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Extrinsically reinforced hybrid speciation within Holarctic ermine (*Mustela* spp.) produces an insular endemic

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Abstract

Aim: Refugial isolation during glaciation is an established driver of speciation; however, the opposing role of interglacial population expansion, secondary contact, and gene flow on the diversification process remains less understood. The consequences of glacial cycling on diversity are complex and especially so for archipelago species, which experience dramatic fluctuations in connectivity in response to both lower sea levels during glacial events and increased fragmentation during glacial recession. We test whether extended refugial isolation has led to the divergence of genetically and morphologically distinct species within Holarctic ermine (*Mustela erminea*), a small cosmopolitan carnivore species that harbours 34 extant subspecies, 14 of which are insular endemics.

Location: Holarctic.

Methods: We use genetic sequences (complete mitochondrial genomes, four nuclear genes) from >100 ermine (stoats) and geometric morphometric data for >200 individuals (27 of the 34 extant subspecies) from across their Holarctic range to provide an integrative perspective on diversification and endemism across this complex landscape. Multiple species delimitation methods (*iBPP, bPTP*) assessed congruence between morphometric and genetic data.

Results: Our results support the recognition of at least three species within the *M. erminea* complex, coincident with three of four genetic clades, tied to diversification in separate glacial refugia. We found substantial geographic variation within each species, with geometric morphometric results largely consistent with historical infraspecific taxonomy.

Main conclusions: Phylogeographic structure mirrors patterns of diversification in other Holarctic species, with a major Nearctic-Palearctic split, but with greater intraspecific morphological diversity. Recognition of insular endemic species *M. haidarum* is consistent with a deep history of refugial persistence and highlights the urgency of mindful management of island populations along North America's North

Pacific Coast. Significant environmental modification (e.g. industrial-scale logging, mining) has been proposed for a number of these islands, which may elevate the risk of extinction of insular palaeoendemics.

1 | INTRODUCTION

Extended isolation in glacial refugia is a documented driver of diversification worldwide (Bennett & Provan, 2008; Hewitt, 1996; Stewart et al., 2010). The cyclic expansion and contraction of glaciers through the Quaternary (2.6 Mya–present) is credited with structuring flora and fauna at the high latitudes (Pielou, 2008), whereby episodes of allopatric refugial isolation lead to genetic and morphological differentiation over time (e.g. mammals, Heaton et al., 1996; Sawyer et al., 2019; plants, DeChaine et al., 2014; insects, Ujvárosi et al., 2010). Subsequent periods of glacial recession, however, are often associated with secondary contact between expanding refugial populations. Secondary contact has been primarily viewed as a homogenizing force, with gene flow often erasing differences accumulated between refugial taxa (Gilman & Behm, 2011). Interestingly, established biotic responses to glaciation by terrestrial species—isolation during glacial advances and expansion following deglaciation—may be reversed in island or archipelago systems where isolation and gene flow are further complicated by fluctuations in sea levels which change interisland and island–mainland connectivity (Esselstyn et al., 2009; Fernández-Palacios et al., 2016; Grant & Grant, 2016; Heaney et al., 2005; Sato, 2016). Glaciation typically fractures the ranges of continental species, however, the retention of water in glaciers also lowers sea levels, thereby increasing connectivity between proximal islands through the exposure of shallow continental shelf (Sato, 2016). In turn, glacial recession can release mainland species from refugial isolation, but correspondingly fragment island systems by inundating shallow areas of continental shelf with water, thus creating dispersal barriers and potentially promoting allopatric divergence (Fernández-Palacios et al., 2016). Islands separated by deeper oceanic barriers (e.g. Ireland relative to the other British Isles) or greater geographic distances (e.g. oceanic archipelagos) likely experience fewer bouts of gene flow due to infrequent connectivity with or colonization by mainland source populations.

Climate-associated changes in sea level influence the evolutionary histories of species on both oceanic (Grant & Grant, 2016; Rocha et al., 2016) and near-shore, continental archipelagos (Colella et al., 2018; Sato, 2016; Slager et al., 2020; Whittaker & Fernandez-Palacios, 2007) spanning climate, elevational, and latitudinal gradients (tropical, Caujapé-Castells et al., 2017; temperate, Craw et al., 2017; arctic, high-elevation sky-islands, Folk et al., 2018; Flantua & Hooghiemstra, 2018). Due to the extended distance of oceanic archipelagos from continental source populations,

hybridization during low sea levels primarily occurs between established, actively diverging sister taxa that inhabit geographically neighbouring islands that are more fully disconnected at higher sea levels, as seen on the islands of Galapagos and Seychelles (Grant & Grant, 2016; Rocha et al., 2016). In contrast, the flora and fauna of near-shore continental archipelagos experience both periodic connectivity with neighbouring islands and frequent colonization or invasion by mainland dispersers, potentially leading to a more complex history of isolation and contact with multiple different populations, that is less dependent on long-distance dispersal. Higher latitude continental (as opposed to oceanic) archipelago flora and fauna, including that of the Alexander Archipelago of Alaska (USA), Haida Gwaii and Arctic archipelagos of Canada, the Japanese Archipelago, and the British Isles, may be particularly impacted by glacial cycling, as these archipelagos also served as glacial refugia for displaced continental species, and have dynamic histories of connectivity and isolation. The periodic influx of novel genetic material into continental archipelago species through introgressive hybridization with either mainland dispersers or neighbouring island populations may contribute to elevated levels of endemism within continental archipelagos (Grant & Grant, 2014; Larsen et al., 2010).

Patterns of gene flow can now be explored in detail using whole-genome sequencing (WGS), which enables fine-scale detection of historical and contemporary introgression through the reconstruction of demographic patterns in response to glaciation. Consistent with the coastal refugium hypothesis (Heusser, 1989), classic morphometrics (Eger, 1990) and WGS of the geographically widespread Holarctic ermine (*Mustela erminea*, King, 1983) have revealed four genetically distinct clades, geographically coincident with three glacial refugia in North America and a fourth that spanned Beringia through the Last Glacial Maximum (LGM, 26.5–19 kya; Colella et al., 2018; Dawson et al., 2014; Fleming & Cook, 2002). One clade, now endemic to two archipelagos along North America's North Pacific Coast (NPC), may represent a distinct species of hybrid origin (Colella et al., 2018). In this case, ancient admixture is hypothesized to have occurred along the NPC during a previous interglacial (~377 Kya; Colella et al., 2018), during secondary contact between the Old World Beringian and New World "East" clades (Fleming & Cook, 2002). Subsequent refugial isolation of the admixed population, potentially within the NPC archipelagos and neighbouring coastline (Colella et al., 2018; Dawson et al., 2014; Eger, 1990), at least since the LGM (~21 Kya) is hypothesized to have promoted allopatric divergence and potentially speciation of
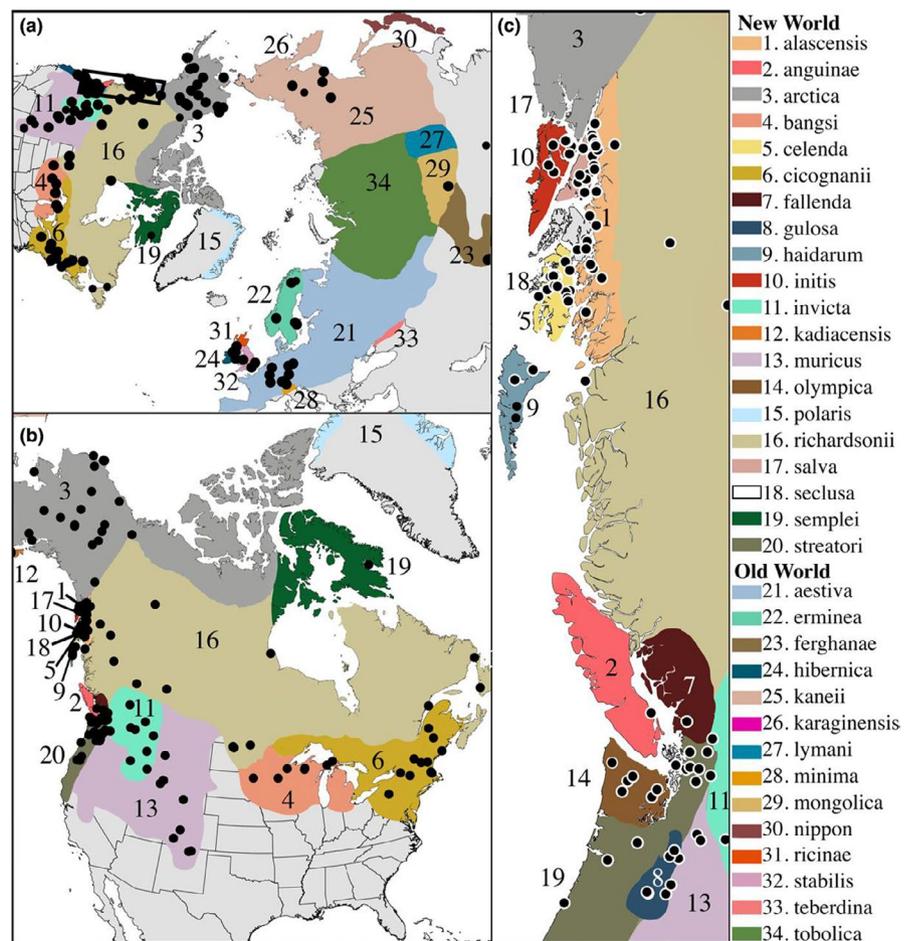
this insular population, which may now represent an evolutionary novelty. Following the LGM, sea levels rose in response to glacial recession, and instead of being released from refugia, many NPC populations remained isolated on islands leading to the evolution of substantial intraspecific diversification. Various numbers of ermine subspecies, from 3 to 34, have been recognized (Corbet, 1978; Ellerman & Morrison-Scott, 1951; King, 1983; Hall, 1951), but with no consensus. Given the shared phylogeographic history of numerous NPC endemics (Sawyer et al., 2019), hybridization and isolation (both refugial and insular) acting as an engine for accumulating endemicity is likely a shared process among similarly distributed taxa and among high-latitude archipelagos (Colella et al., 2018; Patiño et al., 2017; Sawyer et al., 2019; Slager et al., 2020).

Whole-genome sequencing remains expensive, particularly for organisms with large genomes (e.g. plants, mammals), and previous sampling limitations (Colella et al., 2018) did not provide for spatially extensive tests of cryptic speciation within the *M. erminea* complex. An incomplete understanding of species diversity hinders effective management of insular endemics, including seven ermine subspecies endemic to the NPC (Hall, 1951). Proposed habitat modification, including industrial-scale timber harvests and mining in the Tongass National Forest (USDA, 2007a, 2007b; Stewart, 2016), increases the exigency of characterizing cryptic diversity and novel evolutionary processes within the biogeographically distinct "Sitkan District" (Cook & MacDonald, 2001; Dawson et al., 2007). Reduced-representation

genetic and geometric morphometric approaches to species delimitation afford expanded geographic sampling for increased resolution into cryptic species diversity across the complex landscape of the North Pacific. Morphological and genetic changes do not necessarily occur in a regular order (de Quieroz, 1998). Therefore, the inclusion of morphological perspectives in species delimitation enables a more powerful evaluation of congruence across multiple methods and datasets to limit methodological biases (Carstens et al., 2013). Integrative approaches to species delimitation can help identify distinct population segments (DPS) relevant under the U.S. Endangered Species Act (1973), particularly in organisms that span broad, spatially heterogeneous environments where we might expect profound differences in size due to latitudinal clines (Bergmann, 1847) or insularization (Foster, 1964). The rate of insular morphological and molecular evolution in mammals varies substantially (Barton, 1996; Millien, 2006; Raia & Meiri, 2011), presumably due to the combined effects of isolation and limited effective population sizes, which increase the strength of genetic drift, can alter fitness landscapes and can, ultimately, lead to the evolution of novel phenotypes.

Here, we use the geographically widespread ermine as a model to understand the nuanced role of climate cycling in the accumulation of diversity within continental archipelagos. We integrate geometric morphometric and genetic datasets with expanded sampling from across the Holarctic range of ermine (sampling 27 of 34 nominal subspecies) to test for cryptic diversity. Specifically, we aim to

FIGURE 1 Map of ermine subspecies distributions based on Hall (1951) and IUCN distribution data (www.iucn.org) with individual sampling localities indicated by black dots. (a) Polar view of the northern hemisphere; (b) North America; (c) North America's North Pacific Coast (NPC), geographic limits correspond to the extent-indicator box in (a). The NPC Island clade is distributed across two islands in the Haida Gwaii Archipelago of British Columbia (Graham and Moresby islands; *haidarum*), on Prince of Wales Island (*celenda*) in the Alexander Archipelago of Southeast Alaska, and possibly on neighboring Suemez Island (*seclusa*)

New World
1. alascensis
2. anguinae
3. arctica
4. bangsi
5. celenda
6. cicognanii
7. fallenda
8. gulosa
9. haidarum
10. initis
11. invicta
12. kadiacensis
13. muricus
14. olympica
15. polaris
16. richardsonii
17. salva
18. seclusa
19. semplei
20. streatori
Old World
21. aestiva
22. erminea
23. ferghanae
24. hibernica
25. kaneii
26. karaginensis
27. lymani
28. minima
29. mongolica
30. nippon
31. ricinae
32. stabilis
33. teberdina
34. tobolica

determine the species status of the NPC Island clade, which may represent an evolutionary novelty in mammals and provide rare insight into a constructive role for interglacial hybridization in the diversification of archipelago systems that may be broadly relevant to high-latitude refugial archipelagos.

2 | METHODS

2.1 | Geometric morphometric methods

We imaged the ventral aspect (*norma basalis*) of the crania of 277 adult male ermine specimens representing 27 of the 34 extant subspecies (19 of 20 New World, 8 of 14 Old World subspecies) and all four genetic clades, although sampling is biased towards New World localities. Although the number of ermine subspecies remains contentious, we chose to assess the most diverse estimates (Hall, 1951), hypothesizing that a subset therein (as proposed by Corbet, 1978 or King, 1983) would be identified as distinct. Ermine

FIGURE 2 The ventral aspect of a landmarked male ermine specimen from the University of Alaska Museum of the North (UAM:Mamm:93279). Landmark abbreviations correspond to the descriptions in Supporting Information S1

are strongly sexually dimorphic (Hall, 1951; King, 1983); therefore, following Abramov and Baryshnikov (2000) we restricted morphological sampling to males only, as species diagnosis within mustelids remains consistent even when sex is unknown (Bornholdt et al., 2013). Crania were loaned from the University of New Mexico Museum of Southwestern Biology (MSB), the University of Alaska Museum of the North (UAM), the Museum of Vertebrate Zoology (MVZ) at the University of California Berkley and the Smithsonian National Museum of Natural History (USNM). We selected only adult specimens, by requiring the presence of fused cranial sutures and complete eruption of all adult teeth (Dayan & Simberloff, 1994; Hall, 1951; Peters et al., 2010). Images were collected using a macro lens on a Canon DSLR D5200 fixed 33 cm above the specimen. Specimens were aligned by eye, with the hard palate parallel to the imaging plane. Orientation aimed to maximize the number of reproducible, homologous landmarks available within the same plane of focus. Images were taken at every degree of focus and digitally stacked into a single high-resolution image using the Helicon software suite (Remote and Focus; www.heliconsoft.com). Homologous ventral landmarks ($N = 24$), selected based on comparable studies of cranial morphology in carnivores (Goswami et al., 2011; Peters et al., 2010), were digitized in *TPSdig* (Rohlf, 2006; Supporting Information S1; Figure 2) by the same observer (LMF) to minimize placement error. We estimated landmark variance (*morphol.disparity* function in the *Geomorph* package in *R* v. 3.6.1; Adams et al., 2017; R Core Team, 2017), after landmarking the same specimen image five times on different days to assess placement accuracy. Only the right side of each skull was landmarked to prevent confounding issues associated with fluctuating asymmetry. Unless noted, all statistical analyses were conducted in *Geomorph* (Adams et al., 2017). At least one landmark was missing from 106 specimens. For each specimen with missing data, individuals lacked an average of 2.03 landmarks (range 1–7). Missing landmarks were estimated using the *estimate.missing* function within geographic populations (e.g. island) or subspecies, if geography was not obviously disjointed. A general Procrustes analysis (GPA) eliminated variance caused by rotation, translation, and scale based on the unit centroid size (CS, the square root of the sum of squared distances of all landmarks from their centroid). Nine outliers were identified (*plotOutliers*), based on distance from the mean shape (above the uppermost and below the lowermost quartiles) and removed from downstream analyses. An additional GPA was run on the final curated dataset, excluding outliers, agnostic of a priori subspecies identifications.

We ran an allometric ANOVA (*procD.allometry*) on the GPA-adjusted coordinates to test for the influence of size (cranium CS, Klingenberg, 2016) on shape variation in male *M. erminea* ($p < .05$). We extracted residual shape variation and ran a Procrustes ANOVA (*procD.lm*) to test which factors (genetic clade, subspecies, collection locality, or insular/continental collection locality) most influence shape variation. Pairwise Procrustes ANOVAs between subspecies and clades tested for significant differences between groups ($p < .05$) with the expectation that traditionally defined morphological subspecies would lack significant differentiation once size was
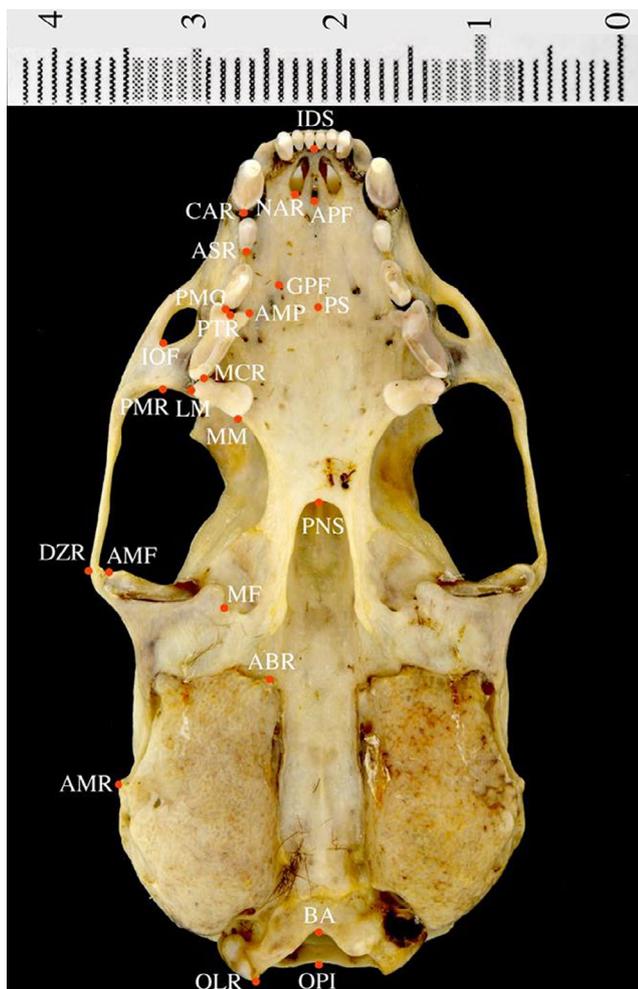
eliminated from our analysis. To assess morphological separation among subspecies and genetic clades, we conducted a principal component analysis (PCA). To simplify PCA visualization, we also averaged principal components within each subspecies and within each genetic clade and plotted groupwise averages. We estimated mean shapes (*mshape*) for each group (subspecies and clade) and used displacement plots (*plotRefToTarget*) to visualize differences between groups. Mean CS ($\pm SD$) was calculated and contrasted between groups as a proxy for overall size (Bookstein, 1996; Slice et al., 1996). A standard linear regression (*lm* function in base R) estimated the strength of the relationship (R^2) between size and latitude. CS was plotted against collection latitude to visualize agreement with Bergmann's latitudinal rule (Bergmann, 1847).

In addition to testing for differentiation among predefined subspecies and genetic clades, we also ran an uninformed cluster analysis for all New World specimens, for which we had greater sampling depth and subspecies representation, to determine the best partitioning scheme for our morphological data (*kmeans* function in the *flexclust* R package; Leisch, 2006). We used the Rand, Jaccard, and Fowlkes–Mallows index (*randIndex* function; Hubert & Arabie, 1985; Rand, 1971) to compare agreement among kmeans clustering schemes and genetic clusters identified using genetic and WGS data (Colella et al., 2018; Dawson et al., 2014). The Rand Index varies between zero and one, with one indicating that two clustering schemes are identical.

To place New World morphological variation into a broader context, we added limited geometric morphometric coordinate data from 44 Old World ermine, representing eight of 14 Old World subspecies. Differences were visualized using PCA and linear regression to assess the relationship between CS and collection latitude. We contrasted allometric trends between Old and New World ermine and tested for differences in size and shape between subspecies and genetic clades (Old World samples pooled with the Beringia clade) using pairwise ANOVAs, corrected for multiple comparisons. Displacement plots were used to visualize mean shape differences between New and Old World ermine.

2.2 | Molecular methods

DNA was extracted from liver tissue loaned from MSB and UAM following the protocol in Sonsthagen et al. (2004). Mitochondrial genomes were amplified in five fragments using the primers in Supporting Information S2. To build upon nuclear sequences available in GenBank, four nuclear genes (agouti signalling protein [*ASIP*], feline sarcoma [*FES*], growth hormone receptor [*GHR*] and serotonin receptor 1b [*HTR1B*]) were amplified following Dawson et al.'s (2014) PCR protocol. Nuclear PCR products were pooled with mitogenome fragments for parallel-tagged amplicon sequencing. Library preparation followed the Nextera XT DNA Sample Preparation Guide (Illumina 2012, San Diego, California, USA) for sequencing on an Illumina MiSeq Small Genome Analyzer at the U.S. Geological Survey Alaska Science Center (Anchorage, AK, USA). We used a 2×250 bp

Reagent Kit with 10% PhiX. Individual samples were recovered by identifying individual barcodes and adaptors, and quality score trimming was performed with default settings using *MiSeq Reporter Software* (Illumina, San Diego, CA, USA). Paired-end reads were assembled and mapped to their respective GenBank reference sequences in *CLC Genomics* v. 7.5 (https://www.qiagenbioinfomratics.com/). GenBank identifiers for reference sequences are available in the Supporting Methods. Nuclear ambiguities were called when two alleles were present at a 0.3 frequency threshold. Loci were aligned via *MUSCLE* v. 7 (Edgar, 2004).

We used *Integrative Bayesian Phylogenetics and Phylogeography* (*iBPP*; Solís-Lemus et al., 2015) to integrate coalescent modelling of multi-locus divergence with the evolution of morphological traits to delimit species. This method builds on the *Bayesian Phylogenetics and Phylogeography* (*BPP*) model for coalescent species delimitation (Yang & Rannala, 2010), conditioned on a Brownian motion model of trait evolution, and was run for combined datasets and again for molecular and morphological datasets independently. Three- and four-taxon species trees, estimated by Colella et al. (2018) and Dawson et al. (2014) using maximum-likelihood and Bayesian inference on multi-locus genetic data, were used as guide trees: (I) ((Beringia, NPC), East/West)) and (II) ((Beringia, NPC), (East, West)). Individuals were sorted into clades based on Dawson et al. (2014) haplotype assignment, collection locality, and genetic clade assignment, with East and West clades combined for three-species tests. Genetic data included three mitochondrial (complete mitochondrial genomes, cytochrome *b*, and control region) and four nuclear loci. Nuclear sequences from individuals collected within the Alaska–Canada hybrid zone were excluded (Colella et al., 2018), as Bayesian inference assumes no recent gene flow (Solís-Lemus et al., 2015). Traits included CS and principal components (PCs) from GPA-adjusted morphometric coordinates ($N = 48$), as geometric morphometric characters are not completely independent and PCs are not necessarily evolutionarily independent. Fine-tuning parameters were auto-adjusted (finetune = 1) to yield appropriate step lengths (GBtj 2, GBspr, 0.0002; update θ_S, 0.001; update τ_S, 1; mixing step, 0.01; change locus rates, 0.005). To test the impact of various parameter combinations, we assessed four distinct demographic scenarios corresponding to large (or small) ancestral population sizes with relatively deep (or shallow) divergence times to estimate the support for putative species. Tested parameters included the following: $\theta = G(1,10)$ and $\tau = G(1, 10)$, $\theta = G(1,10)$ and $\tau = G(2, 2,000)$, $\theta = G(2, 2,000)$ and $\tau = G(1, 10)$, and $\theta = G(2, 2,000)$ and $\tau = G(2, 2,000)$, where θ and τ correspond to the ancestral population sizes and divergence times, respectively, and G specified a gamma distribution for the prior. We adjusted inheritance scalars (mtDNA = 0.25, nuDNA = 1). We conducted five runs for each guide tree with different random seeds. Following Berriman et al. (2018), the MCMC chain was run for 2.5×10^6 generations, with a 2×10^5 burn-in, sampling every 250 generations. Pooled across runs, a posterior probability of > 0.90 was considered significant support for a descendant species.

As an additional delimitation test, we used the *bPTP* Web server available at: species.h-its.org/ptp/ (Zhang et al., 2013). *bPTP* generates ML and Bayesian support values following Poisson tree

processes. *bPTP* was run for the ML mitochondrial and nuclear phylogenies generated by Colella et al. (2018) based on 10 ermine WGS. However, because *bPTP* is not designed to accommodate multi-locus or SNP data, we then ran each locus generated as part of this study (mitochondrial genomes, *ASIP*, *FES*, *GHR*, *HTR1B*) independently and as a concatenated supermatrix with corresponding sequences from other *Mustela* species, as available through GenBank (Supporting Methods). Each *bPTP* iteration was run against the species-level ML phylogeny generated in *RAxML* (10,000 iterations, random seed; Stamatakis, 2014) for 100,000 generation with 0.1 burn-in, 100 thinning and a random seed, and convergence was assessed through visual inspection of trace output.

3 | RESULTS

Procrustes variance around landmarks averaged 0.0003, indicating high precision in landmark digitization. Ten percent of the total shape variation in New World ermine was correlated with size (Supporting Information S3). After removing allometric variation, a priori subspecies assignment was the most influential variable examined, accounting for almost 16% of size-free variation, followed by collection locality and genetic clade assignment (7% each; Supporting Information S4). Whether a specimen was collected on an island

versus from a mainland locality did not significantly influence size-free shape variation (Supporting Information S4). Although most factors examined contributed significantly to shape variation, 69% of shape variation remained unexplained. Pairwise ANOVAs between the 19 sampled New World subspecies found significant shape and size differentiation (Supporting Information S5). Intraspecific systematic results and discussion are available in the Supporting Information. We found significant morphological differentiation in both size and shape among the four genetic clades (Table 1), with the exception of the East and West clades. Comparison between mean clade shapes (Figures 3 and 4) demonstrated strong shape similarity between sister clades: East–West and NPC–Beringia.

Principal component analysis plots visualized differences in subspecies, genetic clades, and insular versus continental populations (Figure 4; Supporting Information S6). Despite significant shape differences between many subspecies, the sheer number of subspecies and sampled individuals makes visualization of comprehensive PCA plots difficult (Supporting Information S6). To simplify, we averaged PCs for each subspecies and each genetic clade to visualize the distribution of shape diversity in New World *M. erminea* (Figure 4). Distribution of these groups in PC space was consistent with recent genomic investigations, documenting similarity between more closely related sister clades (e.g. Beringia-NPC and East–West). Consistent with our ANOVA results, the mean shape of the East and West clades did not differ dramatically (Figure 3). While the palaeoendemic NPC Island clade is the most morphologically distinct (Figures 3 and 4), its phenotype is also most similar to its sister, the Beringia clade (Colella et al., 2018). Both clades share a posteriorly shifted rostral and palatal region and anteroposteriorly compressed braincase, relative to the East clade (Figure 3). The West clade is morphologically similar to its geographic neighbour and sister, the East clade. Within New World ermine, the Beringia clade has the largest CS (Table 2; Figures 3 and 4), followed by the NPC Island clade, and the West clade has the smallest CS.

Uninformed cluster analyses aligned more closely with genetic clade assignments than subspecific assignments, although neither
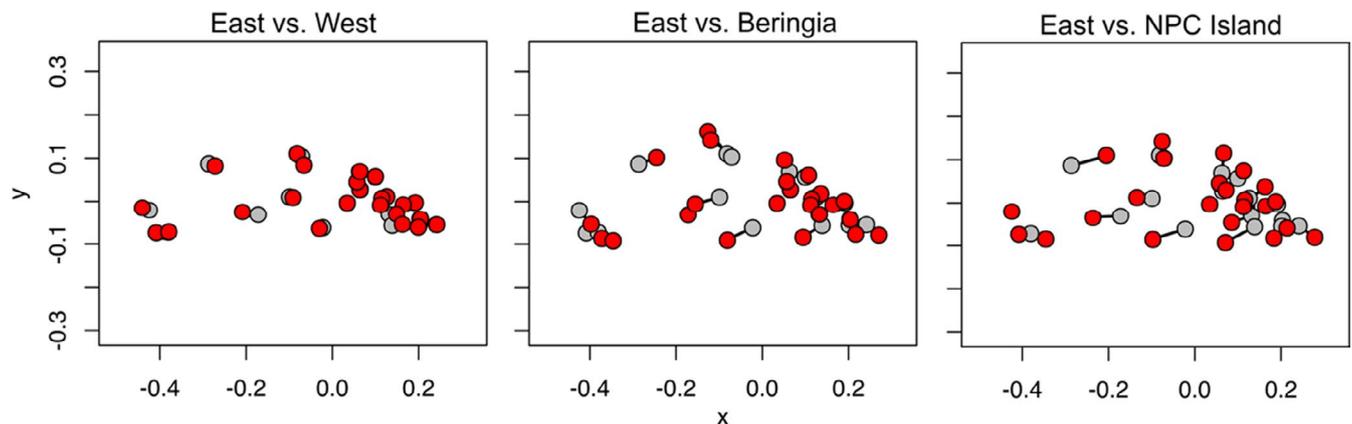
TABLE 1 Pairwise ANOVA tests between genetic clades, with Old World samples included within the Beringia clade. Significance is denoted in italics ($p < 0.005$). The top triangle shows pairwise tests on mean centroid size, and the bottom triangle shows pairwise tests of shape difference

| Clade	East	Beringia	NPC	West
East	—	*0.001*	*0.008*	0.273
Beringia	*0.001*	—	*0.001*	*0.001*
NPC	*0.001*	*0.001*	—	*0.004*
West	0.411	*0.001*	*0.001*	—

FIGURE 3 Mean shape differences between the East clade (gray) and all other genetic clades (red): (left) West, (center) Beringia, and (right) NPC Island. Displacement diagrams demonstrate shape similarity between East and West and differentiation between the East clade and Old World affiliated Beringia and NPC Island clades. NPC is the most morphologically distinct population
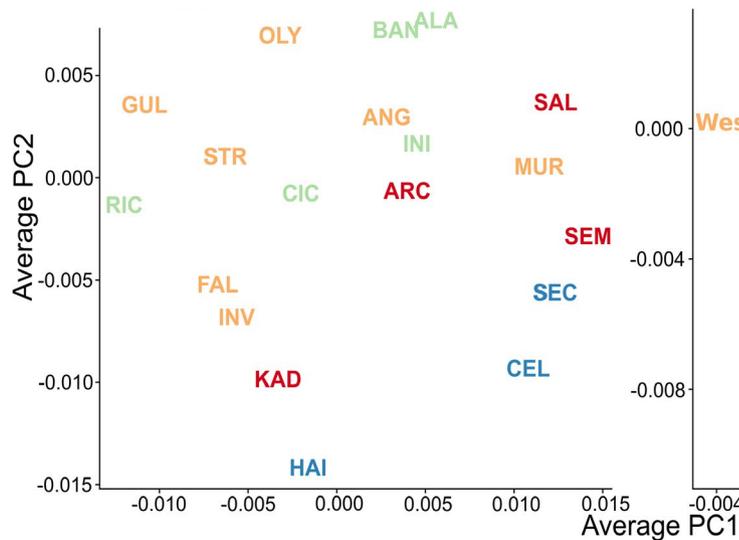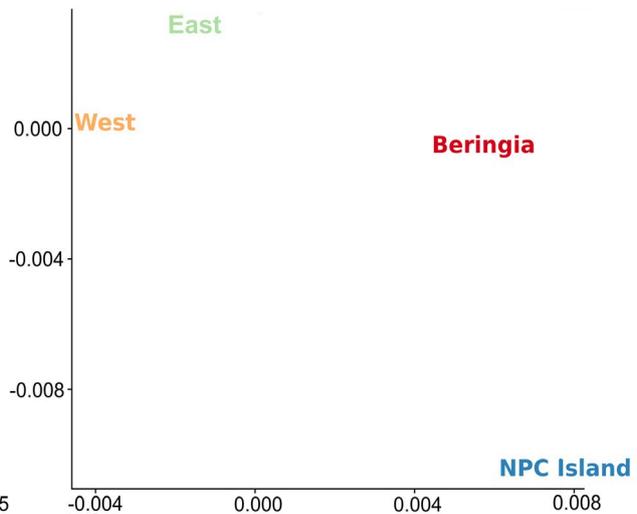
FIGURE 4 (a) Estimated geographic distributions of *Mustela erminea* genetic clades based on the IUCN distribution of the species complex and the distribution of mitochondrial haplotypes (Dawson et al. 2014). Principal component analysis (PCA) of residual shape (or "size free") variation with principal components (PC) one and two averaged by subspecies (b) and genetic clades (c). Colors correspond to genetic clade assignment and subspecies name abbreviations are listed in Table 2

classification scheme matched a priori cluster assignments with 100% accuracy (results not shown). Two clusters (K2) had highest overall Rand index (0.095) when comparing genetic clade and cluster assignments, consistent with the Old versus New World split. Our expectation of four clusters (0.104) had the second highest Rand index when compared to genetic clades. When contrasted against subspecific assignment, this method under-predicts subspecific diversity, recognizing only 11 clusters (Rand index = 0.090).

Worldwide, ermine conform to clinal variation expected with Bergmann's rule ($R^2 = 0.19$, $p < .001$; Supporting Information S7, S8, S11). We found a significant portion of shape variation (13.5%) in the combined New and Old World dataset was influenced by allometry (results not shown). New World ermine increase in size with increasing latitude consistent with the thermoregulatory hypothesis (Bergmann's rule), while Old World specimens decrease in size with increasing latitude (Supporting Information S8), but the Old World relationship is non-significant and requires additional sampling. Despite smaller Old World sample sizes, the negative relationship between CS and latitude is significant ($p < .001$) when all Old World subspecies are considered together ($R^2 = 0.36$) and for insular Old World subspecies ($R^2 = 0.37$). Using CS as a proxy for body size, *M. e. arctica* is the largest New World subspecies and *M. e. olympica* the smallest. Subspecies *M. e. richardsonii* is the most

geographically widespread and also spans the greatest range of CS values (Supporting Information S8; Table 2). *Mustela e. erminea* and *M. e. kaneii* are the largest bodied Old World subspecies sampled, and *M. e. aestiva* the smallest sampled, although additional sampling from these regions is necessary to refine these analyses.

After removing shape variation correlated with allometry, we found significant size and shape differentiation ($p < .01$) between New and Old World ermine (Supporting Information S8–S13). New World ermine have a more elongated braincase, compressed rostrum and anteriorly shifted facial structure relative to the few sampled Old World ermine (Supporting Information S9). For this combined dataset, subspecies assignment had the highest correlation with shape variation of any factor examined (19%), followed by collection locality (9%; Supporting Information S10). Again, 65% of shape variation remained unexplained by the factors examined. With Old World samples included as part of the contiguous Holarctic Beringia clade, the CS of this clade increases to 5,099 (±374), demonstrating that Old World ermine are larger than New World and solidifying Beringia as the largest bodied genetic clade (Table 2). Within Old World ermine, most subspecies do not differ from one another in size and few differ significantly in shape, excluding two of the three Old World island populations examined (*M. e. hibernica*, Ireland, and *M. e. stabilis*, Great Britain). Compared with New World subspecies,

TABLE 2 Geometric morphometric (GMM) and molecular (Molec.) subspecific (Subspp.) sampling (N), type localities, average group centroid size (CS), ± a standard deviation (SD), and genetic clade assignments

	Subspecies	Abbrev.	GMM N	Molec. N	Type locality	Mean subspp. CS (±SD)	Clade	Mean clade CS (±SD)
New World	alascensis	ALA	21	28	North Pacific Coast, AK, USA	4,769 (±232)	East	4,502 (±411)
	bangsi	BAN	18		Minnesota, USA	4,883 (±213)		
	cicognanii	CIC	18	1	Eastern USA	4,716 (±183)		
	initis	INI	11	11	Baranof Island, AK, USA	4,674 (±228)		
	richardsonii	RIC	18	30	Central Canada	4,851 (±417)		
	semplei	SEM	1[a]		Southampton Island, Canada	5,319[b]		
	anguinae	ANG	1[a]		Vancouver Island, BC, Canada	4,395[b]	West	4,347 (±316)
	fallenda	FAL	9		BC, Canada	4,342 (±335)		
	gulosa	GUL	19		Washington, USA	4,076 (±102)		
	invicta	INV	11	6	Idaho, USA	4,517 (±123)		
	muricus	MUR	10	6	Western USA	3,817 (±219)		
	olympica	OLY	8		Olympic Peninsula, USA	3,925 (±215)		
	streatori	STR	19		West coast USA	4,209 (±181)		
	celenda	CEL	20		Prince of Wales Island, AK, USA	4,816 (±232)	NPC	4,735 (±268)
	haidarum	HAI	6	7	Haida Gwaii Islands, BC, Canada	4,493 (±240)		
	seclusa	SEC	1[a]		Suemez Island, AK, USA	4,888[b]		
	arctica	ARC	20	7	Central Alaska, USA	5,181 (±251)	NW Beringia	5,099 (±374)
	kadiacensis	KAD	9		Kodiak Island, AK, USA	5,155 (±223)		
	salva	SAL	19	8	Admiralty Island, AK, USA	4,680 (±249)		
Old World	aestiva	AES	11		Germany	5,547 (±280)	OW Beringia	
	erminea	ERM	6		Scandinavia	5,255 (±314)		
	ferghanae	FERG	3[a]		Northern India	4,585 (±161)		
	hibernica	HIB	6		Ireland	5,412 (±180)		
	kaneii	KAN	11	7	Western Siberia, Russia	4,923 (±314)		
	mongolica	MON	1[a]	1	Mongolia	5,672[b]		
	ricinae	RICIN	1[a]		Scotland	5,722[b]		
	stabilis	STA	5		Great Britain	5,616 (±355)		

[a]Low sample sizes removed from select analyses.
[b]Sample size too low to estimate a standard deviation.

there is mixed support for the morphological differentiation of several Old World subspecies, likely a consequence of low sample sizes. For example, four Old World subspecies (*hibernica*, *stabilis*, *aestiva* and *erminea*) exhibit significant size and shape differentiation, while 2 (*mongolica* and *ricinae*) show limited or inconsistent differentiation, and others differ only in shape, but not size (*ferghanae* and *kaneii*; Supporting Information S5); however, this may be an artefact of small samples sizes.

3.1 | Species delimitation

Newly generated sequences (57 mitochondrial genomes, 43 *ASIP*, 37 *FES*, 66 *GHR* and 78 *HTR1B*) were aligned with available GenBank resources (1 mitochondrial genome, 32 cytochrome *b*, 42 control region, 23 *ASIP*, 24 *FES*, 21 *GHR* and 22 *HTR1B*) to expand geographic coverage of ermine (Supporting Information S13). Mitochondrial genome phylogenies (Figure 5) consistently separated Beringia, NPC, East, and West lineages with strong support, while nuclear phylogenies had mixed support. Various prior values (θ and τ) did not impact *iBPP* results. We consistently identified at least three species with 100% posterior probability (PP), using integrated morphology and genetic data (Supporting Information S15). Delimited species correspond to Beringia, NPC Island, and combined East and West clades. Tests of four species, which recognize both the East and West clades, were also supported (>90% PP; Supporting Information S15). Genetic data alone parsed four species within the *M. erminea* species complex; however, tests of geometric morphometric data independently failed to parse the East and West clades as distinct species.

bPTP species delimitation, which integrates both nuclear and mitochondrial DNA, differentially identified some or all ermine clades as distinct species depending on the number of individuals examined. Tests of the nuclear SNP and mitochondrial genome phylogenies from Colella et al. (2018), with *M. putorius* as an outgroup, parsed all four refugial clades as distinct species (Bayesian) or grouped NPC and Beringia clades into a single species separate from East and West species (ML; Supporting Information S15), but with low support values. *bPTP* is designed for single-locus analyses, however, and assumes independent inheritance; therefore, low support values, particularly for genomic SNP data, are unsurprising. Analyses of mitochondrial genomes generated as part of this study, combined with mitogenomes from additional *Mustela* species, support four species within the *M. erminea* complex corresponding to the four genetic clades (Figure 5). This result remained consistent when our data was down-sampled to three individuals per clade, with varying support for an additional species within the NPC Island clade (0.56 and 0.30 PP), that did not appear to be geographically distinct. When a single representative of each clade was assessed, *bPTP* did not parse any species within *M. erminea*, but the same model also did not identify numerous other well-established *Mustela* species as distinct, including endangered *M. nigripes*, domestic *M. putorius*, and Old World polecats (*M. eversmanii* and *M. siberica*, Figure 5). Nuclear loci had mixed results (Supporting Information S16). On average, 290 nucleotide differences separate NPC and Beringia clade mitochondrial genomes. There are 476 mitochondrial differences between the NPC and East clades and 413 differences between East and Beringia clades, with percent pairwise differences ranging from 2% to 3% for mitochondrial genomes and from 0.8% to 3.2% for cytochrome *b* (East–West: 0.8%, East–Beringia: 3.2%).

FIGURE 5 Ultrametric maximum-likelihood phylogeny (left) based on complete mitochondrial genomes from each ermine clade and additional species within the genus *Mustela*, collected from GenBank. All nodes are highly supported (100 bootstrap support). Colored boxes (right) display maximum likelihood (ML) and Bayesian (B) support values (%) for *bPTP* species delimitation utilizing both mitochondrial and nuclear sequence data. Our "expectation" was that each node represents a distinct species, results for each *bPTP* run (All mitochondrial genomes [All], three representatives of each species [three rep.], and a single representative of each species [one rep.]) demonstrate variable support for a number of *Mustela* species. * indicates 100% support. 29* indicates runs where an additional species was identified within the NPC Island clade (with 56% support)
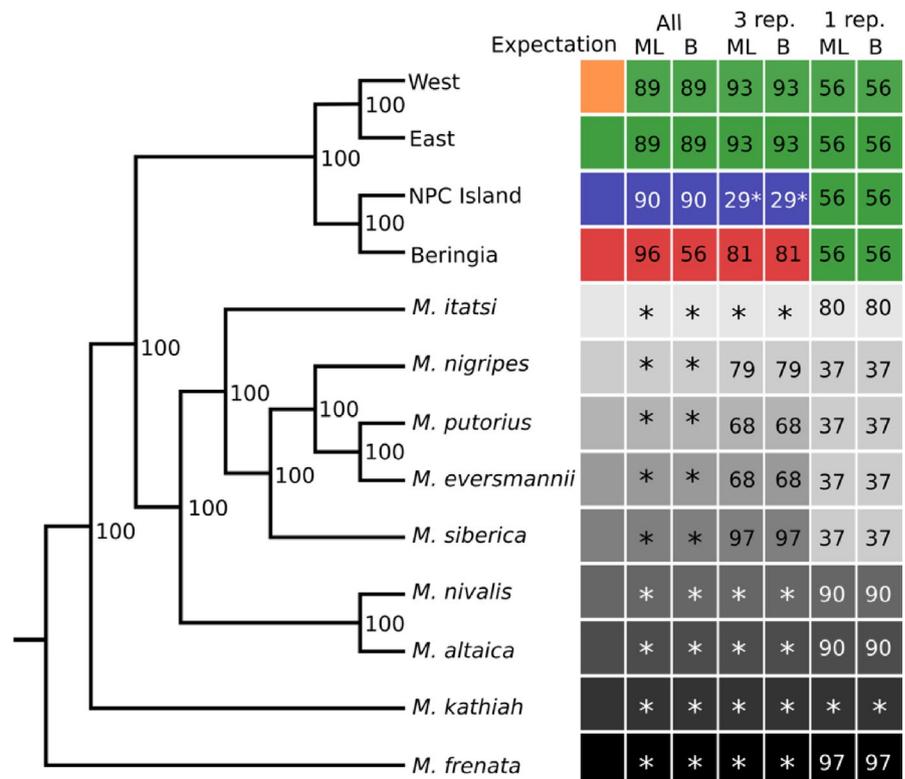
4 | DISCUSSION

The role of Pleistocene climate cycles in shaping diversity is especially complex for island systems. Opposite of patterns observed for continental species, lower sea levels during glaciation increase interisland connectivity and potentially foster genetic exchange, while rising sea levels in response to deglaciation fractures insular systems, isolating islands from source populations. These alternating, climate-mediated episodes of allopatry and connectivity are well characterized (Lawrence et al., 2010; McClymont et al., 2013), yet further nuanced for near-shore continental archipelagos compared with oceanic archipelagos for two reasons. First, continental archipelagos oscillate between connectivity with neighbouring islands and connectivity with major continental landmasses during glacial and interglacial cycles, respectively. Proximity to multiple potential source populations suggests that gene flow may occur more frequently among populations that inhabit continental archipelagos, relative to those on oceanic archipelagos which rely disproportionally on long-distance dispersal to facilitate gene flow. The frequency and duration of genetic exchange among islands and neighbouring continents is further mediated by the amplitude of glacial cycles and strength of geographic barriers (Kinoshita et al., 2019; Sato, 2016). Second, although some continental archipelagos were historically ice-covered through glacial maxima, others served as ice-free refugia that enabled geographically isolated persistence and divergence of peripheral terrestrial populations through ice ages (Byun et al., 1997; Kinoshita et al., 2019; Shafer et al., 2010). Together, episodic vicariance and connectivity, shaped by both climate and geographic complexity, have combined to produced elevated levels of insular endemism in continental archipelagos, despite their proximity to mainland source populations (Patiño et al., 2017; Alexander Archipelago, Alaska, USA, Dawson et al., 2007, Sawyer et al., 2019; Canary Islands, Spain, Caujapé-Castells et al., 2017; Haida Gwaii, British Columbia, Canada, Foster, 1965; Japanese Archipelago, Sato, 2016).

Connectivity and hybridization have been historically viewed as homogenizing forces (Cody, 2006; Whittaker & Fernández-Palacios, 2007); however, episodic bouts of gene flow and geographic isolation may synergistically elevate levels of insular endemism. Hybridization upon secondary contact introduces novel genetic material into small, otherwise isolated populations. Introgressed variants can accumulate cyclically (high allelic turn-over) or gradually overtime depending on the duration of isolation and contact. Introgressed variation may occasionally form the genetic framework necessary for rapid evolution of novel phenotypes, occasionally observed in island systems (Alcala & Vuilleumier, 2014; Caujapé-Castells et al., 2017; Larsen et al., 2010). For ermine, climate-mediated gene flow appears to have acted as a biodiversity "pump," periodically introducing novel variation (April et al., 2013; Avise et al., 1998; Colella et al., 2018; Haffer, 1969; Irl et al., 2017) that was slowly shaped through extended allopatry and a combination of neutral and selective evolutionary processes.

Morphological and genetic analyses are consistent with the hypothesis of Colella et al. (2018) that Haida ermine (*M. haidarum*,

Preble, 1898), as originally described, is a distinct species and represents a specialized case of hybrid speciation in mammals driven by extrinsic reproductive barriers (e.g. geographic isolation; Ottenburghs, 2018). Ancient hybridization between two diverging species is hypothesized to have occurred prior to the LGM (> 300 kya; Colella et al., 2018). We hypothesize that genetic mixing along the NPC was followed by extended geographic isolation of the hybrid population, first in a coastal glacial refugium (through the LGM) and later on at least three islands along the NPC, after sea levels rose in the late Pleistocene. Extended refugial and, now, insular isolation have provided sufficient time for speciation to occur. An influx of novel genetic material, followed by extended allopatry, may have contributed to the rapid divergence of insular endemic Haida ermine (Alcala & Vuilleumier, 2014). Divergence date estimates, based on a log-normal ermine fossil calibration (1.8 Mya, King, 1983) and complete mitochondrial genomes, suggest an initial split between Old World (NPC and Beringia) and New World (East and West) clades around 4.5 Mya. Subsequent divergence of Haida ermine (NPC) from the Beringia clade is dated to 2 Mya (Colella et al., 2018), again, sufficient for speciation to have occurred. The early hybrid history of *M. haidarum* along the NPC may be analogous to the contemporary ermine hybrid zone observed along the northern Alaska–Canada border today (Colella et al., 2018). The ancient hybrid signature evident in Haida ermine today may persist only as a consequence of subsequent and extended allopatric isolation, while the continental hybrid zone is expected to be more prone to break down over time and will ultimately contribute less to diversification processes. The geologic complexity of archipelagos may disproportionately preserve evidence of historical introgression, which may otherwise be lost through homogenization upon secondary contact (Currat et al., 2008). Integration of genomic evidence of introgression with more spatially extensive sampling and species delimitation methods clarifies of the varied impacts of range contraction and expansion, gene flow and diversification across the high latitudes, a framework that is essential for anticipating the evolutionary impacts of rapid environmental change now underway and projected into the future (Hope et al., 2013). Additional insular sampling and comparative analyses across varied taxa will better illuminate the generality of climate-driven isolation and contact as a mechanism of diversification.

The frequency, duration, and evolutionary impact of gene flow on island populations varies across space, time, and taxonomy depending on the geological history of the area, the strength and size of vicariant barriers, and the colonization and reproductive capacities of different organisms. At higher latitudes, we anticipate climate-mediated connectivity to have a greater impact on shaping the diversity of continental archipelagos, and particularly for those that also served as glacial refugia, as opposed to those that were post-glacially colonized. For example, stoats in Ireland exhibit greater genetic diversity than neighbouring stoat populations in the United Kingdom (UK), suggesting in situ refugial persistence through the LGM, similar to the refugial persistence of Haida ermine along the NPC of North America (Martinkova et al., 2007). In contrast, genetic similarity between stoats in the UK and those in continental Europe suggests

that the English Channel acts as a semi-porous or incomplete barrier to gene flow, while the deeper Irish Sea appears to have enabled the extended allopatric differentiation of Ireland stoats. Whether select glacial cycles were sufficient in magnitude to enable rare bouts of gene flow between UK and Ireland stoats remains to be explored from a genomic perspective. Similarly, there are two extant stoat lineages in the Japanese Archipelago. Early stoat migrants colonized Honshu Island of central Japan, while more recent colonists were restricted to northern Hokkaido Island, which was more often accessible by a land bridge to Sakhalin Island during glacial advances, but separated from Honshu Island by the deep Tsugaru Strait (Kurose et al., 1999, 2005; Sato, 2016). Similar distributional and introgression patterns have been observed in hare of the genus *Lepus* (Kinoshita et al., 2019). Introgression coincident with climatic cycling has been identified among east Asian mountain hares (*Lepus timidus*) and Manchurian hares (*L. mandshuricus*); however, similar to ermine, no introgression was found in Japanese hares (*L. brachyurus*) on the more isolated island of Honshu (Kinoshita et al., 2019). Interestingly, Corbet (1978) historically recognized only three ermine subspecies throughout the Holarctic: one in Ireland, one on Honshu Island, and one widespread throughout Eurasia and North America. Although Corbet (1978) did not sample ermine from the Alexanderor Haida Gwaii archipelagos, his hypothesis recognizes the evolutionary distinctiveness of refugial continental archipelagos and is consistent with our hypothesis that climate-driven cycles of connectivity and isolation may lead to the accumulation of endemicity in these areas.

Identification of a hybrid carnivore species that is endemic to the Alexander and Haida Gwaii archipelagos suggests that the geographic complexity of continental archipelagos may foster homoploid hybrid speciation or speciation with gene flow at an elevated frequency (i.e. hybridization without a change in chromosome number; Grant & Grant, 2014, 2016; Larsen et al., 2010; Schumer et al., 2014). Insular hybrid divergence of a non-volant mammal, with limited dispersal capacities relative to bats (Larsen et al., 2010) or birds (Grant & Grant, 2014, 2016), suggests that homoploid hybrid speciation may be more common in continental archipelagos, relative to oceanic. Secondary contact can occur more frequently within continental archipelagos through either interisland connectivity or dispersal from neighbouring coastlines, whereas gene flow in oceanic archipelagos relies on the vagaries of long-distance dispersal. Haida ermine meet at least two of the three criteria proposed by Schumer et al. (2014) for homoploid hybrid speciation, including: (a) demonstrated genetic isolation, in this case, geographic isolation prevents interbreeding between insular and continental lineages, although the presence of reproductive barriers has not been assessed, and (b) evidence of hybridization (e.g. Colella et al., 2018). The third criterion (c) hybrid-derived isolation remains to be explored from a molecular perspective. This proposed model of hybrid speciation invokes extrinsic reproductive barriers, unrecognized by classic models of hybrid speciation (Arnold, 1992), which primarily include: (a) fusion or homogenization, (b) maintenance of hybrid or tension zones, (c) reinforcement, and (d) hybrid speciation through intrinsic barriers (e.g. recombinational speciation, "Criterion 3"; Schumer et al., 2014).

Ottenburghs (2018) distinguishes between type I ("intrinsic") and type II ("extrinsic") hybrid speciation to account for additional processes driving reproductive isolation (e.g. vicariance) whereby Haida ermine represent an example of extrinsically mediated, type II homoploid hybrid speciation. Ultimately, this cyclic, deep-time process has important implications for continued discoveries of cryptic diversity in these regions and the conservation of endemism across complex landscapes.

4.1 | Implications for endemism

Archipelagos are renown hotspots of endemism (Brooks et al., 2002; Mittermeier et al., 2011), and the islands along North America's NPC are no exception, with >27 endemic mammal taxa (Cook et al., 2006; Dawson et al., 2007; MacDonald & Cook, 1996; Sawyer et al., 2019). Under a morphological species concept (Cronquist, 1978), cranial morphometrics support the recognition of three species within *M. erminea*; however, under a phylogenetic species concept (Baum & Shaw, 1995; Cracraft, 1983; Donoghue, 1985) both WGS (Colella et al., 2018) and amplicon genetic data (this study) would elevate all four clades to full species status. Nonetheless, because morphological and genetic changes do not occur in a predictable order, the evaluation of both data types independently highlights important differences in the mode and tempo of differentiation (de Queiroz, 1998). For example, while the *M. erminea* species complex exhibits significant morphological variation across geography (three species, with 22 to 34 subspecies therein; Eger, 1990; Hall, 1951), morphology alone does not detect significant divergence between East and West clades. That disparity is consistent with previous morphological investigations that identified clinal variation in size among North American ermine, explained by local adaptation to temperature and precipitation rather than geographic distance (Eger, 1990). Different patterns among molecules and morphology may be unsurprising for mustelids, which are known to exhibit extensive ecomorphological variation (Dumont et al., 2015; Law et al., 2018). Therefore, under the general lineage concept of species (Florio et al., 2012; De Queiroz, 2007), which cumulatively integrates and equally weights various lines of evidence (e.g. genetic, morphological) to support lineage separation, our results indicate that the *M. erminea* complex is comprised of at least three species: insular endemic *M. haidarum* and two geographically widespread continental species, one primarily Old World and one New World, a result that roughly mirrors phylogeographic breaks of other Holarctic mammals (brown bear, Matsuhashi et al., 2001; moose, Hundertmark et al., 2002; red fox, Kutschera et al., 2013; wolverine, Zigouris et al., 2013).

Beyond measured morphological and molecular differences between taxonomic units or within "the grey area of species delimitation," consideration of geography and taxon-specific biology (e.g. dispersal distances, colonization potential, mating strategies, life history) should also be weighed in the diagnosis of species. Although closely allied with its Beringian sister (*M. erminea*, Supporting Information S15; Kurose et al., 2005), Haida ermine are

geographically isolated. In contrast, the East and West clades exhibit only moderate geographic structuring across the Rocky Mountains (Figure 4), with divergence dated to ~1 Mya (Colella et al., 2018), leading to the conservative resolution of uniting these clades under a single species epithet (collectively, *M. richardsonii*, Bonaparte, 1838). Ecomorphological plasticity among mustelids and the role of spatio-temporal and geographic variation in shaping morphological variation are reflected in 30 morphologically distinct ermine subspecies also supported by these analyses (Table 3 and Supporting Information). This result is better aligned with New World estimates of ermine subspecific diversity proposed by Hall (1951) than the fewer subspecies proposed by Corbet (1978) or King (1983). Our proposed nomenclature change would elevate the oldest named taxon from the range of each clade. The original species epithet (*Mustela erminea*, Linnaeus, 1758) is assigned to the Beringia clade (holotype: USNM14062/23010 [skull/skin], type locality: Europe, later revised to Uppsala, Sweden; Cabrera, 1913; King, 1983), which spans much of Eurasia and into Alaska, consistent with sequence data from Kurose et al. (2005). We recommend the nomen *Mustela richardsonii* Bonaparte, 1838, for the most widespread continental North American species, corresponding to the combined East and West genetic clades. Although no holotype was established in the original species description (Bonaparte, 1838), NHMUK ZOO 1843.3.3.4 at the British Museum is a presumed lectotype for this species. Last, *M. haidarum* (Preble, 1898) represents the most divergent NPC Island species and includes weasels found on Prince of Wales and Suemez islands in the Alexander Archipelago of Southeast Alaska and on Graham and Moresby islands of the Haida Gwaii Archipelago of British Columbia, Canada (type specimen: USNM94430, collected in 1898 on Graham Island; Preble, 1898).

If the NPC was completely ice-covered throughout the LGM (Klein, 1965; Lesnek et al. 2018, Lesnek et al. 2020), there would be a low expectation of endemism in this region. In contrast, frequent discoveries of deeply divergent endemics along the NPC (Barry & Tallmon, 2010; Dawson et al., 2007; Sawyer et al., 2019) provide mounting evidence for the existence of one and possibly multiple coastal refugia along the NPC (Ager, 2019; Baichtal & Carlson, 2010; Carrara et al., 2003, 2007). Our results suggest that conservation efforts focus on insular endemics (Cook et al., 2006; Sikes & Stockbridge, 2013), as their unique molecular and morphological characteristics may rise to the species level with the analysis of additional data streams. Re-evaluation of cryptic diversity along the NPC is warranted and urgent given anthropogenic changes now underway and planned on numerous coastal islands (USDA, 2007a,b; Stewart, 2016). Old-growth timber harvests within the Tongass National Forest and industrial-scale mining have reduced available forest habitat on these islands (USDA, 2007a,b; Stewart, 2016) and may disproportionately impact insular endemics, such as the Haida ermine, and other non-volant species. Expanding human populations and other impacts (e.g. increasing tourism) along the NPC and the geographic proximity of these islands to the mainland also increases risks of anthropogenic wildlife introductions of invasive species or pathogens that may compete with or immunologically decimate

TABLE 3 Proposed revised ermine taxonomy recognizing three evolutionarily independent *Mustela* species coincident with phylogeography and at least 22 subspecies therein. Twelve additional subspecies require further examination: * indicates low sample sizes in this study, ** indicates unexamined

Proposed species	Subspecies	Authority and year	Req additional sampling
Erminea	*aestiva*	Kerr, 1792	
	arctica	Merriam, 1896	
	erminea	Linnaeus, 1758	
	ferghanae	Thomas, 1895	
	hibernica	Thomas and Barrett-Hamilton, 1895	
	kadiacensis	Merriam, 1896	
	kaneii	Baird, 1857	
	karaginensis	Jurgenson, 1936	**
	lymani	Hollister, 1912	**
	minima	Cavazza, 1912	**
	mongolica	Ognev, 1928	*
	nippon	Cabrera, 1913	**
	polaris	Barrett-Hamilton, 1904	**
	ricinae	Miller, 1907	*
	salva	Hall, 1944	
	stabilis	Barrett-Hamilton, 1904	
	teberdina	Korneev, 1941	**
	tobolica	Ognev, 1923	**
Haidarum	*celenda*	Hall, 1944	
	haidarum	Preble, 1898	
	seclusa	Hall, 1944	*
Richardsonii	*alascensis*	Merriam, 1896	
	anguinae	Hall, 1932	*
	bangsi	Hall, 1945	
	cicognanii	Bonaparte, 1838	
	fallenda	Hall, 1945	
	gulosa	Hall, 1945	
	initis	Hall, 1945	
	invicta	Hall, 1945	
	muricus	Bangs, 1899	
	olympica	Hall, 1945	
	richardsonii	Bonaparte, 1838	
	semplei	Sutton and Hamilton, 1932	*
	streatori	Merriam, 1896	

naïve endemics (Ritchie & Johnson, 2009). For example, multiple pathogens common to pets, including canine distemper and parvoviruses, have negatively impacted wild mustelids (Keller et al., 2012; Williams et al., 1988), and the devastating reports of recent

transmission of SARS-CoV-2 from humans to mustelids are yet another potential conservation challenge (Franklin & Bevins, 2020; Gryseels et al., 2020; Molenaar et al., 2020). Given our still rudimentary understanding of much of the diversity in large northern archipelagos, threats to insular endemic diversity should be better quantified to preemptively inform management decisions.

DATA AVAILABILITY STATEMENT

Sequence data are available on GenBank (Accession Numbers: MK584176–584284; MK602925–603008; MK603010–603014; MK603869–603900; MK603869–603915; MK609859–609895). Landmark coordinate data (TPS files) and associated images (.JPG) are available from the Dryad Digital Repository: http://dx.doi.org/10.5061dryad.754vq8n.

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BIOSKETCH

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