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# A recovery network leads to the natural recolonization of an archipelago and a potential trailing edge refuge

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*Abstract.* Rapid environmental change is reshaping ecosystems and driving species loss globally. Carnivore populations have declined and retracted rapidly and have been the target of numerous translocation projects. Success, however, is complicated when these efforts occur in novel ecosystems. Identifying refuges, locations that are resistant to environmental change, within a translocation framework should improve population recovery and persistence. American martens (*Martes americana*) are the most frequently translocated carnivore in North America. As elsewhere, martens were extirpated across much of the Great Lakes region by the 1930s and, despite multiple translocations beginning in the 1950s, martens remain of regional conservation concern. Surprisingly, martens were rediscovered in 2014 on the Apostle Islands of Lake Superior after a putative absence of >40 yr. To identify the source of martens to the islands and understand connectivity of the reintroduction network, we collected genetic data on martens from the archipelago and from all regional reintroduction sites. In total, we genotyped 483 individual martens, 43 of which inhabited the Apostle Islands (densities 0.42–1.46 $km^{-2}$). Coalescent analyses supported the contemporary recolonization of the Apostle Islands with progenitors likely originating from Michigan, which were sourced from Ontario. We also identified movements by a first-order relative between the Apostle Islands and the recovery network. We detected some regional gene flow, but in an unexpected direction: individuals moving from the islands to the mainland. Our findings suggest that the Apostle Islands were naturally recolonized by progeny of translocated individuals and now act as a source back to the reintroduction sites on the mainland. We suggest that the Apostle Islands, given its protection from disturbance, complex forest structure, and reduced carnivore competition, will act as a potential refuge for marten along their trailing range boundary and a central node for regional recovery. Our work reveals that translocations, even those occurring along southern range boundaries, can create recovery networks that function like natural metapopulations. Identifying refuges, locations that are resistant to environmental change, within these recovery networks can further improve species recovery, even within novel environments. Future translocation planning should a priori identify potential refuges and sources to improve short-term recovery and long-term persistence.

*Key words:* *American marten; Apostle Islands National Lakeshore; coalescence; heterogeneity;* Martes americana*; population genetics; reintroduction.*

## Introduction

Rapid environmental change is reshaping the composition and structure of ecosystems globally. In particular, the combination of land-use and climate change have isolated and extirpated numerous vertebrate populations (Laliberte and Ripple 2004). Recovering these populations has motivated conservation biologists for over a century (Seddon et al 2014). Environmental change presents challenges for conservation because recovery must occur in novel ecosystems—systems that are dissimilar to historical baselines and often without analog elsewhere (Radeloff et al. 2015). A species response to

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novelty is often unknown, and complicates efforts to recover declining or extirpated populations (Hobbs et al. 2006). Species recovery, then, represents a "wicked problem" in conservation, in which multiple and complex drivers need to be simultaneously addressed to arrive at potential solutions (Defries and Nagendra 2017).

Translocations are used to repatriate species to areas once occupied or augment existing populations (Griffith et al. 1989, Seddon et al. 2007). Although identifying factors that lead to translocation success can be difficult (Fischer and Lindenmayer 2000), successful translocations generally occur in high-quality habitat, featuring a large number of incipient individuals (Deredec and Courchamp 2007, Tracy et al. 2011). However, many translocations are unsuccessful, because they increasingly occur in novel ecosystems and fail to mitigate conditions that led to the initial extirpation (Armstrong and Seddon 2008, Osborne and Seddon 2012). To improve translocation success, biogeographical concepts like metapopulation dynamics are increasingly being integrated into reintroduction biology, especially to the identification of potential refugia (Armstrong and Seddon 2008).

Refuge or "pseudosource" (Vuilleumier et al. 2007, Elkin and Possingham 2008) populations are large and demographically growing populations that provide consistent immigrants that can enhance recruitment for the recipient populations and, therefore, increase the viability for the overall metapopulation (Boudjemadi et al. 1999, Hastings and Botsford 2006). Recently, a broader refugial concept has gained traction in the identification of areas that provide intermediate refuges and long-term refugia from biotic and abiotic conditions to create population holdouts in the face of rapid land-use and climatic change (Keppel et al. 2012, Monsarrat et al. 2019). Although the importance of refuges in ecology and conservation biology are widely recognized (Akçakaya et al. 2006), and would be ideal targets for translocations and species recovery, they are rarely identified prior to reintroductions (although see Struebig et al. [2015], Conner et al. [2018]). Indeed, information on those fundamental attributes of a potential refuge including resistance to environmental change (i.e., landscapes that resemble historical conditions and are protected from future perturbations), connectivity (i.e., the potential for dispersers to naturally recolonize surrounding areas), and demographic potential (i.e., a net exporter of individuals) are rarely documented, even though they would enhance both translocation success and the future persistence of recovering populations.

Centuries of land-use change have altered forest structure and composition across North America, and these legacies are critical to addressing current conservation challenges (Hall et al. 2002, Foster et al. 2003). Like elsewhere in North America, the Great Lakes region historically was forested, and compositionally and structurally complex until the late 1800s when the region was largely cut over by commercial logging (Schulte et al. 2007). This historic legacy has left contemporary forests in the Great Lakes region that are different in composition and structure: 44% loss of medium- to large-diameter trees, a threefold increase in early successional species, and a near complete loss of eastern hemlock (*Tsuga canadensis*) and pine (*Pinus* spp.) forest cover (22% to 1% [White and Mladenoff 1994, Rhemtulla et al. 2009]). Concomitant with regional forest change and homogeneity, a number of forest carnivores that were once widespread—American martens (*Martes americana*), fishers (*Pekania pennanti*), Canada lynx (*Lynx canadensis*), gray wolves (*Canis lupus*)—were extirpated from most of the Great Lakes region (Petersen et al. 1977, Thiel 1987, Mech 1995, Williams et al. 2007) or persisted in small and isolated populations (De Vos 1964).

Because of the disproportionate effects of carnivores on ecosystems (Estes et al. 2011, Ritchie et al. 2012) and their global decline in abundance and distribution (Ripple et al. 2014), carnivores are among the most frequently translocated species (Seddon et al. 2005). However, because of slow life histories, large spatial requirements, and low population densities, translocations are often unsuccessful (Griffith et al. 1989, Miller et al. 1999). American martens are the most frequently translocated (>50 times) carnivore in North America, yet translocation success rate is low (<50%; Powell et al. 2012, Manlick et al. 2016). Along their southern range boundary in the Great Lakes region, martens were extirpated by the 1930s, with only a small population remaining in northeastern Minnesota (Mech and Rogers 1977). In the 1950s, the first translocations occurred with the release of 10 adult martens (Pacific marten, *M. caurina*) from Montana and British Columbia to the Apostle Islands, Wisconsin (Woodford and Dumyahn 2011). Pacific martens were considered to be American martens at the time, but are now considered to be nonnative in this region. The last reported observation on the Apostle Islands occurred in 1969, and the translocation was considered a failure (Kohn and Eckstein 1987). Beginning in the 1970s and continuing to 2010, martens were reintroduced to mainland Wisconsin in two disjunct areas in the Chequamegon and Nicolet National Forest (Woodford et al. 2013). Martens were translocated from Minnesota to the Chequamegon National Forest and from Ontario and Colorado to the Nicolet National Forest (Williams et al. 2007). During this time, Michigan continued reintroduction efforts, sourcing martens from Ontario. Thus, dozens of translocations spanning 60 yr has created a recovery network—similar to a natural metapopulations but emerging from human agency—that features multiple subpopulations of martens occurring in areas of varying habitat quality and demographic potential, but with unknown connectivity. Consequently, long-term viability of this species is uncertain (Skalski et al. 2011, Manlick et al. 2016, Grauer et al. 2019). Unexpectedly, a marten was observed in 2014 on an Apostle Island, motivating research that has uncovered past

photographic records dating martens back to 2010. To date, martens have been detected on 8 of 22 islands (Allen et al. 2018).

Since 2004, martens have been noninvasively genotyped (Pauli et al. 2010) across the Great Lakes region, resulting in the genetic tagging of >800 individuals (Williams et al. 2009, Williams and Scribner 2010, Koen et al. 2012, Manlick et al. 2016, Grauer et al. 2017, Manlick et al. 2018, Grauer et al. 2019). Genetic tagging of martens has quantified the demographic attributes and processes of subpopulations (Williams et al. 2009, Manlick et al. 2016, Grauer et al. 2019), impact of augmentation on a reintroduced population (Manlick et al. 2016), influence of immigration on recovering populations (Grauer et al. 2019), effect of founding populations (Williams and Scribner 2010, Grauer et al. 2017, Manlick et al. 2018), and landscape features that influence genetic structure (Koen et al. 2012, Howell et al. 2016). Despite extensive research on individual translocations, it is unclear how well these subpopulations are connected and how the relationships of these subpopulations could create a recovery network and aid in species recovery along this trailing range boundary.

Herein, we describe a recovery network following extensive translocations and explore the potential role of sites to act as a current and future refuge for recovery. We employed a combination of genetic data and coalescence simulations to identify the source and timing of marten recolonization of the Apostle Islands, estimate the genetic structure and diversity of each subpopulation and across all subpopulations, and to quantify the degree of and directionality of connectivity within the potential recovery network. Ultimately, through our regional analysis, we aimed to understand how decades of disjunct translocations can shape species recovery at regional and landscape scales and assess the differential importance that individual subpopulations play in species recovery. Additionally, we explored the fundamental attributes leading to the colonization and expansion of a repatriated species to inform future translocation planning.

## Methods

### *Sampling*

To quantify levels of genetic diversity within and levels of differentiation among subpopulations, and gene flow within a recovery network, we used previously genotyped individuals from seven putative subpopulations (Fig. 1a). We used genetic samples from individuals in two geographically disjunct subpopulations in Wisconsin (WI-CF: $N = 48$ and WI-NF: $N = 46$; 2007–2017 [Manlick et al. 2016, Grauer et al. 2017]), three putative subpopulations in Michigan identified from genetic assignment tests (MI-Central, MI-Eastern, MI-Western; $N = 65$ per population; 2004 [Williams and Scribner 2010]), individuals from Minnesota ($N = 61$; 2008–2010) that were used for the most recent augmentation into Wisconsin (Woodford et al. 2013, Manlick et al. 2016), and harvested martens from Ontario ($N = 61$; 2004–2005 [Manlick et al. 2016, Grauer et al. 2017]). Lastly, we used samples of Pacific martens from Colorado ($N = 29$ [Grauer et al. 2017]), as this is the most likely species that was translocated to the Apostle Islands in the 1950s (Woodford and Dumyahn 2011). In total, 440 genotyped martens from the recovery network were included in our analyses (Fig. 1a). On the Apostle Islands (WI-AI), we collected hair samples from noninvasive hair traps (modified from Pauli et al. [2008]) set at random locations with a minimum of 500 m apart in 2017 and 2018. Given the discrete nature of the populations, historical translocation events, and local management strategies, we maintained the use of previously identified and geographic populations in our analyses.

### *Genotyping and individual identification*

We extracted DNA from hair samples using QIAamp DNA micro kit (Qiagen, Valencia, California, USA) in a room dedicated to low-quality DNA samples. We developed a species-specific quantitative polymerase chain reaction (PCR) assay for American marten designed from previously published mitochondrial DNA (mtDNA) sequences obtained from GenBank (see Appendix S1: Table S1 and Supporting Methods for detailed description). Samples that were positive for marten mitochondrial DNA were genotyped at 14 polymorphic microsatellite loci: Ma1, Ma2, Ma5, Ma7, Ma8, Ma11, Ma14, Ma19, Gg3, Gg7, and Tt4 (Davis and Strobeck 1998); and Mer022, Mer041, and Mvis072 (Fleming et al. 1999). We combined microsatellite loci into two multiplexes (MP1: Ma1, Ma2, Ma11, Ma14, Gg7, Mer022; MP2: Ma5, Ma7, Ma8, Ma19, Tt4, Gg3, Mer041, Mvis072) and validated amplification and fragment lengths from previously genotyped individuals. For Multiplex 1, PCRs were conducted in 10-μL reactions containing 2 μL of DNA, 2X Multiplex PCR Mastermix (Qiagen), and labeled primers (FAM, VIC, and NED) with the following concentrations: Ma1 (0.2 μmol/L), Ma2 (0.2 μmol/L), Ma11 (0.15 μmol/L), Ma14 (0.5 μmol/L), Gg7 (0.08 μmol/L), and Mer022 (0.5 μmol/L). For Multiplex 2, PCRs were conducted in 10-μL reactions containing 2 μL of DNA, 2X Multiplex PCR Mastermix (Qiagen), 1XL Q-solution (Qiagen), and labeled primers (FAM, VIC, and NED) with the following concentrations: Ma5 (0.2 μmol/L), Ma7 (0.2 μmol/L), Ma8 (0.2 μmol/L), Mer041 (0.2 μmol/L), Mvis072 (0.2 μmol/L), Gg3 (0.15 μmol/L), Ma19 (0.1 μmol/L), and Tt4 (0.05 μmol/L). PCR conditions for both multiplexes included an initial denature at 94°C for 15 min, 40 cycles of 94°C for 30 s, 57 for 90 s, 72°C for 60 s, and a final elongation at 60°C for 30 min. We analyzed samples on an ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, California, USA), and scored microsatellite alleles using GeneMapper® Software 5

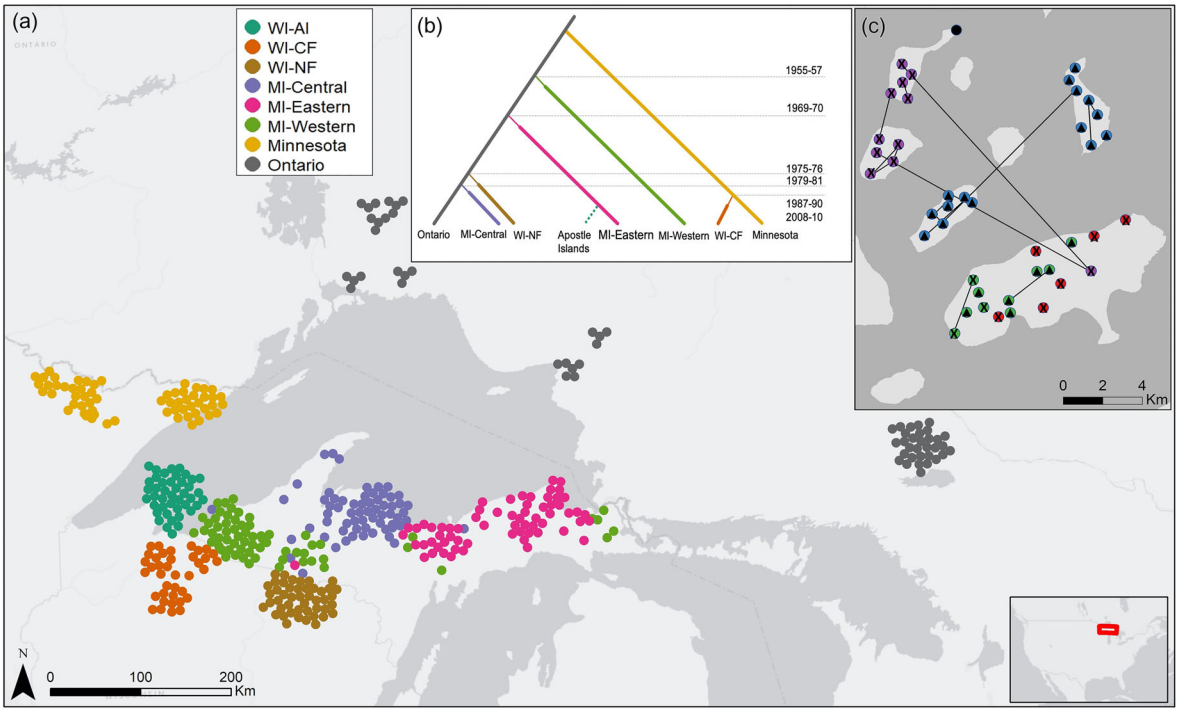


FIG. 1. Map of American marten (*Martes americana*) samples collected from the regional recovery network: Apostle Islands, Wisconsin, United States (WI-AI), Chequamegon National Forest, Wisconsin, United States (WI-CF), Nicolet National Forest, Wisconsin, United States (WI-NF), central Upper Michigan (MI-Central), eastern Upper Michigan (MI-Eastern), western Upper Michigan (MI-Western), Minnesota, and Ontario used to identify source and connectivity. A location jitter was placed on individual points for viewing (a). An example diagram of the tree topology used to test alternate colonization scenarios with dates of historical translocation events (b). For full set of scenarios see Appendix S1: Fig. S1. Individual clustering assignments of American marten (*Martes americana*) sampled from the Apostle Islands, Wisconsin, United States (WI-AI) from STRUCTURE using the admixture ancestry model with correlated allele frequencies. Different colors represent unique genetic clusters from $K = 4$ with black circle representing individuals that had $q$ values <50% admixture proportions. For $K = 2$, individual cluster assignments are represented with black × and triangle. Black lines represent first order relatives (parent-offspring or full-sibships) consistent at 95% confidence (c).

(Applied Biosystems). Samples were genotyped independently in triplicate and we required two replicates to confirm a heterozygous genotype and three replicates to confirm a homozygous genotype at each locus to account for allelic dropout and false alleles. Samples that amplified >3 loci, but <10 loci were rerun in triplicate. All samples were scored from 3 to 6 independent PCR reactions to minimize genotyping errors (Taberlet et al. 1996) and unresolved loci (i.e., did not meet required replication) were censored at the given locus. We assessed power to discriminate between individuals by calculating the probability of identity ($P_{ID}$) and the probability of identity siblings ($P_{IDSIB}$ [Waits et al. 2001]) in CERVUS (Kalinowski et al. 2007). We also calculated a genotype accumulation curve in *poppr* (Kamvar et al. 2014) in R (R Development Core Team 2020) that randomly samples loci and counts the number of multilocus genotypes observed. We had enough power to identify unique individuals with a minimum of seven loci and subsequently removed all samples that failed to amplify at <7 loci (50% genotyped). Genotyping error rate in replicate PCR reactions was calculated using the R (R Development Core Team 2020) package *ConGenR* (Lonsinger and Waits 2015). Once consensus genotypes were confirmed, we grouped replicate genotypes to identify unique martens from the hair samples using *allelematch* in R (Galpern et al. 2012, R Development Core Team 2020). Because of DNA template quality of noninvasive samples, genotyping errors can occur and inflate the number of unique genotypes. We accounted for mismatches in samples that would still be assigned to the same individual by identifying an accepted number of allele mismatches using the amUniqueProfile function in *allelematch* ($N = 2$; Galpern et al. 2012).

### *Genetic diversity and differentiation*

We tested loci for deviations from Hardy–Weinberg proportions and linkage disequilibrium in Genepop (Raymond and Rousset 1995, Rousset 2008) applying a sequential Bonferroni correction to account for multiple tests (Rice 1989). For all subpopulations, we estimated genetic diversity by calculating the average number of alleles, allelic richness using rarefaction, private alleles,

observed and expected heterozygosity with packages *DiveRsity* (Keenan et al. 2013) and *poppr* (Kamvar et al. 2014) in R (R Development Core Team 2020). Additionally, we estimated genetic diversity measures within five of the Apostle Islands as well as contemporary effective population size ($N_e$) using the linkage disequilibrium method with random mating (Waples 2006, Waples and Do 2010) implemented in NeESTIMATOR (Do et al. 2014). We evaluated estimates of $N_e$ with allele frequencies greater than >0.02 and >0.01 to account for potential upward bias due to rare alleles (Waples and Do 2010). The Linkage disequilibrium method assumes discrete generations, random mating, and closed populations (Waples and England 2011); however, this method can perform well when $N_e$ is small, as observed in these populations (Robinson and Moyer 2013).

To identify genetic differentiation between subpopulations, we first calculated pairwise $G'_{ST}$ (Hedrick 2005), $D$ (Jost 2008), and $F_{ST}$ (Weir and Cockerham 1984) with 95% confidence intervals using 5,000 permutations in *DiveRsity* (Keenan et al. 2013). We used a discriminant analysis of principle components (DAPC) on multilocus genotypes to visualize and predict group membership of individuals from the Apostle Islands with individuals from the other subpopulations. We constructed a DAPC that only included putative subpopulations in the recovery network and predicted placement of individuals from the Apostle Islands by centering and scaling individuals to the DAPC constructed from individuals from the mainland (Jombart 2008, Jombart et al. 2010). We calculated the optimal number of principle components to retain using the alpha-score optimization (Jombart 2008, Jombart et al. 2010).

In addition, to quantify genetic relationships within the archipelago, we inferred genetic clusters of martens on the Apostle Islands to identify genetic similarities across islands. We implemented clustering algorithms in Structure v2.3.4 with 500,000 Markov chain Monte Carlo iterations after 100,000 burn-in using admixture ancestry model with correlated allele frequencies (Pritchard et al. 2000). We ran 10 replicates for each $K = 1$–$10$ and the most supported $K$ was determined by examining the change in the mean posterior probability across $K$ (mean Ln $P(K)$) and by estimating $\Delta K$ (Evanno et al. 2005). Replicate runs at each supported $K$ were merged and aligned using CLUMPP (Jakobsson and Rosenberg 2007). We assigned individuals to genetic clusters when admixture proportions were ≥0.5 otherwise individuals were left unassigned. Bayesian clustering was conducted using functions or wrapper functions in the R package *strataG* (Archer et al. 2017, R Development Core Team 2020).

### *Evaluation of colonization scenarios*

To identify the most likely source of martens on the Apostle Islands, we tested three hypotheses: (1) pre-extirpation holdout, (2) 1950s translocation holdout, and (3) contemporary colonization. A pre-extirpation holdout would be a relic lineage that has persisted undetected since before regionwide extirpation and would represent an evolutionary significant unit and a high priority for conservation efforts. In contrast, a 1950s translocation holdout from human-aided translocation, featuring a different and exotic species of marten (Pacific marten), would complicate future management decisions and disqualify the archipelago as a refuge for American marten. A contemporary colonization would signify that martens have dispersed to the islands from the mainland and in recent time suggest the Apostle Islands are an important refuge for martens. Both a pre-extirpation holdout and contemporary colonization would signify an important subpopulation within the recovery network. We defined a pre-extirpation scenario as a single model that had the marten population on the Apostle Islands splitting from an Ontario source before regional extirpation in the 1920s. We modeled a contemporary recolonization with six different scenarios where the marten population on the Apostle Islands split from a source within the recovery network after 1920. We tested competing scenarios in an approximate Bayesian computational (ABC) framework (Beaumont 2010, Bertorelle et al. 2010).

### *Simulations, model selection, and parameter estimation*

We modeled all colonization scenarios with the known source and timing of translocation events of martens in the region (Williams et al. 2007), but varied by the location and timing of the branch leading to the current sample of individuals from the Apostle Islands for a total of seven potential models (Fig. 1b; see Appendix S1: Fig. S1 for all tree topologies). We included parameters of the contemporary effective population size, timing of translocation or splitting event, reintroduction effective population size, and duration of the bottleneck following reintroduction (Table 1, Fig. 1b). We simulated historical parameters from a uniform distribution and the minimum and maximum values were obtained from demographic data and records on reintroduction events (Table 1). Specifically, priors on current effective population size for the Wisconsin and Upper Michigan populations were informed by abundance estimates or genetic data (Skalski et al. 2011, Manlick et al. 2016, Grauer et al. 2019). We used the timing of reintroduction events and the number of martens released during reintroduction to inform priors on timing parameters (t2, t3, t4, t5, t6) and reintroduction effective population size (Table 1; Williams et al. 2007). Consequently, the timing of colonization for the Apostle Islands had to occur concurrent with or after the establishment of the mainland population given the scenario. All timing parameters were estimated in generations and we considered a generation time of 5 yr for martens (Clark et al. 1987). We implemented a generalized stepwise mutation model, and the mean mutation rate was bound between $8.1 \times 10^{-3}$ and $8.0 \times 10^{-5}$ as extreme values observed in

mammalian microsatellites (Peery et al. 2012). We summarized data sets with all available one- and two-sample summary statistics in DIY ABC (see Cornuet et al. [2014] for complete list) and simulated 30,000 replicates per candidate model ($N = 210{,}000$) in DIYABC (Cornuet et al. 2014).

We used a random forest method for model selection and estimate posterior probabilities of competing models using 500 trees for each random forest analysis implemented in the package *abcrf* (Pudlo et al. 2016, Raynal et al. 2019) in R (R Development Core Team 2020). We included all summary statistics ($N = 256$) and the linear discriminant analysis axes in the random forest analysis as model selection is robust to the choice of summary statistics (Pudlo et al. 2016, Fraimout et al. 2017). We evaluated model selection and inference by comparing classification votes, prior error rates, and recording out-of-bag error rates that assess the proportion of data sets that are misassigned to alternate models. We also performed a linear discriminant analysis on the simulated and observed data sets to visualize model fit to the observed data in the R package *abcrf* (Pudlo et al. 2016, R Development Core Team 2020). We conducted posterior model checking in DIYABC by simulating 100,000 data sets of the most supported model and selected a posterior sample of 10,000 closest to the observed data following a rejection step and local regression treatment (Cornuet et al. 2010). We estimated summary statistics from 1,000 new simulated data sets drawn from the posterior distribution. We compared simulated summary

Table 1. Description of parameters and priors used for all colonization scenarios and estimated parameter values from the most supported model from the approximate Bayesian computation analysis.

| Parameter | Population | Description | Prior | Posterior estimate | | |
|---|---|---|---|---|---|---|
| | | | | Median | Q2.5 | Q97.5 |
| N1 | Apostle Island | Contemporary effective population size | 1–25 | 14 | 3 | 24 |
| N2 | WI-CF | Contemporary effective population size | 10–100 | 52 | 12 | 98 |
| N3 | MI-Central | Contemporary effective population size | 10–1,000 | 424 | 18 | 957 |
| N4 | Minnesota | Contemporary effective population size | 10–10,000 | 5,753.14 | 589 | 9,760 |
| N5 | WI-NF | Contemporary effective population size | 10–250 | 102 | 14 | 245 |
| N6 | Ontario | Contemporary effective population size | 10–10,000 | 4,875 | 777.875 | 9,449 |
| N7 | MI-Western | Contemporary effective population size | 10–1,000 | 425 | 21 | 977 |
| N8 | MI-Eastern | Contemporary effective population size | 10–1,000 | 424 | 22 | 977 |
| t1 | Apostle Island | Timing of colonization from source | 1–10,000 | 4 | 2 | 9 |
| t2 | WI-CF | Time of reintroduction | 1–6 | 3 | 1 | 6 |
| t3 | MI-Central | Time of reintroduction | 6–8 | 7 | 6 | 8 |
| t4 | WI-NF | Time of reintroduction | 6–8 | 7 | 6 | 8 |
| t5 | MI-Eastern | Time of reintroduction | 9–10 | 9 | 9 | 10 |
| t6 | MI-Western | Time of reintroduction | 11–12 | 12 | 11 | 12 |
| t7 | Minnesota | Split from Ontario | 50–500 | 234 | 58 | 478 |
| N3r | MI-Central | Reintroduction effective population size | 5–500 | 91 | 13 | 465 |
| N5r | WI-NF | Reintroduction effective population size | 5–500 | 213 | 21 | 489 |
| N8r | MI-Eastern | Reintroduction effective population size | 5–250 | 28 | 5 | 226 |
| N7r | MI-Western | Reintroduction effective population size | 5–100 | 56 | 12 | 96 |
| N2r | WI-CF | Reintroduction effective population size | 5–500 | 238 | 35 | 480 |
| rb(WI-CF) | WI-CF | Duration of reintroduction bottleneck | 1–6 | 4 | 1 | 6 |
| rb(MI-C) | MI-Central | Duration of reintroduction bottleneck | 1–8 | 5 | 1 | 8 |
| rb(WI-NF) | WI-NF | Duration of reintroduction bottleneck | 1–8 | 5 | 1 | 8 |
| rb(MI-E) | MI-Eastern | Duration of reintroduction bottleneck | 1–10 | 6 | 2 | 10 |
| rb(MI-W) | MI-Western | Duration of reintroduction bottleneck | 1–12 | 7 | 2 | 12 |

*Notes:* Prior values are minimum and maximum simulated values from a uniform distribution. Contemporary effective population sizes were informed by current population size estimates or genetic data (Skalski et al. 2011, Manlick et al. 2016, Grauer et al. 2019). Historical release dates and the number of released individuals informed parameters for the timing of reintroductions and reintroduction effective population sizes (Williams et al. 2007). Priors for the duration of reintroduction bottleneck was set as the time of reintroduction to present. All timing parameters are in generations. Contemporary effective population size for the Apostle Islands, Wisconsin, United States (N1), Chequamegon National Forest, Wisconsin, United States (N2), central Upper Michigan (N3), Minnesota (N4), Nicolet National Forest, Wisconsin, United States (N5), Ontario (N6), western Upper Michigan (N7), and eastern Upper Michigan (N8). Translocation time or population splitting are labeled t1 for the Apostle Islands, t2 for Chequamegon National Forest, Wisconsin, United States, t3 for central Upper Michigan, t4 for Nicolet National Forest, WI, t5 for eastern Upper Michigan, t6 for western Upper Michigan, and t7 for Minnesota. Timing parameters with "rb" represent duration of bottleneck following translocation to the Chequamegon National Forest, WI (rb(WI-CF)), central Upper Michigan (rb(MI-C)), Nicolet National Forest, Wisconsin, United States (rb(WI-NF), eastern Upper Michigan (rb(MI-E)), and western Upper Michigan (rb(MI-W)). Effective population size of translocated population in the Chequamegon National Forest, WI (N2r), central Upper Michigan (N3r), Nicolet National Forest, WI (N5r), western Upper Michigan (N7r), and eastern Upper Michigan (N8r).

statistics to observed summary statistics by computing posterior predictive *P* values that identified the probability that simulated summary statistics are more extreme than observed statistics (Bertorelle et al. 2010, Cornuet et al. 2010).

Lastly, we estimated posterior parameter densities from the most supported model using a random forest regression with 500 trees from 30,000 simulated data sets (Raynal et al. 2019). We evaluated our ability to estimate parameters by comparing the correlation between simulated and predicted parameter values from the random forest regression. We visually compared prior and posterior parameter densities from the most supported model.

### *Relatedness and dispersal detection*

To identify interisland connectivity, we used estimates of relatedness between individuals to infer likely pedigree relationship. On the Apostle Islands, we estimated relatedness and identified first-order relationships (i.e., parent–offspring pairs or full-sibships) consistent at 95% confidence using a maximum-likelihood approach in ML-RELATE (Kalinowski et al. 2006). We also analyzed a combined data set following the same procedure in ML-RELATE (Kalinowski et al. 2006) that included individuals from the closest subpopulation with the islands. We included the combined data set due to the proximity and previous sampling effort (2012–2013) that estimated >65% of the population ($N = 22.6$ [confidence interval (CI) 16.89–37.03] [Manlick et al. 2018]). Related individuals would suggest recent movement between the two locations and that contemporary connectivity occurs.

Relatedness estimation relies on the frequency of alleles in the population, but often the true frequency of alleles is unknown from observed genetic data. Thus, pedigree relationships can be influenced by the number of alleles, sampling effort, and population structure. We assessed our power given our observed alleles and sensitivity under alternate allele frequency distributions to infer relationships with simulations (see Appendix S1: Table S6 and Supporting Methods for more details). For the Apostle Island data set and the combined data set of the Apostle Islands and the closest subpopulation, we simulated individuals with known relationships from our observed allele frequencies and compared simulated group means in the R-package *related* (Pew et al. 2015, R Development Core Team 2020). For the combined data set of the Apostle Islands and closest subpopulation, we also evaluated the consistency in relationships under two alternate allele frequencies that do not assume Hardy–Weinberg proportions to estimate expected genotypic frequencies. We tested the sensitivity of our first-order relationships by simulating pedigree relationships from observed allele frequencies and two alternate allele frequency distributions (uniform and triangular) of our observed alleles.

### *Gene flow*

Pairwise gene flow was quantified to assess the degree of connectivity within the recovery network. By identifying differences in the directionality of gene flow, we can explore relationships (i.e., sources) between subpopulations. We estimated the direction and rate of contemporary gene flow among pairs of populations. Using Bayesian posterior probabilities, we estimated recent gene flow (2–3 generations) by assigning individuals to source populations based on population allele frequencies while accounting for inbreeding (BAYESASS 3.0 [Wilson and Rannala 2003]). We did not include historical reintroduction sources (Minnesota and Ontario), as geographical distance and barriers would make gene flow implausible. We used $10^7$ Markov chain Monte Carlo replications after a burn-in of $10^6$ runs. Mixing parameters were adjusted to achieve recommended acceptance rate ($a = 0.25$, $f = 0.30$ [Wilson and Rannala 2003]). We generated 10 independent runs with random starting seeds and evaluated trace files to confirm convergence and consistency across runs.

To explore directionality of contemporary gene flow among our sampled sites, we generated a network graph of relative gene flow. Following Sundqvist et al. (2016), we compared pairwise measures of genetic differentiation between combined population pairs (i.e., pooled individuals) to each separate population of the pair. Relative gene flow within the network (i.e., gene flow scaled to the highest relative value) was estimated from $G_{ST}$ (Nei and Chesser 1983) and significant directionality was tested using 95% confidence limits from 1,000 bootstrap iterations using the divMigrate function in the R-package *DiveRsity* (Keenan et al. 2013, R Development Core Team 2020).

## Results

### *Genetic diversity and differentiation*

We identified 43 unique individuals from 303 hair samples collected on five Apostle Islands. Genotyping error rate per locus ranged from 0% to 6.3% across PCR replicates (i.e., the ratio between observed allelic differences between replicates and the total number of comparisons) for all noninvasive hair samples collected on the Apostle Islands. We had high power to discriminate individuals with $P_{ID}$ and $P_{IDSIB}$ values of $5 \times 10^{-8}$ and $6 \times 10^{-4}$, respectively. The martens on the Apostle Islands had the lowest levels of genetic diversity compared to subpopulations in the recovery network: allelic richness ($A_r$; range 2.29–6.43), observed heterozygosity ($H_o$; range 0.51–0.67), and expected heterozygosity ($H_e$; range 0.49–0.79). We did not observe any private alleles between the Apostle Islands and other subpopulations (Appendix S1: Table S2). The effective population size estimated for the Apostle Islands was 12.2 (95% CI: 8.8–16.9) and 6.8 (4.0–9.4), with rare allele thresholds of

0.02 and 0.01, respectively. Contrary to marten populations on the mainland, the observed heterozygosity was larger than expected for martens on the individual islands. Comparing genetic diversity within the Apostle Islands revealed that martens on Stockton Island had the highest percentage of private alleles (Pa: 24.1%) and highest allelic richness ($A_r$; 2.62; Appendix S1: Table S3).

Martens on the Apostle Islands clustered closely (Fig. 2) and exhibited low pairwise genetic differentiation ($G'_{ST}$: 0.08–0.20; $D$: 0.02–0.11; Appendix S1: Table S4) to all other subpopulations, and exhibited the closest relationship to marten from MI-Eastern subpopulation. Martens from the Apostle Islands differed the most from Minnesota and WI-CF (Fig. 2b). In addition, all subpopulations were discrete (Fig. 2a) and showed substantial genetic differentiation from Pacific martens ($G'_{ST}$: 0.48; $D$: 0.39; Appendix S1: Table S4).

We identified population genetic structure between islands of the archipelago and $\Delta K$ showed support for two and four genetic clusters that occurred across islands (Appendix S1: Fig. S2). For $K = 4$, two sets of two islands clustered together, and Stockton Island, the largest colonized island (40 km$^2$) in the archipelago, had two additional genetic clusters (Fig. 1c). We observed generally concordant grouping of islands when $K = 2$ clusters were considered with martens on Stockton Island having membership to both clusters (Fig. 1c). Average membership ($q$ values) to a given cluster was high regardless of whether 2 ($q = 0.92$) or 4 ($q = 0.84$) clusters was considered (Appendix S1: Fig. S3).

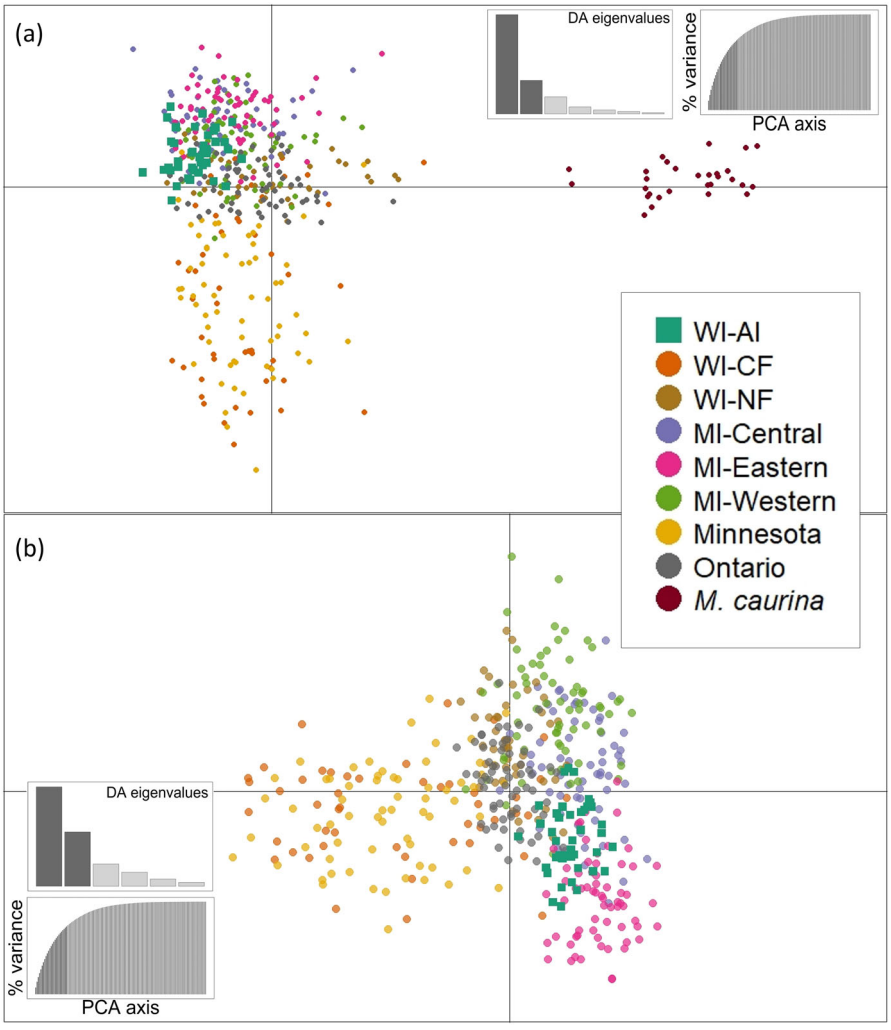


FIG. 2. Discriminant analysis of principle components of American marten (*Martes americana*) populations from the regional recovery network: Chequamegon National Forest, Wisconsin, United States (WI-CF), Nicolet National Forest, Wisconsin, United States (WI-NF), central Upper Michigan (MI-Central), eastern Upper Michigan (MI-Eastern), western Upper Michigan (MI-Western), Minnesota, Ontario, and with (a) and without (b) Pacific marten (*Martes caurina*). Predicted position of martens from the Apostle Islands (WI-AI) within the discriminant functions are symbolized with squares. Scatterplots of individuals along the first two discriminant functions. Included insets show the number of principal components analysis axis retained and discriminant functions eigenvalues.

*Evaluation of colonization scenarios*

We compared results from our two general colonization scenarios of the Apostle Islands (pre-extirpation holdout vs. contemporary recolonization) based on the number classification votes for all random forest trees for each scenario in our ABC framework. Given that genetic differentiation and clustering revealed a translocation holdout from the 1950s was implausible, we eliminated Pacific marten from the ABC analysis. We found little support for a pre-extirpation model (14% of votes), whereas a contemporary colonization scenario was strongly supported with various models receiving 86% of the votes. The most supported contemporary source was from eastern Upper Michigan (36% of votes; posterior probability = 0.54) and two times the votes as the next closest model. The out-of-bag error rates (range 0–0.20) revealed some uncertainty in distinguishing between different contemporary mainland sources (Appendix S1: Table S5). Simulated summary statistics of the top model generally captured the observed data in both the linear discriminate analysis and posterior predictive *P* values with 22 out of 256 summary statistics had *P* values ≤0.05. We estimated contemporary effective population size of the Apostle Islands (N1) at 14 (95% highest density interval [HDI]: 3–24; Table 1) and the timing of colonization (t1) at four generations (95% HDI: 2–9; Table 1). The posterior distribution for N1 and t1 showed clear peaks above prior values and high correlation between simulated and predicted values ($r \geq 0.82$; Appendix S1: Figs. S4, S5). However, N1 and t1 had estimated 95% posterior distributions that encompassed the range of prior values (Table 1).

*Relatedness and detection of dispersal*

We estimated relatedness and pedigree relationships to identify connectivity within the islands and between the other subpopulations. Our power analysis revealed that for both data sets first-order relationships could be distinguished from half siblings and unrelated individuals (Appendix S1: Supporting Methods). We identified 21 first-order relationships in the Apostle Islands with three occurring across different islands, which suggests that marten dispersal occurs between islands (Fig. 1c). Most of the first-order relationships occurred within individual islands, creating family groups that were also supported by fine-scale genetic structuring across the archipelago (Fig. 1c). We identified a single first-order relationship between the Apostle Islands and the closest subpopulation (WI-CF) and was consistently identified as a first-order relationship at 95% confidence in ML-relate with a simulated uniform and triangular allele frequency distributions (Appendix S1: Supporting Methods).

*Gene flow*

Estimates of recent dispersal rates revealed limited gene flow among sub-populations. Only two pairwise comparisons showed recent gene flow that did not overlap zero with a 95% confidence limit (Fig. 3). Recent gene flow and significant directionality in relative gene flow was observed from the Apostle Islands back to the recovery network (Fig. 3; Appendix S1: Fig. S7). In addition, we estimated recent gene flow between two subpopulations in Michigan and significant directional

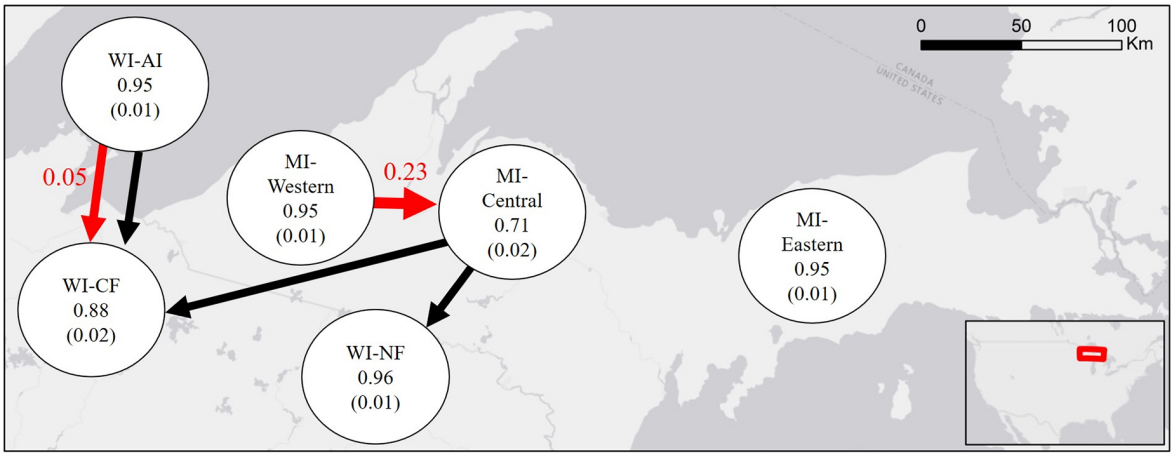


FIG. 3. Indirect gene flow between subpopulation pairs of American marten (*Martes americana*) within a regional recovery network: Apostle Islands (WI-AI), Chequamegon National Forest, Wisconsin, United States (WI-CF), Nicolet National Forest, Wisconsin, United States (WI-NF), central Upper Michigan (MI-Central), eastern Upper Michigan (MI-Eastern), and western Upper Michigan (MI-Western). Values in nodes represent proportion of sampled population from source population with standard deviation in parentheses and red values and arrows represent estimated recent gene flow that did not overlap zero at 95% confidence interval from BAYESASS. Black arrows represent significant directionality of relative gene flow between populations estimated from $G_{ST}$ with 95% confidence from divMigrate.

gene flow from central Michigan to two subpopulations in Wisconsin (Fig. 3; Appendix S1: Fig. S7). The Apostle Islands showed a high percentage of the sampled population that originated from the Apostle Islands (0.95; SD = 0.01) and the central subpopulation in Michigan having the lowest (0.71; SD = 0.02). Results are consistent with the estimated high rate of recent gene flow from the western population in Upper Michigan.

## Discussion

We found that decades of disjunct translocations have formed a recovery network featuring multiple subpopulations occupying areas of varying habitat quality, demographic potential, and connectivity. Within this recovery network we identified a potential refuge, a location resistant to environmental change, that may play a disproportionate role in population recovery along a trailing range boundary. Our results corroborate the observation that, following a long absence, American martens recently recolonized the Apostles Islands from a neighboring mainland population. A translocation holdout from the 1950s is extremely unlikely, given that none of the individuals from the Apostle Islands clustered with Pacific martens and that there was substantial genetic differentiation of Pacific martens with all other subpopulations. Similarly, we found virtually no support for a pre-extirpation holdout as martens on the Apostle Islands held no private alleles and our simulations overwhelmingly supported a recent colonization scenario. Indeed, all lines of evidence point to a recent and regional colonization event to the Apostle Islands: Martens on the Apostle Islands clustered closely with contemporary mainland populations; simulations revealed that martens likely colonized within last two decades; we identified a first-order relative between the island and mainland populations. Identifying the specific source from the mainland had less certainty because of shared ancestry of the many mainland populations. Nevertheless, our top models supported a contemporary recolonization from a source in Upper Michigan that itself was founded by a previous translocation of martens from Ontario (Williams et al. 2007, Williams and Scribner 2010). It is possible that a more complex and reticulate colonization could have occurred featuring multiple founding events admixture and gene flow. Our conclusion, therefore, is based on the most parsimonious explanation for the observed data and the fact that martens on the mainland mate assortatively and do not exhibit admixture (Williams and Scribner 2010, Howell et al. 2016, Grauer et al. 2017). Regardless, our findings indicate that martens on the Apostle Islands are not a relic lineage or an evolutionarily significant unit, nor are they an exotic species from historic human translocations. Instead, martens on the Apostle Islands are from a recent and natural colonization event and appear to be a high-density and growing population, even capable of providing immigrants back to the mainland.

Archipelagic marten we identified shared a first-order relative on the mainland >85 km distant. Given the sample dates of the related individuals (2013 for the mainland and 2017 for the Apostle Islands), it seems plausible that we identified a mainland disperser. If true, this would indicate that the recolonization of the Apostle Islands occurred via a stepping-stone process across the entire network of reintroduction. Martens translocated from Ontario to Upper Michigan dispersed to northern Wisconsin mainland and eventually to Stockton Island. It is worth noting, however, that our relatedness assignment cannot identify directionality of movement. Alternatively, it is possible that we detected a dispersing individual from the archipelago to the mainland. Despite their small body size, martens can disperse long distances (Pauli et al. 2012) and even instances of dispersal >150 km have been observed (Slough 1989, Johnson et al. 2009). The proximity of the Chequamegon National Forest area to the Apostle Islands within the recovery network makes it a likely step in the recolonization process. The mainland population appears to be in decline (Manlick et al. 2016), but may still be important for overall connectivity of the region. Stockton Island, the closest of the Apostle Islands known to have marten, is <8 km from the mainland. Interisland distance of ≤2 km is closer than the more distant recolonization of Isle Royale (Manlick et al. 2018). Open water is generally assumed to be a barrier to movement for martens (Buskirk and Ruggiero 1994), and connectivity likely occurs during periods of winter ice cover on Lake Superior. On Lake Superior average ice coverage has declined since 1973 (−2.0% per year [Wang et al. 2012]), but there is generally more consistent annual lake ice connecting the Apostle Islands (Assel 2009).

We observed genetic structuring among islands within the Apostle Islands, likely representing family groups on each island. Indeed, most first-order relative pairs (86%) documented occurred on the same island. The naïve densities of martens on the islands are high (0.42–1.46 $km^{-2}$), especially compared to recent estimates on the mainland of Wisconsin (<0.08 $km^{-2}$ [Manlick et al 2016, Grauer et al. 2019]) and are comparable to density estimates generated from locations featuring high-quality habitat and high prey densities (Francis and Stephenson 1972, Soutiere 1979, Thompson and Colgan 1994). High densities of martens on the Apostle Islands are likely a combination of reduced competition with other carnivores (Allen et al. 2018) and high-quality habitat potentially featuring greater abundance of preferred prey items. On the mainland, marten populations could be limited in part by preferred prey availability; instead they are reliant on shrews (*Blarina brevicauda*, *Sorex* spp.) and scavenging white-tailed deer (*Odocoileus virginianus*) carrion (Carlson et al. 2014).

Across the region small-mammal communities are changing, with declines in northern species (Myers et al. 2009). On the Apostle Island, though, red-backed voles (*Myodes* spp.), a preferred prey of American martens

across their distributional range, appear to be the most abundant of all small mammal species (Mallinger et al. 2019). Despite being logged in the past, the Apostle Islands have forest composition and complexity that is more similar to pre-European settlement and pre-extirpation of martens that may be attributed to an absence or low intensity of deer herbivory, fire, and forest disturbance (Beals and Cottam 1960). Indeed, Canada yew (*Taxus canadensis*), functionally extirpated from the mainland because of white-tailed deer (*Odocoileus virginianus*) herbivory and fire (Windels and Flaspohler 2011), and mountain maple (*Acer spicatum*) are abundant in the understory because of the absence or low density of deer on most islands. In addition, Canada yew is sensitive to fire and forest disturbance (Windels and Flaspohler 2011), and the Apostle Islands may also provide refuge from disturbance regimes (i.e., timber extraction) on the mainland. The structural complexity likely drives both prey availability (Thompson and Colgan 1987, Carey and Johnson 1995) and marten foraging success (Andruskiw et al. 2008) as well as reduced predation risk (Thompson and Colgan 1994). The Apostle Islands, then, may possess historic forest heterogeneity that simultaneously attenuates predation and enhances foraging and acts as an important refuge for this endangered species. Whether this immediate refuge translates into a refugia, a site that is resilient to long-term landscape and climate change, is yet to be seen.

Even though marten density on each island appears to be high, the number of overall individuals and effective population size is low and, thus, vulnerable to stochastic events. It is likely that the Apostle Islands have the lowest effective population size within the recovery network due to isolation and limitations on available habitat. Thus, within the recovery network, subpopulations in Michigan will be essential to persistence because of the large area of continuous forest. It is also notable that we did not detect contemporary gene flow from the recovery network to the Apostle Islands; however, the temporal differences in samples between the Apostle Islands and other samples may have contributed to our nondetection. Although samples from across the recovery network were sampled asynchronously, they were all collected within at least three generations of each other, so allele frequencies of subpopulations were likely unaffected. If our observation of limited dispersal back to the islands is correct, there is limited potential for demographic or genetic rescue from the mainland populations (Whiteley et al. 2015). Given the small population size and the low genetic diversity on the archipelago, population declines, or genetic inbreeding should be monitored, as they increase the probability of extinction (Mills and Smouse 1994). However, we did identify interisland movement of first-order relatives, revealing that discrete island-bound groups are not completely isolated. It is possible that the islands may function as a metapopulation that is demographically independent but exhibits some degree of functional connectivity (Hanski 1991). We hypothesize that physical space limitations on each of the small islands necessitates the movement of individuals among islands and to the mainland, even across an unequivocally hostile matrix of ice cover.

Our estimated directionality of contemporary dispersal from the islands to the mainland was unexpected. Indeed, both analyses for contemporary gene flow revealed low levels of directional dispersal from the Apostle Islands to the mainland. We hypothesize that this movement of individuals from the archipelago back to the mainland is a result of demographic pressure from a growing marten population that is spatially constrained by island size. Interestingly, a paradigm shift in island biogeography has emerged that suggests island-to-mainland colonization might be more common than previously assumed (Bellemain and Ricklefs 2008), and has been observed among diverse taxa (Jønsson et al. 2010, Tavares et al. 2018, Rowe et al. 2019). Thus, the traditional view of islands as vulnerable sinks may not hold in novel systems that have risen from rapid environmental change where the isolation from mainland disturbances, competition, and disease can act as important refuges. Indeed, the isolation afforded by islands has been used in the extreme to avert extinction by "marooning" threatened species (Williams 1977, Abbott 2000, Saunders and Norton 2001). Rather than a last resort, we believe that such islands can act as particularly important subpopulations in a recovery network when they possess the attributes of a refuge.

Carnivore translocations are a primary tool for conservation and management (Linnell et al. 1997, Lewis et al. 2012) and identifying refuges a priori would likely improve persistence, recovery, and success. Decades of regional translocations have operated as a landscape-scale experiment in the processes that influence the recovery of an extirpated carnivore. Subpopulations in the recovery network display different levels of establishment and persistence, yet even underperforming subpopulations (i.e., pseudo-sinks) can play a role in the expansion of recovery across the landscape. Although carnivore life histories generally complicate translocation success, vagile species with great dispersal power have the potential to expand the area of recovery after establishment and improve regional persistence.

Our work reveals the potential of a reintroduction network to precipitate a natural and unexpected colonization. In addition, the natural recolonization likely contributes to the overall regional viability by both expanding and strengthening the network of recovery via directional flow of individuals back into the original network. It appears that natural recolonization occurred in an ideal spot within the recovery network for improved regional viability and constitutes a refuge exhibiting connectivity to the network, a high density of individuals, and high-quality habitat that resembles historic conditions that are protected from both human and natural perturbations. Importantly, conservation efforts would benefit from identifying putative refuges a

priori and targeting them for translocations. The identification of such areas should extend beyond habitat suitability, and included an assessment of ecological novelty, resistance to future environmental change, connectivity to remnant populations or other translocation sites, and demographic potential. In general, these targeted refuges represent valuable targets, especially at range boundaries, for species recovery and long-term persistence. The complex problem of species recovery in novel ecosystems will require the continued identification and evaluation of various strategies, including refuges, and conservation biologists should be prepared for the emergence of new and even unexpected mechanisms that promote regional recovery.

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## Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2416/full

## Open Research

Data (Smith et al. 2021) are available in the Dryad digital repository: https://doi.org/10.5061/dryad.jwstqjq8f.