 1 Geographic locations and population grouping of the sable (circles) and Japanese marten (triangles) used in the MIG-seq analyses. Sample localities are coloured according to the highest proportion of cluster assignment in the admixture analysis with $K=5$ in Figure 2b. The numbers in parentheses after the population names indicate the number of individuals examined after filtering for the full data set. Further details are provided in Table S1. Grey dotted lines show a sea depth of −130 m, the maximum sea-level drop in the last glacial maximum. Arrows I–III indicate possible migration routes for the sable between the continent and SHSK islands. The SHSK islands formed a paleo-peninsula during glacial periods due to shallow straits (arrows I–III). Bar IV indicates the Tsugaru Strait separating Hokkaido and Honshu, while bar V indicates the Korea (Tsushima) Strait separating the continent and Honshu, both of which are deeper than −130 m. Insets: A photo of a sable taken in Hokkaido by Masahiro Iijima, and a map showing the area around the Southern Kuril Islands with sea depth indications of −130, −150 and −200 m.

with vegetation shifts due to climate changes (Kinoshita et al., 2015; Li et al., 2021; Malyarchuk et al., 2014; Stojak & Jędrzejewska, 2022). The sable shows considerable variation in morphological characters across its distribution range (Monakhov, 2015), and the SHSK populations have unique pelage colours and skull traits as compared to continental populations (Monakhov, 2016). These intra-specific variations could be linked to phylogeographic history and local adaptation (Monakhov, 2015). In our previous study, two distinctive mtDNA lineages were identified from Sakhalin, only one of which expanded to Hokkaido and the southern Kuril Islands (Kinoshita et al., 2015). It was proposed that this phylogeographic pattern could be explained by repeated migrations from the continent (Kinoshita et al., 2015). In more detail of the hypothesis, only the earlier migration wave expanded across the paleo-SHSK Peninsula, while subsequent migration waves with different mitochondrial lineages may have colonized Sakhalin and mixed with the earlier lineage.

An alternative hypothesis is also possible to explain the multiple lineages in Sakhalin and the fewer lineages in Hokkaido and the Southern Kuril Islands. The reduction of genetic diversity from Sakhalin to Hokkaido and particularly in the southern Kuril Islands may have resulted from a founder effect that occurred through long-distance expansion and genetic drift in each island. In this stepping-stone migration scenario, it could be predicted that Sakhalin directly accepted colonizer from the continent with a large population size and high level of genetic diversity (several lineages as ancestral polymorphism). Then, as the colonizers proceeded to migrate to Hokkaido and the Southern Kuril Islands, genetic drift would have occurred at the migration front, resulting in a decline in genetic diversity. The above two possible hypotheses (repeated migrations or stepping-stone migration), however, have not been fully tested either for sables or other terrestrial animals possessing multiple distinctive lineages across the SHSK. Demographic inferences based on the previous mtDNA analyses of limited sable samples should be tested by genome-wide variation with more samples and compared with possible alternative scenarios.

In this study, we aimed to analyse genome-wide single nucleotide polymorphisms (SNPs) and mtDNA with an unprecedentedly large sample set covering SHSK sable populations. We adopted several population genetics approaches to test possible scenarios (hypotheses) of colonization and diversification of the SHSK sable under Quaternary climate changes. We also discussed the influence of Quaternary climate changes in the boreal forest community on the SHSK islands system.

2 | MATERIALS AND METHODS

2.1 | Samples in this study

In total, 162 sable samples from Hokkaido, Sakhalin, the southern Kuril Islands and the continental Russian Far East were subjected to sequencing for SNP analyses. In addition, 25 samples of Japanese marten (*M. melampus*) from native HSK populations and the introduced Hokkaido population were included in the analyses as an outgroup. Some samples were filtered out during data processing for SNP analyses as described below (Table 1; S1). Samples considered were either from our previous mtDNA study (Kinoshita et al., 2015; Sato et al., 2011) or newly obtained from muscle tissues of road-killed animals or local hunters. No animals were killed for the purpose of this study. The mtDNA sequences from this study and Kinoshita et al. (2015) were also analysed as described below (Table 1; S1). Total genomic DNA was extracted from tissues preserved in ethanol using the conventional phenol-chloroform method (Sambrook & Russell, 2001) or a DNeasy Blood and Tissue Kit (QIAGEN, Hilden, Germany).

2.2 | MIG-seq library preparation and SNP discovery

To obtain genome-wide polymorphisms from extracted genomic DNA, we employed the multiplexed ISSR (inter-simple sequence repeat) genotyping by sequencing (MIG-seq) method (Suyama & Matsuki, 2015), in which loci between two SSRs were targeted for amplification using the polymerase chain reaction (PCR). All the processes for generating an MIG-seq library followed the protocol described in Suyama et al. (2022). In the first round of PCR, a primer set with repeated motifs and anchor sequences: $(ACT)_4TG$, $(CTA)_4TG$, $(TTG)_4AC$, $(GTT)_4CC$, $(GTT)_4TC$, $(GTG)_4AC$, $(GT)_6TC$ and $(TG)_6AC$ were selected. The library generated after the second round of PCR, which included each index for sample identification and Illumina adapter sequences, was sequenced on the MiSeq platform (Illumina, San Diego, CA, USA), using a MiSeq Reagent Kit v.3 (150 cycles) (Illumina).

To trim Illumina adapter sequences and low-quality reads, we used Trimmomatic (Bolger, Lohse, & Usadel, 2014). Trimmed reads were processed using the following parameters, keeping paired-end reads: SLIDINGWINDOW:4:15, CROP:79, HEADCROP:2 and MINLEN:75. Six samples with less than 10,000 reads were removed from subsequent analyses. Processed reads for each sample were mapped to the sable reference genome ASM1258336v1 assembled by Liu et al. (2020) using the Burrows-Wheeler Aligner (BWA) program v.0.7.12 (Li & Durbin, 2009) and the BWA-MEM algorithm with default parameters. The SAM files obtained by read mapping were converted into BAM files using SAMtools (Li et al., 2009). All 180 samples were subjected to mapping analysis with quality ≥30,

TABLE 1 Summary of diversity indexes of the sable populations.

		Genetic diversity based on called genotypes by MIG-seq				Genetic diversity based on the *ND2* sequences		
Species	Population	n^1	n^2	π	PHG^3	n^4	π	h
The sable	Khabarovsk (Kha)	20	19	0.1608 (SE 0.0056)	0.146 (SE 0.011)	82	0.0050 (SE 0.0027)	0.8958 (SE 0.0156)
	Primorsky (Pri)	20	20	0.1526 (SE 0.0055)	0.170 (SE 0.031)	80	0.0053 (SE 0.0029)	0.8449 (SE 0.0250)
	Kha + Pri	40	39	0.1600 (SE 0.0053)	0.159 (SE 0.027)			
	Sakhalin	45	43	0.1651 (SE 0.0054)	0.158 (SE 0.022)	89	0.0050 (SE 0.0027)	0.7978 (SE 0.0258)
	Hokkaido	56	53	0.1447 (SE 0.0055)	0.136 (SE 0.013)	62	0.0007 (SE 0.0006)	0.5621 (SE 0.0615)
	Iturup	21	16	0.0846 (SE 0.0052)	0.084 (SE 0.015)	21	No variation	
The Japanese marten (outgroup)	Native	14	14					
	Introduced	11	11					

Abbreviations: *h*, haplotype diversity; 1, total sample number subjected for MIG-seq; 2, sample number of the full data set after filtering; 3, average proportion of heterozygous genotypes (number heterozygous genotypes/number of sites in an individual); 4, sample number used in the *ND2* locus analyses including database sequences previously analysed in Kinoshita et al. (2015); π, nucleotide diversity; *h*, haplotype diversit.

yielding 24,541–219,912 reads (mean mapping rate: 0.95, SD: 0.08). The BAM files were used as input to Analysis of Next Generation Sequencing Data SOFTWARE (ANGSD v.0.929; Korneliussen et al., 2014) to filter sites and estimate genotype likelihoods, which were calculated in an empirical Bayesian framework. To identify samples with a high proportion of missing data, we performed a preliminary run of the ANGSD analysis using the following filters: minimum base quality 20 and mapping quality 30, polymorphism p value threshold 10^{-6}, minimum minor allele frequency (MAF) 0.05 and at least 80% individuals passing the filters. In this preliminary run, four samples were found to have >50% missing loci; ANGSD analyses were performed again after removing those samples. We explored two data sets: The first data set comprised both sable and Japanese marten individuals (full dataset), and the second comprised only sable individuals (sable-only data set). Both data sets were analysed in ANGSD with filters as used for the preliminary run, except that MAF was set to be 0.01 to exclude singletons thought to represent sequencing errors. We obtained 7135 SNPs in the full data set and 5844 SNPs in the sable-only data set. We selected unlinked loci using ngsLG (Fox et al., 2019) with parameters *max_kb_dist* 5, *field_weight* 7 and *min_weight* 0.5, using 2747 SNPs from the full data set and 2030 SNPs from the sable-only data set for analyses based on genotype likelihoods. We performed SNP calling of the full and sable-only data sets for downstream analyses that cannot be performed using genotype likelihood data. Specifically, we converted genotype likelihoods to PLINK format files (Chang et al., 2015; Purcell et al., 2007) in ANGSD by setting a genotype posterior probability of 0.90 as a cut-off to select high-confidence variants.

2.3 | Individual-based analyses of SNP data

To explore genetic variation of sables in our sampling localities, we conducted three individual-based analyses using genotype likelihoods from the full and sable-only data sets. Initially, we obtained a covariance matrix and performed individual-level principal component analysis (PCA) using PCAngsd v.0.982 (Meisner & Albrechtsen, 2018) with default parameters. To estimate shared ancestry, individual admixture proportions using NgsAdmix were estimated (Skotte et al., 2013). We performed 10 independent runs for each K from 1 to 8 using default parameter settings. The most likely K was estimated using the ΔK statistics method described in Evanno et al. (2005) and mean posterior probability by CLUMPAK (Kopelman et al., 2015). We calculated pairwise genetic distances between individuals based on genotype likelihoods under a p-distance model using ngsDist (Vieira et al., 2016) with the option–*avg_nuc_dist* and constructed a NeighborNet tree using SplitsTree v.4.14.5 (Huson & Bryant, 2006).

2.4 | Population-based analyses of SNP data

We estimated population-level genetic diversity and evolutionary history using the called genotypes for the full and sable-only data sets, with different filtering strategies for each downstream analysis. Initially, nucleotide diversity (π) for each population and proportion of heterozygous genotypes for each individual (number of heterozygous genotypes/total number of genotypes for that individual) were computed based on the full data set using STACKS populations v.1.44 (Catchen et al., 2013) and Tassel v.5.2.79 (Bradbury et al., 2007); then, average proportion of heterozygous genotypes (PHG) was calculated for each population. Here, we filtered out SNPs shared by less than five individuals in each population and SNPs with proportions of missing data of >20% and heterozygosity of 50% among individuals using TASSEL, yielding 1084 SNPs across 176 individuals in the full data set.

Using the same filtered data set, we investigated migration events in a phylogenetic context using TreeMix v.1.12 (Pickrell & Pritchard, 2012). TreeMix estimates a maximum likelihood (ML) tree of populations, and the direction and weight of gene flow based on allele frequencies. We ran TreeMix for different numbers of migration events from *m0* (no migration events) to *m5* (five migration events) and assessed the best value of *m* using the R package BITE (Milanesi et al., 2017). The robustness of nodes in the inferred tree was estimated through 100 bootstrap replicates using TreeMix.bootstrap.sh and plotted using BITE. In all TreeMix analysis runs, Japanese martens were used as an outgroup.

To investigate evolutionary relationships among populations in a coalescent framework, we estimated a species tree using SNAPP (Bryant et al., 2012) within BEAST v.2.4.7 (Bouckaert et al., 2014). As this method is computationally intensive and requires a lower level of missing data, we subsampled the full data set to include three individuals from each population with the lowest proportion of missing sites. All missing and high heterozygosity (>50%) sites in the selected individuals were filtered from called genotypes using TASSEL. In the final analysis, 432 SNPs from 21 individuals in the sable and Japanese marten populations were subjected to species tree construction and estimation of divergence time. We used the *snapp_prep.rb* script to generate an input file for SNAPP. Based on the speciation time for sable and Japanese marten estimated from mtDNA sequences (Kinoshita et al., 2015), we calibrated the tree height to be 1.08 million years ago (Mya) with a standard deviation of 0.15 under a log normal distribution model. The MCMC analysis was run for 5×10^7 generations, with trees sampled every 5000 generations. We confirmed convergence to the stationary posterior distribution and sufficient ESS (effective sample size) for each parameter in the log file (>200) using the program Tracer v.1.6 (Rambaut et al., 2018). The population trees were visualized using DensiTree v.2.4.7 (part of the BEAST package). To check estimated divergence time for each node, a maximum clade credibility tree with median node heights was obtained using TreeAnnotator v.2.4.7 (part of the BEAST package) and visualized using FigTree v.1.4.2 (https://tree.bio.ed.ac.uk/software/figtree/).

To assess possible scenarios of genetic divergence for the SHSK sable, we performed Approximate Bayesian Computation (ABC) with machine learning Random Forest approach (Breiman, 2001) using DIYABC-RF v.1.2.1 (Collin et al., 2021) The program was able to consider splitting and admixing events among populations with estimates of times and population sizes. For this analysis, we prepared two SNP data sets. One was 'four-pops data' (continent, Sakhalin, Hokkaido and Iturup) and comprised called genotypes of the sable-only data set with individuals from Primorsky and Khabarovsk merged into a single population as preceding analyses showed non-significant genetic differentiation between these. The second was 'three-pops data' (continent, Hokkaido and Iturup), in which the Sakhalin population was excluded from the four-pops data, to test whether multiple migration waves might have reached Hokkaido from the continent. Both SNP data sets were filtered using TASSEL, which was shared by more than 80% of individuals in each population, resulting in 472 SNPs in the four-pops data and 501 SNPs in the three-pops data. Considering the geographic structure of SHSK as a single-island chain (as shown with arrows I–III in Figure 1), we performed a two-step model choice analysis for the four-pops data. In the step 1, we tested 12 scenarios for four-pops data; a single colonization event from the continent to SHSK assuming stepping-stone migration (Scenario 1), and multiple migrations without admixture (Scenarios 2–4) or with admixture among lineages derived from different waves of migration (Scenarios 5–12) (Figure S2). To improve the robustness of the step 1 analysis, we performed model choice again only for top three supported scenarios and additional Scenario 1′, wherein a greater number of events related to population size change were considered for insular populations (Figure S2). For the three-pops data, we tested three simplified scenarios by assuming two or one migration events to Hokkaido and Iturup without admixture (Scenarios 13 and 14) or with a single admixture event for the Hokkaido population (Scenarios 15) (Figure S3). For the four- and three-pops data, we adopted prior setting of parameters for effective population sizes and numbers of generations as listed in Tables S2 and S3. All prior values were drawn from uniform distributions and an additional condition was applied to specify $t1 < t2 < t3$. We assumed changes in the effective population size of the ancestral population before the split at $t3$ (i.e. Na) and the first colonizer on the islands between $t2$ and $t3$ (i.e. Nb) in some scenarios to improve the efficiency of ABC simulation. We ran 100,000 simulations per scenario for the four- and three-pops data. Using all summary statistics as well as the optional axes of a linear discriminant analysis (LDA), a random forest estimation was conducted to determine the best-fit model and to estimate parameters under the chosen model. The number of trees in the random forest was set to 1000. For all our DIYABC-RF analyses, we confirmed that our observed data were located within the clouds of simulated data sets on the LDA projection and verified sufficiency of 1000 trees by the plotting of error metrics as a function of the number of trees in the forest (Figure S4). The best-fit model was chosen based on the number of classification votes and then the posterior probability for that scenario as well as global and local error rates were estimated to assess the choice of scenario and the quality of prediction.

2.5 | mtDNA sequence analysis

We sequenced 976 bp of the mitochondrial NADH dehydrogenase subunit 2 (*ND2*) gene for 140 newly obtained sable samples from SHSK (Table S1) using the previously described method (Kinoshita et al., 2015). The sequences were aligned with *ND2* sequences from the 279 sable samples analysed in our previous study (Kinoshita et al., 2015). To infer relationships of the observed haplotypes from the *ND2* sequence data set, a median-joining network was reconstructed using the program Popart v.1.7 (Leigh & Bryant, 2015). For genetic diversity indices among populations, we calculated nucleotide diversity (π) and haplotype diversity (h) using Arlequin v.3.5.2.2 (Excoffier & Lischer, 2010).

3 | RESULTS

3.1 | Nuclear SNP detection and population structure

In the present study, using the MIG-seq method, we obtained nuclear SNPs as genotype likelihoods for a full data set comprising sable and Japanese marten as well as a sable-only data set. After filtering, we retained unlinked 2747 SNPs from 176 individuals (151 sables and 25 Japanese martens, Table 1) of the full data set and 2030 SNPs from 151 individuals of the sable-only data set.

To explore the potential population structure, we performed three individual-based analyses using genotype likelihoods for the full and sable-only data sets. PCA using the full dataset showed that the two marten species were clearly separated in PC1 (Figure 2a). The sable populations from the continent and SHSK were dispersed along the PC2 axis, showing three clusters (continent-Sakhalin, Hokkaido and Iturup). Individuals from Primorsky, Khabarovsk and Sakhalin were positioned close to each other. This pattern was observed consistently in the sable-only data set (Figure S1). It should be noted that no genetically intermediate individuals between sable and Japanese marten were observed in Hokkaido (Figure 2a), where the two species are parapatrically distributed (Hirakawa et al., 2015), indicating no or negligible impacts of interspecific hybridization or introgression in our samples.

Similar divergence patterns were uncovered in admixture analyses using NgsAdmix. At $K=2$ for the full data set, two species were clearly separated (Figure 2b). Among the sable populations, as K value increased, a clear separation between continent+Sakhalin and Hokkaido+Iturup was initially observed, followed by separation between Hokkaido and Iturup, and then between the continent and Sakhalin. At $K=5$ for the full data set (Figure 2b) and $K=4$ for the sable data set (Figure S1), each individual was assigned to the continent/Sakhalin/Hokkaido/Iturup. In analyses using higher K values, subclusters within the Hokkaido population were inferred ($K=6$ and 7 in Figure 2b), while the two continental populations of Primorsky

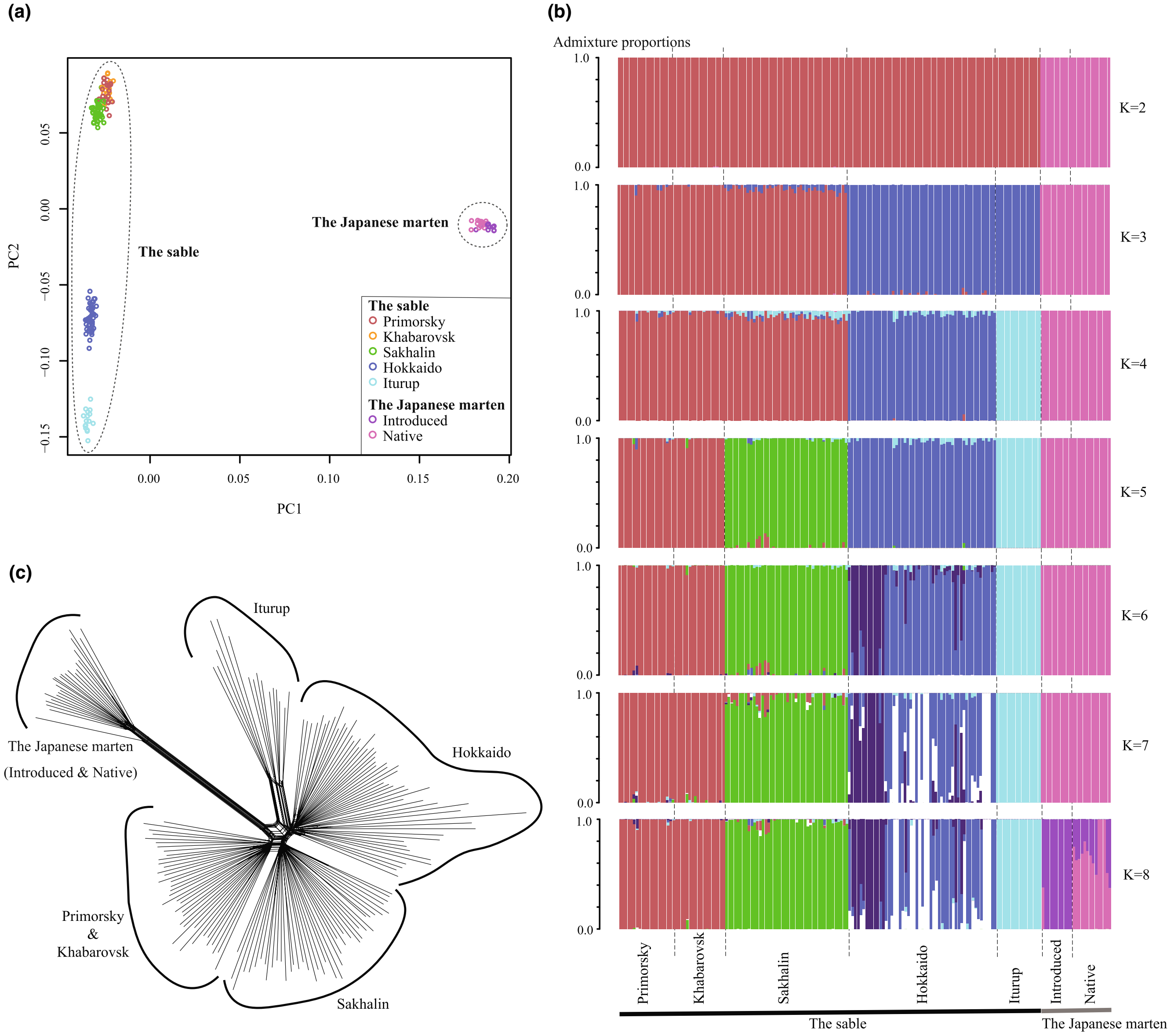

FIGURE 2 Genetic structure based on genotype likelihood data from MIG-seq for the full data set comprised of the sable and Japanese marten (a) PCA analysis using PCAngsd. The clustering with dotted lines corresponds to the two species. (b) Admixture panels produced by NgsAdmix for *K* values from 2 to 8. Each vertical bar indicates an individual, and the y-axis represents the admixture proportion for potential ancestral populations. (c) Phylogenetic relationships of the sable and Japanese marten inferred using NeighborNet analysis implemented in SplitsTree.

and Khabarovsk showed different genetic proportion tendencies only at $K=8$ for the sable-only data set (Figure S1). The best *K* values based on ΔK were estimated to be $K=3$ and $K=2$ for the full and sable-only data sets, respectively, although the highest mean posterior probability was obtained at $K=8$ (Figure S5).

NeighborNet analysis based on the genetic distance matrix showed a result mostly consistent with the PCA and admixture analyses (Figure 2c). The two species were clearly separated, and sable individuals constituted the four major clusters corresponding to each locality (the continent, Sakhalin, Hokkaido and Iturup). The continent, Sakhalin and Hokkaido clusters had shorter branches from the ancestral node, while the Iturup cluster had longer branches.

3.2 | Genetic diversity and population history

For the population-based analyses, genotype likelihoods were converted to called genotypes. Genetic diversity indices were summarized in Table 1. Estimated genetic diversity was similar among the continental populations (π=0.153–0.161, PHG=0.146–0.170) and the Sakhalin population (π=0.165, PHG=0.158). They were slightly lower in the Hokkaido population (π=0.144, PHG=0.136), but they were nearly halved in the Iturup population (π=0.085, PHG=0.084).

To estimate the phylogeny of the sable populations using a Bayesian coalescent-based approach, we constructed a population tree using SNAPP (Figure 3a). The Iturup population diverged first from the other sable populations, with Hokkaido and Sakhalin branching off in that order. The two continental populations showed shallow divergence indicating almost no differentiation. Although the topology should be interpreted carefully because of an inability to assume gene flow among diverged populations in SNAPP models, the most recent common ancestor between the Iturup and other populations was estimated at 0.178 Mya (95% highest posterior density [HPD] 0.115–0.250 Mya with a posterior probability of 1.00), indicating that the Iturup population has been genetically isolated since the late Middle Pleistocene. The divergences for Sakhalin and Hokkaido from the continent were estimated to be more recent (Figure 3a), possibly caused by recent gene flow from the continent after the initial colonization.

To infer population phylogeny allowing gene flow after divergence, we conducted TreeMix analysis considering migration edges and drift parameters. Although the TreeMix analysis did not strongly support gene flow among the sable populations, the fraction *f* explaining variance in the sample covariance matrix of allele frequencies for the three migrations was slightly higher than that of the other migration number settings (Figure S6a). The topology of the inferred ML tree was not different between $m=0$ and $m=3$ (Figures 3b and S6b). The sable populations were divided into continental and insular groups, while the nodal support for the insular group had $a<50\%$ bootstrap value. The Hokkaido and Iturup populations appeared linked to each other, supported by $a>90\%$ bootstrap value, although the Iturup population has a long branch along the *x*-axis indicating strong genetic drift. Assuming the three migration edges, the strongest gene flow was estimated to be from the Khabarovsk to the Sakhalin population, followed by that from the ancestral lineage of the continental populations to the Hokkaido population, and from the Primorsky population to the common ancestor of the Hokkaido and Iturup populations (Figure 3b). No gene flow to Iturup was suggested, even when increasing the migration edges to 5.

In the ABC analysis of the four-pops data, we compared a single stepping-stone migration (Scenario 1) and 11 repeated migration scenarios (Scenarios 2–12) (Figure S2). Scenario 11, which assumed two admixture events following initial colonization to the Islands (Figure 3c) received the highest percentage of the classification votes at 60.5% and resulted in high posterior probability (PP = 0.596 with global and local errors of 0.399 and 0.484, respectively) (Table S4). Following Scenario 11, Scenario 6 (11.2% of votes) and scenario 12 (10.3% of votes) were supported, in which one or two admixture events for Sakhalin and Hokkaido populations were assumed. In contrast, Scenarios 1, assuming just a single stepping-stone migration, received only 0.3% votes and the other nine scenarios were received 0.1%–4.5% votes. To improve the prediction quality, we repeated model choice analysis focusing on Senarios 6, 11 and 12, as well as on Scenario 1′ which we modified to account for population size changes in insular populations. Scenario 11 was selected again as the best-fit model with 66.2% of votes and 0.714 PP accompanied by global and local errors of 0.283 and 0.323, respectively (Table S4). Estimated values for each parameter of Scenario 11 are listed in Table S5. The expected value of initial colonization to SHSK at *t*3 was estimated to be 1.84×10^5 generations ago (95% confidence interval (CI): 8.61×10^4–2.88×10^5), and the subsequent admixture events at *t*2 and *t*1 were estimated to be 5.62×10^4 (95% CI: 2.28×10^4–9.59×10^4) and 2.63×10^4 (95% CI: 0.89×10^4–5.10×10^4) generations ago, respectively. The expected values of admixture proportion of ra at t1 and rb at t2 were 0.634 (95% CI:

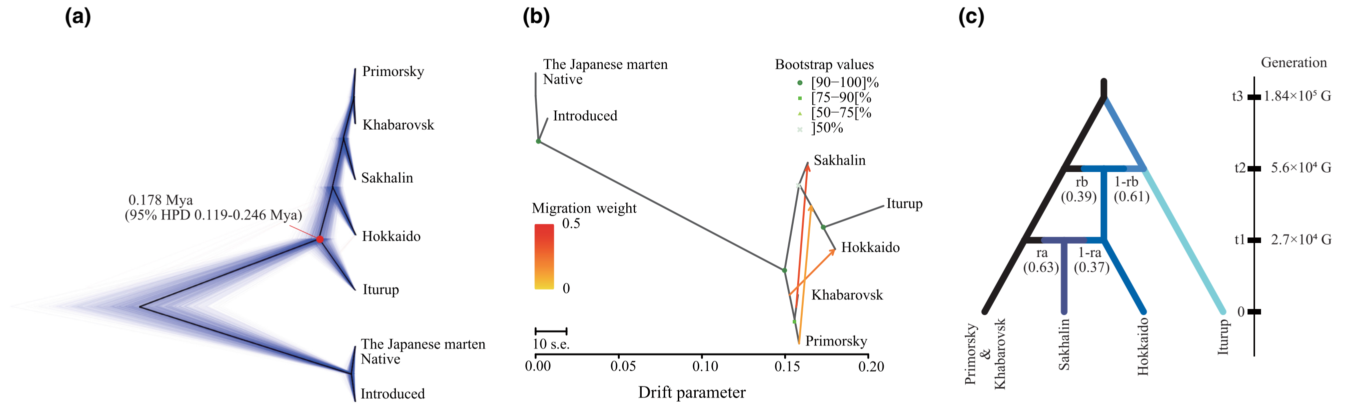

FIGURE 3 Population relationships and demography based on called genotype data from MIG-seq. (a) Multispecies coalescent tree clouds inferred for sable and Japanese marten populations in SNAPP analysis. The tree was constructed using 21 samples obtained by selecting three samples from each population with the lowest missing rate of SNPs. The consensus coalescent tree is represented with dark lines, with the estimated divergence time on the node of the split between the Iturup and other sable populations. (b) Graph of admixture with three migration edges ($m=3$) constructed using TreeMix based on the full data set. Arrows on the tree indicate the direction of gene flow, and the colours of the arrows reflect the migration weight (the fraction of ancestry derived from the migration edge). (c) Schematic of the best demographic scenario selected using DIYABC-RF analysis based on the four-pops data. Generations are shown on the *y*-axis (*t*0–*t*3) and admixture proportions from two parental populations are shown with *ra* and 1 − *ra* at *t*1, and *rb* and 1 − *rb* at *t*2. Darker colours of branches reflect genetic closeness to the continental populations based on recent divergence or high levels of gene flow. Competing scenarios are shown in Figure S3. Prior setting of the time of divergence and admixture events (*t*), the admixture rate during admixture events between two parental populations (*r*) and effective population size for each population are summarized in Table S2, and estimated values are given in Table S5.

0.446–0.798) and 0.392 (95% CI: 0.072–0.674), respectively. The ABC analysis for the three-pops data showed that Scenario 15 had the highest support among the three scenarios (77.9% of votes and PP = 0.811 accompanied with global and local errors of 0.269 and 0.337, respectively) (Table S4). In Scenario 15, the Hokkaido population experienced an admixture event with the continental populations (*t*1) after the initial colonization event of the ancestral insular population (*t*2). The expected value of admixture proportion *ra* at *t*1 was 0.394 (95% CI: 0.108–0.658) (Table S6).

3.3 | Mitochondrial DNA lineages by the *ND2* marker

In total, 419 mtDNA *ND2* sequences of sable across the distribution range were subjected to haplotype network analysis (Figure 4 and Table 1). We recognized several clusters (R1a, R1b, R1c, H1, R2 and R3), all of which corresponded to the six clades reported previously (Kinoshita et al., 2015). Nine haplotypes from Sakhalin were newly identified in this study and clustered into the R1b, R2 or H1 clades (Figure 4). The proportions of the haplotype clusters in 89 Sakhalin individuals were 71.9% in R2, 23.6% in H1 and 4.5% in R1b. Some R2 haplotypes from Sakhalin showed a starlike structure in the network (Figure 4). The Hokkaido and Iturup populations were found to possess haplotypes only from the H1 cluster. H1 haplotypes across SHSK also showed a star-like structure, in which the central haplotype and four of seven tip haplotypes were from Hokkaido. The genetic diversity of the Sakhalin population ($\pi = 0.0050$, $h = 0.80$) was as high as those of the Khabarovsk ($\pi = 0.0050$, $h = 0.90$) and Primrosy ($\pi = 0.0053$, $h = 0.84$) populations (Table 1). In contrast, the genetic diversity of the Hokkaido population was low ($\pi = 0.0007$, $h = 0.56$) and no genetic diversity was observed in the Iturup population due to detection of only a single haplotype.

4 | DISCUSSION

Previous studies on the faunal assembly in northern island systems in response to climate changes and the formation of land bridges during glacial periods have been actively investigated primarily in the British Isles and Ireland, as well as the islands of the northwest coast of North America (e.g. Colella et al., 2021; da Silva Coelho et al., 2023; Kotlík et al., 2018; Montgomery et al., 2014; Shafer et al., 2010). Those studies often focused on the dynamics of glacier development during the Last Glacial, the presence of ice-free refugia that allowed species to survive and the colonization process after the glacial period in the Holocene. However, the SHSK region and the mainland of northeastern Asia were not extensively covered by massive icesheets even during glacial periods (Igarashi, 2016; Leipe et al., 2015; Saito et al., 2014; Vandenberghe et al., 2014), offering the potential to gain insights into the historical population dynamics of boreal and arctic biota since before the last glacial period, which is difficult to infer in Europe or North

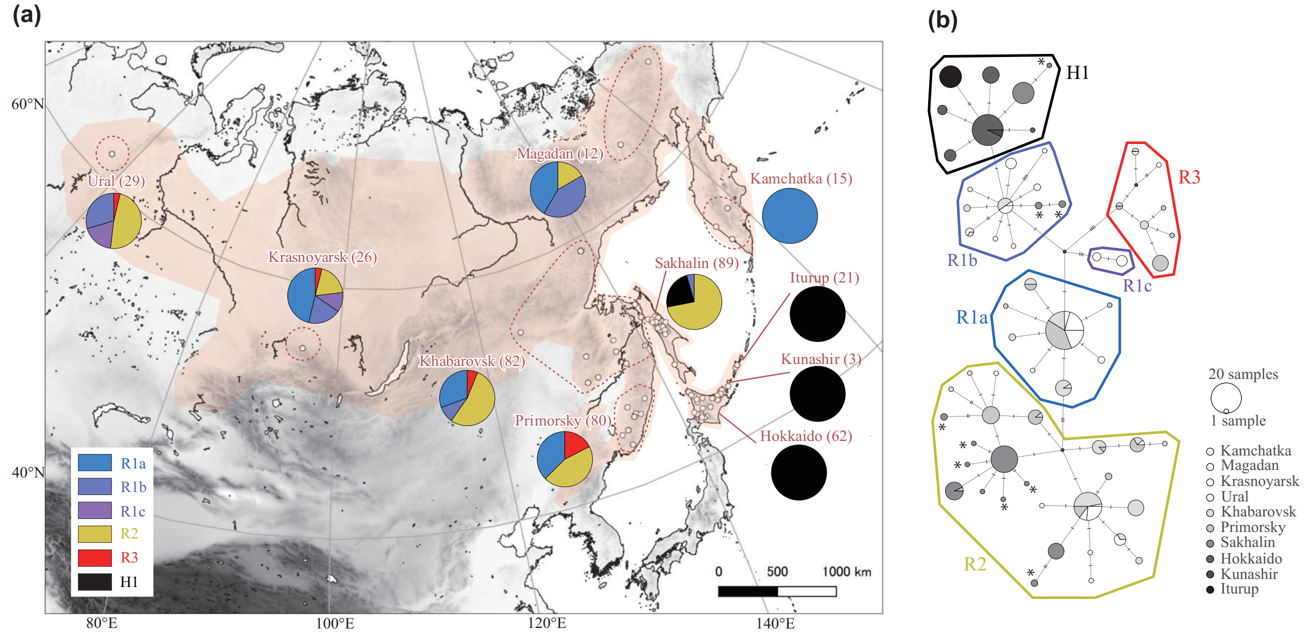

FIGURE 4 Haplotype analysis of mitochondrial *ND2* data. (a) Geographic locations and population grouping for samples used in mitochondrial *ND2* analyses. The numbers in parentheses after the name of a population indicate the number of individuals examined. Further details are provided in Table S1. Pie charts under population names show the proportion of the mitochondrial clades in (b). The distribution ranges shown in translucent red shading were adopted from the IUCN red list version 2022-2. (b) Median-joining haplotype network based on 976 bp of the *ND2* locus from 419 sable individuals. Newly identified haplotypes in this study are marked with an asterisk, while the other haplotypes were reported in Kinoshita et al. (2015). The clade names on the haplotype network are according to Kinoshita et al. (2015).

America where such information was often swept away by the effect of massive ice sheets. Our phylogeographic analyses of sable populations in the SHSK have revealed the complicated genetic population structure across the islands and shed light on the deep evolutionary history since before the last glacial.

4.1 | Genetic structure and colonization scenario for SHSK sable

The present study using genome-wide nuclear SNP data revealed genetic differentiation among Hokkaido, Iturup and continental populations of sable, while the Sakhalin population showed more genetic affinity to continental populations. The genetic diversity of the Sakhalin population is as high as that of the continental populations in both the nuclear SNP and mtDNA analyses, while the genetic diversity apparently declined in the Hokkaido and Iturup populations (Table 1). To explain this genetic diversity pattern across SHSK, we employed a coalescent simulation analysis taking both the single stepping-stone migration and repeated migrations scenarios into account as two competing hypotheses. We demonstrated that repeated migration events contributed to the contemporary genetic diversity of the sable across SHSK. The best scenario selected by the ABC analysis indicated that, after an ancestral lineage of SHSK populations separated from the continental population and expanded to Iturup, the first admixture occurred between the continental populations and Sakhalin+Hokkaido ancestor, and a second admixture between continental and Sakhalin lineages (Figure 3c). The ABC analysis, omitting the Sakhalin population, also suggested that Hokkaido received at least two migration waves from the continent (Figure S3 and Table S4). In contrast, the Iturup population would have been isolated since the initial colonization event without subsequent gene flow from the continent via Sakhalin and Hokkaido in the TreeMix analysis (Figure 3b). The SNAPP analysis also yielded a consistent result whereby the coalescence of the Iturup population with the others was older than that of the Sakhalin and Hokkaido populations (Figure 3a). According to these results, the stronger effects of repeated migrations closer to the continent, and conversely, the ancient colonization and a greater period of isolation farther from the continent contributed to the contemporary genetic diversity and differentiation of sable populations on the SHSK island.

4.2 | Forest corridors and refugia in the SHSK island system

Vegetation shifts are also crucial factors for lineage assemblage and differentiation on continental island systems at higher latitudes (Colella et al., 2021; Kotlík et al., 2018; Montgomery et al., 2014). Forest dependency in terrestrial organisms would have determined their success of migration via land bridges and persistence on islands during glacial periods (Colella et al., 2021; Garg et al., 2018; Heaney et al., 2005). It has been suggested that Quaternary climate changes dramatically changed the vegetation on the SHSK and HSK islands (Allen et al., 2010; Igarashi, 2016; Qiu et al., 2011; Takahara et al., 2010). The timing of the migration and persistence of forest-dependent marten species implies the formation of forest corridors and refugia on islands and land bridges (Colella et al., 2021; Montgomery et al., 2014; O'Reilly et al., 2021). Assuming a generation time of 2 years for sable (Monakhov, 2005), the first divergence between insular and continental populations was estimated to have occurred at 0.37 Mya (0.17–0.58 Mya) based on the divergence at t3 in Figure 3c and Table S5, and the admixture events in the islands were estimated to have occurred at 0.05–0.11 Mya (0.02–0.19 Mya) based on *t*1–*t*2 in Figure 3c and Table S5. Similarly, mitochondrial lineages of squirrels (*Pteromys volans* and *Sciurus vulgaris*) in Hokkaido were estimated to have diverged from the continental lineages around 0.3 Mya (Oshida et al., 2005; Sato, 2017). These estimates imply that forest corridors occasionally emerged on the paleo-SHSK peninsula during the Middle Pleistocene and beyond. Thus, the sable would have been able to migrate on several occasions.

Despite the influence of repeated migrations from the continent both to the Sakhalin and Hokkaido populations (Figure 3c and Table S4), the Sakhalin population was genetically much closer to the continental populations compared to the Hokkaido population (Figures 2 and S1). This difference could be attributed to the proximity of Sakhalin to the continent, with just a shallow strait separating them. To migrate from the continent to Hokkaido and Iturup, it is necessary to pass through Sakhalin (see Figure 1). In addition, the heterogeneity of vegetation across the paleo-SHSK Peninsula, especially forest fragmentations, would have also played a crucial role in restricting gene flows from the continent and promoting genetic differentiation among SHSK populations, considering the forest dependency of the sable. The maximum extent of permafrost during the last glacial period almost fully covered Sakhalin, increasing forest fragmentation and land openness favoured by tundra steppe faunal elements (Kirillova & Tesakov, 2008; Leipe et al., 2015; Saito et al., 2014; Vandenberghe et al., 2014). Previous studies of some cold-adapted trees have revealed the existence of a phylogeographic boundary in central Sakhalin, suggesting past distribution gaps and secondary contact between northern-migrated continental lineages and southern-resident insular lineages in Sakhalin (Aizawa et al., 2007, 2009; Khatab et al., 2008; Polezhaeva et al., 2010; Semerikova et al., 2011). This history probably had a high impact on migration and the persistence of the sable. At the same time, cold-adapted needleleaf-tree forests characterized by *Larix* developed in Hokkaido during the last glacial period (Igarashi, 2016). The forests persisting in Hokkaido during glacial periods might support the early sable colonization and keep the mitochondrial genetic diversity of the H1 clade in Hokkaido higher than in Sakhalin (Figure 4).

The Iturup Island represents the end of the SHSK migration route for several terrestrial organisms in northeastern Asia. We clarified that the Iturup sables were the most differentiated among the individuals examined. Only a few studies have investigated the phylogeny of terrestrial animals in the southern Kuril Islands (e.g. Hirata et al., 2017; Ohdachi et al., 2001) and the historical faunal assembly remains largely unknown. The area around Iturup comprises one of the most active volcanic island regions in the world, with violent eruptions in the past 50,000 years (e.g. a large eruption in southern Iturup ca. 9500 years ago with a volcanic explosivity index of 6+) (Simkin & Siebert, 1994; Smirnov et al., 2017). These would have greatly altered the geographic structure and played important roles in vegetation shift in the area, in combination with global climate changes and sea-level oscillations (Gorshkov, 1970; Razjigaeva et al., 2002, 2013; Razzhigaeva et al., 2016). However, information on paleogeographic and vegetation dynamics prior to the last glacial period remains inadequate. The present study provides important insights into the origin of a forest biota element (the sable) on the island dating prior to the last glacial period, suggesting the presence of forest corridors at that time and a long-standing forest habitat. The skull size of the Iturup sable is significantly greater than those of continental populations in the Far East, while skulls from Sakhalin and Hokkaido are relatively small (Monakhov, 2016). The Iturup sable likely evolved independently due to long-term isolation on a marginal island.

4.3 | Remaining issues for the evolutionary history of the sable in Hokkaido

We found a signature indicating that the sable population in Hokkaido could be divided into several genetic subclusters (Figures 2b and S1). This may be a result of past forest fragmentation within the island during glacial periods (Igarashi, 2016), which would have forced the sable to retreat into micro-refugia and promoted genetic diversification within the island. Similar patterns have been suggested for other terrestrial mammals in Hokkaido (Inoue et al., 2022; Kawai et al., 2013; Kinoshita et al., 2012; Noda et al., 2016; Suzuki et al., 2015). Alternatively, the outcome could be a result of severe hunting pressure prior to prohibition in 1920 (Hirakawa et al., 2015). Population declines and fragmentation over the past hundred years could have led to differentiation among local populations within Hokkaido due to strong genetic drift, as reported for Blakiston's fish owl (*Bubo blakistoni*; Omote et al., 2015) and sika deer (*Cervus nippon*; Nabata et al., 2004).

The population size of the sable in Hokkaido appears to have recovered, but rapid replacement by the Japanese marten introduced from Honshu to Hokkaido around 1940 poses a severe threat to the sable in the western part of Hokkaido (Hirakawa et al., 2015; Murakami & Ohtaishi, 2000). The two species were clearly distinguishable in our analyses, and a previous study using mtDNA did not find signatures of hybridization or introgression (Inoue et al., 2010). However, a more thorough investigation is needed to understand the genomic impacts of ongoing replacement by the Japanese marten in Hokkaido, as interspecies hybridization and introgression have been reported between sable and pine marten (*M. martes*) (Modorov et al., 2020; Monakhov, 2022; Rozhnov et al., 2013), as well as between American marten (*M. americana*) and Pacific marten (*M. caurina*) in distribution boundary areas (Lucid et al., 2020).

Although the MIG-seq method allowed us to reveal a backbone of evolutionary history of the sable across SHSK, this covers only a very small portion of the genome. In this study, we conducted analyses comparing scenarios with a selection of simplified scenarios to the best of our ability. However, we believe that more comprehensive data sets, such as whole genome sequencing data, could enable the examination of more complex scenarios involving a greater number of gene flow events and fluctuations in population sizes, such as population bottlenecks and dispersals. It has been reported that the sable in Hokkaido possesses a unique haplotype of the coat colour-related gene *Mc1r* that is phylogenetically close to those of Japanese and American martens (Ishida et al., 2013). Unique genetic diversity of the Hokkaido sable, shaped by repeated isolation and admixture as observed in this study, possibly with ancestral polymorphism and/or ancient introgression (Ishida et al., 2013), could have contributed to long-term persistence and local adaptation on the island. In previous studies of the mountain hare (Kinoshita et al., 2019) and brown bear (de Jong et al., 2023), it has been suggested that ancient introgression with geographically distant species on the continent contributed to genetic uniqueness in the Hokkaido population, because of past distribution shifts induced by climate changes. Further study using denser genome-wide polymorphisms to focus on loci under natural selection will provide a more detailed evolutionary history of the SHSK sable addressing local adaptation on the islands in response to climate changes.

5 | CONCLUSIONS

The SHSK continental island system serves as one of the southernmost habitats for many boreal organisms in the Palearctic, allowing colonization through a paleo-peninsula formed during the glacial periods. Our genome-wide and comprehensive sampling approaches demonstrated that the sable experienced repeated migrations from the continent to SHSK and partial admixture events of multiple lineages at least since the Middle Pleistocene. This implies the existence of forest corridors and refugia on the paleo-SHSK Peninsula during the last several glacial periods. The SHSK may represent a good system for comparison with other continental island systems at high latitudes, including those in Europe and North America (e.g. Colella et al., 2021; da Silva Coelho et al., 2023; Kotlík et al., 2018; Montgomery et al., 2014; Shafer et al., 2010). The system offers more robust and variable insights into how cold-adapted organisms have responded to climate changes in the Quaternary, and how this may continue into the future.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data collected to this study are freely available: raw data of MIG-seq are deposited in DDBJ under accession numbers DRR466510–466685 (Submission) and PRJDB15868 (BioProject); *ND2* sequences are deposited in DDBJ under accession numbers: LC768322–LC768461.

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BIOSKETCH

The research team is interested in the ecology and evolutionary history of marten species.

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Vladimir Monakhov is a zoologist and ecologist at the Institute of Plant and Animal Ecology of the RAS. His main interests include craniology, phenetics, population structure, and hunting management of the sable and pine marten. The most significant development is the study and generalization of the results of mass introductions of sable in western and eastern Siberia.

Alexey Kryukov is an ornithologist and evolutionary geneticist, engaging in the research of speciation and species isolation, natural hybrid zones and phylogeography. He studies a wide range of vertebrate groups from amphibians to mammals by utilizing the integrative approach.

Liubov Frisman is a theriologist and evolutionary geneticist at the Far Eastern Branch of RAS, focuses on speciation, isolation's impact on population structure, and the history of area formation. Using an integrated approach, she primarily studies small mammals. Her current research examines the genetic structure's response to isolation in various rodent species and monitors the population structure of the sable in the Middle Amur region.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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