Mechanisms of species recovery for a forest carnivore in a changing landscape

By

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Dissertation abstract

Land-use and climate change are reshaping ecosystems and driving species loss globally. Such rapid environmental change presents unique challenges for conservation efforts as recovery is now occurring in novel ecosystems. Species recovery, in particular, represents a "wicked problem" in conservation, in which many complex drivers need to be considered to arrive at potential solutions. My dissertation focuses on the recovery of American marten (*Martes americana*) – a small forest carnivore of conservation concern – in the Great Lakes Region to identify important features and mechanisms that influence persistence. Through my dissertation, I explored the role of a rediscovered population on an archipelago to act as a regional refugia and model how connectivity affects future genetic and demographic potential. In addition, I examined potential mechanisms contributing to recovery including linking landscape conditions to demographic outcomes and the role of competition on dietary niches.

Chapter 1 identified the source of martens that recolonized the Apostle Islands in Lake Superior after a nearly 50-year absence. In addition, I used genetic data of martens from the archipelago and from regional populations to understand connectivity following decades of regional translocations. Coalescent analyses supported a contemporary recolonization of the Apostle Islands, and we identified some regional gene flow. My findings suggest that the islands can act as a refuge for martens regionally due to the protection from disturbance, complex forest structure, and reduced carnivore competition and a central node for regional recovery.

Chapter 2 assessed how seasonal heterogeneity influences survival and compared common forest metrics to explicit measures of habitat complexity. Ecological heterogeneity promotes species persistence and diversity, but environmental change has altered fundamental patterns of heterogeneity. I modeled the survival of martens from a long-term spatially explicit dataset and show how differences in snow depth relate to survival differences at historical translocation sites. Our work links heterogeneity to fitness and joins a growing body of research highlighting the role of snow as habitat and argue for the inclusion of important seasonal conditions into management and recovery plans.

Chapter 3 explored the role of competition and environmental context (e.g., availability and aggregation of resources and competitors) to shape niche variation and foraging tactics. To test how competition between martens and fishers shapes their niche variation and foraging tactics, I explored proportional diets and partitioning across a gradient of competition in the Great Lakes Region. Fishers and martens generally consumed different prey: fishers consumed larger-bodied prey and martens consumed smaller-bodied prey. However, in the absence of martens, fishers consumed a greater proportion of smaller prey. Fishers adjusted their niche in the face of a subordinate, but superior, exploitative competitor. These findings highlight the underappreciated role of the subordinate competitor in shaping the dietary niche of a dominant competitor.

Chapter 4 simulated and projected the demographic and genetic potential of martens inhabiting the Apostle Islands. Building from Chapter 1, the Apostle Islands appear to be a refugia, however, it is unknown how connectivity will influence population persistence and genetic diversity as ice cover has declined since the 1970s. I simulated changing ice cover conditions within the archipelago and tested the sensitivity of genetic erosion and persistence using an individual-based model. Our work revealed that martens would be resilient to moderate changes in ice cover, but a complete loss of regional and island connectivity resulted in rapid genetic erosion. Identifying thresholds in connectivity that maintain small populations but provide protection from disturbances will be essential features of refugia.

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ADDENDUM

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

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Running head: Recolonization of a potential refuge

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 years. 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.

Keywords: 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 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). While 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). While 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 American, 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 (Thiel 1987; Petersen et al. 1977; Mech 1995; Williams et al. 2007) or persisted in small and isolated populations (De Vos 1964).

Due to 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, due to 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 marten at the time but are now considered to be non-native 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 years has created a recovery network – similar to a natural metapopulations but emerging from human agency – that features multiple sub-populations 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 non-invasively 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; Manlick et al. 2016; Grauer et al. 2017; Manlick et al. 2018; Grauer et al. 2019; Koen et al. 2012). 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 sub-populations 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 sub-populations, and gene flow within a recovery network, we used previously genotyped individuals from seven putative sub-populations (Fig. 1a). We used genetic samples from individuals in two geographically disjunct sub-populations in Wisconsin (WI-CF: N = 48 and WI-NF: N = 46; 2007-2017; Grauer et al. 2017; Manlick et al. 2016), three putative sub-populations 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; Grauer et al. 2017; Manlick et al. 2016). 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 non-invasive hair traps (modified from Pauli et al. 2008) set at random locations with a minimum of 500 meters 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, CA) in a room dedicated to low quality DNA samples. We developed a species-specific quantitative 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, Tt4 (Davis and Strobeck 1998) and Mer022, Mer041, and Mvis072 (Fleming et al. 2002). 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, polymerase chain reactions were conducted in 10 μL reactions containing 2 μL of DNA, 2X Multiplex PCR Mastermix (Qiagen, Valencia, CA), and labelled primers (FAM, VIC, and NED) with the following concentrations: Ma1 (0.2 μM), Ma2 (0.2 μM), Ma11 (0.15 μM), Ma14 (0.5 μM), Gg7 (0.08 μM), Mer022 (0.5 μM). For Multiplex 2, polymerase chain reactions were conducted in 10 μL reactions containing 2 μL of DNA, 2X Multiplex PCR Mastermix (Qiagen, Valencia, CA), 1XL Q-solution (Qiagen, Valencia, CA), and labelled primers (FAM, VIC, and NED) with the following concentrations: Ma5 (0.2 μM), Ma7 (0.2 μM), Ma8 (0.2 μM), Mer041 (0.2 μM), Mvis072 (0.2 μM), Gg3 (0.15 μM), Ma19 (0.1 μM), and Tt4 (0.05 μM). 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, CA, USA), and scored microsatellite alleles using GeneMapper® Software 5 (Applied Biosystems, Foster City, CA, USA). 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 re-run in triplicate. All samples were scored from 3-6 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 Core Team 2020) that randomly samples loci and counts the number of multi-locus genotypes observed. We had enough power to identity unique individuals with a minimum of 7 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 Core Team 2019) 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 Core Team 2019). Due to DNA template quality of non-invasive 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 sub-populations, 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 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 sub-populations, we first calculated pairwise G'_{ST} (Hedrick 2005), D (Jost 2008), and F_{ST} (Weir and Cockerham 1984) with 95% confidence intervals using 5000 permutations in *DiveRsity* (Keenan et al. 2013). We used a discriminant analysis of principle components (DAPC) on multi-locus genotypes to visualize and predict group membership of individuals from the Apostle Islands with individuals from the other sub-populations. We constructed a DAPC that only included putative sub-populations 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 et al. 2010). We calculated the optimal number of principle components to retain using the alpha-score optimization (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 ΔK (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 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, (3) contemporary colonization. A pre-extirpation holdout would be a relic lineage that has persisted undetected since before region wide 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 sub-population 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 6 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 7 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 years for martens (Clark et al. 1987). We implemented a generalized stepwise mutation model, and the mean mutation rate was bound between 8.1 x 10^{-3} to 8.0 x 10^{-5} as extreme values observed in mammalian microsatellites (Peery et al. 2012). We summarized datasets 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 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 datasets 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 Core Team 2020). We conducted posterior model checking in DIYABC by simulating 100,000 datasets 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 datasets drawn from the posterior distribution. We compared simulated summary 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 datasets (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 inter-island 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 dataset following the same procedure in ML-RELATE (Kalinowski et al. 2006) that included individuals from the closest sub-population with the islands. We included the combined dataset due to the proximity and previous sampling effort (2012-2013) that estimated >65% of the population (N = 22.6 (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 dataset and the combined dataset of the Apostle Islands and the closest sub-population, 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 Core Team 2020). For the combined dataset of the Apostle Islands and closest sub-population, 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 between within the recovery network. By identifying differences in the directionality of gene flow, we can explore relationships (i.e., sources) between sub-populations. 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 1000 bootstrap iterations using the divMigrate function in the R-package *DiveRsity* (Keenan et al. 2013; R Core Team 2019).

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 non-invasive hair samples collected on the Apostle Islands. We had high power to discriminate individuals with P_{ID} and P_{IDSIB} values of 5×10^{-8} and 6×10^{-4}, respectively. The martens on the Apostle Islands had the lowest levels of genetic diversity compared to sub-populations 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 sub-populations (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 sub-populations, and exhibited the closest relationship to marten from MI-Eastern sub-population.

Martens from the Apostle Islands differed the most from Minnesota and WI-CF (Fig. 2b). In addition, all sub-populations 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 ΔK showed support for 2 and 4 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).

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), while 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% HDI: 3-24; Table 1) and the timing of colonization (t1) at 4 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: Fig. S4 and Fig. 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 datasets first order relationships could be distinguished from half siblings and unrelated individuals (Supporting Methods). We identified 21 first order relationships in the Apostle Islands with three occurring across different islands that suggests 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 sub-population (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 (Supporting Methods).

Geneflow

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 sub-populations in Michigan and significant directional gene flow from central Michigan to two sub-populations 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 sub-population 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 sub-populations 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 sub-populations. 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 2 decades; we identified a first-order relative between the island and mainland populations. Identifying the specific source from the mainland had less certainty due to shared ancestry of the many mainland populations. Nevertheless, our top models supported a contemporary recolonization from a source in Upper Michigan that itself 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. Inter-island 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, 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 due to white-tailed deer (*Odocoileus virginianus*) herbivory and fire (Windels and Flaspohler 2011), and mountain maple (*Acer spicatum*) are abundant in the understory due to 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, sub-populations in Michigan will be essential to persistence due to the largest 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 non-detection. While samples from across the recovery network were sampled asynchronously, they were all collected within at least three generations of each other, and allele frequencies of subpopulations were, thus, 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 inter-island 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 exhibit some degree of functional connectivity (Hanski 1991). We hypothesize that physical space limitations on each of the small island 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 sub-populations 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. Sub-populations in the recovery network display different levels of establishment and persistence, yet even underperforming sub-populations (i.e., pseudo-sinks) can play a role in the expansion of recovery across the landscape. While 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 target 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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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. 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, WI (N1), Chequamegon National Forest, WI (N2), central Upper Michigan (N3), Minnesota (N4), Nicolet National Forest, WI (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, WI, 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, WI (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).

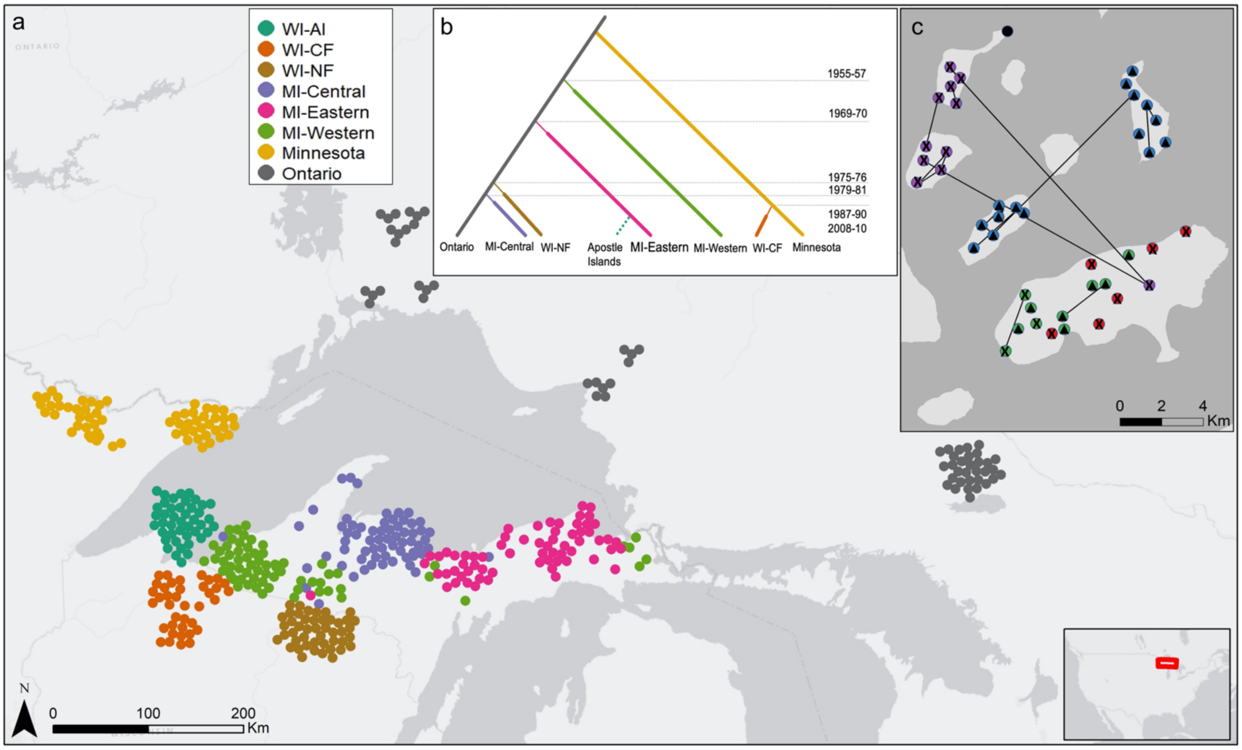
				Posterior estimate		
Parameter	**Population**	**Description**	**Prior**	**Median**	**Q2.5**	**Q97.5**
N1	Apostle Is.	Contemporary effective population size	1 - 25	14	3	24
N2	WI-CF	Contemporary effective population size	10 - 100	52	12	98
N3	MI-Central	Contemporary effective population size	10 - 1000	424	18	957
N4	Minnesota	Contemporary effective population size	10 - 10000	5753.14	589	9760
N5	WI-NF	Contemporary effective population size	10 - 250	102	14	245
N6	Ontario	Contemporary effective population size	10 - 10000	4875	777.875	9449
N7	MI-Western	Contemporary effective population size	10 - 1000	425	21	977
N8	MI-Eastern	Contemporary effective population size	10 - 1000	424	22	977
t1	Apostle Is.	Timing of colonization from source	1 - 10000	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

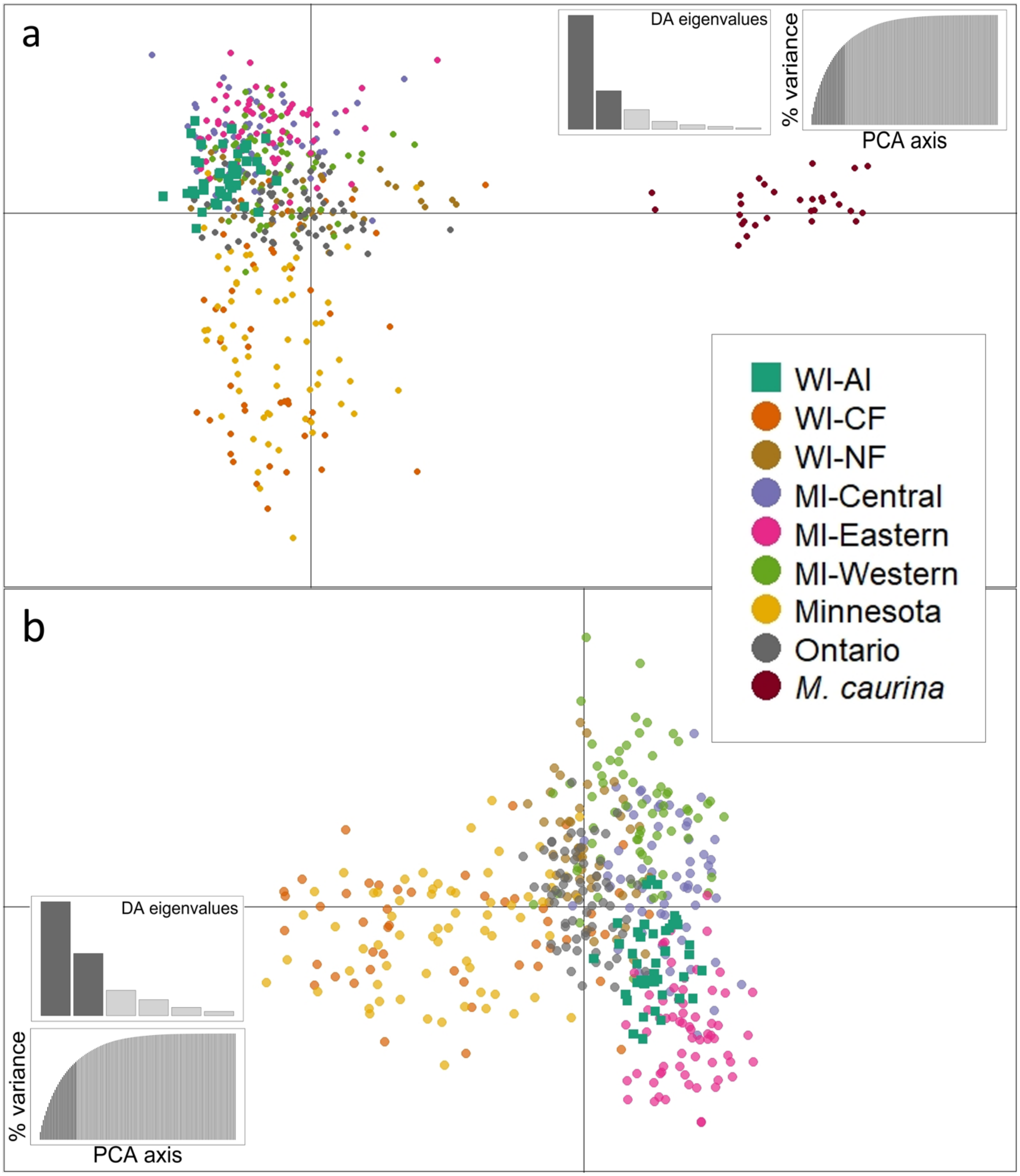
t5	MI-Eastern	Time of reintroduction	9 - 10	9	9	10
t6	MI-Western	Time of reintroduction	11 - 12	12	11	12
t7	Minnesota	Split from Ontario	50 - 500	234	58	478
N3r	MI-Central	Reintroduction effective population size	5 - 500	91	13	465
N5r	WI-NF	Reintroduction effective population size	5 - 500	213	21	489
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

Figure 1: Map of American marten (*Martes americana*) samples collected from the regional recovery network: Apostle Islands, WI (WI-AI),Chequamegon National Forest, WI (WI-CF), Nicolet National Forest, WI (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 Figure S1. Individual clustering assignments of American marten (*Martes americana*) sampled from the Apostle Islands, WI (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 X and triangle. Black lines represent first order relatives (parent-offspring or full-sibships) consistent at 95% confidence (c).

Figure 2: Discriminant analysis of principle components of American marten (*Martes americana*) populations from the regional recovery network: Chequamegon National Forest, WI (WI-CF), Nicolet National Forest, WI (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 PCA axis retained and discriminant functions eigenvalues.

Figure 3: Indirect gene flow between sub-population pairs of American marten (*Martes americana*) within a regional recovery network: Apostle Islands (WI-AI), Chequamegon National Forest, WI (WI-CF), Nicolet National Forest, WI (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.


a
WI-AI
WI-CF
WI-NF
MI-Central
MI-Eastern
MI-Western
Minnesota
Ontario
N
0
100
200
Km
b
1955-57
1969-70
1975-76
1979-81
1987-90
2008-10
Ontario
MI-Central
WI-NF
Apostle Islands
MI-Eastern
MI-Western
WI-CF
Minnesota
c
0
2
4
Km


a
DA eigenvalues
% variance
PCA axis
WI-AI
WI-CF
WI-NF
MI-Central
MI-Eastern
MI-Western
Minnesota
Ontario
M. caurina
b
DA eigenvalues
% variance
PCA axis

Supporting Information – Appendix S1

Smith MM, Gilbert JH, Olson ER, Scribner KT, Van Deelen TR, Van Stappen JF, Williams BW, Woodford JE, Pauli JN. A recovery network leads to the natural recolonization of an archipelago and a potential trailing edge refuge. Ecological Applications.

Supporting Methods

Quantitative PCR species identification

We developed a species-specific quantitative PCR assay (qPCR) for American marten designed from previously published sequences of the cytochrome b region of the mitochondrial DNA (N = 166) from GenBank. Sequences were aligned using ClustalX2 (Larkin *et al.* 2007) and consensus sequences were compiled using MEGA7 (Kumar et al. 2016). We compared consensus sequences of martens to fisher (*Pekania pennanti*) and weasel (*Mustela* sp.) species sequences to identify locations that maximize differences in the 3' end of the forward and reverse primer and in the middle of the probe to ensure assay specificity (Appendix S1: Table S1). The resulting assay was tested against isolated DNA from non-invasively collected hair samples or tissue in a panel of 10 American martens, 5 fisher, and 5 weasel species. We analyzed each sample in duplicate in a reaction that included 3 µL of DNA template in a total volume of 15 µL. Reactions were run using 2X PrimeTime Gene Expression Master Mix (IDT, Coralville, IA), 0.2 µM of each primer, and 0.2 µM of probe on an Eppendorf Mastercycler® RealPlex2 (Hauppauge, NY). Reactions activated for 15 minutes at 95°C then ran for 40 cycles of 94°C for 60s followed by 60°C for 60s. All qPCR plates included negative controls to test for contamination. All of the samples from the target species tested positive and all of the samples from non-target species tested negative.

Relatedness power and sensitivity

We simulated individuals with known relationships in the R-package *related* to determine our overall power to distinguish between pedigree relationships (Pew et al. 2015). Pedigree relationships included: Parent-offspring, Full-siblings, Half-siblings, and unrelated pairs. We simulated relatedness estimates and distribution within each pedigree relationship for two datasets: The Apostle Islands and a combined dataset of the Apostle Islands plus the Chequamegon National Forest. Relatedness values are estimated from a modified likelihood estimator that performs well with small sample sizes (Wang 2007). We compared these simulated group means using analysis of variance (ANOVA) and a pairwise comparison of groups with Tukey's HSD in R (R Core Team 2020). Additionally, we compared differences in effect sizes using Cohen's d (d; Cohen 1988) between groups with R-package *effsize* (Torchiano 2019).

We found the group means to be statistically different for the Apostle Islands dataset ($F(3,396) = 141$; $p < 0.0001$) and the Apostle Islands plus Chequamegon National Forest dataset ($F(3,396) = 194.1$; $p < 0.0001$). Specifically, for both datasets, we found that all pairwise comparisons of means between pedigree groups were different except the group means between parent-offspring and full-siblings (Appendix S1: Fig. S6, Table S6). For both datasets (i.e., the Apostle Islands only and the Apostle Islands plus Chequamegon), we estimated what is considered a large effect size (Cohen 1988) between parent-offspring and unrelated ($d = 3.1$ and 3.2, respectively) and full-siblings and unrelated ($d = 2.5$ and 2.5, respectively) relationships. In other words, there would be approximately 0.95 or greater probability that parent-offspring or full-sibling pair would have a larger relatedness estimate than an unrelated pair when both are chosen at random and sufficient power to distinguish between first order relatives (i.e., parent-offspring and full-siblings) and unrelated individuals.

Estimates of relatedness generally assume that individuals come from a single panmictic population. To account for potential bias in relatedness estimates of our combined dataset that included individuals from the Apostle Islands plus the Chequamegon National Forest, we simulated two alternate allele frequency distributions that do not assume Hardy-Weinberg Proportions. For a given locus, we pulled from a uniform distribution between 0 and 1 for each observed allele and then normalized across the locus to sum to 1 and repeated for all loci (following Hunter et al. 2020). This approach was repeated for a triangular distribution between 0 and 1 with a mode of 0.5. Then, we simulated new individuals with known pedigree relationships using the uniform and triangular distribution of allele frequencies with the familysim() function in *related (*Pew et al. 2015). The identified first order pair (i.e., parent-offspring or full-sibling) with the observed allele frequencies from the Apostle Islands and the Chequamegon National Forest were then added to the simulated individuals with both uniform and triangular allele frequency distributions. With the uniform and triangular allele frequency distribution, we re-estimated the pedigree relationship consistent at 95% confidence in ML-relate (Kalinowski et al. 2006). The Apostle Islands and Chequamegon National Forest pair was consistently identified as full-siblings with the observed, uniform, and triangular allele frequency distributions. Thus, we are confident that the population structure from combining individuals did not alter inferred relationships.

Table S1: Quantitative PCR assay design for American marten (*Martes americana*).

Forward Primer	CCTTGGAATCTGCCTAATCCTAC
Reverse Primer	RTATGGAAGCCCCATTGGCA
Probe	6FAM-ACACTACACATCAGATACAGCCACAGCC-IBFQ

Table S2: Measures of genetic diversity of American marten (*Martes americana*) from regional populations in the Great Lakes. Number of individuals (*N*), allelic richness (A_r) using rarefaction, percent private alleles (*Pa (%)*), observed heterozygosity (H_O), and expected heterozygosity (H_E). Sub-populations had 1 to 8 loci out of Hardy-Weinberg proportions. Across all sub-populations, 2 out of 78 locus pairs exhibited linkage disequilibrium. Regional recovery network: Apostle Islands, WI (WI-AI), Chequamegon National Forest, WI (WI-CF), central Upper Michigan (MI-Central), Nicolet National Forest, WI (WI-NF), eastern Upper Michigan (MI-Eastern), western Upper Michigan (MI-Western), Minnesota, and Ontario.

	N	A_r	*Pa (%)*	H_o	H_e
WI-AI	43	2.29	0.0%	0.51	0.49
WI-CF	48	4.23	8.5%	0.58	0.64
WI-NF	46	6.43	19.3%	0.58	0.79
MI-Central	65	3.48	0.0%	0.64	0.64
MI-Western	65	3.72	0.0%	0.65	0.64
MI-Eastern	65	3.04	0.0%	0.55	0.55
Minnesota	61	3.91	1.3%	0.56	0.62
Ontario	61	3.97	0.0%	0.67	0.69

Table S3: Genetic diversity of American marten (*Martes americana*) across the Apostle Island, WI including year sampled and area of island (Km^2). Number of individuals (*N*), allelic richness (A_r) using rarefaction, percent private alleles (*Pa (%)*), observed heterozygosity (H_O), and expected heterozygosity (H_E).

	Year sampled	*Area* (Km^2)	*N*	A_r	*Pa (%)*	H_o	H_e
Otter	2018	5.4	5	2.15	1.5%	0.43	0.35
Rocky	2018	4.5	6	2.14	0.0%	0.51	0.40
Cat	2017	5.5	8	2.27	1.9%	0.57	0.43
Manitou	2017	5.5	7	2.21	0.0%	0.63	0.43
Stockton	2017	40.7	17	2.62	24.1%	0.46	0.45

Table S4: Mean estimates of G’st (above the diagonal) and D (below the diagonal) as measures of genetic differentiation between American marten (*Martes americana*) sub-populations from the regional recovery network. Fst values appear below the dashed line. All pairwise comparisons had confidence limits that did not overlap zero, except WI-CF and Minnesota. Apostle Islands, WI (WI-AI), Chequamegon National Forest, WI (WI-CF), central Upper Michigan (MI-Central), Nicolet National Forest, WI (WI-NF), eastern Upper Michigan (MI-Eastern), western Upper Michigan (MI-Western), Minnesota (MN).

	WI-AI	WI-CF	WI-NF	MI-Central	MI-Western	MI-Eastern	MN	Ontario	*M. caurina*
WI-AI		0.25	0.17	0.20	0.20	0.08	0.23	0.17	0.63
WI-CF	0.11		0.07	0.16	0.16	0.18	0.01	0.05	0.47
WI-NF	0.11	0.06		0.04	0.05	0.12	0.08	0.05	0.42
MI-Central	0.08	0.06	0.02		0.07	0.11	0.15	0.04	0.45
MI-Western	0.06	0.07	0.03	0.03		0.15	0.16	0.05	0.45
MI-Eastern	0.02	0.07	0.06	0.06	0.07		0.18	0.08	0.52
MN	0.10	0.00	0.05	0.05	0.05	0.06		0.06	0.48
Ontario	0.09	0.03	0.03	0.02	0.03	0.02	0.02		0.48
M. caurina	0.39	0.29	0.28	0.23	0.22	0.26	0.29	0.31	

WI-AI								
WI-CF	0.12							
WI-NF	0.14	0.05						
MI-Central	0.11	0.09	0.03					
MI-Western	0.13	0.09	0.04	0.04				
MI-Eastern	0.06	0.11	0.10	0.07	0.10			
MN	0.12	0.00	0.05	0.09	0.09	0.11		
Ontario	0.12	0.03	0.03	0.03	0.04	0.06	0.03	
M. caurina	0.47	0.32	0.25	0.34	0.34	0.42	0.33	0.31

Table S5: The proportion of correct assignments to each model from the random forest classifier. Models are represented in the table as the potential source population of American marten (*Martes Americana*) to the Apostle Islands, WI. Correct assignments are on the diagonal and out-of-bag-error rates off diagonal for a random forest analysis using 30,000 simulations per model (N = 210,000) and 500 trees. Source populations consisted of Ontario, Canada, central Upper Michigan (MI-Central), Nicolet National Forest, WI (WI-NF), eastern Upper Michigan (MI-Eastern), western Upper Michigan (MI-Western), Chequamegon National Forest, WI (WI-CF), and Minnesota.

	Ontario	MI-Central	WI-NF	MI-Eastern	MI-Western	WI-CF	Minnesota
Ontario	0.67	0.20	0.02	0.01	0.01	0.01	0.04
MI-Central	0.16	0.79	0	0	0.01	0	0
WI-NF	0.04	0	0.74	0.08	0.06	0.05	0.02
MI-Eastern	0.04	0	0.08	0.67	0.10	0.08	0.01
MI-Western	0.04	0	0.08	0.12	0.67	0.15	0.01
WI-CF	0.03	0	0.08	0.11	0.16	0.70	0.01
Minnesota	0.02	0	0	0	0	0	0.92

Table S6: Results from Tukey's HSD comparing group means between pedigree relationships from simulated individuals with known relationships from observed allele frequency distributions on the Apostle Islands and a combined dataset including the Apostle Islands plus the Chequamegon National Forest in Wisconsin (WI-CF).

Apostle Islands				
	Difference	Lower	Upper	p-adjusted
Parent-offspring – full-sibling	-0.04	-0.11	0.03	0.39
Parent-offspring – half-sibling	0.27	0.20	0.33	0.00
Parent-offspring – unrelated	-0.47	-0.53	-0.40	0.00
Full-sibling – half-sibling	0.22	0.16	0.29	0.00
Full-sibling – unrelated	-0.43	-0.49	-0.36	0.00
Half-sibling – unrelated	-0.20	-0.27	-0.13	0.00
Apostle Islands plus Chequamegon National Forest				
Parent-offspring – full-sibling	-0.02	-0.08	0.03	0.73
Parent-offspring – half-sibling	0.28	0.22	0.33	0.00
Parent-offspring – unrelated	-0.46	-0.52	-0.40	0.00

Full-sibling – half-sibling	0.25	0.20	0.31	0.00
Full-sibling – unrelated	-0.44	-0.49	-0.38	0.00
Half-sibling – unrelated	-0.18	-0.24	-0.13	0.00

Figure S1: Model scenarios for testing alternate colonization scenarios of American marten (*Martes americana*) to the Apostle Islands, WI. All models shared a common tree topology based on source population of historical translocations and timing of translocation or population splitting event. Translocation time or population splitting are labeled t1 for the Apostle Islands (WI-AI), t2 for Chequamegon National Forest, WI (WI-CF), t3 for central Upper Michigan (MI-central), t4 for Nicolet National Forest, WI (WI-NF), t5 for eastern Upper Michigan (MI-eastern), t6 for western Upper Michigan (MI-western), and t7 for Minnesota. Timing parameters with "rb" represent duration of bottleneck following translocation for the Chequamegon National Forest, WI (rb(WI-CF)), central Upper Michigan (rb(MI-C)), Nicolet National Forest, WI (rb(WI-NF), eastern Upper Michigan (rb(MI-E)), and western Upper Michigan (rb(MI-W)).Each potential source population is represented by a different color and the thinner line at translocation event represents estimate of effective population size from the number of individuals translocated. Dates on the right represent year of reintroductions. A total of seven scenarios were modeled that changed the Apostle Island branch location to each potential source population. Timing parameters are not to scale.

Figure S2: Rate of change in likelihood distribution of K = 1 to 10 from STRUCTURE using the admixture ancestry model with correlated allele frequencies (Pritchard et al. 2000; Evanno et al. 2005) when evaluating the genetic structure of American martens (*Martes americana*) from the Apostle Islands, Wisconsin.

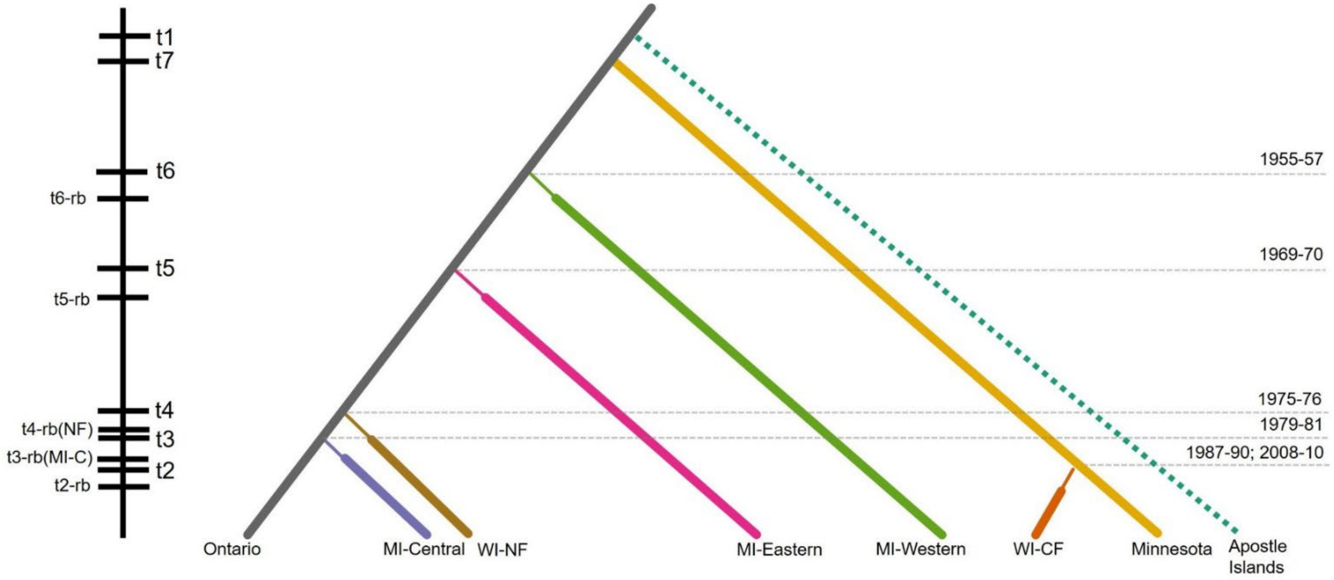
Figure S3: Assignment of genetic cluster from STRUCTURE using the admixture ancestry model with correlated allele frequencies (Pritchard et al. 2000) when K = 2 (a) and K = 4 (b) when evaluating the genetic structure of American martens (*Martes americana*) from the Apostle Islands, Wisconsin. Each vertical bar represents an individual and bars are divided by probability of cluster membership using a gray scale color theme.

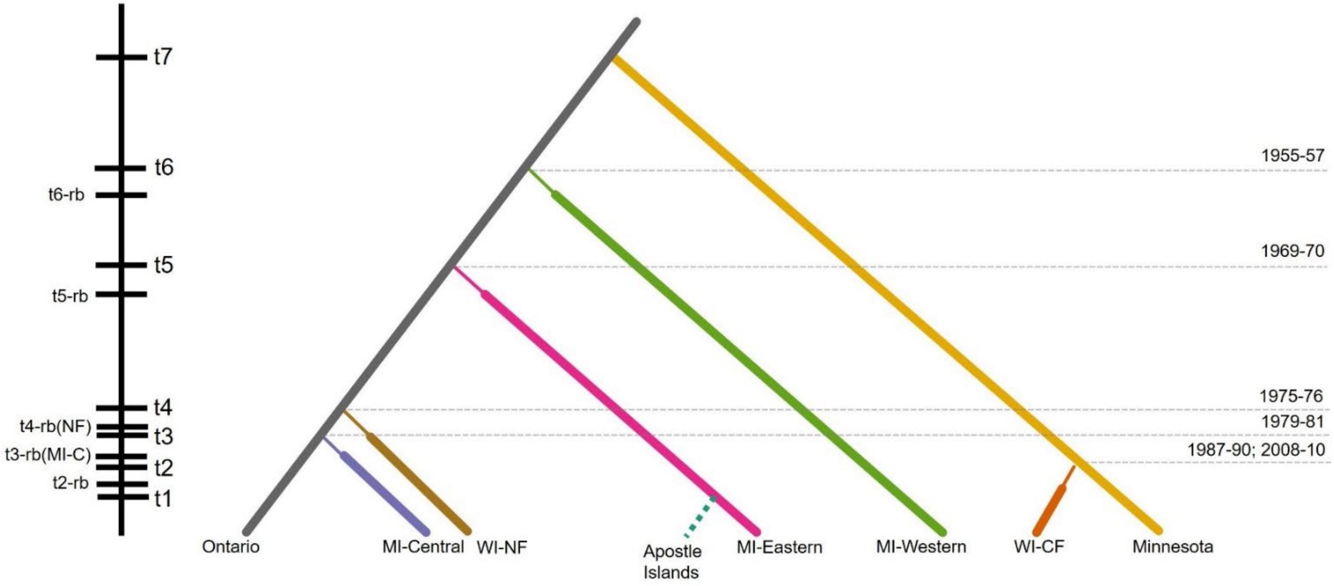
Figure S4: Correlations between simulated and predicted parameter values from a random forest regression procedure. Parameter estimates were from the most supported model that described the colonization of American marten (*Martes americana*) to the Apostle Islands, WI. The most supported model from the approximate Bayesian computation analysis identified a recent colonization event from a marten population in eastern Michigan. Contemporary effective population size for the Apostle Islands, WI (N1), Chequamegon National Forest, WI (N2), central Upper Michigan (N3), Minnesota (N4), Nicolet National Forest, WI (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, WI, 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 for the Chequamegon National Forest, WI (rb(WI-CF)), central Upper Michigan (rb(MI-C)), Nicolet National Forest, WI (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).

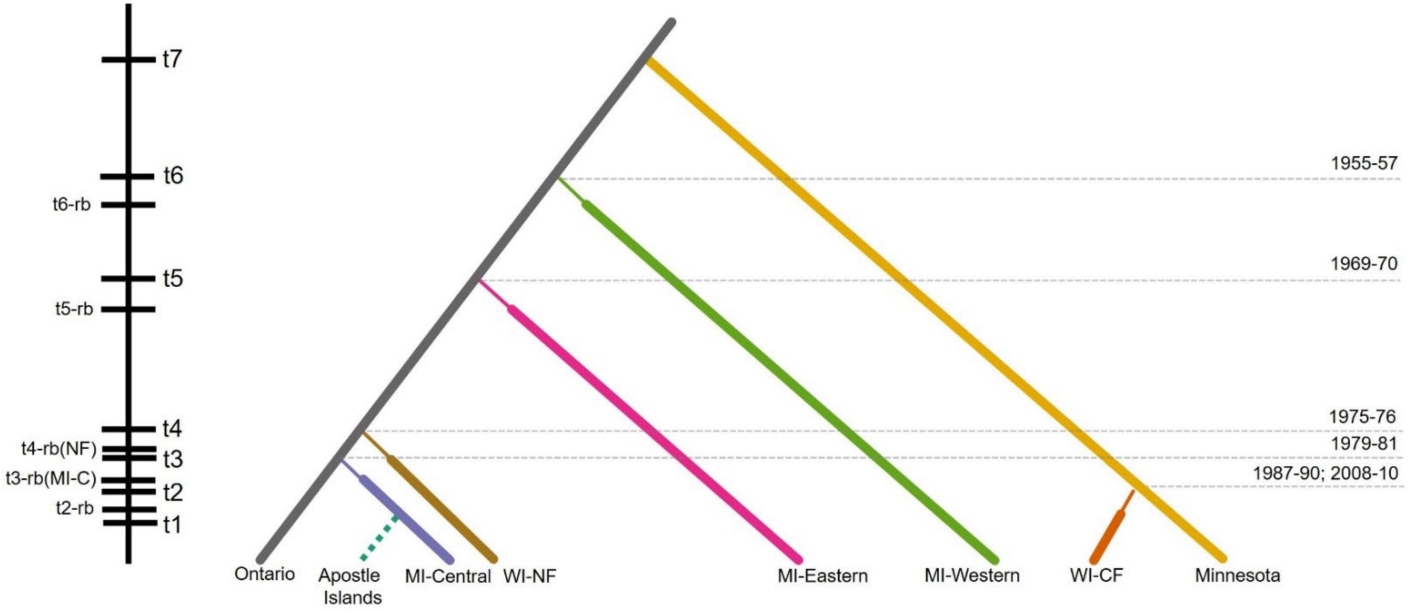
Figure S5: Prior (gray lines) and posterior (black lines) density of parameter values from the random forest regression procedure. Parameter densities were from the most supported model that described the colonization of American marten (*Martes ameriana*) to the Apostle Islands, WI. The most supported model from the approximate Bayesian computation analysis identified a recent colonization event from a marten population in eastern Michigan. Contemporary effective population size for the Apostle Islands, WI (N1), Chequamegon National Forest, WI (N2), central Upper Michigan (N3), Minnesota (N4), Nicolet National Forest, WI (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, WI, 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 for the Chequamegon National Forest, WI (rb(WI-CF)), central Upper Michigan (rb(MI-C)), Nicolet National Forest, WI (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).

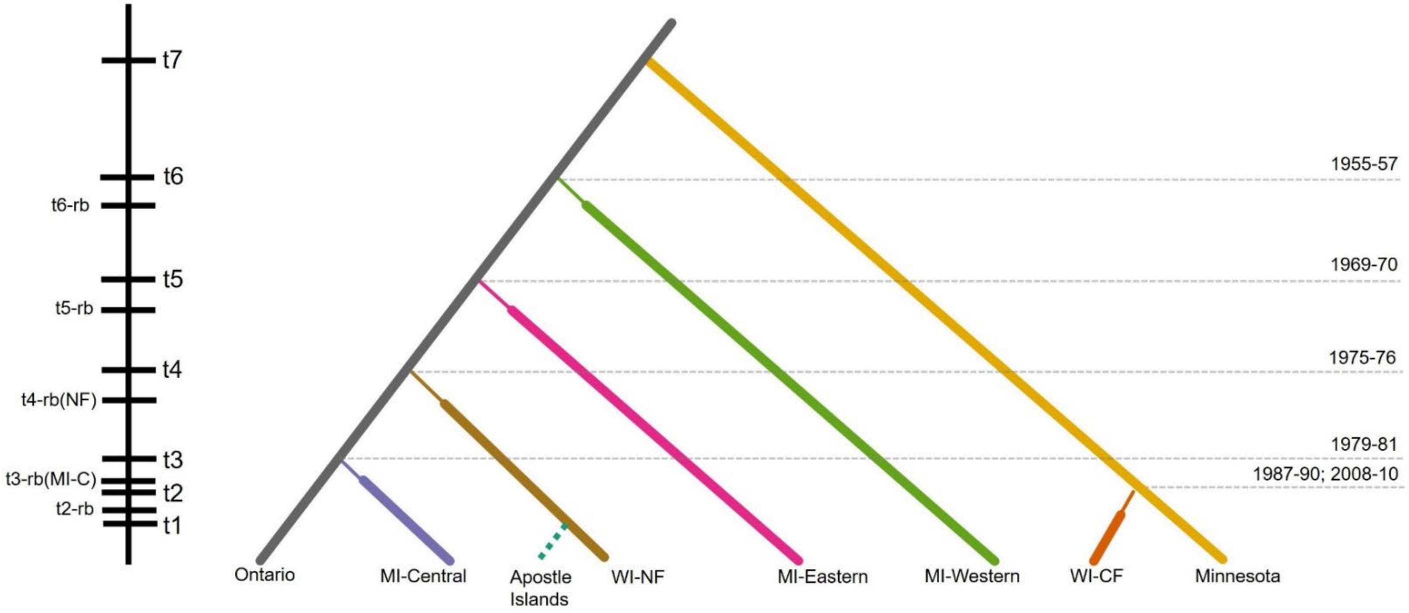
Figure S6: Simulated pedigree relationships and relatedness estimation from observed allele frequency distribution of American martens (*Martes americana*) in the (a) Apostle Islands and (b) a combined dataset of the Apostle Islands plus the Chequamegon National Forest, Wisconsin. Different color boxplot represents statistically significant groups from Tukey’s HSD. Expected relatedness values: Half-siblings – 0.25, Parent-offspring – 0.5, full-siblings – 0.5, unrelated – 0.

Figure S7: Relative migration network between regional populations of American martens (*Martes americana*) in Wisconsin and Upper Michigan. (A) Complete network with no filter threshold. (B) Relative migration network showing significant pairwise directionality in relative migration estimates from 1000 bootstraps. Regional populations consisted of the Apostle Islands, WI (WI-AI), Chequamegon National Forest, WI (WI-CF), central Michigan (MI-Central), Nicolet National Forest, WI (WI-NF), eastern Michigan (MI-Eastern), western Michigan (MI-Western).


t1
t7
t6
t6-rb
t5
t5-rb
t4
t4-rb(NF)
t3
t3-rb(MI-C)
t2
t2-rb
1955-57
1969-70
1975-76
1979-81
1987-90; 2008-10
Ontario
MI-Central
WI-NF
MI-Eastern
MI-Western
WI-CF
Minnesota
Apostle Islands


t7
t6
t6-rb
t5
t5-rb
t4
t4-rb(NF)
t3
t3-rb(MI-C)
t2
t2-rb
t1
1955-57
1969-70
1975-76
1979-81
1987-90; 2008-10
Ontario
MI-Central
WI-NF
Apostle Islands
MI-Eastern
MI-Western
WI-CF
Minnesota


t7
t6
t6-rb
t5
t5-rb
t4
t4-rb(NF)
t3
t3-rb(MI-C)
t2
t2-rb
t1
1955-57
1969-70
1975-76
1979-81
1987-90; 2008-10
Ontario
Apostle Islands
MI-Central
WI-NF
MI-Eastern
MI-Western
WI-CF
Minnesota


t7
t6
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t1
1955-57
1969-70
1975-76
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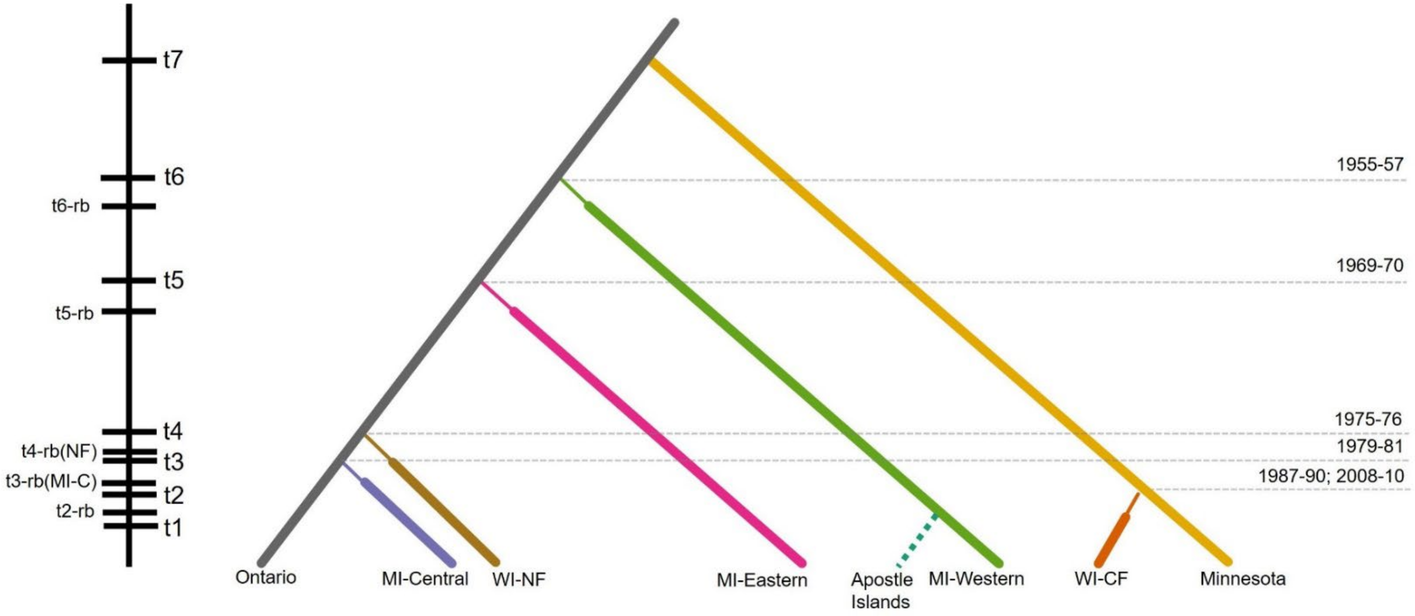
1987-90; 2008-10
Ontario
MI-Central
Apostle Islands
WI-NF
MI-Eastern
MI-Western
WI-CF
Minnesota


t7
t6
t6-rb
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t4-rb(NF)
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t3-rb(MI-C)
t2
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t1
1955-57
1969-70
1975-76
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1987-90; 2008-10
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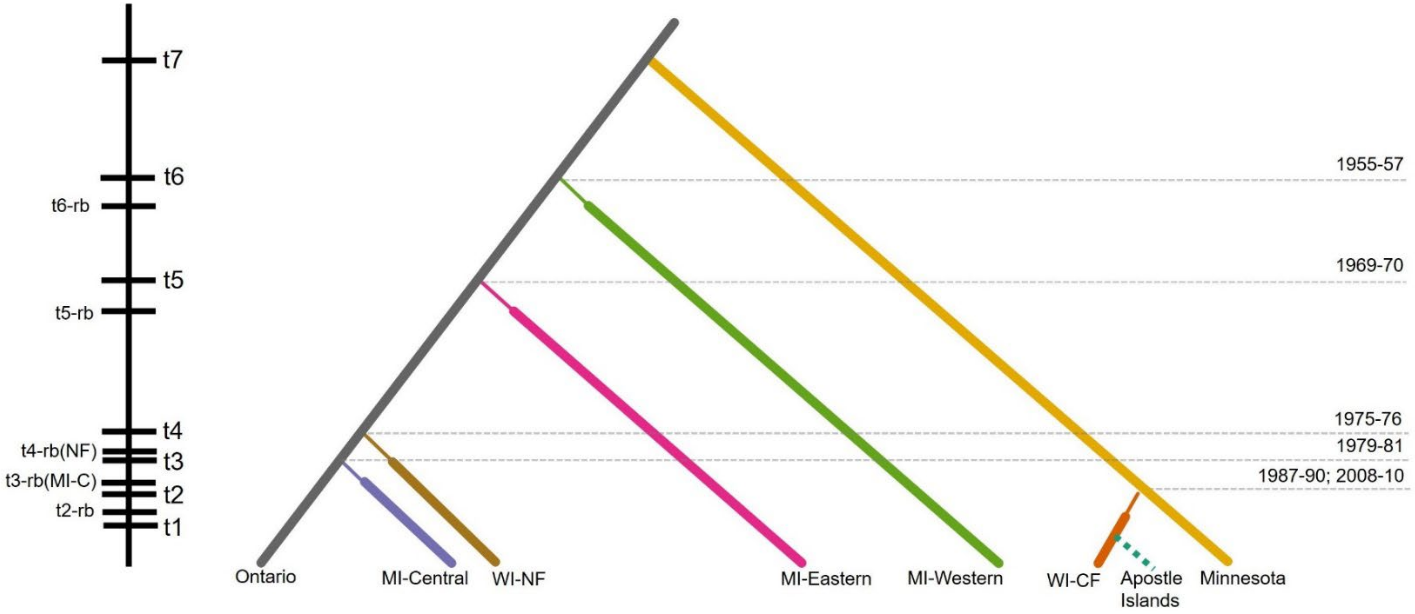
Apostle Islands
MI-Western
WI-CF
Minnesota


t7
t6
t6-rb
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t3-rb(MI-C)
t2
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t1
1955-57
1969-70
1975-76
1979-81
1987-90; 2008-10
Ontario
MI-Central
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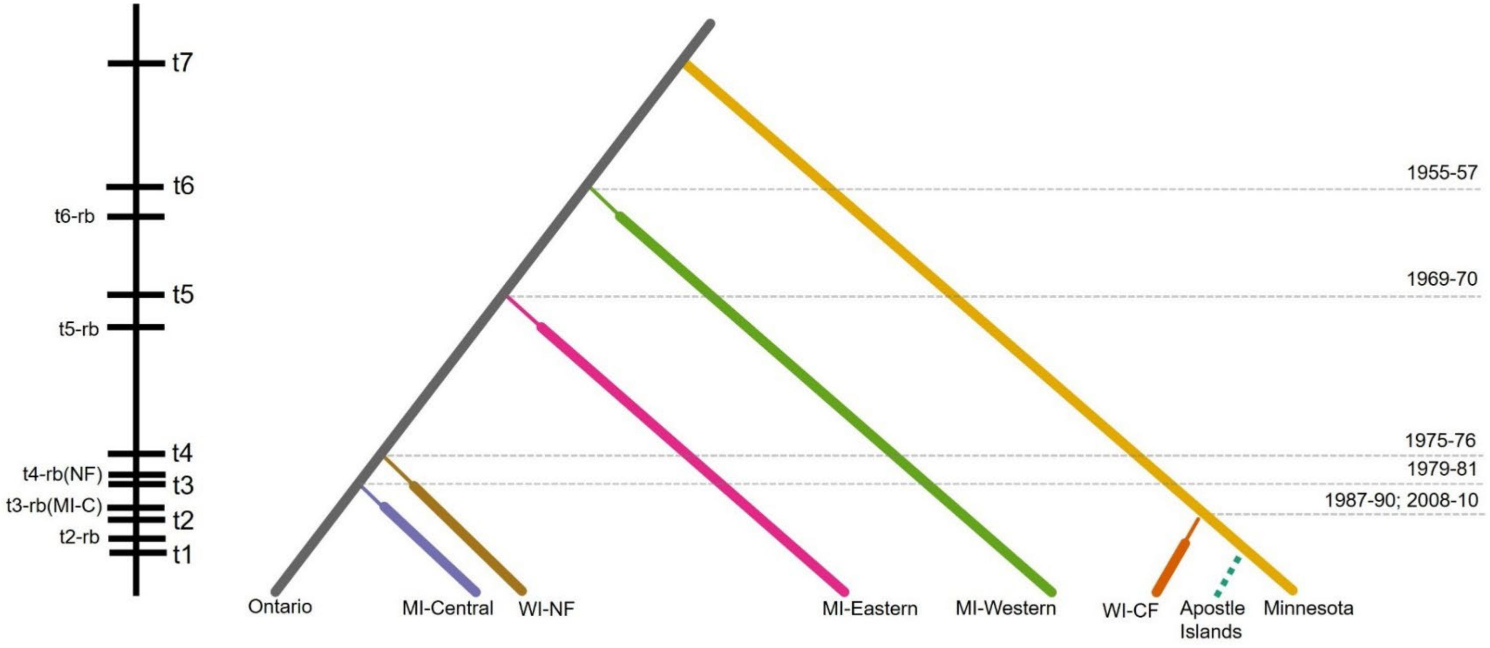
WI-CF
Apostle Islands
Minnesota


t7
t6
t6-rb
t5
t5-rb
t4
t4-rb(NF)
t3
t3-rb(MI-C)
t2
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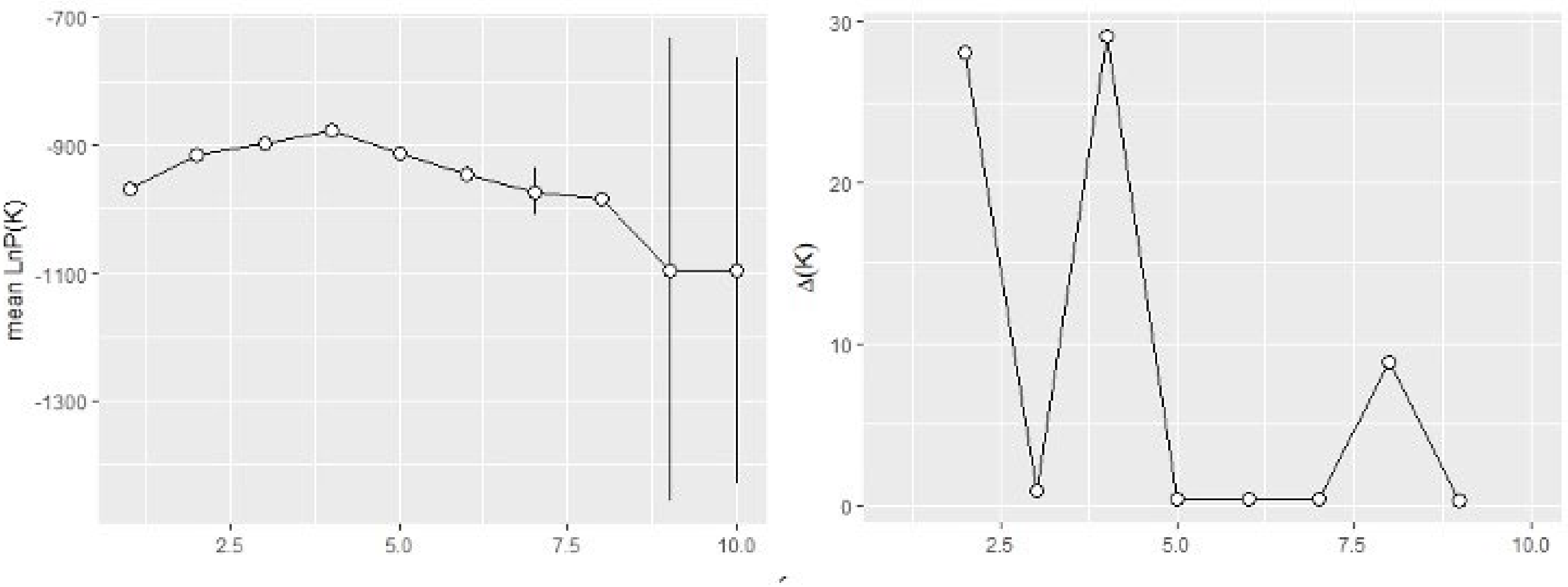
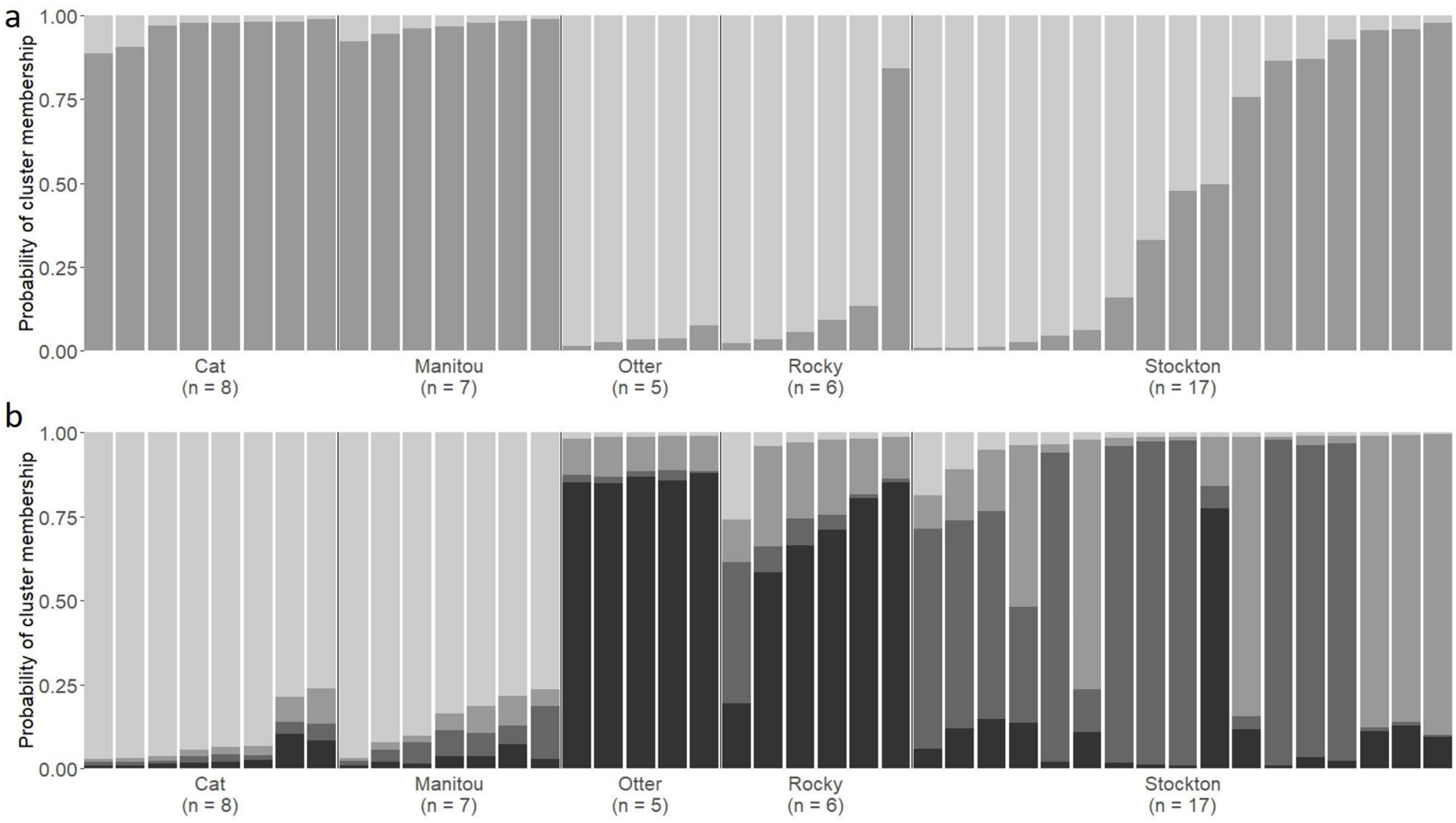
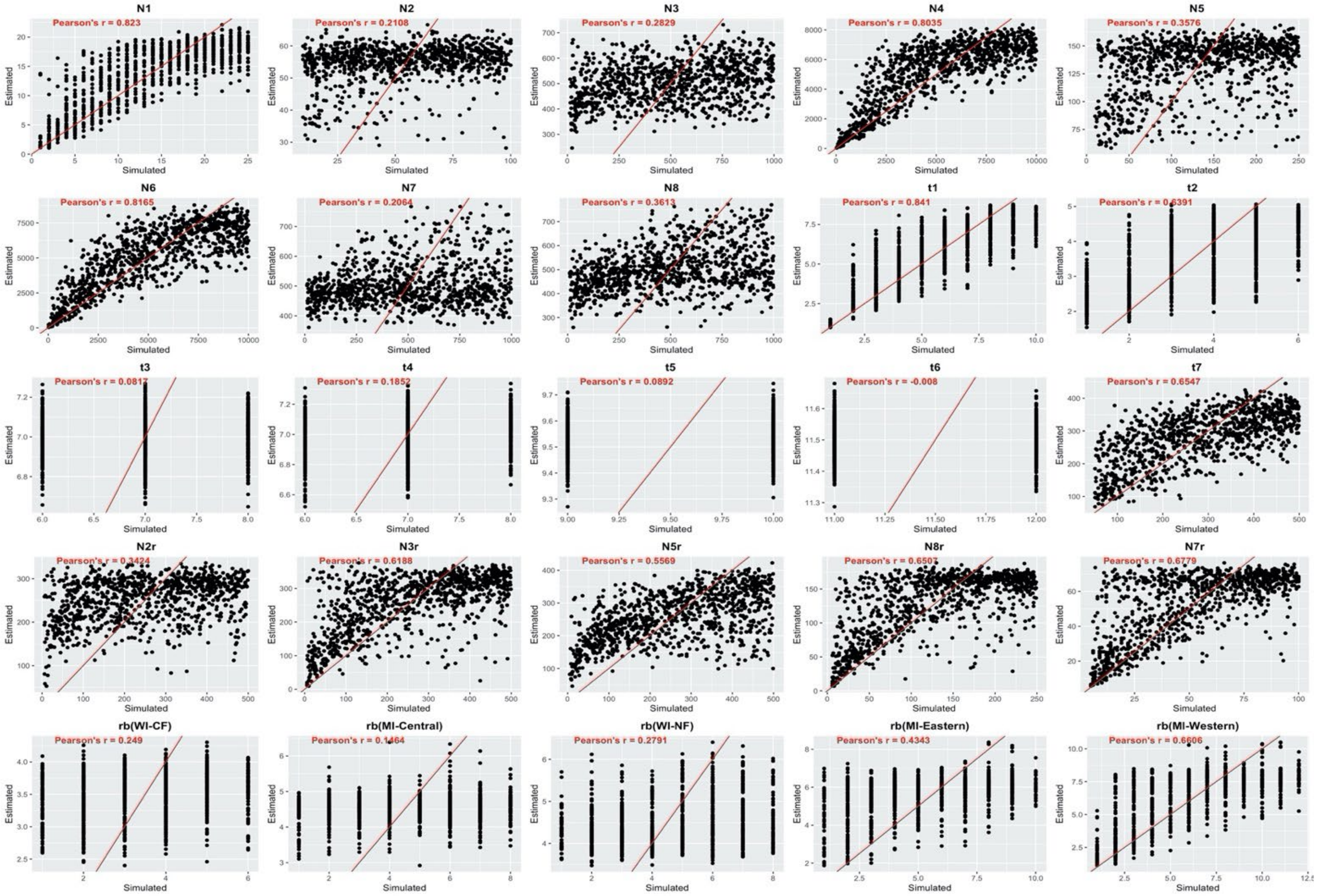
t1
1955-57
1969-70
1975-76
1979-81
1987-90; 2008-10
Ontario
MI-Central
WI-NF
MI-Eastern
MI-Western
WI-CF
Apostle Islands
Minnesota


-700
-900
-1100
-1300
mean LnP(K)
2.5
5.0
7.5
10.0
30
20
10
0
Δ(K)
2.5
5.0
7.5
10.0


a
b
Probability of cluster membership
1.00
0.75
0.50
0.25
0.00
Cat
(n = 8)
Manitou
(n = 7)
Otter
(n = 5)
Rocky
(n = 6)
Stockton
(n = 17)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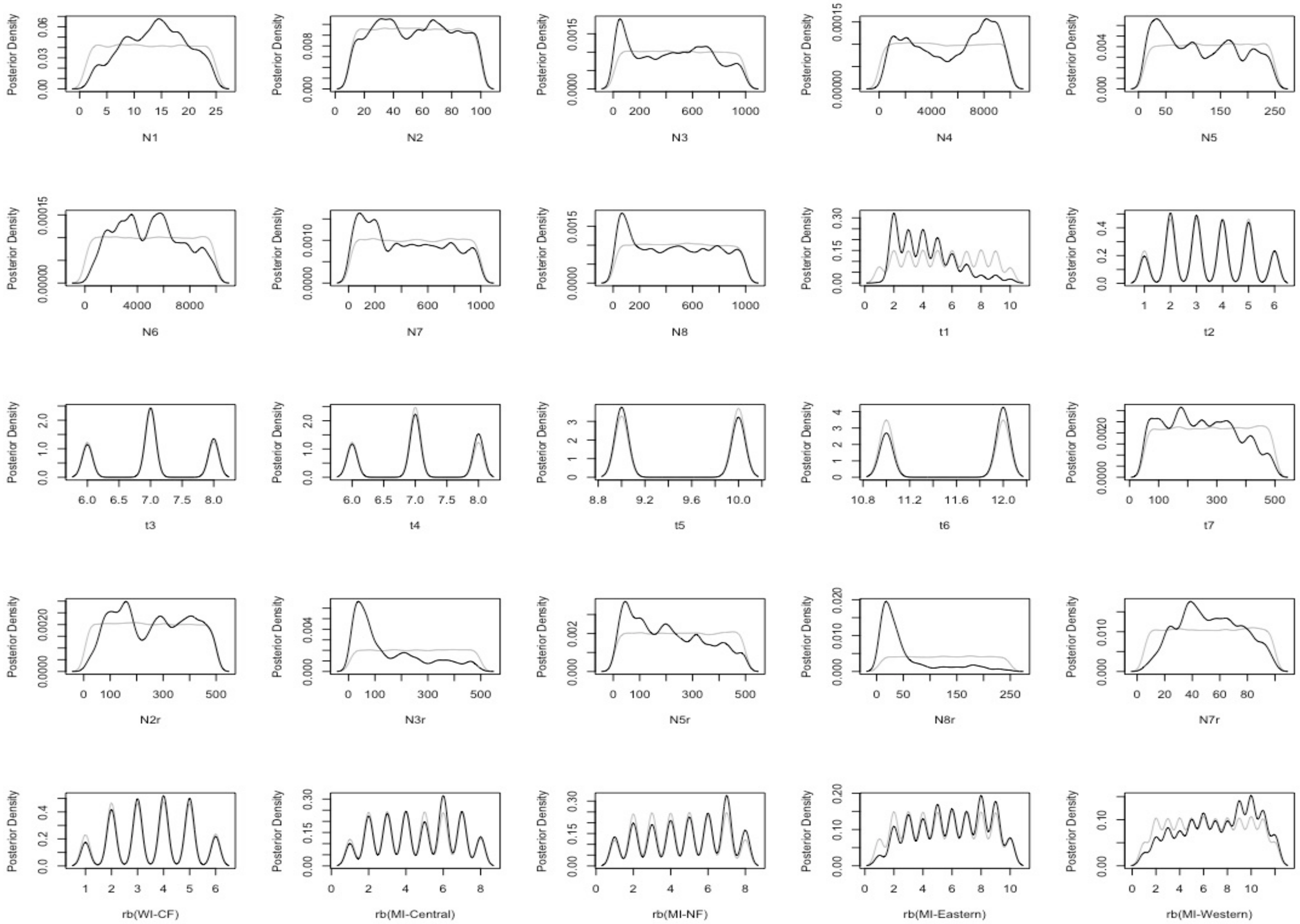
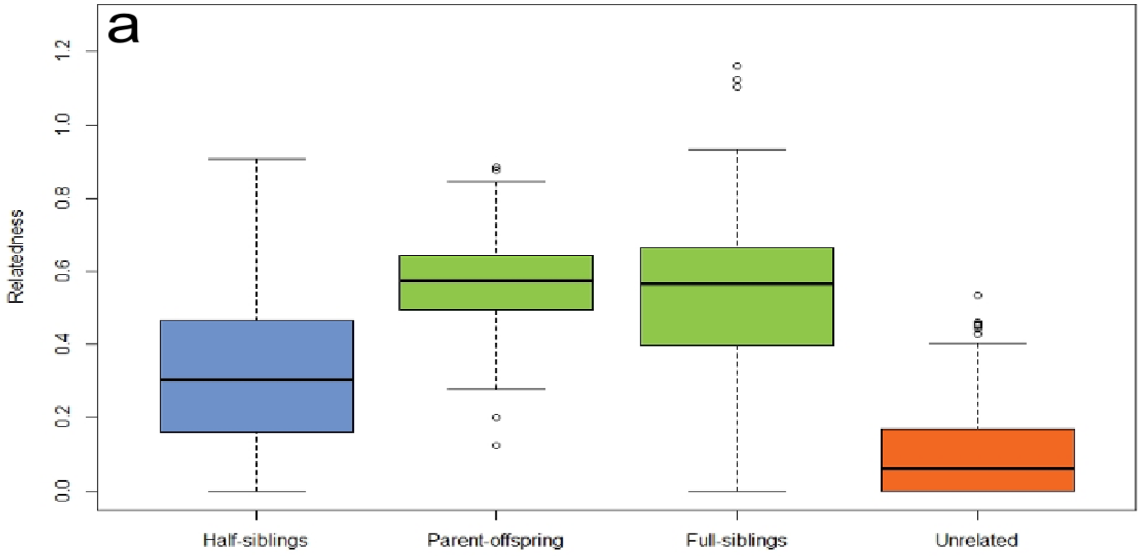
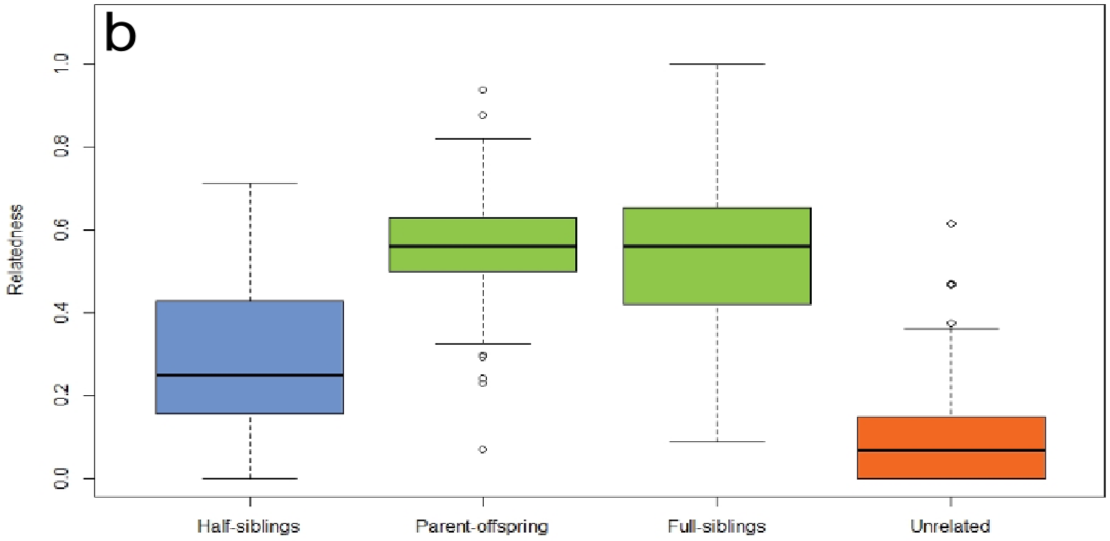
Pearson's r = 0.823
N2
Pearson's r = 0.2108
N3
Pearson's r = 0.2829
N4
Pearson's r = 0.8035
N5
Pearson's r = 0.3576
N6
Pearson's r = 0.8165
N7
Pearson's r = 0.2064
N8
Pearson's r = 0.3613
t1
Pearson's r = 0.841
t2
Pearson's r = 0.6391
t3
Pearson's r = 0.0812
t4
Pearson's r = 0.1852
t5
Pearson's r = 0.0892
t6
Pearson's r = -0.008
t7
Pearson's r = 0.6547
N2r
Pearson's r = 0.3424
N3r
Pearson's r = 0.6188
N5r
Pearson's r = 0.5569
N8r
Pearson's r = 0.6507
N7r
Pearson's r = 0.6779
rb(WI-CF)
Pearson's r = 0.249
rb(MI-Central)
Pearson's r = 0.1464
rb(WI-NF)
Pearson's r = 0.2791
rb(MI-Eastern)
Pearson's r = 0.4343
rb(MI-Western)
Pearson's r = 0.6606
Estimated
Simulated


Posterior Density
N1
N2
N3
N4
N5
N6
N7
N8
t1
t2
t3
t4
t5
t6
t7
N2r
N3r
N5r
N8r
N7r
rb(WI-CF)
rb(MI-Central)
rb(MI-NF)
rb(MI-Eastern)
rb(MI-Western)


a
Relatedness
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Half-siblings
Parent-offspring
Full-siblings
Unrelated


b
Relatedness
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0.2
0.4
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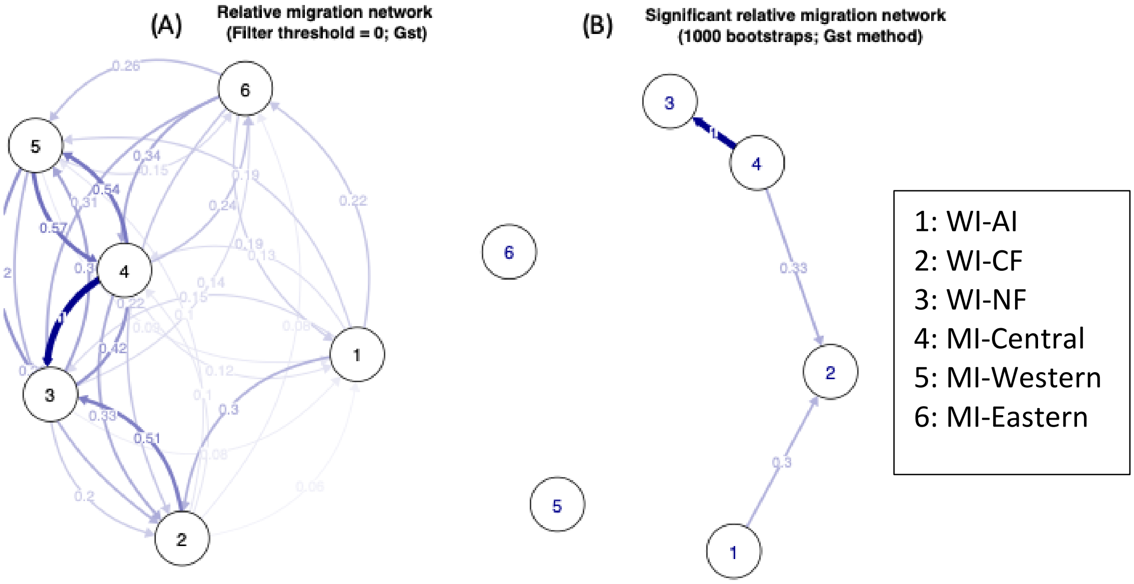
Half-siblings
Parent-offspring
Full-siblings
Unrelated



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Seasonality drives the survival landscape of a recovering forest carnivore in a changing world

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Abstract

Ecological heterogeneity promotes species persistence and diversity. Environmental change has, however, eroded patterns of heterogeneity globally, stifling species recovery. To test the effects of seasonal heterogeneity on a reintroduced carnivore, American martens (*Martes americana*), we compared metrics of local and season-specific heterogeneity to traditional forest metrics on the survival of 242 individuals across 8 years and predicted a survival landscape for 13 reintroduction sites. We found that heterogeneity – created by forest structure in the growing season and snow in the winter – improved survival and outperformed traditional forest metrics. Spatial variation in heterogeneity created a distinct survival landscape, but seasonal change in heterogeneity generated temporal discordance. All translocation sites possessed high forest heterogeneity but there were greater differences in winter heterogeneity; recovery sites with the poorest snow conditions had the lowest viability. Our work links heterogeneity across seasons to fitness and suggests that management strategies that increase seasonal aspects of heterogeneity may help to recover other sensitive species to continuing environmental change.

Introduction

Ecological heterogeneity, or the variability of an environmental property, are abiotic and biotic characteristics that vary temporally and spatially (Li & Reynolds 1995). Many ecological processes are sensitive to this variation and heterogeneity generally increases biodiversity by promoting species coexistence and persistence (Tews et al. 2004). Widespread land-use change has, however, transformed ecosystems, and altered fundamental patterns of heterogeneity (e.g., Jones et al. 2020a). Unlike natural disturbance regimes that typically promote spatial heterogeneity, the intensity and duration of land-use often simplifies structure and species composition to reduce spatial variation (Foley et al. 2005). The homogenization of forested systems, and fauna that rely on them, generally benefits a few generalists to the detriment of specialists.

Many ecosystems, especially in latitudinal extremes, also exhibit strong temporal heterogeneity (e.g., seasonality; Levins 1968). For instance, temperate forest structure varies seasonally from growth and subsequent abscission of leaves, and seasonal snowfall modifies the structure of the forest floor. While snow depth can have a homogenizing effect on the above-snow community, it increases heterogeneity by creating spatially distributed refugia and vertical complexity across the landscape for plants and animals, especially as the subnivium (Pauli et al. 2013). Climate change is altering abiotic conditions and changes are particularly pronounced across mid-latitudes and during the shoulder seasons (Choi et al. 2010). Notably, there have been substantial reductions in snow cover duration, spatial extent, and depth, and formation of the subnivium is projected to decline sharply under future climate scenarios (Thompson et al. 2021). Changing climate is altering the timing and duration of seasonality that has driven species adaptations and community structure.

Land use and climate change drive species persistence and have isolated and extirpated numerous vertebrate populations (Laliberte & Ripple 2004). Recovering these populations has motivated the reintroduction of species to areas once occupied or to augment existing populations. Indeed, the rewilding of species has been proposed to not only recover individual species but to restore ecological processes and resiliency (Perino et al. 2019). However, species recovery increasingly occurs in novel systems unlike historical baselines. For example, the Laurentian Forest of the Great Lakes Region was compositionally and structurally complex until the late 1800s when the region was commercially logged. Now, contemporary forests are dominated by different species at early successional stages (Rhemtulla et al. 2009). This forest loss and homogenization contributed to the decline or regional extirpation of several forest carnivores and snow-adapted species including American martens (*Martes americana*), fishers (*Pekania pennanti*), Canada lynx (*Lynx canadensis*), and gray wolves (*Canis lupus*) (Thiel 1987; Mech 1995; Williams et al. 2007). Complicating recovery for many snow-adapted species is the continued attenuation of winter conditions. Spring snow melt now occurs nearly 2 weeks earlier (Mioduszewski et al. 2015), and the snow season is projected to shorten by >1.5 months by the end of the 21st century (Ashley et al. 2020). Consequently, the loss of snow cover may affect species persistence and community structure.

Along their southern range boundary in the Great Lakes Region, American martens were extirpated by the 1930s and only a small population in northeastern Minnesota persisted. Across the region, dozens of translocations spanning 60 years have reestablished populations (Williams et al. 2007; Woodford et al. 2013), but sites vary in their recovery and long-term viability is uncertain (Skalski et al. 2011; Manlick et al. 2017; Grauer et al. 2019). American martens are considered deep snow specialists and conifer old-growth obligates (Buskirk and Powell 1994;

Proulx et al. 2005). However, broader habitat associations have been identified, suggesting that other attributes like heterogeneity, rather than a particular forest type or age, may be important for population persistence. Heterogeneity in forest stands likely improves both prey availability and foraging success (Andruskiw et al. 2008) as well as reducing predation risk (Thompson & Colgan 1994). Additionally, martens are adapted for snow, including small body size and low-foot loading, and can exploit the subnivium and deep snowpack, conferring a competitive advantage over other carnivores in snow-covered environments (Sherburne & Bissonette 1994; Krohn et al. 2005). Despite the potential importance of heterogeneity in both the summer and winter for martens, the effect on fitness has not been quantified. Linking spatially and temporally heterogeneous environmental features to demographic processes and individual fitness remains a global challenge for species recovery (Peery et al. 2012; Griffith et al. 2016).

To test the effect of landscape conditions and seasonal heterogeneity on survival, we used mortality events of martens from a long-term spatially explicit dataset. We hypothesized that martens are complexity specialists and rely on heterogeneity over traditional metrics of forest composition and age for persistence and to promote coexistence. We predicted that heterogeneity would increase survival of martens, driven by vegetation during periods of primary growth and abiotic conditions from subnivium formation (i.e., snow depth) during winter months. We compared the response of survival to a suite of landscape variables that included measures of heterogeneity and traditional forest metrics that represent landscape composition and configuration during two seasonal time periods: snow-free (1 May to 31 October) and snow-on (1 November to 30 April). Using these relationships, we then projected a contemporary survival landscape for 13 translocation sites to evaluate the potential limitations of each site within this recovery network. Ultimately, our work aims to compare landscape conditions and seasonal heterogeneity to fitness, and its importance in species reintroductions and recovery.

Methods

Capturing, monitoring, and activity areas

From 2007-2015, we captured martens using Tomahawk (Tomahawk Live Trap, Hazelhurst, WI) cage traps (models 106 and 108) that were baited with white-tailed deer (*Odocoileus virginianus*) or American beaver (*Castor canadensis*) meat and had commercial scent lure applied. Traps were covered with natural vegetation or other material and checked daily. We administered a 10:1 injection of ketamine and xylazine and monitored vitals during anesthesia (Kreeger et al. 2002). We fitted radio-collars (MI-2, 31 grams, Holohil Systems Ltd., Ontario, Canada) on captured martens (n = 242) in northern Minnesota (Fig. 1). We obtained year-round weekly radiolocations from the ground and aircraft and investigated mortality events within 1-3 days of mortality signal. We removed from analysis any individuals that were ear-tagged only (n = 3), had <8 days between capture and mortality (n = 8) or slipped their collar (n = 3), and martens captured as juveniles that did not transition to sub-adults due to being lost from monitoring or mortality (n = 26). We included all other sub-adult and adult martens in the final dataset (n = 202). To summarize environmental conditions encountered by individuals, we extracted landscape variables and measures of heterogeneity within 95% kernel density estimates (hereafter, activity areas; for individuals with ≥18 relocations) and from buffered activity areas (4.71 Km^2; for individuals with <18 relocations; see Appendix S1 for additional details). We estimated activity areas from all available relocations regardless of season as overall home ranges are relatively static across seasons (e.g., Phillips et al. 1998; Martin et al. 2021).

Quantifying landscape heterogeneity

We identified a set of variables that characterized potentially important drivers of marten survival, allowing for a comparison between heterogeneity metrics (i.e., complexity of vegetation, land cover, and abiotic conditions) and landscape variables representing composition and configuration. We derived metrics of forest composition, configuration, and complexity using the National Land Cover Dataset (Fig. 1) and the R (R Core Team 2021) package *landscapemetrics* (Hesselbarth et al. 2019). We combined forest cover classes from NLCD (deciduous, evergreen, and mixed forest) and calculated the largest patch index, edge density, radius of gyration (i.e., the average distance an organism can move within a patch), and correlation length (i.e., the physical connectedness of the landscape) within activity areas to represent established landscape metrics (Cushman et al. 2008). In addition, we quantified land cover complexity by calculating joint entropy (i.e., land cover complexity) that identifies the frequency and probability of adjacencies between cells of different land cover classes (Nowosad & Stepinski 2019). We matched the time the individual was alive on the landscape to the closest available NLCD year (2008, 2011, 2013, 2016) to estimate and update our landscape metrics for each individual that survived multiple years.

To characterize vegetation complexity, we used measures of image texture (Haralick et al. 1973) that have been associated with foliage height diversity (Wood et al. 2012), successional stage (Jakubauskas 1997), and structural complexity (Tuanmu & Jetz 2015). Land cover classification simplifies the landscape to discrete cover types and may fail to capture heterogeneity within cover types and important ecological heterogeneity (Cushman et al. 2010; Frazier & Kedron 2017). We selected 2nd order entropy and correlation (i.e., vegetation complexity) as two uncorrelated measures of image texture to capture heterogeneity in vegetation and habitat complexity within marten activity areas. Second-order entropy and correlation were calculated within individual activity areas from a gray-level co-occurrence matrix (GLCM) derived from composite images of greenness following Farwell et al. (2021). We estimated the percent and standard deviation of annual canopy cover from a Landsat-based canopy cover map for Minnesota (Vogeler et al. 2018). We quantified the average and standard deviation of forest age within marten activity areas from a 2018 dataset developed by the USFS Forest Inventory and Analysis (Wilson et al. 2018).

We summarized abiotic complexity as the elevation and the standard deviation in elevation from a 1 arc-second (~30 m) digital elevation model (3D Elevation Program, USGS) during the snow-free season. During the snow-on season, we quantified abiotic complexity by snow depth (mm) from the Snow Data Assimilation System (National Operational Hydrologic Remote Sensing Center) and the percent of frozen ground without snow during the winter (Fig. 1; FWOS; Gudex-Cross et al. 2021). We used both snow measures to represent the importance of the subnivium for martens (Sherburne & Bissonette 1994) that adds complexity through the vertical profile of the snowpack. We accounted for temporal variation throughout the seasons by estimating landscape variables and heterogeneity at the time of mortality either to the closest month or year the mortality occurred.

Survival analysis

To test the influence of landscape variables and heterogeneity on survival, we modeled mortality risk from time-to-event data using a Bayesian framework (P. F. Jones et al. 2020). We developed a set of eight *a priori* models that characterized potentially important drivers of marten survival and allowed for comparison between heterogeneity and landscape variables:

vegetation complexity, forest age, forest connectivity, area and edge metrics, abiotic complexity, canopy cover, and land cover complexity (Table 1). In addition, we modeled an interaction between vegetation complexity and abiotic complexity during the snow-on period. We did not include landscape variables in the same model if they exhibited collinearity (Pearson's correlation coefficient ≥ 0.5).

We used a recurrent time horizon based on a biological calendar year starting on 1 May and ending on 30 April (Fieberg and Delgiudice 2009). Individuals could contribute multiple individual-years to the risk sample if they survived multiple biological years. We tested the effect of landscape heterogeneity using separate seasonal models for snow-free (1 May to 31 October) and snow-on (1 November to 30 April), representing the seasonal shifts of forested systems in this region. We used staggered entry and right censored individuals that had collar failure, were lost to detection, or survived the seasonal timeframe. We assumed censoring was independent of fate; if individuals lost during monitoring were true mortality events, we would underestimate mortality during both seasons. For example, mortality in the snow-on season due to trapping could be underestimated if trappers did not report harvested individuals with collars, however, only two individuals went missing during the trapping season.

We estimated a baseline hazard function and log hazard coefficients. Briefly, the Poisson random variable (dN_{ij}) had a mean intensity equal to an indicator of an individual's status in the risk set (I_{ij}), the baseline hazard function ($d\Lambda_{0j}$), and log hazard coefficient (β) of the ith individual. We ran 3 chains of 50 000 iterations and removed the first 5000 iterations as burn-in and then thinned posterior samples to every fifth sample. We used vague priors for all parameters including β ~ Normal(0, 10) and ($d\Lambda_{0j}$ ~ Gamma($d\Lambda_{0j}^{*}$, c). The baseline hazard ($d\Lambda_{0j}$) was distributed as a gamma process prior that is centered around a prior estimate of the baseline hazard ($d\Lambda^*_{0j}$) and a dispersion parameter (c = 0.001; Ibrahim 2001). Small values of c correspond to weak prior knowledge (P. F. Jones et al. 2020). We used Markov chain Monte Carlo sampling to derive parameter estimates from posterior distributions with the R (R Core Team 2021) package Nimble (de Valpine et al. 2017). We assessed model convergence with trace plots and Gelman-Rubin statistics (*R hat* < 1.1) and evaluated competing models and a null model (N = 6; Table 1) for each season using WAIC (Watanabe 2010). We considered the most supported model to have the lowest WAIC value and compared competing models by ΔWAIC. We centered and scaled each covariate and present standardized beta-coefficients and Bayesian credible intervals (BCI) in our results to compare relative effects of landscape variables and heterogeneity on sub-adult and adult marten survivorship. We also estimated cause-specific mortality rates during the snow-on season with a Bayesian cumulative incidence function (P. F. Jones et al. 2020; see Appendix S1 for additional details).

Survival landscape

We projected a survival landscape using the survival probabilities from the most supported seasonal models and the 25th, 50th, and 75th percentile of predictor values averaged over the study period (2007-2015). We spatially extrapolated model predictions by estimating seasonal survival rates to the end of each season as a function of each pixel value (DeCesare et al. 2014). We multiplied seasonal survival probabilities after resampling to estimate a cumulative annual survival probability. To detect seasonal incongruences in survival, we calculated the difference between snow-on and snow-free survival probabilities across the landscape.

Finally, we used the most supported survival model from the Minnesota study area to extrapolate the contemporary (2011-2020) probability of survival at all regional reintroduction sites (Williams et al. 2007; Fig. 1). Because recovery of these reintroductions has varied, we used landscape features correlated to survival to identify potential demographic limitations of these past reintroductions. We predicted contemporary survival from each reintroduction site by averaging landscape variables over the last 10 years (2011-2020) and extracted values buffered by our study area in Minnesota (167 241 hectares; see Appendix S1 for additional details). We compared the mean and range of landscape variables from our training dataset (i.e., observed values used in our Bayesian survival model) and testing dataset (i.e., contemporary values extracted from buffered reintroduction sites) and masked analysis to only observed values. We compared predicted survival at reintroduction sites and identified sites with sub-adult/adult survival <0.75, which has previously been identified as generally indicative of vulnerable or declining populations (Buskirk et al. 2012),

Results

Survival modeling

We observed 119 mortality events including 36 during the snow-free season and 83 during the snow-on season. We had 61 natural mortality events, and most were from predation (89%) and nearly all were attributed to mammalian carnivores (94%). We observed 58 human-related mortality events, and all were attributed to trapping. We estimated snow-free survivorship (0.85, BCI: 0.80, 0.89) to be 24% higher than snow-on survivorship (0.61, BCI: 0.54, 0.67) including trapped and natural mortality. During the snow-on period, adult mortality associated with trapping was higher (CIF = 0.31, BCI: 0.23, 0.39) than natural causes (CIF = 0.09, BCI: 0.06, 0.13). Males (CIF = 0.36, BCI: 0.25, 0.49) were approximately 10% more likely to be trapped than females (CIF = 0.25, BCI: 0.15, 0.38) but had a lower probability of natural mortality (CIF = 0.06, BCI: 0.03, 0.11) than females (CIF = 0.11, BCI: 0.06, 0.19). However, 95% Bayesian credible intervals overlapped for both mortality sources (Fig. S1). Thus, we did not include variables of sex or age class in modeling the effects of landscape variables and heterogeneity.

Metrics of heterogeneity were the most supported models, yet the heterogeneity metric differed by season (Table 1). Vegetation complexity (2nd order entropy) was negatively related to the mortality hazard (i.e., positively to survival) during the snow-free season (β = -1.94, BCI: -2.57, -1.31; Fig. 2). During the snow-on season, abiotic complexity (i.e., snow depth) reduced the mortality hazard and increased survival (β = -2.51, BCI: -3.00, -2.04; Fig. 2). No other covariate was important in either season when evaluating their 95% credible intervals (Fig. 2). Similar to our overall survival modeling, snow depth reduced the mortality hazard and increased survival for both trapping (β = -2.90, BCI: -3.57, -2.28) and natural (β = -1.91, BCI: -2.71, -1.06) mortality events (Fig. S2). In addition, two related measures (radius of gyration and correlation length) that estimate average distance to forest edge and physical connectedness of forest within activity areas reduced the hazard of natural mortality, but had no effect on trapping related mortality (Fig. S2).

Survival landscape

Survival during the snow-on season exhibited a notable decrease from east to west driven by snow conditions, while during the snow-free season survival was spatially patchy and was higher in areas around complex forest stands (Fig. 3a, b). Cumulative survival and the difference in survival between seasons were driven by lower survival during the snow-free season and the east-west trend in survival during the snow-on (Fig. 3c, d). In particular, the lower survival during the snow-free season in the northeast portion of the landscape created differences in survival between seasons, but the most extreme differences occurred due to lower survival during the snow-on season from both mortality sources, especially in the southwest portion of our study area (Fig. 3d).

Regionally, predicted survival was high during the snow-free season across all translocation sites with little difference between sites (Fig. 4a, b). There was, however, much more variability in survival during the snow-on season influencing demographic outcomes (range: 0.56, 0.93; Fig. 4b). Indeed, the four most southern translocation sites had predicted survival <0.75.

Discussion

Using mortality events from a large and unique long-term spatially explicit dataset, our work compared the response of survival to a suite of landscape variables that included measures of heterogeneity and traditional forest metrics. We predicted that heterogeneity would increase survival of martens and would likely be dictated by seasonality in this system. We found that heterogeneity improved survival of martens, but the landscape feature varied seasonally.

In the snow-free season, areas with greater vegetation complexity conferred higher survival. Complex forest likely improves fitness by providing the structural characteristics that increase foraging success (Andruskiw et al. 2008) and reduce predation risk (Thompson & Colgan 1994). While martens are often considered older-forest specialists, forest age, area, or canopy cover were not correlated with survival. Previous research has identified a high degree of plasticity in marten habitat suitability and selection across their range, and at times no association with indices of old growth forests. (e.g., Moriarty et al. 2021). Moreover, other putative specialists of old growth – northern flying squirrels (*Glaucomys sabrinus*; Smith et al. 2005), spotted owls (*Strix occidentalis*; Tempel et al. 2014) and fishers (Sauder & Rachlow 2015; Parsons et al. 2019) – have also been associated with a variety of seral stages as well as heterogeneity. While attributes of old growth forests are beneficial to meet some life-history needs (e.g., large trees for reproduction), heterogeneity can be more important for other components of demography (e.g., adult survival) and may even confer larger impacts to population growth (Heppell et al. 2000; Sæther & Bakke 2000).

Across northern latitudes forests are temporally dynamic and are typified by snow that transforms the physical environment for part of the year. We found that abiotic conditions in the snow-on season (i.e., snow depth) reduced mortality associated with both trapping and predation. Deep snow likely makes trapping and access more difficult, in addition to reducing above ground movements of martens that can be energetically expensive (Gilbert et al. 2009), while also providing the necessary refuge from predators. Given attenuating snow conditions from climate change, snow conditions may be important tools for guiding trapping regulations. Martens had a higher probability of survival as snow depth increased, likely attributable to depth being a key component of subnivium formation and beneficial thermal properties (Thompson et al. 2018). Moving across deep snow increases energetic cost even for a snow-adapted species (Martin et al. 2020), but the benefits of deep snow (i.e., avoiding predators, accessing the subnivium) appear disproportionate to the cost. Previous research has identified snow as an important predictor of habitat use (Shirk et al. 2014; Martin et al. 2021) and behavior (Sherburne & Bissonette 1994; Gilbert et al. 2009), but the fitness response we have as shown here links snow to the persistence of populations.

Along their southern range boundary, snowpack is projected to continue to decline, leaving only lake effect zones in the Great Lakes Region as snow and subnivium holdouts (Thompson et al. 2021). Not only is snow contracting spatially, but the snow season is shortening and spring melt is 2 weeks earlier than 50 years ago (Choi et al. 2010). For martens, as well as other snow-adapted species, the risk of mortality can be high during periods when complexity is lowest from the transition between winter conditions and vegetative green-up, which is often the case during shoulder seasons (i.e., spring and fall; Wilson et al. 2019). We identified areas where habitat (vegetation complexity) that enhances survival rates in one season is not matched with other seasons (snow depth), leading to important mismatches in survival. Climate change may, then, amplify seasonal differences and ultimately accentuate the costs on survival.

Lessons for management

Ultimately, changes in the depth and duration of the snowpack, especially outside of subnivium holdouts, will likely favor less snow-adapted species, intensify competition with martens, and potentially drive local or regional extirpations. Indeed, heterogeneity can structure carnivore communities (Fedriani et al. 1999; Chesson 2000) and promote biodiversity by providing more resources, refuges, and niche space (Udy et al. 2021; Thomsen et al. 2022). Increasing heterogeneity may even select for behaviorally diverse populations that could further increase population resiliency to continued environmental change (Mortelliti and Brehm 2020).

Resource managers face the challenge of mitigating species losses due to environmental change often through intensive management practices (e.g., habitat modification, translocations). Practices that emulate natural disturbances have gained prominence as potential management strategies that add heterogeneity to many systems. Forests of the Great Lakes Region were historically disturbed by wind-induced tree fall or infrequent fire, but the vast majority of stand replacing disturbance is now from harvest activities which has decreased structural complexity and simplified forest layers (Vogeler et al. 2020). Practices that mimic the size and intensity of natural disturbances can be tools to restore heterogeneity in many forested landscapes and create more resilient forests to environmental change (Messier et al. 2021).

Reintroductions often focus on identifying habitat during the summer. Indeed, the contemporary forest at translocations sites in the Great Lakes Region appear well suited for marten survival during the summer. Martens regionally appear to have higher survival during summer periods than winter even where trapping does not occur (McCann et al. 2010). However, rarely have winter conditions and snow been explicitly considered in reintroduction or recovery plans. Consequently, populations at translocation sites with lower winter survival (≤ 0.75) have remained near release sites and their viability remains uncertain (Manlick et al. 2017). In contrast, reintroduced populations featuring higher predicted survival (> 0.75) during the snow-on season are the same ones that have expanded their distribution (Williams et al. 2007) and even dispersed into neighboring declining populations (Smith et al. 2021). In areas where martens are legally harvested, but where populations may be less abundant, managers may need to consider adjusting harvest season timing, length, or limits to offset potential increases in harvest and natural mortality stemming from reduced snowpack associated with climate change.

Our work joins the growing body of research revealing that snow is habitat and should be considered in management plans and even managed to promote its quality and extent (Zuckerberg & Pauli 2018). While addressing global climate change is limited at the scale of local management, heterogeneity and forest floor complexity can prolong snow retention (Lundquist et al. 2013) and provide managers a tool to mediate eroding snow conditions. Indeed, management strategies that manage the subnivium as a seasonal habitat and enhance its formation and persistence are indirect approaches to mitigate climate change consequences.

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Table 1: Model selection results comparing relative support for the influence of forest and abiotic conditions on sub-adult and adult American marten (*Martes americana*) survival in northern Minnesota, USA. The most supported model according to WAIC is in bold and relative support compared to alternative hypotheses is estimated by ΔWAIC. Entropy and correlation are 2nd order image textures derived from Enhanced Vegetation Index of Landsat 5 and 8 images. SD: standard deviation. FWOS: percent of days with frozen ground without snow. LPI: largest patch index.

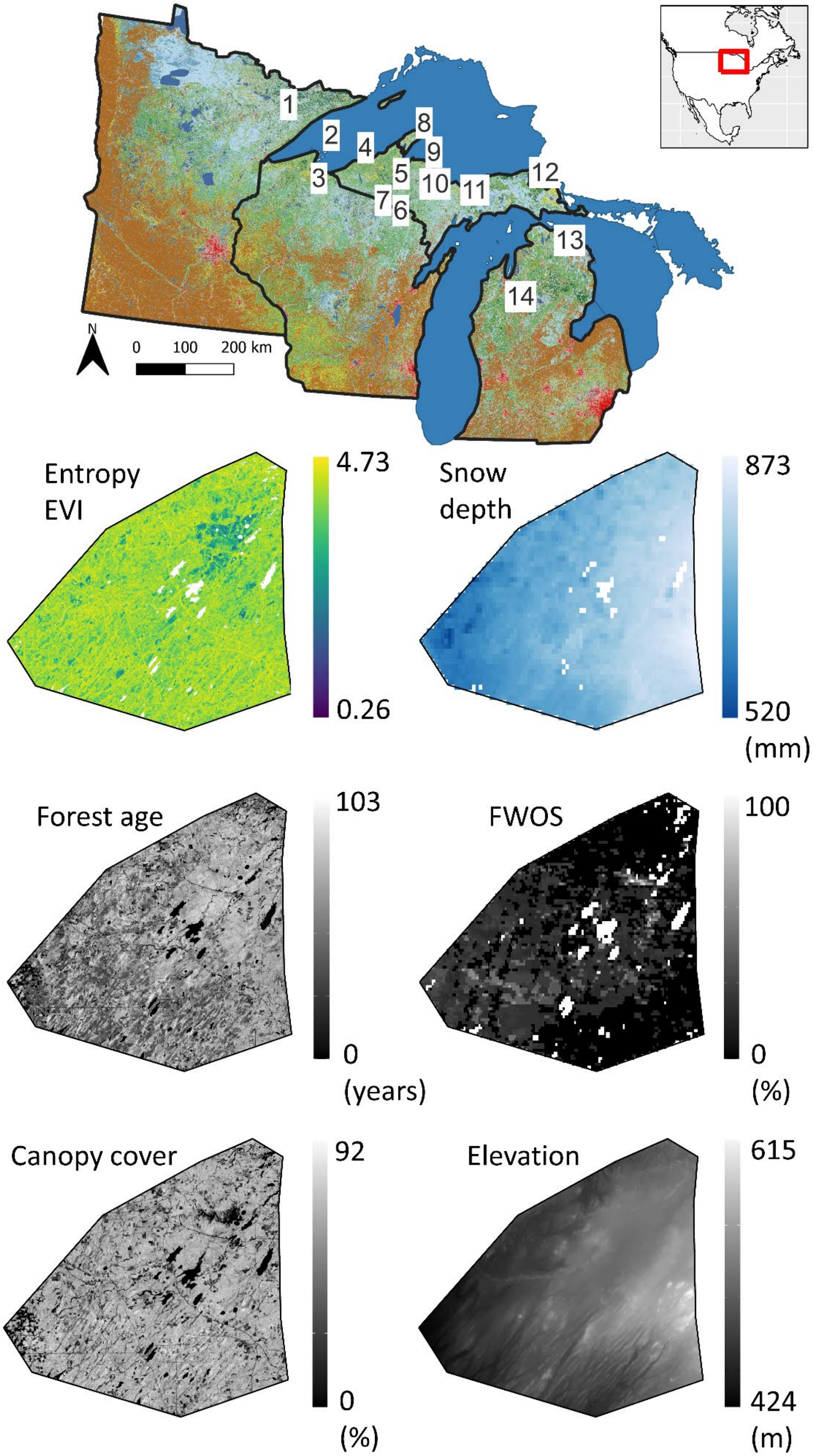
		Snow-free		Snow-on	
Model	k	WAIC	ΔWAIC	WAIC	ΔWAIC
H1. Vegetation complexity (entropy + correlation)	2	**520.32**	**0**	922.61	107.85
H2. Forest age (forest age + forest age SD)	2	563.72	43.40	921.72	106.96
H3. Abiotic complexity (Snow-free: elevation + elevation SD) (Snow-on: snow depth + FWOS)	2	559.91	39.59	**814.76**	**0**
H4. Area and edge metrics (LPI + edge density + radius of gyration)	3	561.22	40.91	923.86	109.17
H5. Forest connectivity (correlation length)	1	562.58	40.36	920.13	105.37
H6. Land cover complexity (joint entropy)	1	561.44	41.12	920.78	106.02
H7. Canopy cover (% canopy cover)	1	562.64	42.32	921.06	106.30
H8. Interaction (snow depth + entropy + entropy * snow depth)	3	–	–	817.65	2.89
H9. Null	0	560.68	42.26	918.36	103.60

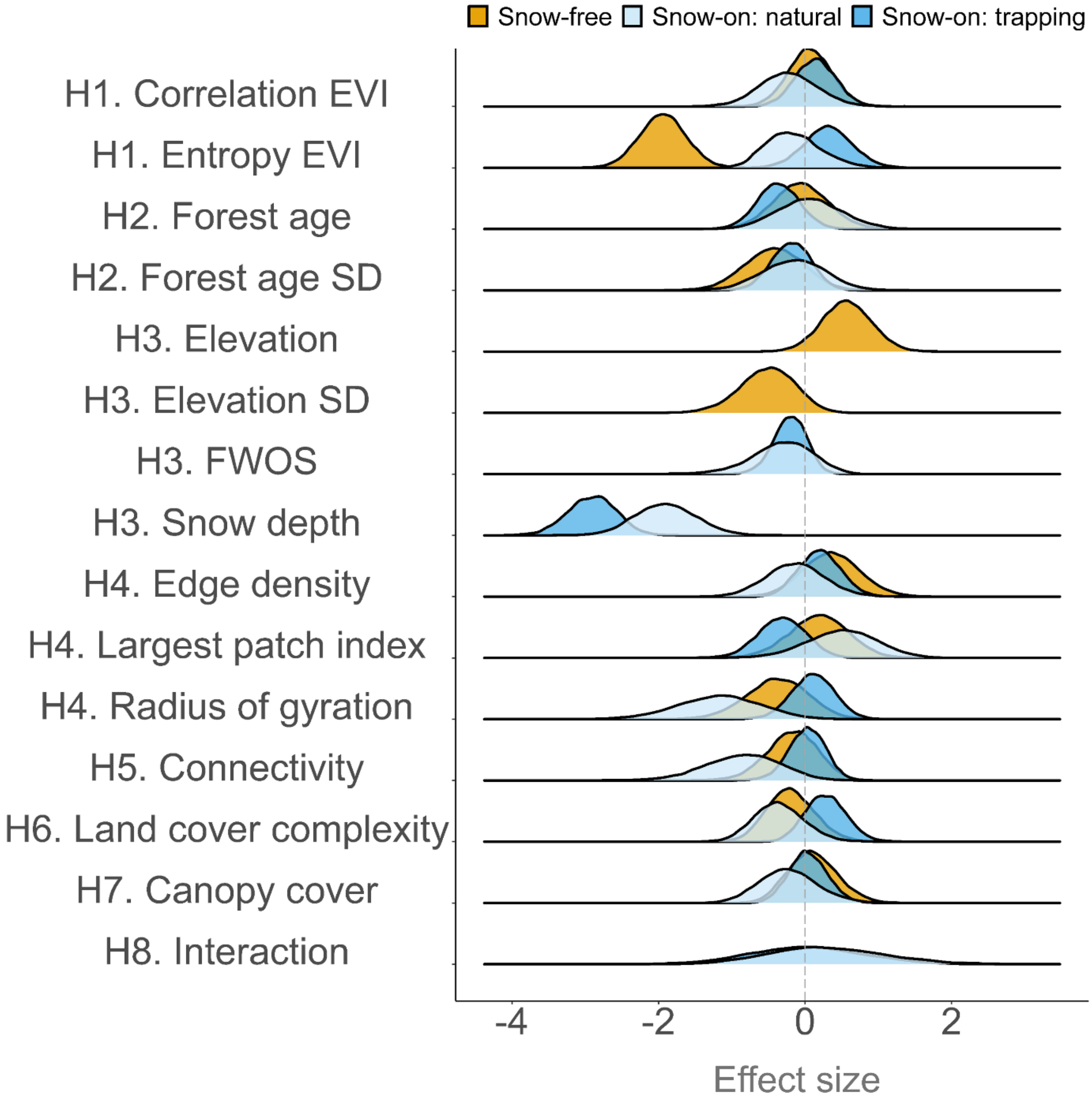
Figure 1: Regional land cover from the 2016 National Land Cover Database and reintroduction sites (numbers) of American marten (*Martes americana*). Examples of landscape variables and measures of heterogeneity within the Minnesota study area (1) including (from left to right) entropy − a 2nd order image texture derived from Enhanced Vegetation Index of Landsat 5 and 8 images, snow depth (mm), forest age (years), FWOS − percent of days with frozen ground without snow, canopy cover (%), and elevation (m).

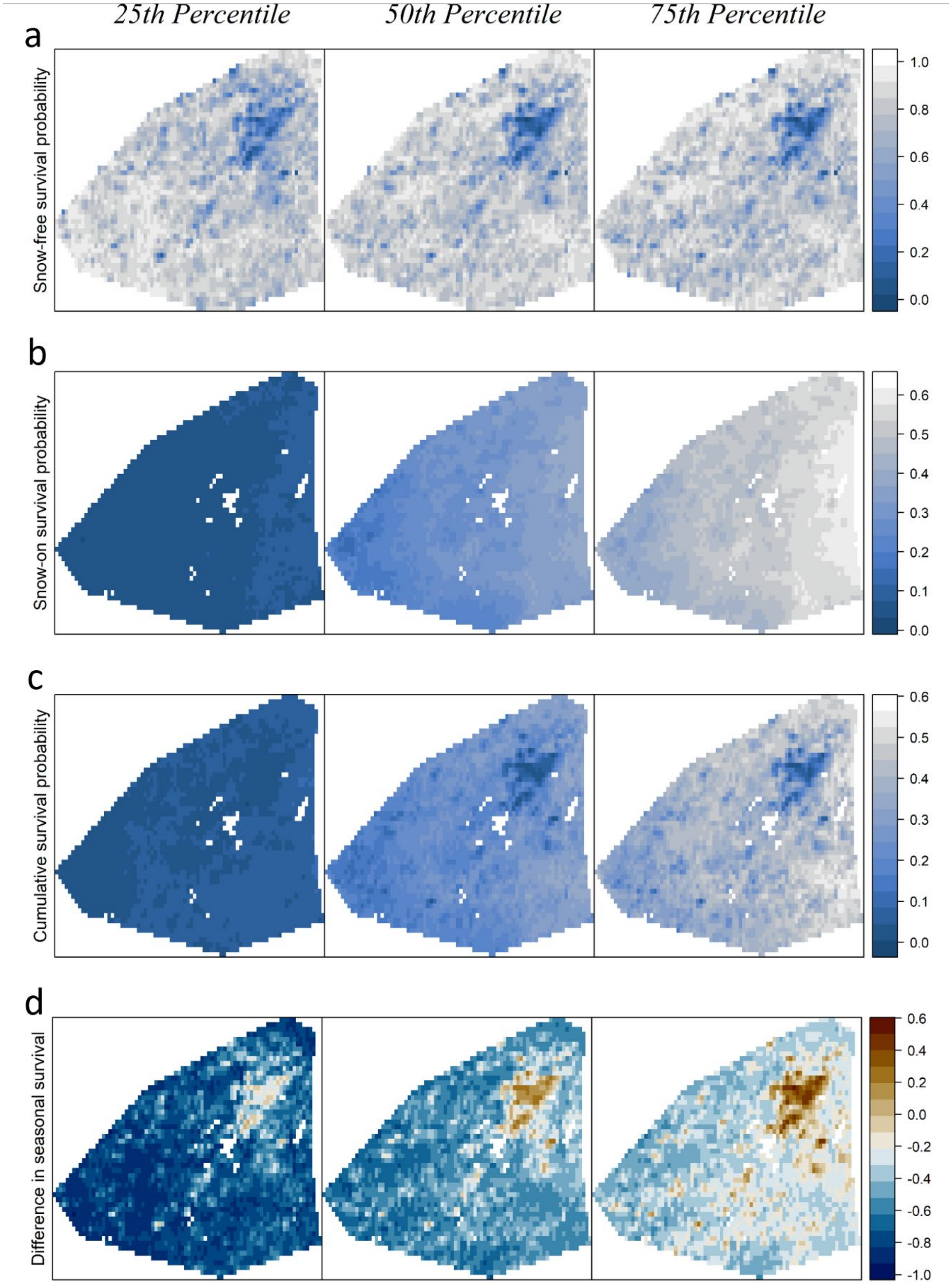
Figure 2: Posterior densities of beta-coefficients from an *a priori* model set (see Table 1) estimated from a Bayesian proportional hazards model for seasonal mortality risk of sub-adult and adult American marten (*Martes americana*) in Minnesota, USA. Snow-free (1 May – 31 Oct), Snow-on (1 Nov – 30 April). Entropy and correlation are 2nd order image textures derived from Enhanced Vegetation Index of Landsat 5 and 8 images. SD: standard deviation, FWOS: percent of days with frozen ground without snow, Interaction: snow depth x entropy.

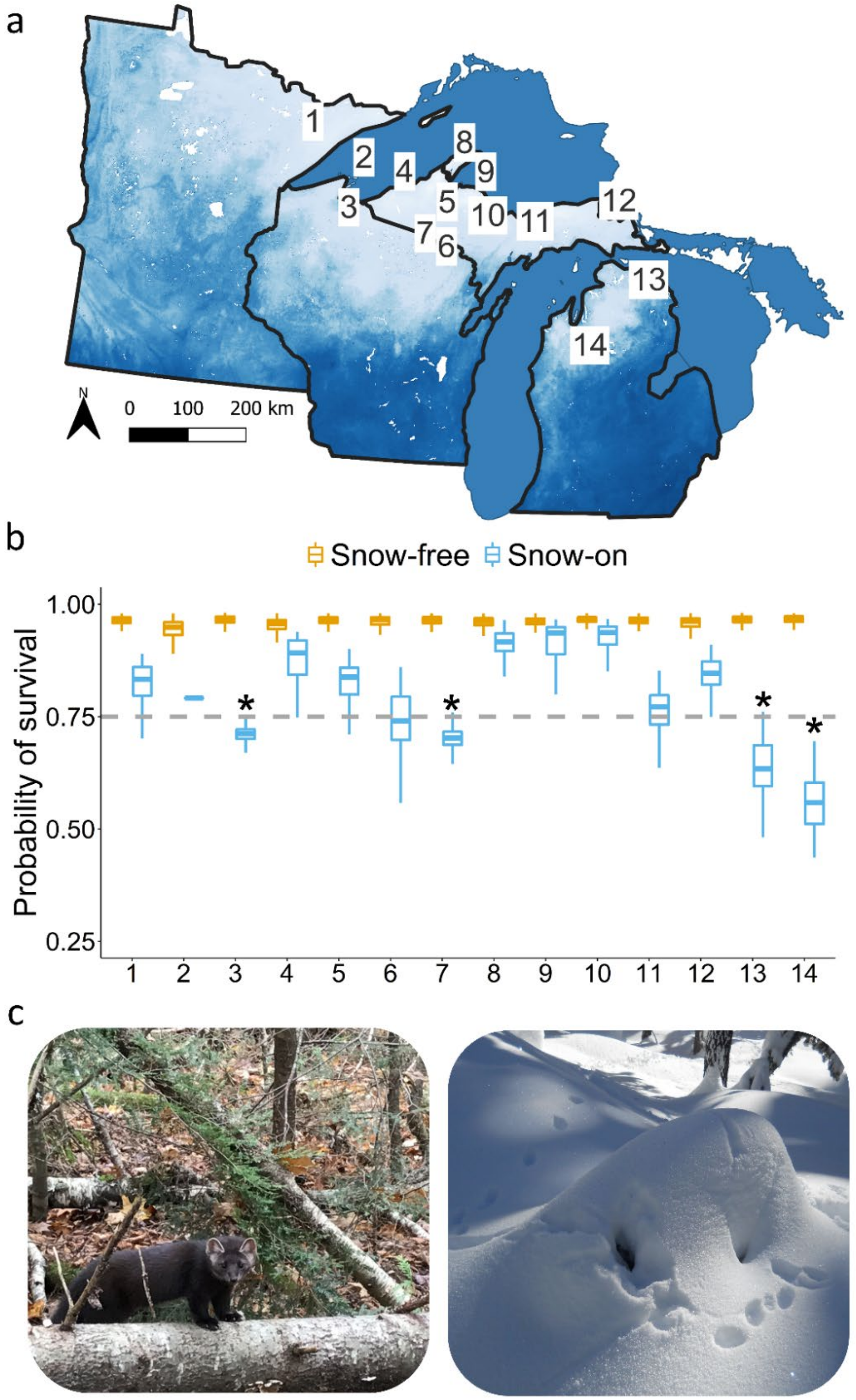
Figure 3: Predicted survival landscapes from seasonal Bayesian proportional hazards models of sub-adult and adult American martens (*Martes americana*) in northern Minnesota, USA. Spatial survival probabilities during the snow-off season (1 May – 31 Oct) (a), snow-on season (1 Nov – 30 Apr) (b), cumulative annual survival probability (c), and the difference in seasonal survival probabilities (d; positive values occurred when snow-on survival probability was greater than snow-off and negative when snow-off survival probability was greater) estimated from the 25th, 50th, and 75th percentile from averaged entropy and snow depth across the years of the study (2007-2015).

Figure 4: Reintroduction sites of American marten (*Martes americana*) in the Great Lakes Region, and the northern Minnesota study area with average snow depth from 2011-2020 (increasing from blue to white) (a). Boxplot summarizing the predicted survival estimates at each site based on modeled relationships from Bayesian survival models of sub-adult and adult martens in northern Minnesota (snow-off: 1 May – 31 Oct; snow-on: 1 Nov – 30 Apr) (b). Dotted horizontal line denotes 0.75 annual survival, a threshold previously identified for population growth rate in American martens (Buskirk et al. 2012); sites with interquartile ranges that fell below and did not overlap 0.75 with an asterisk (*). Photographs of a marten moving along a downed tree and example of a subnivium access point (c).


1
2
3
4
5
6
7
8
9
10
11
12
13
14
N
0
100
200 km
Entropy EVI
4.73
0.26
Snow depth
873
520
(mm)
Forest age
103
0
(years)
FWOS
100
0
(%)
Canopy cover
92
0
(%)
Elevation
615
424
(m)


Snow-free
Snow-on: natural
Snow-on: trapping
H1. Correlation EVI
H1. Entropy EVI
H2. Forest age
H2. Forest age SD
H3. Elevation
H3. Elevation SD
H3. FWOS
H3. Snow depth
H4. Edge density
H4. Largest patch index
H4. Radius of gyration
H5. Connectivity
H6. Land cover complexity
H7. Canopy cover
H8. Interaction
-4
-2
0
2
Effect size


25th Percentile
50th Percentile
75th Percentile
a
Snow-free survival probability
1.0
0.8
0.6
0.4
0.2
0.0
b
Snow-on survival probability
0.6
0.5
0.4
0.3
0.2
0.1
0.0
c
Cumulative survival probability
0.6
0.5
0.4
0.3
0.2
0.1
0.0
d
Difference in seasonal survival
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0


a
1
2
3
4
5
6
7
8
9
10
11
12
13
14
N
0
100
200 km
b
Snow-free
Snow-on
Probability of survival
1.00
0.75
0.50
0.25
*
*
*
*
1
2
3
4
5
6
7
8
9
10
11
12
13
14
c

Supporting Information – Appendix S1

Smith, M.M., Erb, J.D., & Pauli, J.N. Seasonality drives the survival landscape of a recovering forest carnivore in a changing world.

Estimating activity areas

We removed all locations >8 km (the average juvenile dispersal distance; Johnson et al. 2009) from capture point to avoid overestimation of activity area due to dispersal events. We used a plug-in bandwidth selector and calculated 95% KDEs using the *ks* (Duong 2007) R (R Core Team 2021) package. To identify the minimum number of relocations needed to represent an average adult activity area, we used 95% KDE estimates for all individuals identified as adults at time of capture and fitted a segmented regression on the area of the KDE by the number of relocations using the R (R Core Team 2020) package *segmented* (Muggeo 2008). We estimated a minimum of 18 locations needed to capture the area of an adult activity area (n = 71).

Quantifying landscape heterogeneity

To characterize vegetation complexity, we selected 2nd order entropy and correlation as two uncorrelated measures of image texture to capture heterogeneity in vegetation and capture habitat complexity within marten activity areas. Second order Entropy and correlation were calculated within individual activity areas from a gray-level co-occurrence matrix (GLCM) derived from composite images of greenness following Farwell et al. (2020; 2021). We extracted peak greenness from the 90th percentile of Enhanced Vegetation Index (EVI) composites from all available images for both seasonal timeframes. Specifically, we obtained Landsat 5 (2008-2011) and 8 (2013-2015) corrected Surface Reflectance Tier 1 data; all processing was performed in

Google Earth Engine (GEE; http://earthengine.google.org). Landsat images were not available for 2012, we used the average of 2010 and 2011to estimate metrics of image texture for that year. We excluded pixels from Landsat imagery that contained water, clouds, or cloud shadows using product quality assessment bands, and those mapped as permanent water bodies (Hansen et al. 2013). To calculate 2nd order image textures of entropy and correlation, we used the *glcmTexture* function in GEE after we converted EVI composite values to unsigned 8-bit integers, to limit the size of the GLCM and avoid matrices that are too sparsely populated to calculate robust values (Culbert et al. 2012). After finding high correlation between smaller (4 x 4) and larger (16 x 16 and 32x32) window sizes, we selected a moving window extent of 5.76 ha for Landsat imagery (8 x 8 pixels; 30-m resolution) to capture relatively fine-scale changes in vegetative structure and after finding high correlation between. We then extracted the mean 2nd order entropy and correlation values from within individual marten activity areas and accounted for temporal heterogeneity of vegetative complexity by estimating values from EVI images across the season if the individual survived or from the month the mortality occurred.

To account for temporal variation, we estimated landscape variables and heterogeneity at the time of mortality. For example, we described abiotic complexity during snow-on season by extracting the average snow depth within an activity area; if a marten died during the snow-on season, then snow depth was estimated from the month the mortality occurred.

Survival analysis

We estimated contemporary survival at translocation sites from predictors by averaging over the last 10 years (2011-2020). We buffered each translocation site by the size of the Minnesota study area (167 241 hectares) besides the Apostle Islands, WI. Instead, we summarized the probability of survival across all islands within the Apostle Islands National Lakeshore to better account for available terrestrial habitat. Snow depth was not available for the Apostle Islands, and we used an average value of snow depth from northern Bayfield Peninsula, WI (mean distance = 10.16 km). To account for phenological differences between reintroduction sites, we narrowed the dates for Landsat image collection to the peak of the growing season (1 May – 31 August). We compared the mean and range of landscape variables from our training dataset (i.e., observed values used in our Bayesian survival model) and testing dataset (i.e., contemporary values extracted from buffered translocation sites). We found our testing data to be representative of the training dataset, but masked entropy values that fell outside of the training dataset (Table S1).

Cause-specific mortality

We observed 58 human-related and 25 natural caused mortalities during the snow-on season. The only source of human mortality observed was from trapping. Natural caused mortalities were either from predation (88%), possible injury or predation (4%), illness (4%), or a perforated large intestine from ingested bone (4%). Mortality associated with trapping was higher (CIF = 0.31, BCI: 0.23, 0.39) compared to natural causes (CIF = 0.09, BCI: 0.06, 0.13). Males (CIF = 0.36, BCI: 0.25, 0.49) were approximately 10% more likely to be trapped than females (CIF = 0.25, BCI: 0.15, 0.38) and had a lower probability of natural mortality (CIF = 0.06, BCI: 0.03, 0.11) compared to females (CIF = 0.11, BCI: 0.06, 0.19), but 95% Bayesian credible intervals overlapped for both mortality sources (Fig. S1).

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Table S1: Comparison of landscape variables from training and testing data used to predicted contemporary (2011-2020) survival at translocation sites (2-14) and our study area (1) from seasonal Bayesian proportional hazards models of sub-adult and adult American martens (*Martes americana*) in northern Minnesota, USA.

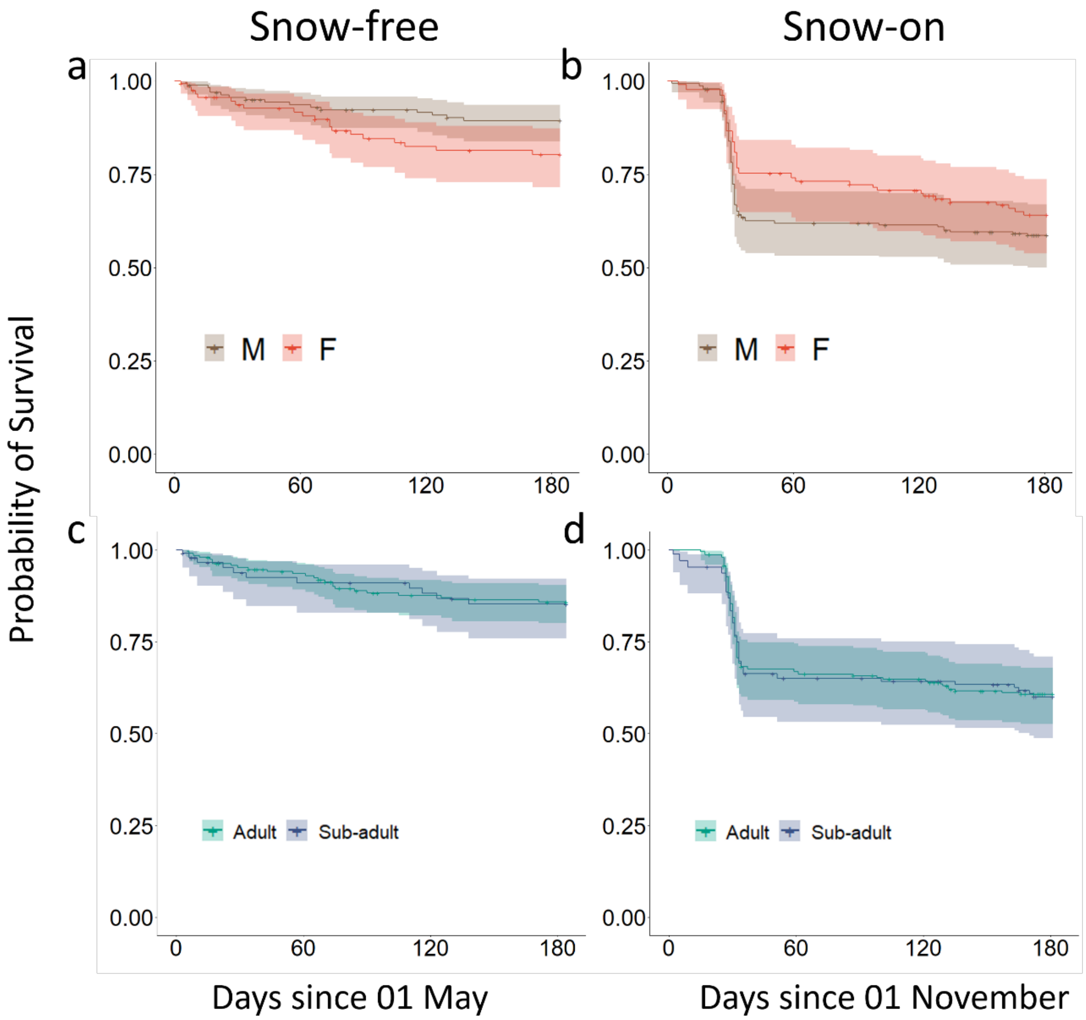
	Entropy		Snow depth (mm)	
	Mean	Range	Mean	Range
Training data	4.14	3.24, 4.41	658	0, 1172
Testing data				
1	4.15	0.17, 4.76	749	501, 862
2	3.77	2.22, 4.76	696	696
3	4.21	0.26, 4.84	607	384, 663
4	3.95	1.54, 4.77	852	623, 1008
5	4.18	0.95, 4.77	753	601, 886
6	4.14	0.17, 4.76	649	430, 801
7	4.17	0, 4.76	601	355, 739
8	4.09	0, 4.76	939	577, 1142
9	4.11	0, 4.77	959	424, 1151
10	4.22	0, 4.77	981	577, 1155
11	4.16	0, 4.77	666	525, 787
12	4.05	0, 4.81	778	556. 912
13	4.23	1.28, 4.85	544	405, 659
14	4.25	1.50, 4.77	480	344, 592

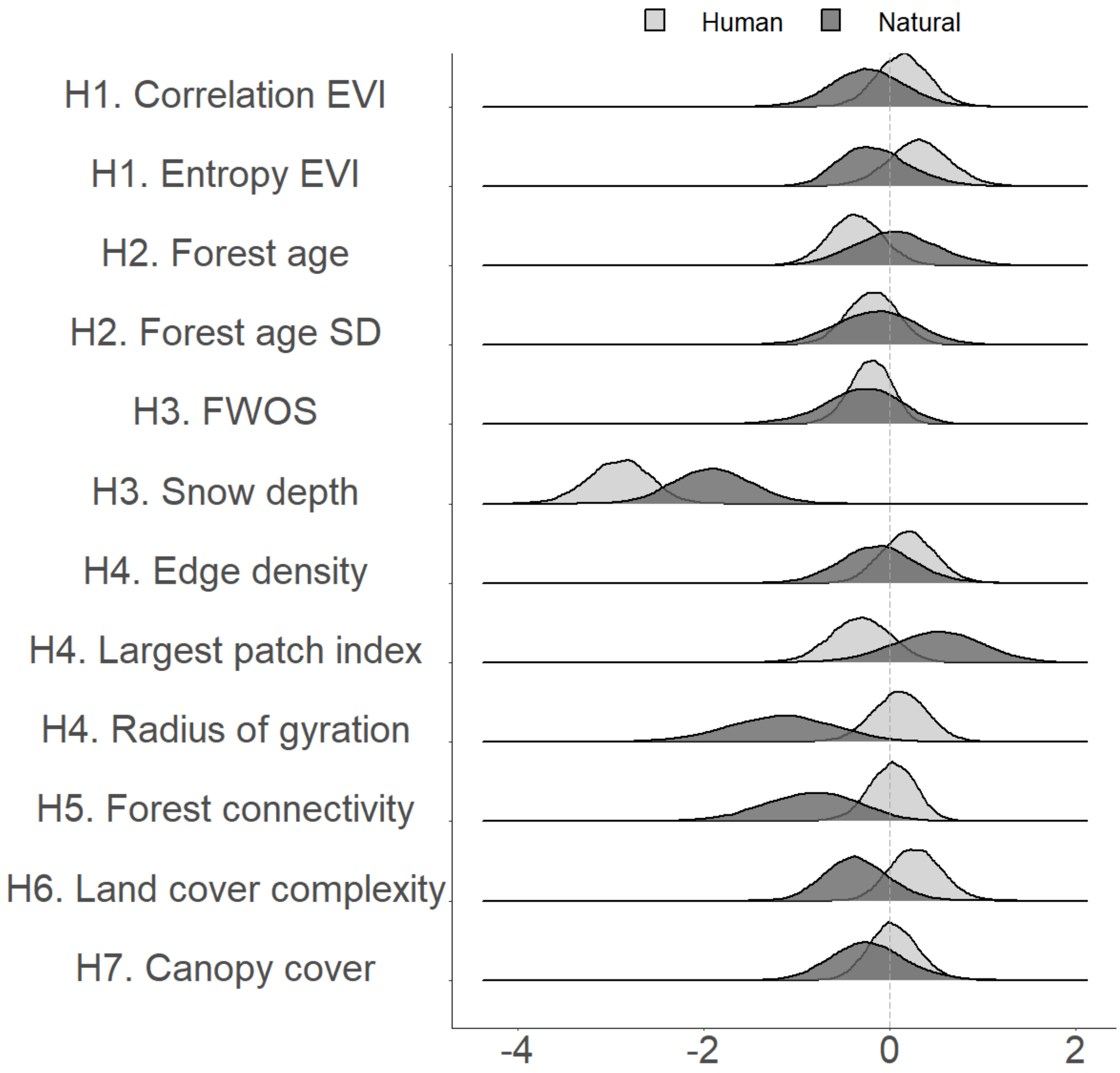
Table S2: Mean, standard deviation (SD), and range of variables from individual activity areas of American marten (*Martes americana*) used to model survival in Minnesota, USA. Snow-free (1 May – 31 Oct), Snow-on (1 Nov – 30 April). Entropy and correlation are 2nd order image textures derived from Enhanced Vegetation Index of Landsat 5 and 8 images. FWOS: percent of days with frozen ground without snow. LPI: largest patch index.

	Snow-free			Snow-on		
	Mean	SD	Range	Mean	SD	Range
Entropy	4.14	0.18	3.24, 4.41	3.74	0.20	2.29, 4.16
Correlation	0.61	0.03	0.50, 0.67	0.52	0.04	0.33, 0.62
Forest age (years)	56	10	34, 102	59	7	40, 77
Elevation (m)	506	29	429, 580	–	–	–
Snow depth (mm)	–	–	–	662	301	0, 1172
FWOS (%)	–	–	–	2.5	5	0, 29.2
LPI	27.0	18.3	0, 79.2	27.4	17.9	0, 79.2
Edge density	58.9	20.3	0, 104.2	59.3	19.5	0, 102.1
Radius of gyration	128.1	52.0	0, 368.0	129.5	51.9	0, 368.0
Correlation length	5864	4179	0, 27138	5952	4161	0, 27591
Joint entropy	2.80	0.67	0.41, 3.94	2.80	0.64	0.41, 3.94
Canopy cover (%)	59	5	30, 69	59	5	30, 69

Figure S1: Median estimates of seasonal survivorship with 95% Bayesian credible intervals by sex (a, b) and age class (b, c) for American martens (*Martes americana*) in northern Minnesota, USA (2007-2015). Sharp reduction in survival during the snow-on season is from trapping related mortality (b, d).

Figure S2: Posterior densities of β parameters estimated from *a priori* model set (see Table 1) from a Bayesian proportional hazards models for cause specific mortality risk of sub-adult and adult American marten (*Martes americana*) in Minnesota, USA. Entropy and correlation are 2nd order image textures derived from Enhanced Vegetation Index of Landsat 5 and 8 images. SD: standard deviation. FWOS: percent of days with frozen ground without snow.


Snow-free
Snow-on
a
b
c
d
Probability of Survival
1.00
0.75
0.50
0.25
0.00
0
60
120
180
M
F
Adult
Sub-adult
Days since 01 May
Days since 01 November


Human
Natural
H1. Correlation EVI
H1. Entropy EVI
H2. Forest age
H2. Forest age SD
H3. FWOS
H3. Snow depth
H4. Edge density
H4. Largest patch index
H4. Radius of gyration
H5. Forest connectivity
H6. Land cover complexity
H7. Canopy cover
-4
-2
0
2

Reciprocated competition between two forest carnivores drives dietary specialization

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Keywords: exploitation, interference, *Martes americana*, niche partitioning, niche overlap, *Pekania pennanti,* stable isotopes

Abstract

1. Competition shapes animal communities, but the strength of the interaction varies spatially depending on the availability and aggregation of resources and competitors. Among carnivores, competition is particularly pronounced with the strongest interactions between similar species with intermediate differences in body size. While ecologists have emphasized interference competition among carnivores based on dominance hierarchies from body size (smaller = subordinate; larger = dominant), the reciprocity of exploitative competition from subordinate species has been overlooked even though efficient exploitation can limit resource availability and influence foraging.

2. Across North America, fishers (*Pekania pennanti*) and martens (*Martes* spp.) are two phylogenetically related forest carnivores that exhibit a high degree of overlap in habitat use and diet and differ in body size by a factor of 2-5x, eliciting particularly strong interspecific competition. In the Great Lakes region, fishers and martens occur both allopatrically and sympatrically; where they co-occur, the numerically dominant species varies spatially. This natural variation in competitors and environmental conditions enables comparisons to understand how interference and exploitative competition alter dietary niche overlap and foraging strategies.

3. We analyzed stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) from 317 martens and 132 fishers, as well as dietary items (n = 629) from 20 different genera, to compare niche size and overlap. We then quantified individual diet specialization and modeled the response to environmental conditions that were hypothesized to influence individual foraging.

4. Martens and fishers exhibited high overlap in both available and core isotopic δ-space, but no overlap of core dietary proportions. When the competitor was absent or rare both martens and fishers consumed more smaller-bodied prey. Notably, the dominant fisher switched from being a

specialist of larger to smaller prey in the absence of the subordinate marten. Environmental context also influenced dietary specialization: increasing land cover diversity and prey abundance reduced specialization in martens whereas vegetation productivity increased specialization for both martens and fishers.

5. Despite an important dominance hierarchy, fishers adjusted their niche in the face of a subordinate, but superior, exploitative competitor. These findings highlight the underappreciated role of the subordinate competitor in shaping the dietary niche of a dominant competitor.

Introduction

Interspecific competition is foundational in structuring animal communities (Grinnell 1917; Holt 1987). Niche-based theories are a useful framework to conceptualize and predict when and to what degree coexisting species will compete (Hutchinson 1959; Macarthur and Levins 1967). In general, coexistence hinges on some form of niche differentiation to partition important and limiting resources (Gause 1934). The myriad resources that species partition has been generally consolidated into the niche meta-axes of space, time, and resources (Chase and Leibold 2003). Species that can differentiate along one or more of these axes should reduce their overlap, competition, and promote coexistence (Letten et al. 2017). However, the partitioning of resources is arguably the most important niche axis (Manlick and Pauli 2020); indeed, shared resources are what competitors partition in space and time. Overlap in resource use can be manifested in two forms of competition: indirectly through exploitative competition where competitors limit the availability of shared resources; or, through interference competition where direct conflict occurs when pursuing shared resources (Birch 1957). The degree of competition, though, typically varies spatially depending on the availability and aggregation of resources and competitors. Heterogenous environments allow for species to exhibit a differential response dependent on interactions between environmental context and degree of competition (Chesson 2000; Amarasekare 2003). Environmental heterogeneity also can create spatial refuges from competition that play a central role in the stability of populations and coexistence of species at broader spatial scales (Hanski and Gilpin 1991; Chesson 2000). Rapid land-use change, however, is altering patterns of competition and has spurred renewed interest in understanding how environmental context of interspecific competition shapes niche variation between competing but coexisting species (Holt 2009).

Competition is particularly pronounced among carnivores (Mammalia: Carnivora) due to specialization in their diets and elevated trophic position (Polis et al. 1989; Palomares and Caro 1999). Carnivore competition is modulated by the environment by either directly creating more advantageous competitive conditions or indirectly through suppression of other competitors (Sivy et al. 2017; Rodriguez Curras 2022). In theory, variation in the local densities of competitors driven by the scale at which interspecific and intraspecific competition occurs can promote coexistence (i.e., heteromyopia; Murrell and Law 2003). However, environmental change has altered niche partitioning among carnivores leading to increased overlap in space (Tucker et al. 2018), time (Gaynor et al. 2018) and resources (Manlick and Pauli 2020). Increased overlap of resources can be particularly problematic for carnivores as the result can be lethal for one of the competitors because they have evolved (e.g., behaviors and morphology) as effective killers (Arim and Marquet 2004; Donadio and Buskirk 2006). Consequently, competition has been implicated as a driver of evolutionary change (Meachen and Samuels 2012), ecosystem functioning (Estes et al. 2011) and the global distribution and abundance of carnivore species (Crooks et al. 2011).

The strongest competitive interactions are predicted between phylogenetically related species that exhibit intermediate differences in body size (Palomares and Caro 1999; Donadio and Buskirk et al. 2006). The consumption of food is the principal resource that drives competition. When relying on the same diet, body size creates a dominance hierarchy due to interference competition – the smaller is subordinate, the larger is dominant – but as body size converges, the risk becomes too great for both species (Palomares and Caro 1999). Conversely, interference competition should be rare as the difference in body size increases (i.e., >10x) because of a divergence in diets that reduce niche overlap. Research often assumes the dominant species, through interference competition, forces the smaller subordinate competitor to alter their dietary niche. Yet, interference competition requires a shared resource to exploit, thus, it would be pragmatic for the less efficient species, regardless of body size, to adjust their niche in the face of exploitative competition. Besides body size, however, the winning of shared resources between carnivores through interference competition can also result from species-specific adaptations including behaviors (e.g., social groups and aggressiveness; Allen et al. 2016). In general, then, the role of subordinate (i.e., smaller) carnivores in structuring competitive interactions has been underappreciated in carnivore ecology.

In North America, fishers (*Pekania pennanti*) and martens (*Martes* spp.) are two such carnivores that are similar in body size (differ by a factor of 2-5x) and exhibit a high degree of overlap in habitats and diet, leading to the potential for interspecific competition (Pauli et al. 2022). In addition, both species have a shared evolutionary history and occur in the same subfamily (Guloninae), leading to similarities in morphology and behavior. Where they co-occur, fishers and martens show little partitioning of habitat (Jensen and Humphries 2019; Manlick et al. 2017a; Zielinski et al. 2017) and activity patterns (McCann et al. 2017; Croose et al. 2019).

Ultimately, spatiotemporal partitioning should have the effect of reducing competition for resources, especially prey. Both species are generalist predators, and often specialize on different prey based on size (Pauli et al. 2022). However, fishers and martens exhibit a high degree of dietary plasticity and dietary overlap is common (Manlick et al. 2017a; Raine 1987; Zielinski and Duncan 2004). Despite these similarities, fishers and martens have coexisted over millennia (Law et al. 2018) and their coexistence has been of interest to ecologists for decades (e.g., Rosenzweig 1966; Dayan et al. 1989; Pauli et al. 2022).

Land-use change has altered forest structure and composition across North America and has resulted in the isolation and extirpation of numerous vertebrate populations (Laliberte & Ripple 2004). Like elsewhere in North America, the Great Lakes Region historically featured forests that were compositionally and structurally complex until the late 1800s when the region was largely cut over by commercial logging (Schulte et al. 2007). This forest loss contributed to regional extirpation of several forest carnivores including American martens (*Martes americana*) and fishers (*Pekania pennanti*) by the early 1900s (Williams et al. 2007). Along this southern range boundary in the Great Lakes Region, natural recolonization and reintroductions have reestablished populations but the distribution remains fragmented and with varying population size and resource availability, leading to uncertainty about long-term coexistence (Skalski et al. 2011; Manlick et al. 2017b; Grauer et al. 2019; Smith et al. 2021). Competition and the lack of preferred prey, especially for martens, has been hypothesized as a contributing factor to their slow recovery in some areas (Carlson et al. 2014; Manlick et al. 2017a). Consequently, this region provided a unique opportunity to better understand how variation in the local abundance of close competitors and putative dominance hierarchy alters dietary niche overlap and foraging strategies for two recovering forest carnivores.

To test how individual- and population-level competition between two carnivores shapes their niche variation and foraging tactics, we explored dietary inputs and partitioning across a gradient of competition in the Great Lakes Region. Our study locations featured areas of sympatry but with variation in the numerically dominate species and areas where each species was isolated from the other, allowing for a unique comparison of a large dataset across levels of inferred competition and environmental conditions. We hypothesized that fishers and martens would partition their diets to avoid niche overlap. This partitioning would mirror body size and follow a dominance hierarchy where the larger fisher would consume larger-bodied prey and exclude martens from these items through interference competition, and where the smaller marten would consume smaller-bodied prey. We also predicted that given the ecological opportunity and the absence of competition, martens would show greater dietary specialization on preferred prey than fishers due to reduced interference competition. To assess foraging overlap and specialization, we used stable isotope analysis (δ^{13}C and δ^{15}N) to assess prey items (n = 629) and the dietary niche of fishers and martens (n = 449). Specifically, we compared size and overlap in available and core dietary niches in isotopic δ-space and proportional dietary space. We then quantified individual specialization in proportional diets and modeled the response to environmental conditions that were hypothesized to influence foraging. Our work aims to better understand how differences in interspecific competition shape dietary niche variation and individual dietary specialization of competing and coexisting species.

Materials and Methods

Sites and samples

We compared the isotopic niche and proportional diets of American martens and fishers at four sites in the Great Lakes Region featuring different levels of interspecific competition based on relative abundance (Fig. 1). On the Apostle Islands, martens are common, and fishers are absent or rare (hereafter, M+0; Allen et al. 2018); in northcentral Minnesota fishers are common and martens are rare (hereafter, F+0; few martens captured over eight years). Two additional sites featured both martens and fishers, with martens being more common than fishers in northeastern Minnesota (hereafter, M+f; few fishers captured over eight years) and the opposite in northern Wisconsin (hereafter, F+m; Manlick et al. 2017; Grauer et al. 2019). Across the sites, we collected samples of marten (n = 317), fisher (n = 132), and dietary items (n = 629) from direct sampling of hair (e.g., non-invasive methods, collared animals, known-fate mortality), muscle of prey items, or soft mast (Supporting information, Table S1). We sampled all primary prey groups including small mammals, birds, deer, and soft mast at each site. To increase sample sizes of dietary items and account for potentially important dietary groups, we supplemented M+f with dietary items from F+0, specifically porcupines (*Erethizon dorsatum*), ruffed grouse (*Bonasa umbellus*), and white-tailed deer (*Odocoileus virginianus*). Soft mast data were shared between M+f and F+0. We used published isotopic values for F+m (Carlson et al. 2014; Manlick et al. 2017; Kirby et al. 2018) and supplemented our samples of fishers in M+f with published isotopic values (Manlick and Pauli 2020; Supporting Information, Table S1). To summarize landscape characteristics, we identified capture or sampling location(s) and buffered by the average activity area for marten (4.71 Km^2) and fisher (19.7 Km^2) for the region (Smith et al. 2022).

Stable isotope analyses

We quantified the isotopic niche and proportional diets of martens and fishers using $\delta^{13}C$ and $\delta^{15}N$ stable isotope analyses (Supporting Information). Samples were collected in the late fall and winter after the annual molt (July to October; Pauli et al. 2009) and, thus, represent assimilated diets from late summer into fall. We applied a tissue-specific trophic discrimination factor (TDF; $\delta^{13}C = 2.6$; $\delta^{15}N = 3.4$; *Vulpes vulpes*; Roth and Hobson 2000). Given that martens and fishers do not assimilate prey keratin (hair), we adjusted the TDF of $\delta^{13}C$ if the prey sample came from hair to account for offsets between the isotopic discrimination of hair and muscle tissue ($\delta^{13}C = 1.3$; Stephens et al. 2022; Supporting Information Table S1).

Isotopic niche

We accounted for differences in the range of $\delta^{13}C$ and $\delta^{15}N$ and diversity of resources across sites by using a standardized multidimensional isotopic space, pooling all organisms before scaling (Cucherousset and Villéger 2015). We compared the isotopic niche size, position, and overlap of martens and fishers among sites using Bayesian ellipses from bulk values of $\delta^{13}C$ and $\delta^{15}N$. We tested for pairwise differences in the means and variances of scaled isotopic values between martens and fishers where they co-occurred (M+f and F+m) using a multi-response permutation procedure (MRPP) with 10,000 iterations in the R (R Core Team 2022) package *VEGAN* (Oksanen et al. 2022). We estimated the size of the isotopic niche and overlap between marten and fisher standard ellipses using a Bayesian framework in the R package *SIBER* (Jackson et al. 2011). To estimate the Bayesian standard ellipses, we ran 3 chains of 40,000 iterations and removed the first 10 000 iterations as burn-in, thinned posterior samples to every tenth sample, and calculated overlap from all posterior estimates. We estimated overlap of the 50% and 95% Bayesian isotopic ellipses as a proportion of the sum of the non-overlapping area where ellipses are distinct (0) to completely identical (1). In addition, we quantified ecological opportunity at each site by the area of the Bayesian isotopic standard ellipse of the available dietary items (e.g., Shaner and Ke 2022).

Proportional diets and overlap

We estimated proportional diets of marten and fisher populations with a Bayesian isotopic mixing model in the R (R Core Team 2022) package *MixSIAR* (Stock et al. 2018). We first identified important functional prey groups and isotopically distinct dietary groups for each site using a K nearest-neighbor randomization test (Supporting Information Fig. S1; Rosing et al. 1998). Using site specific mixing spaces, we estimated proportional dietary inputs of individuals by running 3 chains of 300,000 iterations, removed the first 200,000 iterations as burn-in, and then thinned posterior samples to every 100th sample (Stock et al. 2018). We assessed model convergence with trace plots and Gelman-Rubin statistics (*R hat* ≤ 1.01; Gelman and Rubin 1992).

To make comparisons between sites and species, we *a posteriori* combined sources (i.e., prey) of the Bayesian mixing model using *MixSIAR* (Stock et al. 2018) into the finest resolution of dietary groups consistent across sites prior to comparing overlap of proportional diets. We identified three functional dietary groups shared between sites that included: soft mast, larger-bodied prey (snowshoe hares [*Lepus americanus*], deer [*Odocoileus virginianus*], ruffed grouse [*Bonasa umbellus*], porcupine [*Erethizon dorsatum*]), and smaller-bodied prey (songbirds, mice [*Peromyscus* spp.], shrews [*Blarina brevicauda*, *Sorex* spp.], voles [*Myodes gapperi*], squirrels [*Sciuridae* spp.]; Supporting Information Table S1). For population-level dietary proportions, we compared pairwise differences in posterior distributions by extracting the site-specific marginal posterior distributions for each diet group and species and compared across marten populations and between sympatric marten and fisher populations. We calculated the probability that populations consume different proportions of diet groups and identified significant differences between marginal posterior distributions (Hopkins et al. 2014; Manlick et al. 2019). We also estimated median dietary proportions for each individual and estimated 50% and 95% kernel density estimates of dietary distribution for each population following Manlick et al. (2019). We then estimated proportional dietary overlap using pairwise comparisons of the utilization distribution overlap index (UDOI) using the R package *adehabitathr* (Calenge 2006). We used 50% UDOIs to evaluate overlap of core diets and 95% UDOIs to evaluate overlap of available diets, with estimates ranging from zero (no overlap) to one (complete overlap; Fieberg and Kochanny 2005; Manlick et al. 2019). Although, measures of UDOI typically range from 0 (no overlap) to 1 (100% overlap), they may also exceed 1 if the utilization distributions are nonuniformly distributed and have high overlap (Fieberg and Kochanny 2005).

Specialization

We estimated individual niche specialization and similarity from posterior samples of the Bayesian mixing model (Newsome et al. 2012). The degree of niche specialization ranges from zero (ultra-generalist) to one (ultra-specialist) and can be compared across consumers (Newsome et al. 2012). We also estimated dietary similarity by comparing individual martens relative to the median dietary proportions of their respective population (Newsome et al. 2012). We compared similarity between individual marten dietary proportions and the median fisher proportion for populations where they both occur (M+f and F+m). Similarity values also range from 0 to 1, with higher values representing greater similarity between individual martens and fishers.

We calculated the average enhanced vegetation index, vegetation complexity, Shannon diversity index, and relative prey abundance of small mammals within individual marten and fisher activity areas. We calculated enhanced vegetation index and vegetation complexity (i.e., 2nd order entropy) using Landsat imagery following Farwell et al. (2021). We calculated Shannon diversity index estimates within activity areas using the National Land Cover Dataset (NLCD) and the R (R Core Team 2022) package *landscapemetrics* (Hesselbarth et al. 2019). We matched the time the individual isotopic sample was taken and selected Landsat imagery from the summer preceding the collection and to the closest available NLCD year (2008, 2011, 2013, 2016).

We estimated relative prey abundance at each area as site-specific captures per 100 trap nights of small mammals that included: *Peromyscus* spp., *Blarina brevicauda*, *Sorex* spp., and *Myodes gapperi*. For M+0, martens were assigned island-specific measures of catch per 100 trap nights and matched sampling years of martens on the islands (Malinger et al. 2021). For other sites (F+0, M+f, and F+m), catch per 100 trap nights was estimated by land cover type and associated with deciduous, conifer, mixed forests, and woody wetlands from the NLCD (Supporting Information). Relative prey abundance temporally overlapped with marten and fisher isotopic samples for F+0 and M+f, but did not overlap with marten isotopic samples from F+m. We then calculated the proportion of land cover classes from NLCD within the individual activity area and multiplied by the land cover specific catch per 100 trap nights and summed for all available land cover classes. We matched the time the individual was alive on the landscape to the closest available NLCD year (2001, 2008, 2011, 2013, 2016) to estimate proportional land cover.

We used Bayesian generalized linear models to assess the effects of habitat characteristics and relative resource abundance on individual niche specialization for each species separately. We modeled habitat characteristics and relative resource abundance as fixed effects. To assess site specific responses to specialization, we also included sites as a fixed effect, with either the intercept and slope or just the intercept varying by site. In addition, we only modeled the effects of habitat characteristics on fishers from F+0 and M+f because we lacked specific spatial locations for the F+m site. Given that individual specialization is bounded (0,1), we used regression with a beta distribution and logit link function. All models were implemented in the R package *RStanaRm* (Goodrich et al. 2022). We used weakly informative priors (Normal [0,10] for intercepts and Normal [0,2.5] for coefficients), ran four chains for 3,000 iterations, and discarded the first 1,000 iterations as warmup. To evaluate model convergence, we required *R hat* values <1.01 and visually inspected traceplots (Gelman and Rubin 1992). We compared model performance using expected log predictive density and leave-one-out cross-validation information criterion in the R package *loo* (Vehtari et al., 2022). All variables were scaled and centered prior to model fitting and had Pearson's correlation coefficients |<0.6|. To describe the effects of model variables from parameter estimates, we calculated the 89% highest density interval (HDI) (because 95% HDI is unstable when effective sample size is less than 10,000), probability of direction (pd), and region of practical equivalence (ROPE) using the R package *bayestestR* (Makowski et al. 2019).

Results

Isotopic niche

Ecological opportunity was similar across sites (Supporting Information Fig. S2). Martens and fishers were isotopically different when fishers were uncommon (M+f; $p < 0.001$), but we detected no difference when fishers were common (F+m; $p = 0.14$) using MRPP (Supporting Information Table S2). The area of the isotopic niche increased for martens as fishers became more common (M+0 < M+f < F+m), and fisher isotopic niche size decreased slightly when martens were absent (F+0; Fig 2a,b; Supporting Information Fig. S3). For sites where marten and fishers both occur, overlap occurred at both the 50% and 95% isotopic niche (Fig. 2c,d).

Proportional diets and overlap

Martens and fishers consumed higher proportions of smaller-bodied prey when the competitor was absent or rare (97% and 68%; M+0 and F+0) compared to when both co-occurred (all *p values* < 0.01; Supporting Information Fig. S4a, b). Martens consumed more smaller-bodied prey than fishers, but fishers consumed more larger-bodied prey when they co-occurred (Supporting Information Fig. S4c, d). Fishers consumed the smallest proportion of smaller-bodied prey when martens were numerically dominant (28%; M+f) compared to fishers where martens were uncommon (40%; F+m) or rare (68%; F+0; Supporting information Fig. S4b). The consumption of soft mast was limited for all populations (1.0%-4.8%). There was little to no overlap of core and available diets of martens in absence of fishers (M+0) or for both populations of martens where fishers co-occurred (M+f and F+m; Table 1; Fig. 3). Similarly, there was little to no overlap of core and available diets when fishers co-occurred with martens compared to fishers alone (F+0; Table 1; Fig. 3). However, available diets overlapped (albeit minimally) between marten and fishers when they co-occurred (M+f and F+m), but core diets did not overlap Table 1; Fig. 3a). Martens had substantial overlap in overall dietary space when they co-occurred with fishers, but little overlap in core and available diets (Table 1; Fig. 3a).

Specialization

Individual specialization varied between species and populations (range 0.37 to 0.97) and martens in absence of fishers (M+0) featured the greatest specialization (median = 0.97; Fig. 4). In both populations where marten and fisher co-occurred (M+f and F+m), the numerically subordinate species was more specialized, but fishers specialized on larger-bodied prey and marten on smaller-bodied prey (Fig. 4). Conversely, fishers specialized on smaller-bodied prey when martens were absent (F+m; Fig. 4). Dietary similarity was high (range 0.81, 1.00) within each species and site and between martens to fishers where they co-occurred (M+f and F+m; range 0.83, 1.00).

For both species, the most supported model testing the effect of habitat characteristics and relative resource abundance on individual niche specialization indicted site-specific differences in specialization (i.e., site-specific intercepts) but no differences in the site-specific response of specialization to habitat characteristics (Supporting Information Table S4). For martens, increasing Shannon diversity index and relative prey abundance was correlated to a more generalized foraging tactic (i.e., negative effect), while enhanced vegetation index increased specialization (pd > 95%; Fig. 5), but the strength of effect was marginal (ROPE > 82.4%; Supporting Information Table S5). We found limited support for habitat associations and relative prey abundance influencing fisher specialization, but similar to martens, enhanced vegetation index increased specialization (pd = 88.0%; Fig. 5) though the strength of the effect was marginal (ROPE = 80.4%; Supporting Information Table S6).

Discussion

When sympatric, fishers and martens consumed different prey: fishers consumed larger-bodied prey and martens consumed smaller-bodied prey. The observed dietary differences support the idea that prey partitioning based on size contributes to coexistence (Rosenzweig 1966). Martens consumed more smaller-bodied prey (e.g., small rodents, squirrels, and passerine birds), which are common prey across their range (Buskirk & Macdonald 1984; Zielinski and Duncan 2004). While prey switching is common for martens, the consistent specialization on small mammals, even when other prey sources are equally available, is also supported from previous observations (Ben-David et al. 1997). Similarly, fishers are generalist predators but can specialize on porcupines (Pokallus and Pauli 2015). We estimated that porcupines comprised 19%-37% of fisher diets. We generally found that fishers consumed larger-bodied prey, presumably because larger prey provide greater amounts of metabolizable energy (Golightly et al. 2006; LaPoint et al. 2015).

In the absence of a close competitor (M+0 and F+0), martens and fishers exhibited a reduced isotopic niche breadth and consumed more smaller-bodied prey. Fishers are dietary generalists and due to their larger body size are expected to consume larger prey, but in the absence of martens they consumed a greater proportion of smaller prey in this study. Similarly, smaller-bodied prey was common in fisher scat from southern Maine where martens were likely absent or rare (Arthur et al. 1989). The increased use of larger prey by fishers in the presence of martens suggests they may be less efficient in the search and acquisition of smaller prey. Indeed, we hypothesized that smaller-bodied martens have a competitive advantage in exploiting smaller prey due to the relative differences in overall body size and shorter legs, compared to fishers, that give them the ability to exploit more interstitial and subnviean spaces in forested systems (Andruskiw et al. 2008). Consequently, in the absence of exploitative competition from martens, fishers likely reduced their dietary niche overlap with other carnivores that also rely on larger prey.

The relative abundance of small mammals had minimal or no effect on fisher or marten dietary specialization; suggesting that competition -- not prey availability or habitat context -- is the primary driver behind foraging strategies. Local variation in abundance is common for small mammals (Prevedello et al. 2013; Stephens et al. 2017) and at one site our samples for martens (F+m) were not collected at the same time of small mammal abundance. Consequently, we may have underestimated the importance of prey abundance on dietary specialization. Despite the temporal mismatch in small mammal and marten sampling at F+m, martens nevertheless consumed primarily small mammals even though the site had the lowest average relative abundance. In addition, the relative abundance of larger-bodied prey was not available to further disentangle competitive interactions between species. However, small mammals are a preferred prey item for martens even when other diet items are equally available (Ben-David et al. 1997). Consequently, we concluded that the specialization on smaller-bodied prey is driven by competition that then suggests a potential competitive advantage for martens in their foraging.

Our results suggest that differences in the local abundance of each competitor altered foraging of both species, but not only from a strict body-size dominance hierarchy of interference. Theoretically, we would expect the smaller competitor to be favored in exploitative competition as resources become limited due to lower resource requirements (Persson 1985; Bagchi and Ritchie 2012). Such dietary shifts in the larger competitor have been observed when a smaller competitor has been either introduced (Baldi et al. 2004) or invaded new systems

(Bøhn and Amundsen 2001; Savino and Kolar 1996). It is important to note that investigating such competitive interactions are difficult because of interactions within and between trophic levels. Indeed, fishers and martens in our study areas exist within a larger community of carnivores, although we were unable to investigate how that broader community influenced their foraging behavior. While our study sites feature the same general structure and taxonomic diversity of carnivores, the local abundance likely differs between our sites, which may influence the diet of both fishers and martens. Nevertheless, we would predict the strongest interaction to occur between these two mustelids due to phylogenetic, morphological, and behavioral similarities (Donadio and Buskirk et al. 2006; Pauli et al. 2022).

Interference competition, especially size-mediated competitive interactions among carnivores, is important in structuring communities (Linnell and Strand 2000). However, given the change in dietary specialization of fishers (the dominant competitor) in the absence of martens, it is likely that a trade-off between exploitative and interference ability is important in determining overall effects of competition. Different foraging tactics that make exploitative-interference trade-offs are particularly common among social insects and permits species with different tactics to coexist (Wilson 1971; Holway 1999). For example, small size and inconspicuous behavior ("insinuators") may allow a species to forage in the presence of other competitors or a species may exploit new food sources quickly, but also retreat in the face of interspecific competition ("opportunists"; Wilson 1971). Both foraging tactics can result in high overlap of space, time, and resources with a socially dominant competitor, but such foraging tactics allow coexistence. We observed high overlap between martens and fishers in their isotopic and available dietary niche and dietary overlap is commonly observed among carnivores (e.g., Cupples et al. 2011; Fedriani et al. 2000; Kachel et al. 2022). Thus, even when overlap of the niche meta-axes (i.e., space, time, and resources) appears high, important differences in foraging tactics may mediate competition between species and should be considered.

Our analytical framework used complementary analyses of isotopic δ-space and dietary p-space (Manlick et al. 2019), revealing important differences in niche overlap metrics that would have been missed without this dual approach. Overlap was high for both available and core isotopic δ -space, but overlap of dietary proportions, especially core diets, showed little overlap between fishers and martens. Evaluating both overlap via broader trophic niche and core diet is needed to assess or predict if conditions exist for interspecific competition to limit coexistence. Fitness varies within any niche dimension and this variation contributes to the coexistence of species, and differences between core and available resource overlap may result in different fitness outcomes. Future research would benefit from identifying potential fitness differences between core and available resource overlap as they may be analogous to differences between the persistence and establishment niche (Holt 2009). For example, a population in the core dietary niche may act as a source, much like the lack of overlap in core diets may allow for establishment of new populations. Conversely, sites with high dietary overlap between competitors may theoretically allow coexistence, but populations may not establish, and these areas could act as sinks within the region. Demographic consequences due to niche dynamics and overlap is rarely quantified (e.g., Darimont et al. 2007; Manlick et al. 2021) and disentangling fitness consequences of overlap between core and available diet may further elucidate important thresholds in competition that affect viability or persistence. Ultimately, determining these thresholds will have a greater importance as environmental change continues to alter local abundance and resource availability.

Environmental change will continue to alter species coexistence especially along trailing edges where interactions between competition and prey continue to evolve (Peers et al. 2013). Across the region, small mammal communities are changing, with declines in northern species (Myers et al. 2009; Scott et al. 2022) that will potentially alter how carnivores in this region persist or interact. Habitat loss resulted in the extirpation of fishers and martens across much of the Great Lakes Region by the early 1900s (Williams et al. 2007) and natural recolonization and reintroductions have resulted in the reestablishment of fishers and martens in some areas. However, the persistence, especially of martens, along their southern trailing edge (e.g., at our F+m site) remains uncertain (Manlick et al. 2017; Grauer et al. 2019; Smith et al. 2021). This population of martens may be particularly sensitive to competitive interactions because the environmental context may not benefit the exploitatively superior species (i.e., martens), but rather benefits the superior interference competitor (i.e., fishers); interference competition can have a greater benefit when resources are limited (Case and Gilpin 1974). The environmental context of competitive interactions is increasingly occurring in novel ecosystems and, for many populations, is unlikely to return to conditions where these species have evolved. Consequently, competition refuges (e.g., via spatial separation or habitat heterogeneity), either natural or human aided, may be necessary to mediate novel competitive interactions and promote species persistence.

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Data availability statement

Data will be made available on Figshare upon publication.

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Table 1: Estimation of niche overlap in proportional dietary space from isotopic mixing models of allopatric and sympatric marten and fisher populations in the Great Lakes Region (M+0 marten only; F+0 fisher only; M+f marten are more common than fisher; F+m fisher are more common than marten). Core dietary space is represented by the 50% utilization distribution overlap indices (UDOI) and 95% for available diet. Measures of UDOI range from 0 (no overlap) to 1 (100% overlap). Total overlap of 95% kernel density estimates relative to each pairwise comparison.

Comparison	Core diet	Available diet	Percent overlap
M+0 Marten/F+m Marten	0	0	0/0
M+0 Marten /M+f Marten	0	0	0/0
M+f Marten / F+m Marten	0	0.06	41.1/22.4
F+m Marten / F+m Fisher	0	0	0/0
M+f Marten /M+f fisher	0	0.05	56.5/20.9
F+0 Fisher/F+m Fisher	0	0.08	19.6/62.0
F+0 Fisher/M+f Fisher	0	0	0/0
M+f Fisher/F+m Fisher	0.01	0.21	23.0/71.2

Figure 1: Stable isotope sampling locations of American martens, fishers, and dietary items in the Great Lakes Region. Sites vary by the presence marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common. Forest and woody wetland land cover from the 2016 National Land Cover Database depicted in green.

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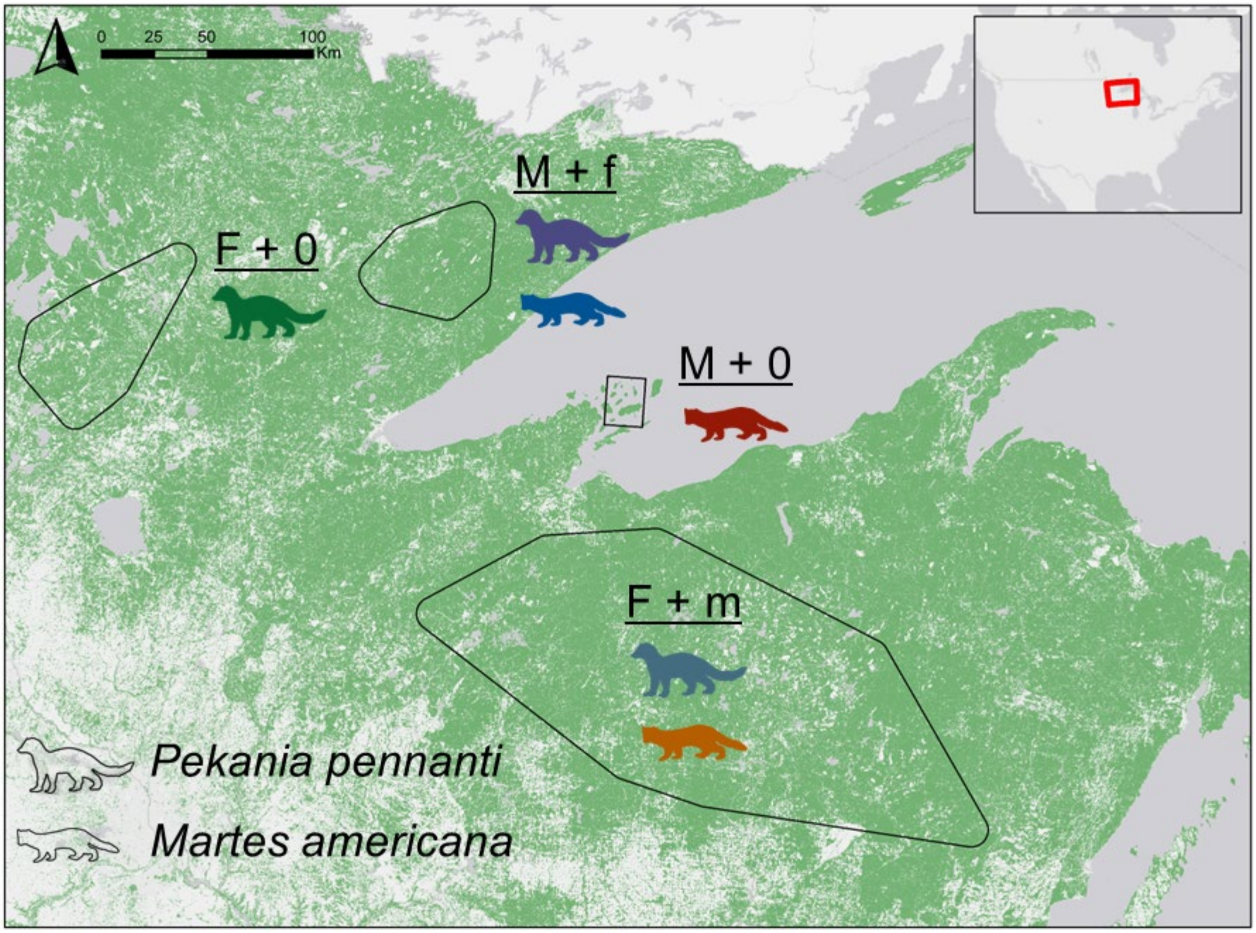
Figure 2: Scaled proportional isotopic values of $\delta^{13}C$ and $\delta^{15}N$ for American martens and fishers in the Great Lakes Region. Comparison of the 50% and 95% Bayesian ellipses for martens (a), fishers (b), and when they co-occur (c,d). Sites vary by the presence marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common.

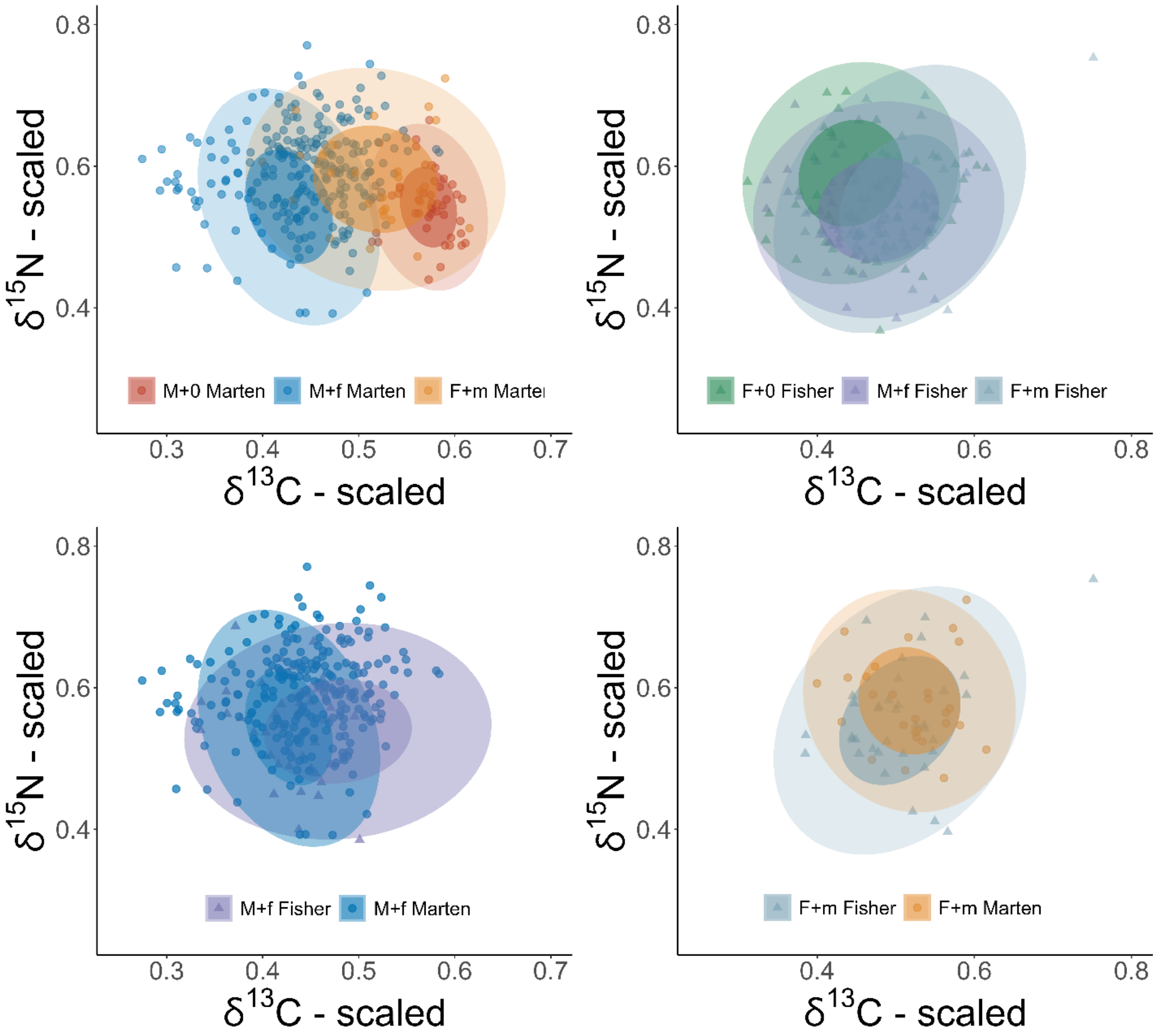
Figure 3: Bi-plot of proportional dietary space for American martens and fishers in the Great Lakes Region from isotopic mixing models. Axes denote proportion (%) of each functional dietary group estimated for each population, points denote estimated individual diets, and polygons denote 50% and 95% proportional dietary space for the population. Sites vary by the presence marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common.

Figure 4: Distribution of individual specialization for American martens and fishers across four sites in the Great Lakes Region (a) and correlation between the proportion of smaller-bodied prey by individual specialization (b). Sites vary by the presence of marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common.

Individual specialization was calculated from proportional dietary inputs estimated from isotopic mixing models. Colored dots represent individual specialization values, red dot represents the median of the population, and black vertical line represents the 89% high density interval. Majority (>50%) dietary group for each population was denoted with a silhouette. Smaller-bodied prey (🐁) consisted of songbirds, mice, shrews, voles, and squirrels, whereas larger-bodied prey (🐇) consisted of snowshoe hares, deer, ruffed grouse, and porcupine.

Figure 5: Parameter estimates from the most supported Bayesian generalized linear model explaining individual specialization as a function of habitat characteristics and relative prey abundance. Individual specialization was calculated from proportional dietary inputs estimated from isotopic mixing models for fishers and martens in the Great Lakes Region.


0
25
50
100
Km
M + f
F + 0
M + 0
F + m
Pekania pennanti
Martes americana


0.8
0.6
0.4
δ15N - scaled
M+0 Marten
M+f Marten
F+m Martei
0.3
0.4
0.5
0.6
0.7
δ13C - scaled
0.8
0.6
0.4
δ15N - scaled
F+0 Fisher
M+f Fisher
F+m Fisher
0.4
0.6
0.8
δ13C - scaled
0.8
0.6
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δ15N - scaled
M+f Fisher
M+f Marten
0.3
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δ13C - scaled
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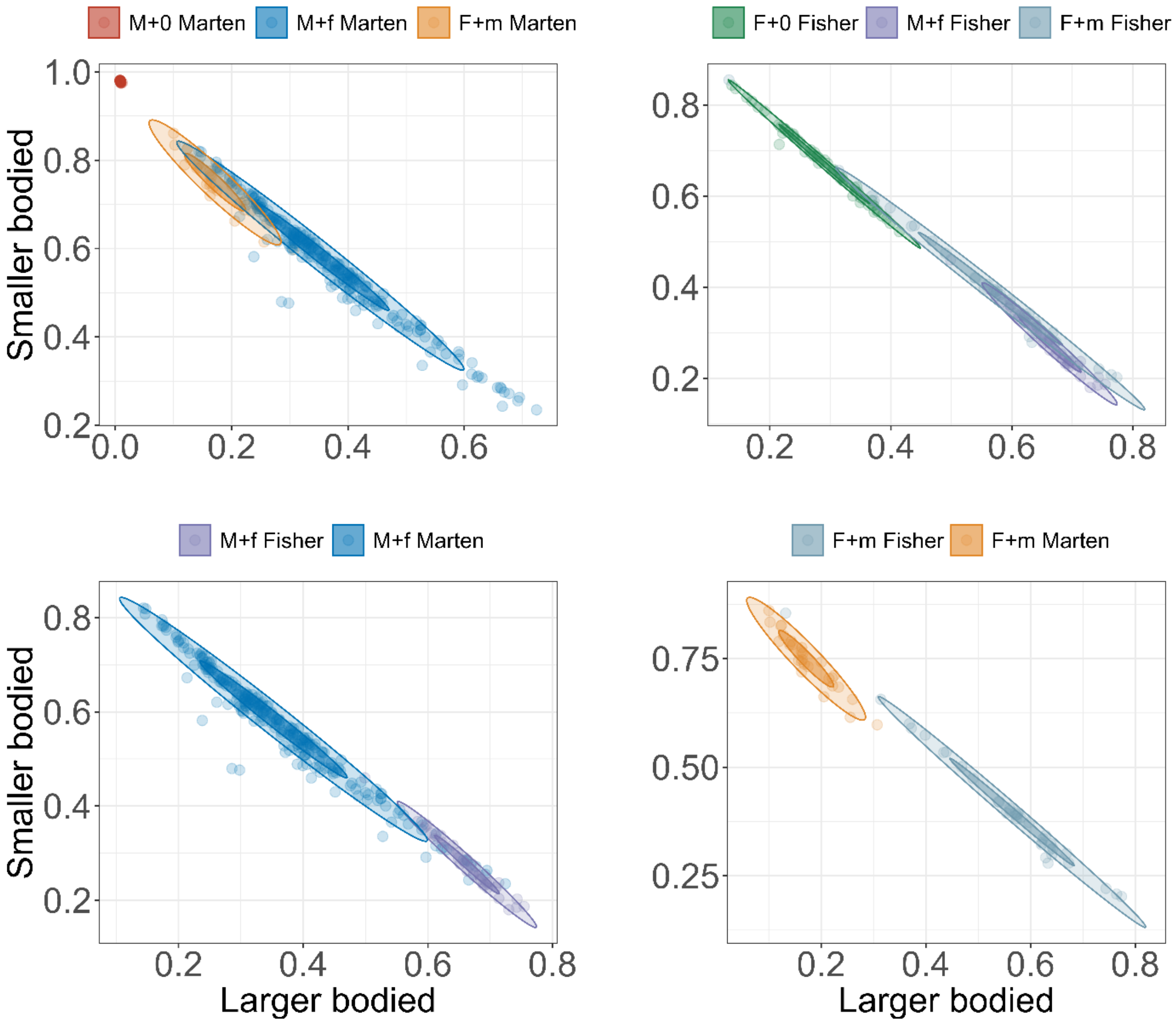
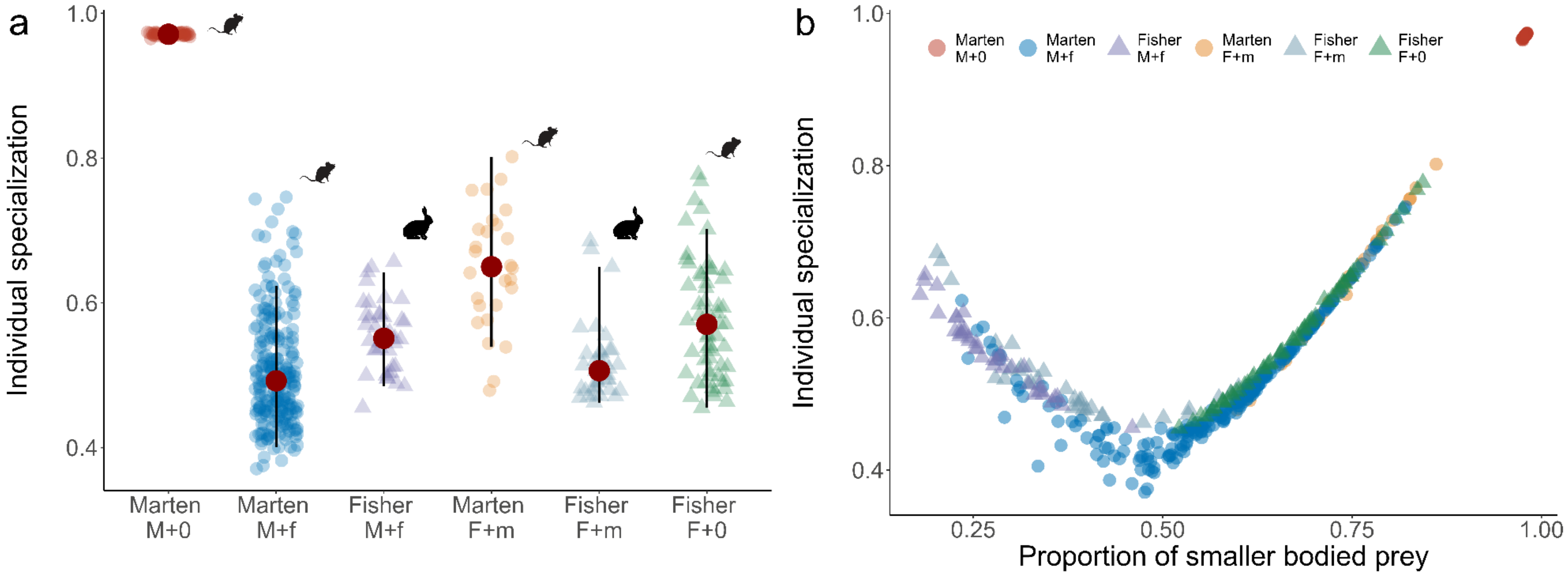
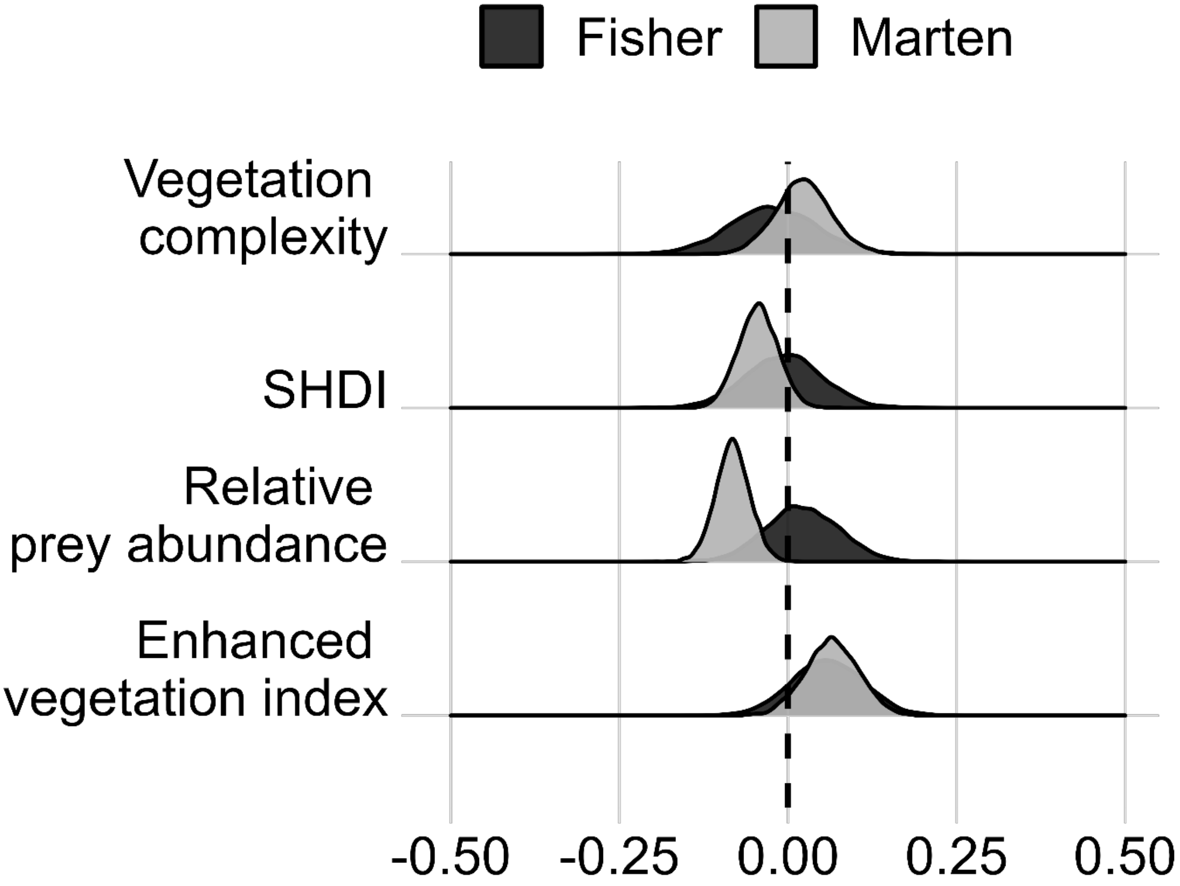
F+m Fisher
F+m Marten
0.4
0.6
0.8
δ13C - scaled


M+0 Marten
M+f Marten
F+m Marten
F+0 Fisher
M+f Fisher
F+m Fisher
Smaller bodied
1.0
0.8
0.6
0.4
0.2
0.0
0.2
0.4
0.6
0.8
M+f Fisher
M+f Marten
F+m Fisher
F+m Marten
0.75
0.50
0.25
Larger bodied
Larger bodied


a
Individual specialization
1.0
0.8
0.6
0.4
Marten M+0
Marten M+f
Fisher M+f
Marten F+m
Fisher F+m
Fisher F+0
b
Individual specialization
1.0
0.8
0.6
0.4
Marten M+0
Marten M+f
Fisher M+f
Marten F+m
Fisher F+m
Fisher F+0
0.25
0.50
0.75
1.00
Proportion of smaller bodied prey


Fisher
Marten
Vegetation complexity
SHDI
Relative prey abundance
Enhanced vegetation index
-0.50
-0.25
0.00
0.25
0.50

Supporting Information

Methods

Stable isotope analyses

Samples were rinsed 3x with a 2:1 chloroform:methanol solution to remove surface contaminants, homogenized, and dried at 56°C for 72 hours or until dry. Analysis of $\delta^{13}C$ and $\delta^{15}N$ was conducted at facilities dedicated to stable isotope analysis. Isotope ratios are reported in delta (δ) notation in per mille (‰) relative to the international standards Vienna Peedee Belemnite and atmospheric nitrogen. Analysis of stable isotopes was conducted at either the UC-Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK), Colorado Plateau Stable Isotope Facility using a Costech ECS4010 Elemental Analyzer coupled to a Thermo Scientific Delta V mass spectrometer (Waltham, MA), or the University of Wyoming Stable Isotope Facility using a Thermo Scientific Delta V mass spectrometer (Waltham, MA). Isotope ratios are reported in delta (δ) notation as parts per mille (‰) following the equation $\delta = (R \text{ sample} / R \text{ standard} - 1) \times 1000$, where R_{sample} and $R_{standard}$ are the ratios of the heavy and light isotopes (13C/12 C or 15N/14N) in a sample and standard, respectively. Analytical precision (standard deviation) was ≤0.2 ‰ for δ13C and δ15N values based on replicate measurements of internal reference materials calibrated to international standards.

Small mammal trapping

For F+0 and M+f, small mammal grids were 5x2 with 20 m intervals (*1600* m^2) and estimates of relative prey abundance for each cover type matched the year of the marten and fisher hair sample. For F+m, small mammal grids were 5x5 with 10 m intervals (*1600* m^2) and did not overlap temporally with marten hair samples. Grids were placed within cover types associated with deciduous, conifer, mixed forests, and woody wetlands from the NLCD.

Table S1: Stable Isotope of American martens (*Martes americana*), fishers (*Pekania pennanti*), and dietary items in the Great Lakes Region. Sites vary by the presence of marten and fisher: M + 0 only martens, F + 0 only fishers, M + f martens are more common, F+m fishers are more common. Sampling was supplemented with published isotopic values under Source, otherwise samples come from this study. To increase sampling sizes of dietary items and account for important dietary groups, we supplemented M + f with dietary items from F + 0 including porcupines (*Erethizon dorsatum*), ruffed grouse (*Bonasa umbellus*), and white-tailed deer (*Odocoileus virginianus*). Soft mast samples were shared between M + f and F + 0.

Site	Dietary Group	Species	Number	Tissue type	Year	Source
M+f		American marten (*Martes americana*)	245	Hair	2008-2014	
		Fisher (*Pekania pennanti*)	39	Hair	2008-2017	Manlick and Pauli 2020 (n = 15)
	Smaller-bodied	Flying squirrel (*Glaucomys* spp.)	12	Muscle	2010-2014	
		Red squirrel (*Tamiasciurus hudsonicus*)	19	Muscle	2007-2014	
		Peromyscus spp.	24	Muscle	2009-2013	
		Eastern chipmunk (*Tamias striatus*)	5	Muscle	2010-2014	
		Southern red-backed vole (*Myodes gapperi*)	25	Muscle	2007, 2009, 2010, 2013	
		Dark-eyed junco (*Junco hyemalis*)	4	Muscle	2013	
		Unknown bird	1	Muscle	2009	
		Shrews (*Blarina* and *Sorex*)	43	Muscle	2009-2014	
	Larger-bodied	Ruffed grouse (*Bonasa umbellus*)	47	Muscle	2009-2014	
		White-tailed deer (*Odocoileus virginianus*)	22	Muscle	2012-2014	
		Snowshoe hare (*Lepus americanus*)	23	Muscle	2009, 2011-2014	
		Porcupine (*Erethizon dorsatum*)	16	Muscle	2008-2015	

	Soft mast	Chokecherry (*Prunus virginiana*)	1		2010	
		Dwarf raspberry (*Rubus pubescens*)	1		2010	
		Gooseberry (*Ribes* sp.)	1		2010	
		Highbush cranberry (*Viburnum trilobum*)	1		2010	
		Nannyberry (*Viburnum lentago*)	1		2010	
		Raspberry (*Rubus* sp.)	1		2010	
		Sarsaparilla (*Aralia* sp.)	1		2010	
		Serviceberry (*Amelanchier* sp.)	1		2010	
F+m		American marten (*Martes americana*)	28	Hair	2005-2013	Carlson et al. 2014; Manlick et al. 2017
		Fisher (*Pekania pennanti*)	36	Hair	2013, 2016, 2017	Carlson et al. 2014; Manlick et al. 2017
	Smaller-bodied	Flying squirrel (*Glaucomys* spp.)	3	Hair	2010-2013	Carlson et al. 2014; Manlick et al. 2017
		Red squirrel (*Tamiasciurus hudsonicus*)	16	Hair	2010-2013	Carlson et al. 2014; Manlick et al. 2017
		Peromyscus spp.	14	Hair	2010-2013	Carlson et al. 2014; Manlick et al. 2017

		Eastern chipmunk (*Tamias striatus*)	5	Hair	2010-2013	Kirby et al. 2018
		Southern red-backed vole (*Myodes gapperi*)	8	Hair	2010-2013	Carlson et al. 2014; Manlick et al. 2017
		Shrews (*Blarina* and *Sorex*)	16	Hair	2010-2013	Carlson et al. 2014; Manlick et al. 2017
	Larger-bodied	Ruffed grouse (*Bonasa umbellus*)	7	Hair	2010-2013	Carlson et al. 2014; Manlick et al. 2017
		White-tailed deer (*Odocoileus virginianus*)	18	Hair	2010-2013	Carlson et al. 2014; Manlick et al. 2017
		Porcupine (*Erethizon dorsatum*)	6	Hair	2007	Kirby et al. 2018
	Soft mast	Unknown	5		2010-2013	Carlson et al. 2014; Manlick et al. 2017
M+0		American marten (*Martes americana*)	41	Hair	2017-2019	
	Smaller-bodied	Red squirrel (*Tamiasciurus hudsonicus*)	14	Hair	2017-2019	
		Peromyscus spp.	11	Hair	2016-2020	
		Southern red-backed vole (*Myodes gapperi*)	12	Hair	2017, 2020	
		Shrews (*Blarina* and *Sorex*)	16	Hair	2018, 2019	

	Larger-bodied	Snowshoe hare (*Lepus americanus*)	5	Hair	2017
	Soft mast	Blueberry (*Vaccinium* sp.)	5		2020
		Raspberries (*Rubus* sp.)	5		2020
		Sarsaparilla (*Aralia* sp.)	6		2020
		Serviceberry (*Amelanchier* sp.)	6		2020
F+0		Fisher (*Pekania pennanti)*	57	Hair	2007-2014
	Smaller-bodied	Red squirrel (*Tamiasciurus hudsonicus*)	41	Muscle	2008-2014
		Peromyscus spp.	34	Muscle	2008-2014
		Southern red-backed vole (*Myodes gapperi*)	32	Muscle	2008-2014
		Shrews (*Blarina* and *Sorex*)	44	Muscle	2009-2014
		Flying squirrel (*Glaucomys* spp.)	13	Muscle	2007-2014
		Gray squirrel (*Sciurus carolinensis*)	16	Muscle	2009-2015
		Eastern chipmunk (*Tamias striatus*)	10	Muscle	2008-2013
		Passerines	3	Muscle	2011, 2014
	Larger-bodied	Ruffed grouse (*Bonasa umbellus*)	46	Muscle	2009-2014
		White-tailed deer (*Odocoileus virginianus*)	17	Muscle	2012-2014
		Porcupine (*Erethizon dorsatum*)	16	Muscle	2009, 2011-2014
		Snowshoe hare (*Lepus americanus*)	6	Muscle	2007, 2008, 2014, 2015
	Soft mast	Chokecherry (*Prunus virginiana*)	1		2010
		Dwarf raspberry (*Rubus pubescens*)	1		2010
		Gooseberry (*Ribes* sp.)	1		2010
		Highbush cranberry (*Viburnum trilobum*)	1		2010

	Nannyberry (*Viburnum lentago*)	1	2010
	Raspberry (*Rubus* sp.)	1	2010
	Sarsaparilla (*Aralia* sp.)	1	2010
	Serviceberry (*Amelanchier* sp.)	1	2010

Table S2: Mean ± standard deviation of scaled $\delta^{15}N$ and scaled $\delta^{13}C$ isotopic values of American marten (*Martes americana*) and Fishers (*Pekania pennanti)*. Study areas vary by the presence marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common.

Site	Species	Mean scaled $\delta^{15}N$	Mean scaled $\delta^{13}C$
M+0	Marten	0.55 ± 0.05	0.57 ± 0.03
F+0	Fisher	0.54 ± 0.06	0.48 ± 0.07
M+f	Marten	0.59 ± 0.06	0.44 ± 0.06
	Fisher	0.54 ± 0.07	0.43 ± 0.04
F+m	Marten	0.58 ± 0.06	0.52 ± 0.06
	Fisher	0.55 ± 0.08	0.51 ± 0.06

Table S3: Mean ± standard deviation, and range of variables in parentheses from activity areas of American marten (*Martes americana*) and Fishers (*Pekania pennanti)* used to model the effect of habitat characteristics and relative resource abundance on niche specialization in the Great Lakes Region. Vegetation complexity (i.e., Entropy) is a 2nd order image textures derived from Enhanced Vegetation Index of Landsat 5 and 8 images. Shannon diversity index was calculated using the National Land Cover Dataset. Study areas vary by the presence marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common.

Site	Species	Vegetation complexity	Relative resource abundance	Enhanced vegetation index	Shannon diversity index
M + 0	Marten	3.85±0.15	10.60±6.44	0.76±0.03	0.91±0.21
		(3.57, 4.10)	(2.80, 23.11)	(0.71, 0.79)	(0.63, 1.38)
F + 0	Fisher	4.16±0.08	15.38±9.63	0.59±0.04	1.26±0.22
		(3.92, 4.33)	(6.37, 48.68)	(0.52, 0.67)	(0.85, 1.74)
M + f	Marten	4.22±0.09	22.14±6.72	0.56±0.05	1.29±0.32
		(3.77, 4.38)	(11.43, 37.60)	(0.40, 0.69)	(0.16, 1.91)
	Fisher	4.23±0.08	21.28±7.32	0.56±0.05	1.32±0.26
		(4.06, 4.36)	(12.30, 36.17	(0.48, 0.67)	(0.74, 1.68)
F + m	Marten	4.17±0.12	9.74±1.53	0.65±0.07	1.25±0.25
		(3.98, 4.41)	(7.13, 11.54)	(0.49, 0.75)	(0.86, 1.95)

Table S4: Model set for American marten (*Martes americana*) and fishers (*Pekania pennanti*) comparing habitat characteristics to individual dietary specialization. Models included study area as a fixed effect letting the intercept and slope or just the intercept to vary by study area to assess site specific responses to specialization. Interactions included all combinations of site by habitat characteristics. Most supported model had lowest leave-one-out-cross-validation information criterion (LOOIC). SE standard error.

Model	Species	LOOIC	SE
Individual specialization ~ vegetation complexity + relative resource abundance + enhanced vegetation index + Shannon diversity index + site	Marten	-799.2	27.3
Individual specialization ~ vegetation complexity + relative resource abundance + enhanced vegetation index + Shannon diversity index + site + Interactions	Marten	-7921.6	27.1
Individual specialization ~ vegetation complexity + relative resource abundance + enhanced vegetation index + Shannon diversity index + site	Fisher	-166.4	5.9
Individual specialization ~ vegetation complexity + relative resource abundance + enhanced vegetation index + Shannon diversity index + site + Interactions	Fisher	-159.0	5.4

Table S5: Parameter estimates from the most supported Bayesian generalized linear model explaining individual specialization as a function of habitat characteristics and relative prey abundance. Individual specialization was calculated from proportional dietary inputs estimated from isotopic mixing models for American martens (*Martes americana*) in the Great Lakes Region. The most supported model had study areas that varied in intercept, but not slope based on leave one out cross-validation information criterion. HDI: highest density interval, pd: probability of direction, ROPE: percent in region of practical equivalence (-0.1,0.1), ESS: effective sample size.

Parameter	Median	89% HDI	pd	ROPE	*R hat*	ESS
Vegetation complexity	0.02	-0.04, 0.09	71.42%	99%	1.00	5411
Relative prey abundance	-0.08	-0.12, -0.04	99.88%	78.1%	1.00	6994
Enhanced vegetation index	0.07	0.00, 0.13	94.58%	82.4%	1.00	5284
Shannon diversity index	-0.04	-0.09, 0.00	93.50%	99.6%	1.00	5208
Intercept – F+m	0.48	0.36, 0.60	100%	0%	1.00	6589
Intercept – M+f	--0.40	-0.54, -0.25	100%	0%	1.00	6344
Intercept – M+0	-2.46	2.23, 2.73	100%	0%	1.00	5196

Table S6: Parameter estimates from the most supported Bayesian generalized linear model explaining individual specialization as a function of habitat characteristics and relative prey abundance. Individual specialization was calculated from proportional dietary inputs estimated from isotopic mixing models for fishers (*Pekania pennanti*) in the Great Lakes Region. The most supported model had study areas that varied in intercept, but not slope based on leave one out cross-validation information criterion. HDI: highest density interval, pd: probability of direction, ROPE: percent in region of practical equivalence (-0.1,0.1), ESS: effective sample size.

Parameter	Median	89% HDI	pd	ROPE	*R hat*	ESS
Vegetation complexity	-0.02	-0.12, 0.08	63.58%	93.2%	1.00	3890
Relative prey abundance	0.02	-0.06, 0.11	65.82%	97.7%	1.00	5186
Enhanced vegetation index	0.06	-0.03, 0.14	88.00%	80.4%	1.00	5528
Shannon diversity index	-0.01	-0.10, 0.09	53.58%	100%	1.00	4106
Intercept – M+f	-0.72	-0.91, -0.52	100%	0%	1.00	4951
Intercept – F+0	0.29	0.19, 0.38	100%	0%	1.00	5576

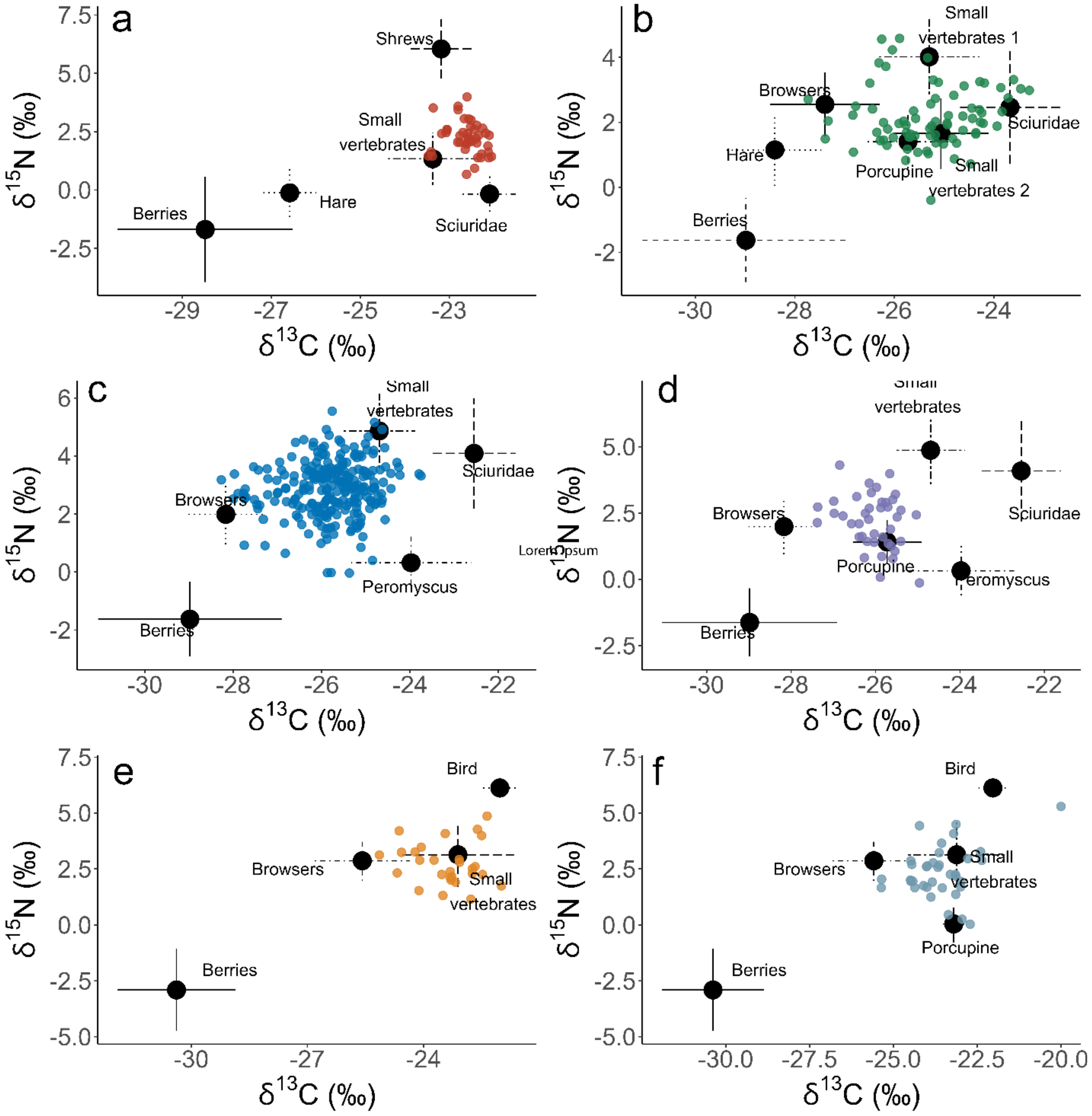


Figure S1: Mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope value and standard deviation of dietary source groups including trophically corrected ($\delta^{13}C = 2.6$ or 1.3 (if prey sample was hair); $\delta^{15}N = 3.4$; *Vulpes vulpes*; Roth and Hobson 2000) marten (Martes americana; a, c, e) and fisher (*Pekania pennanti*; b, d, f) individual values. Martens, fishers, and dietary source groups where unique to each study area in the Great Lakes Region: marten are common, but fishers are rare or absent (M + 0; a), fishers are common, but marten are rare (F + 0; b), both martens and fishers with martens being more common than fishers (M + f; c [marten] and d [fisher]) or fishers being more common than martens (F + m; e [marten]and f [fisher]). Isotope ratios are reported in delta (δ) notation as per mille (‰). We identified isotopically distinct groups and combined prey items when not isotopically distinct including browsers (snowshoe hares [*Lepus americanus*], deer [*Odocoileus virginianus*], ruffed grouse [*Bonasa umbellus*]) and small vertebrates that could include a combination of songbirds, mice (*Peromyscus* spp.), shrews (*Blarina brevicauda*, *Sorex* spp.), and red-backed voles (*Myodes gapperi*) depending on study area.

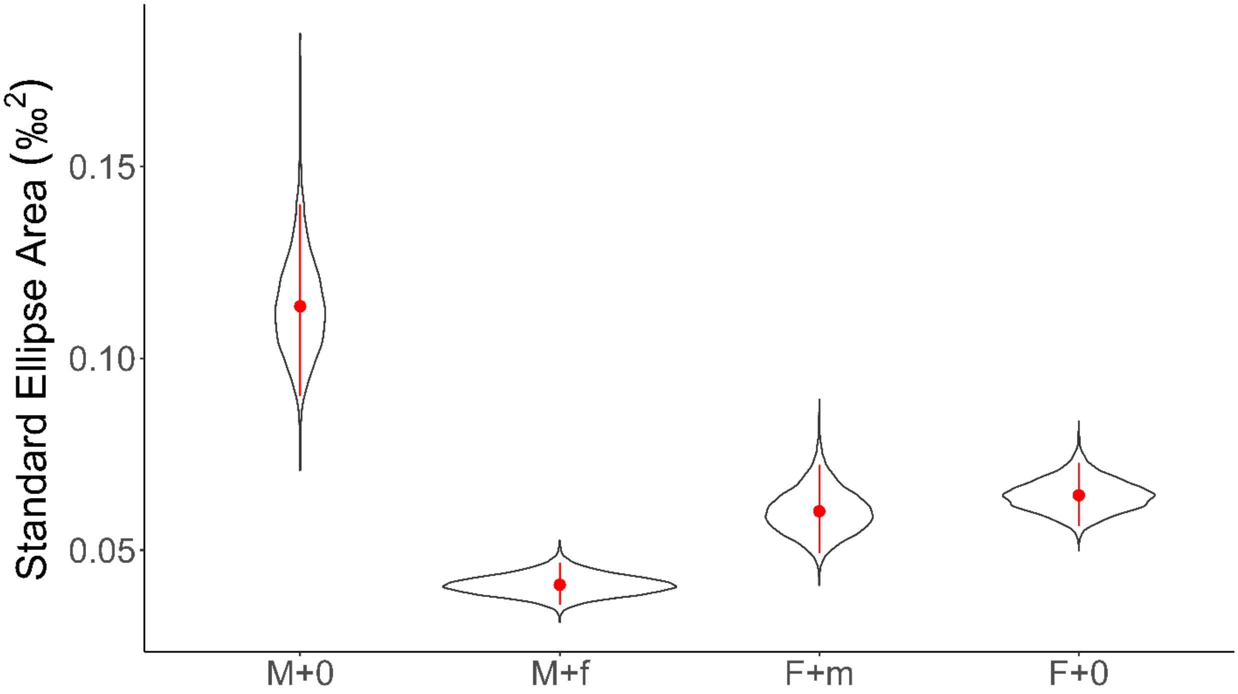


Figure S2: Bayesian standard ellipse area from scaled proportional isotopic values of δ^{13}C and δ^{15}N of dietary items in the Great Lakes Region. Red vertical line denotes the 95% high density interval and red point represents the median ellipse area. Study areas vary by the presence marten and fisher: M+0 only martens (a), F+0 only fishers (b), M+f martens are more common, F+m fishers are more common.

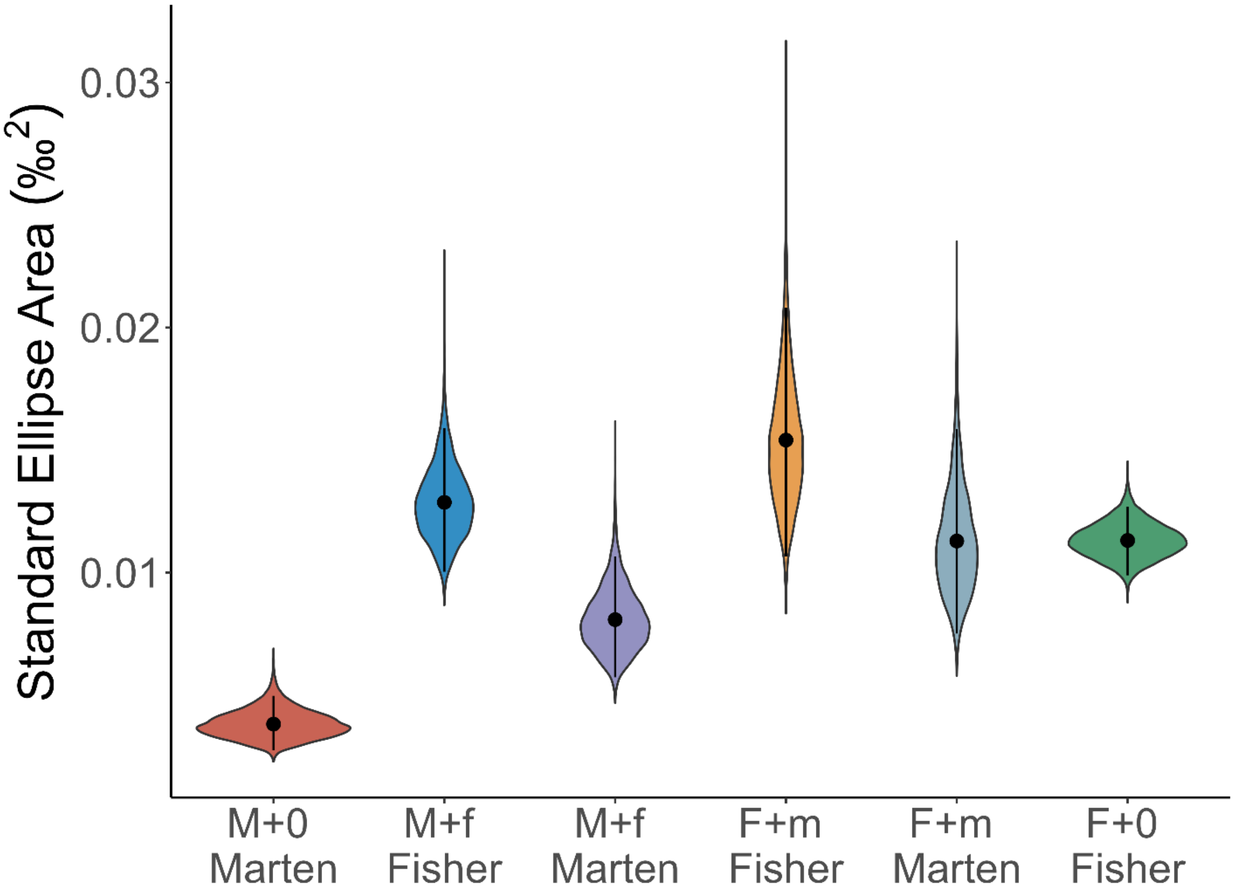


Figure S3: Bayesian standard ellipse area from scaled proportional isotopic values of δ^{13}C and δ^{15}N for American martens (*Martes americana*) and fishers (*Pekania pennanti*) in the Great Lakes Region. Black vertical line denotes the 95% high density interval and black point represents the median ellipse area. Study areas vary by the presence marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common.

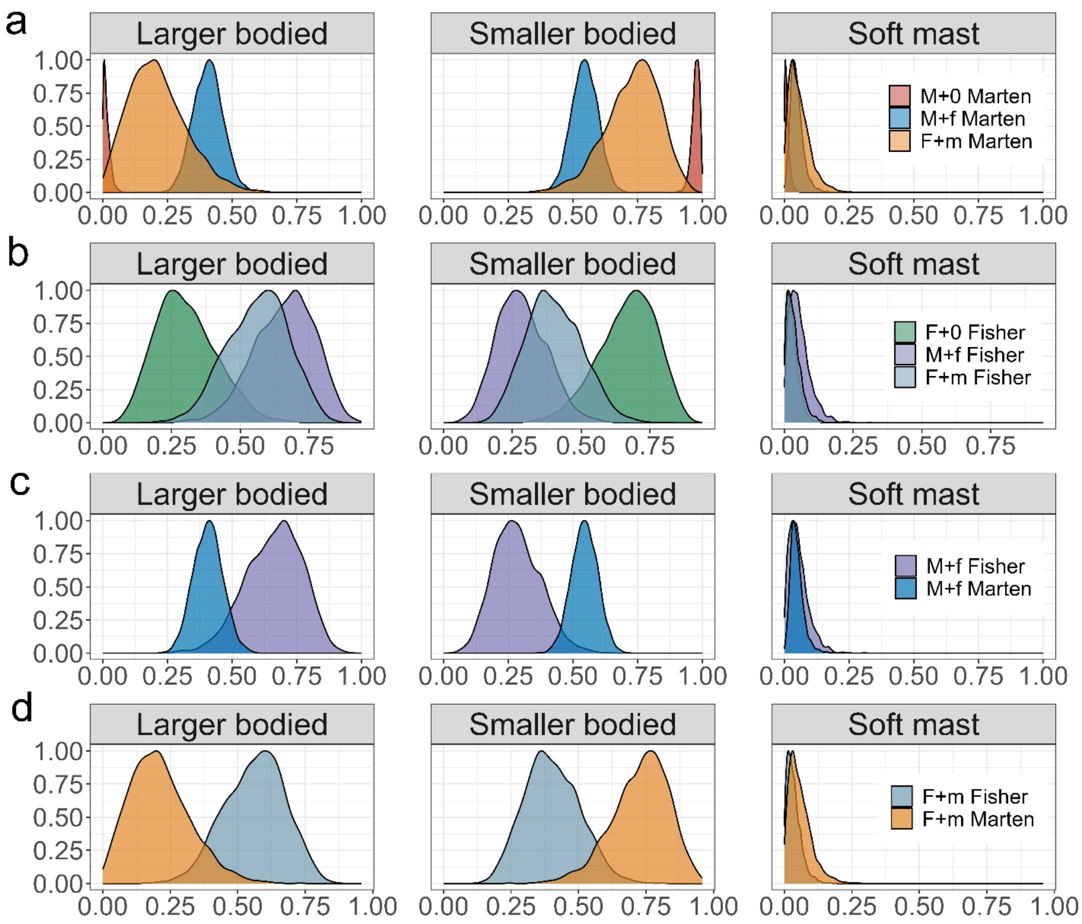


Figure S4: Proportional dietary inputs for American martens (*Martes americana*) and fishers (*Pekania pennanti*) in the Great Lakes Region from isotopic mixing models. To make comparisons possible between sites and species, we *a posteriori* combined sources (i.e., prey) into the finest resolution of dietary groups consistent across sites. We identified three functional dietary groups shared between sites that included: soft mast, larger-bodied prey (snowshoe hares [*Lepus americanus*], deer [*Odocoileus virginianus*], ruffed grouse [*Bonasa umbellus*], porcupine [*Erethizon dorsatum*]), and smaller-bodied prey (songbirds, mice [*Peromyscus* spp.], shrews [*Blarina brevicauda*, *Sorex* spp.], voles [*Myodes gapperi*]*,* squirrels [*Sciuridae* spp.]). Comparisons of only martens (a), only fishers (b), and two sites where martens and fisher co-occur (c,d). Sites vary by the presence marten and fisher: M+0 only martens, F+0 only fishers, M+f martens are more common, F+m fishers are more common.

Connectivity maintains genetic diversity and population persistence within an archipelagic refugia even under declining lake ice

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Abstract

Anthropogenic climate change is impacting environmental conditions with clear and often striking effects on the ecology of species and ecosystem. In response, conservation practitioners have initiated climate adaptation strategies that often include the identification of refugia. Consequently, identifying site-specific conditions that maintain the viability of refugial populations is essential. Often, populations rely on connectivity to enhance persistence and genetic diversity. Islands have been model systems to understand the role of connectivity and metapopulation processes and can be important refugia from environmental change. To better understand how connectivity influences genetic diversity and persistence within an islands system and potential refugia for a climate-sensitive species, we developed a demographically informed individual-based model (IBM) to explicitly test the role of connectivity. We simulated changing ice cover conditions within the Apostle Islands and tested the sensitivity of genetic erosion and persistence for American martens (*Martes americana*). We found that the loss of genetic diversity was resilient to moderate changes in ice cover, but a complete loss of regional and island connectivity resulted in rapid genetic erosion. However, despite the genetic erosion, populations persisted as long as nominal connectivity occurred between the Islands. Our work revealed that martens would be resilient to moderate changes in connectivity within the Apostle Islands and in the short term can act as a regional refugia. Furthermore, predicting how populations will respond within refugia is fundamentally important and will require the evaluation of populations through time. Refugia will likely be strongly dictated by its connectivity to regional populations and size. Thus, identifying thresholds in connectivity that maintain small populations but allow for a degree of isolation from disturbance will provide important features of refugia in space and time.

Introduction

Ongoing anthropogenic climate change is altering environmental conditions globally with pronounced effects on the ecology of species and ecosystems (Parmesan and Yohe 2003; Rosenzweig et al. 2008). Consequently, conservation practitioners and resource managers are increasingly challenged with identifying and applying solutions to mediate the loss of biodiversity in the face of climate change (Stein et al. 2013; LeDee et al. 2020). The identification of refugia -- areas buffered from contemporary climate change to aid in the regional persistence of locally adapted species -- has become an important component of climate adaptation strategies to support the persistence of species, communities, and ecosystems (Keppel et al. 2015; Morelli et al. 2016). Broadly inclusive refugial concepts, in particular, have gained traction to embrace ecological complexity and identify refugia based on varying scale (e.g., spatial and temporal) and function (Keppel et al. 2012; Monsarrat et al. 2019; Morelli et al. 2020). Regardless of the specific scale and function, refugia should allow for the persistence of a population through local favorable environmental (e.g., abiotic or biotic) conditions while the broader regional environment may be unfavorable (Rull 2010). An important requirement of any refugia is to be sufficiently large and of sufficient quality to support a viable population (Ashcroft 2010). Exploring central factors that dictate the qualities of a refugia are essential as climate change management moves from general recommendations to prescriptive actions that address site-specific conditions and population viability (Morelli et al. 2020).

Connectivity, primarily observed through the dispersal of individuals across populations, is particularly critical for spatially structured populations as it can promote metapopulations dynamics that improve resiliency to demographic and environmental stochasticity (Hanski and Gilpin 1991). Indeed, connectivity has been identified as centrally important to the viability of past and contemporary refugia (Epps et al. 2006; Morelli et al. 2017; Heard et al. 2015). Furthermore, connectivity promotes gene flow between populations to increase local genetic diversity, reduce inbreeding, and ameliorate the effects of genetic drift in small populations (Broquet et al. 2010). Despite the importance of genetics on population persistence, applying genetic principles and advances in conservation genetics to conservation planning remains poorly integrated (Pierson et al. 2016; Ralls et al. 2017; Cook and Sgrò 2017), especially in the planning and management of refugia.

Island have been model systems for understanding metapopulation concepts (MacArthur and Wilson 1967) and have since been applied to the conservation of populations in fragmented landscapes (Hanksi and Gaggiotti 2004). Notably, island populations are often maintained by connectivity and in many cases can be as persistent as larger mainland populations even though they are smaller in size (Harrison and Taylor 1997). For example, both theoretical models (Allen 1987) as well as empirical observations on oceanic islands (Schoener and Spiller 1987; Peeters et al. 2020), and habitat islands (Harrison et al. 1988; Taylor et al. 2007) have shown that greater connectivity can substantively enhance population persistence. Nevertheless, island populations are still vulnerable to extinction due to smaller population size and isolation, especially when they are isolated from immigration from the mainland (Frankham 1998). Indeed, most recent extinctions have occurred on islands and remain at risk due to human land-cover change, introduction of non-native species, and disease (Manne et al. 1999; Kier et al. 2009). Interestingly, however, islands can serve as refugia in regions where mainland populations are threatened due to the inherent isolation that protects populations from disturbances, competition (e.g., non-native species), and disease (Burbidge *et al.* 1997). Phylogeographic and fossil evidence support the use of islands as refugia during the last glacial maximum (Shafer et al.

2010; Fleming & Cook 2002), and more recently, 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). For example, the marooning of Koalas other non-volant mammals on coastal islands of Australia and have aided conservation of at-risk species (Burbidge 1999; Menkhorst 2008). Not only can islands protect species from changes on the mainland, but they can also harbor unique genetic diversity and adaptative potential (Wilson et al. 2009). Thus, archipelagos are both intrinsically vulnerable to stochastic events, but can also act as refugia and sources of genetic variability and holdouts for mainland populations under threat from climate change (Keppel *et al.* 2012).

In the Great Lakes Region, the Apostle Islands, are a 22-island archipelago in Lake Superior. On both the archipelago and neighboring mainland, the Laurentian Forests were compositionally and structurally complex until the 1800s when the region was commercially logged (Rhemtulla et al. 2009). Concomitant with this forest loss and simplification, several forest carnivores were extirpated by the early 1900s including American martens (*Martes americana*) (Thiel 1987; Williams et al. 2007), a forest and complexity specialist (Smith et al. 2022) and current state endangered species (Woodford et al. 2013). Serial reintroductions spanning 60 years have reestablished populations of martens on the mainland (Williams et al. 2007; Woodford et al. 2013), but long-term variability is uncertain (Skalski et al. 2011; Manlick et al. 2017; Grauer et al. 2019). Despite the slow recovery, martens naturally recolonized the Apostle Islands from the mainland and regional connectivity likely contributed to the expansion of martens outside of historical translocation sites (Smith et al. 2021). Movement between the Apostle Islands and mainland Wisconsin almost certainly occur only during periods of ice cover on Lake Superior (Allen et al. 2018). Unlike much of the habitat on the mainland, and despite being logged in the past, the Apostle Islands now maintain forest composition and complexity that is similar to pre-European settlement that may be attributed to an absence or low intensity of deer herbivory, fire, and forest disturbance (Beals and Cottam 1960). While the Apostle Islands currently provide an ideal place for martens and climate-sensitive species in the region, it is unknown how connectivity will influence future population persistence and genetic diversity, especially considering ice cover has declined since 1973 (-2.0% per year) and increased in variability (Wang et al. 2012).

Identifying the degree of connectivity to maintain populations within refugia is an important step to anticipate and promote climate change solutions. Herein, we simulated how a climate-sensitive species may respond to changes in connectivity due to climate change. To better understand how connectivity influences genetic diversity and persistence within an islands system and potential refugia, we developed a demographically informed individual-based model (IBM) to explicitly test the role of connectivity among the archipelago and between the mainland. Specifically, we incorporated changing ice cover (i.e., connectivity) within the Apostle Islands and tested the sensitivity of genetic erosion and persistence by simulating baseline conditions, loss of immigration from the mainland, and loss of connectivity among the islands and between the mainland. With this case study, we empirically investigated the influence of climate change on connectivity and evaluated population trends of a climate-sensitive species within a potential refugia.

Methods

Ice cover trends

We obtained daily gridded ice cover data from December 1973 through May 2022 from the Great Lakes Environmental Research Laboratory part of the National Oceanic and Atmospheric Administration (Assel 2005; Yang et al. 2020). We used daily ice cover to estimate the average annual onset, offset, and monthly ice cover within the archipelago. We calculated annual average ice cover using daily values from January 3rd to April 5th as all years (1973-2022) had records during this time. To identify interannual changes in ice cover, we used a Bayesian change point and trend analysis implemented in the R package *Rbeast* (Zhao et al. 2023). We identified likely changepoints and estimated the probability of occurrence to assess contemporary trends in ice cover. We used monthly average ice cover observed within the core islands of marten distribution in the archipelago to parametrize our IBM.

Individual-based model

We designed an individual-based model (NETLOGO; Wilensky 1999) to project the potential effect of changing ice cover on population persistence and genetic diversity of an archipelagic population of martens. The spatial structure of the model consisted of patches that represented five islands within the archipelago (Fig. 1a). The model simulated the life history of individual martens (i.e., agents) through time using a monthly time step. We selected a monthly time step to model the monthly variation in ice cover and account for temporal life history processes. We incorporated two stages of individuals: juveniles (age = 0) and adults (age > 0) with stage specific monthly survival probabilities. Individual attributes of martens included: parents, sex, genotype, and current island location. Genotypes from 11 microsatellite loci were assigned by randomly selecting one of the two alleles from each parent. Martens could reproduce from age 1 and mates were randomly selected from all individuals of reproducing age on the same island. Reproduction took place in the simulated month of July to account for delayed implantation (Jonkel and Weckwerth 1963), but new kits were not added to the landscape until the following simulated month of April. Litter size was randomly assigned for individual females each year from a weighted probability between zero and three kits (Lacy and Clark 1993).

We modeled connectivity as two separate processes as either dispersal from within the archipelago or immigration from the mainland. First, we required ice to be present given the proportion of monthly ice cover and then by a probability that a marten would move across the ice and reach an island. Dispersal only occurred among juveniles and at the end of their first year (Johnson et al. 2009). Immigrants and dispersers would only be recruited into the population if the carrying capacity was not exceeded and we set a carrying capacity of 1.5 martens/Km^2 (Francis and Stephenson 1972) for each island based on area (Fig. 1a). Immigrants were assigned alleles based on a probability that was proportional to the observed allele frequencies from the founding population (Smith et al. 2021). A random set of juveniles and new immigrants could be recruited into the population if the maximum population size was not exceeded (for overview, design concept, and details protocol see Supporting Information).

Parameter inference

We used our IBM to simulate the past colonization process of the Apostle Islands to inform model parameterization of future projections. Previous research quantified genetic diversity, population size, and timing of colonization (Smith et al. 2021). We used the estimated timing of colonization to test three different scenarios by adjusting the number of time steps within our IBM to test a colonization event of 45 years, 20 years, and 10 years since the initial data collection in 2017 (Smith et al. 2021). Our time points match the median and 95% credible interval of the timing of colonization from coalescent simulations (Smith et al. 2021). We used the observed percentage of ice cover during each month and year to parameterize the probability of ice for the dispersal and immigration procedure of our IBM. We used an approximate Bayesian computation framework for model selection and parameter inference. We approximated the posterior distribution of four model parameters of monthly adult survival (S_A), monthly juvenile survival (S_J), probability of immigration (P_I), and probability of dispersal (P_D). Parameters were sampled from a uniform distribution and the minimum and maximum values for adult and juvenile survival were obtained from the literature (Buskirk et al. 2012). We used Latin hypercube sampling implemented in the R (R Core Team 2023) package *nlrx* (Salecker et al. 2019) to sample 150 000 parameter sets for each colonization scenario. We compared models using rejection methods implemented in the R package *abc* (Csillery et al. 2012) and selected the scenario that had the highest posterior probability approximated by the proportion of accepted simulations (Pritchard et al. 1999). We used summary statistics of observed heterozygosity, number of alleles, and population size by island. We performed a goodness-of-fit test on the most supported scenario by comparing the distance between accepted summary statistics to observed and computed a Bayesian p-value. In addition, we performed a posterior predictive check (Gelman et al. 2003) using the median parameter value from the posterior distribution and compared with the observed data using 10000 simulations of our IBM.

Future projections

We simulated a starting population forward in time for 200 years and estimated observed heterozygosity and inbreeding at each time step. Inbreeding coefficients (*F*) were calculated using the R package *pedigree* (Coster 2013) from a reconstructed pedigree based on known parents and observed heterozygosity was calculated from multi-locus genotypes of each individual following Hervey et al. (2021). Additionally, we calculated the probability of extinction for each island as the frequency of simulations where the population size was equal to zero. To account for monthly variation in ice cover, we randomly simulated the probability of ice formation as a beta distribution using the monthly mean and variance from observed values within the archipelago.

We tested the sensitivity of our simulations to changes in ice cover by reducing the mean or increasing the variance of the percentage of ice cover by 20% and 40% while keeping either the mean or variance constant. To test the resilience of the archipelago as a refugia, we compared baseline treatments of current mean ice cover to simulations that removed immigration of new individuals from the mainland, but maintained connectivity among the islands and a condition where the islands were no longer connected to each other and the mainland. We initiated the forward projections for all conditions based on individuals identified on each island and their multi-locus genotype (Smith et al. 2021). We simulated 100 replicates of each condition.

Results

Ice trends

Ice cover within the archipelago exhibited strong annual variation (Fig. 1b), Mean seasonal ice cover ranged from 22% to 99% and the on-set generally occurred during the middle of December and lasted until the middle of April (Fig 1b). Change point and trend analysis supported a single change point in 1998 (prob = 0.80). From 1973 to 1997, the annual trend in percent of ice cover was 85% and declined by 28% to an average of 61% ice cover from 1998 to

2022 (Fig 1c). Consequently, we used the average mean and variance from monthly percent ice cover from 1998 to 2022 as our baseline for our future projections.

Parameter inference

We found that a colonization time of 10 years received the highest proportion of accepted simulations (71%) and highest posterior model probability (0.92). In addition, this scenario provided a good fit to the observed data ($p = 0.38$). The posterior distribution for all estimated parameters showed clear peaks above prior values and the observed data was included within the posterior predictive distributions (Supporting Information Fig. S1 and Fig S2). We subsequently used the median value of S_A (0.99), S_J (0.94), P_I (0.12), and P_D (0.22) from the 10-year model to parameterize future projections (Fig. S1).

Future projections

Projected inbreeding increased and observed heterozygosity decreased over the 200-year simulation regardless of condition (Fig. 1; Fig. 2). We found that both inbreeding and observed heterozygosity were resilient to increases in the monthly variance of ice cover (Fig. 2), and to a $\leq$40% reduction in the monthly ice cover (Table 1; Fig. 2). The loss of immigrants from the mainland resulted in a large decline in heterozygosity (41.8%) and a large increase (66.6%) in inbreeding compared to baseline condition (Table 1; Fig. 3). The largest relative change from baseline occurred between projected inbreeding and observed heterozygosity when immigration from the mainland and dispersal among the islands were absent (Table 1; Fig. 3). No simulated marten population went extinct under baseline conditions or when martens could disperse among the islands (Fig. 4). However, when immigration from the mainland and dispersal was removed from the simulation, the smallest islands by area and carrying capacity had a ≥75% probability of extinction within 100 years (Fig. 4). The largest island (Stockton) was the only location predicted to persist even when connectivity from the mainland and other islands were absent (Fig. 4).

Discussion

The loss of genetic diversity was resilient even to moderate changes in ice cover, but a complete loss of regional and island connectivity resulted in rapid genetic erosion. Indeed, reductions in ice cover (20% and 40%) resulted in only a minimal loss of genetic diversity. However, substantial genetic erosion occurred when immigration from the mainland or dispersal between the islands was not possible. Furthermore, isolation from the regional metapopulation (i.e., no immigration from the mainland) contributed the most to reductions in genetic diversity. Interestingly, despite genetic erosion, the largest island remained populated under all connectivity scenarios. Generally, these results support what conservation biologists have long known: connectivity and area play an important role in understanding demographic and genetic trajectories of populations. Across taxa, incorporating metapopulation processes and connectivity has improved population persistence and genetic diversity of historical refugia (Morelli et al. 2017), and in reserve design (Cabeza 2003; Williams et al. 2005). However, identifying thresholds in connectivity that lead to different population outcomes is important for local and management-relevant scales. Here, we showed limited change in genetic diversity and no change in the islands occupied if nominal connectivity remained in the system.

Simulations that project populations forward in time within refugia are a necessary tool for local, species-specific management. Even though complex individual interactions can be incorporated into IBMs, important assumptions are required. Notably, we assumed low genetic diversity will result in low fitness and low phenotypic variation that will contribute to extirpation risk of the refugia. However, recent debate has proposed that minimizing deleterious variation and not maximizing genetic diversity should take priority when assessing extirpation risk (Kyriazis et al. 2021). Although, this recommendation is counter to previous empirical evidence of the benefits of genetic diversity to ameliorate inbreeding depression (Frankham et al. 2017; Ralls et al. 2020). Regardless, inbreeding depression was not included in our individual-based model and our approach likely underestimated the severity and timing of genetic erosion and population persistence. Conversely, kin avoidance or giving preference for new migrants may lessen the rate of inbreeding and genetic erosion as highly related individuals are avoided and similarly was not included in our modeling approach. Given uncertainties surrounding environmental and demographic consequences due to climate change, our simulations should not be considered to predict the timing of actions, but instead highlight the critical importance that connectivity will play for this putative refugia and a likely scenario for many refugia.

The resiliency observed supports the idea that the Apostle Islands can act as refugia for martens in the short-term when ice conditions are likely to not drop below thresholds for immigration to occur. Indeed, the Apostle Islands have been federally protected since 1970 and 80% is federally designated as wilderness (Public Law 108-447, Division E, Section 140). This designation provides protection from large-scale disturbance (e.g., timber extraction and fire) that contributes to forests that are compositionally and structurally more complex than on the mainland (Beals and Cottam 1960). In addition, Canada yew (*Taxus canadensis*), functionally extirpated from the mainland, and mountain maple (*Acer spicatum*) are abundant in the understory due to the absence or low density of deer (*Odocoileus virginianus*) and fire (Windels and Flaspohler 2011). The structural forest complexity likely contributes to prey availability

(Thompson and Colgan 1987; Carey and Johnson 1995), marten foraging success (Andruskiw et al. 2008), and reduced predation risk (Thompson and Colgan 1994). In the short-term, then, the Apostle Islands may act as an important refugia for this endangered species. Beyond martens, regional changes in winter conditions have been implicated in range reductions of winter-adapted species (Myers et al. 2009; Wilson et al. 2019; Smith et al. 2022). In particular, small mammal communities are changing with declines in northern species on the mainland (Myers et al. 2009) but remain abundant on the archipelago (Mallinger et al. 2019). The Apostle Islands may act as an important refugia for other climate-sensitive species as winter conditions change in the region.

While not a requirement of climate change refugia, it is likely that many will feature small populations with varying degrees of connectivity (Ashcroft 2010) and the potential to become more isolated as the effect of climate change moves from decades to centuries. Consequently, species-specific management under climate change will require planning actions across temporal scales. Our simulations suggest that if the archipelago becomes completely isolated, likely common for many refugia, martens would be increasingly vulnerable to extirpation. Indeed, a more proactive strategy would be needed to maintain genetic health. Active human interventions have become increasingly recommended for climate change adaptation (Ledee et al. 2020). For example, genetic rescue (i.e., assisted geneflow) can alleviate the negative effects of low genetic variation by managing geneflow (Mills and Allendorf 1996; Hedrick et al. 2011) but remains a controversial approach (Edmands 2007; Frankham et al. 2011; Whiteley et al. 2015). Regardless, approaches that act to restore connectivity or mimic metapopulation processes that restore geneflow will likely be essential strategies when refugia become isolated.

Movement of individuals across ice, especially sea ice in the Artic, has played a critical role structuring and maintaining genetic diversity (Geffen et al. 2007; Peeters et al. 2020). Even within Lake Superior, immigration, and periodic gene flow of wolves to Isle Royale maintained genetic health and will continue to be important for future persistence (Hedrick et al. 2015; Hervey et al. 2021). Critically, climate adaptation will require predicting site-specific responses and the incorporation of simulations to project population level outcomes that can guide future planning. In tandem with simulations, climate adaptation planning for refugia should include genetic monitoring to track changes in connectivity and identify when management action is needed. In addition, if action is required, the proliferation of genomic techniques make it possible to identifying the underlying loci contributing to inbreeding depression beyond the often considered nongenetic factors (Allendorf et al. 2010; Whiteley et al. 2015).

Addressing the effect of climate change on wildlife species is a complex problem, but new strategies are emerging (Schuurman et al. 2021). However, predicting how populations will respond is fundamentally important and will require the continued identification and evaluation of various strategies, including refugia. Our work reveals that a climate-sensitive species would be resilient to moderate changes in connectivity within a potential refugia. However, connectivity to the broader metapopulation would be necessary to maintain persistence and buffer genetic erosion. This suggests that longevity of a refugia will likely be strongly dictated by its connectivity to regional populations and size. Thus, identifying thresholds in connectivity that maintain a degree of isolation from disturbance, but allow for metapopulation processes will provide important features of refugia in space and time.

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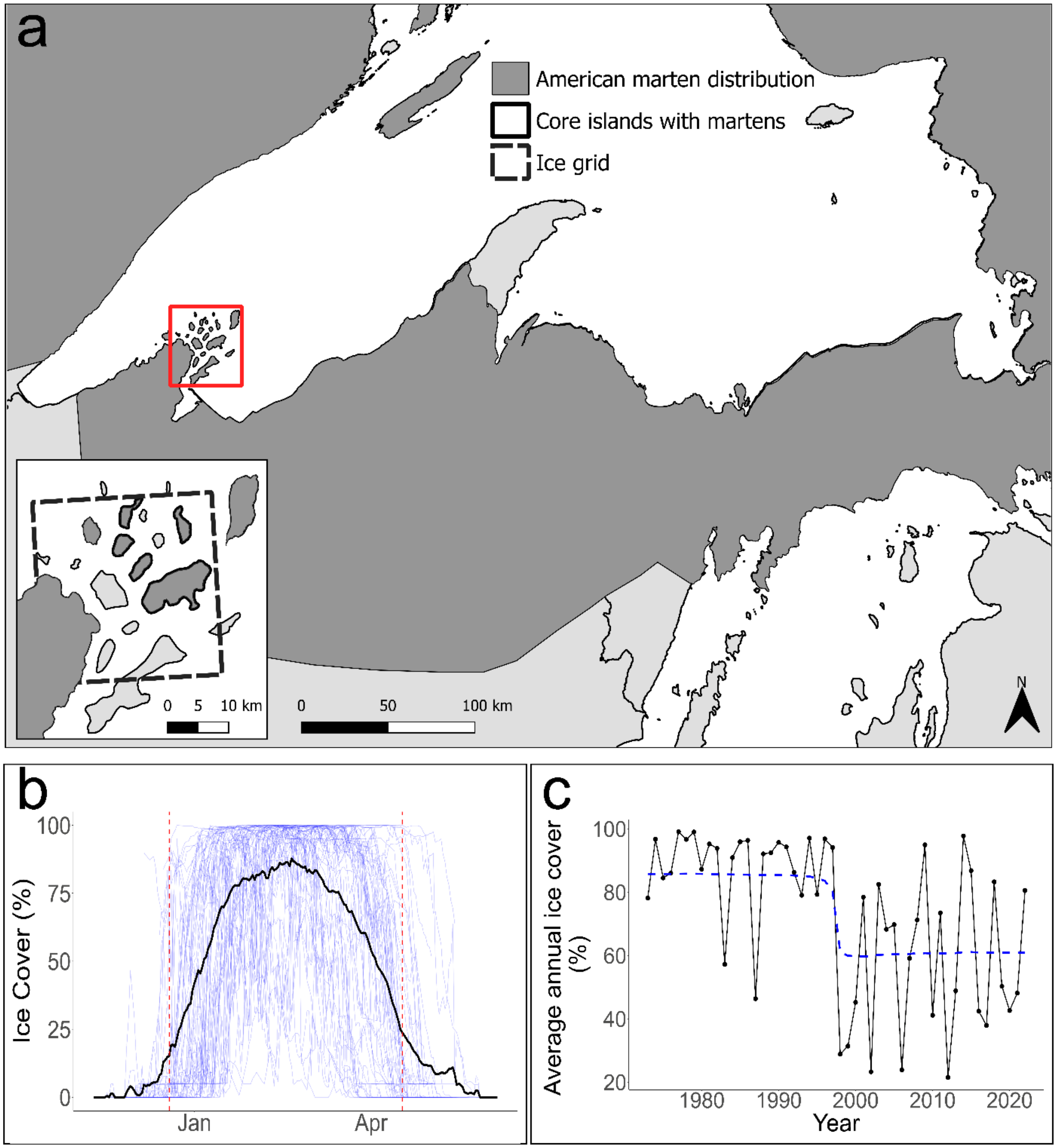
Table 1: Projected observed heterozygosity and inbreeding of baseline ice conditions (1998-2022), loss of immigration from the mainland and a loss of immigration from the mainland and dispersal among the islands. Mean estimates (SD, % relative change from baseline) at 50, 100, and 200 years from 100 replicates of a simulated individual-based model of American martens (*Martes americana*) on the Apostle Islands, WI.

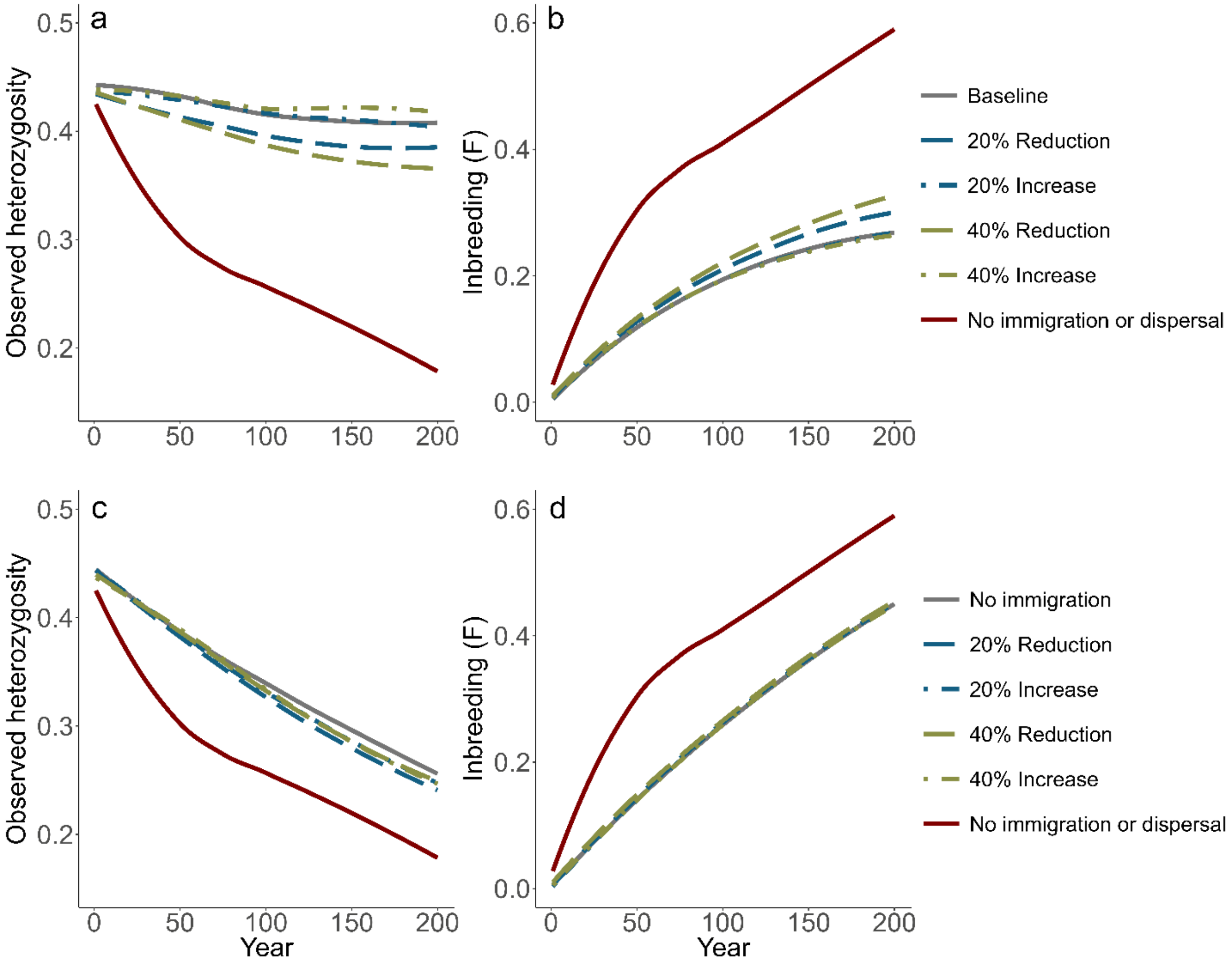
	Observed heterozygosity		
	50 years	100 years	200 years
Baseline	0.43 (0.14, -)	0.41 (0.14, -)	0.41 (0.15, -)
No immigration	0.39 (0.13, -9.8)	0.34 (0.13, -20.5)	0.25 (0.12, -41.8)
No immigration and dispersal	0.30 (0.16, -31.0)	0.26 (0.14, -37.5)	0.18 (0.11, -57.0)
	Inbreeding (F)		
	50 years	100 years	200 years
Baseline	0.12 (0.06, -)	0.19 (0.07, -)	0.27 (0.09, -)
No immigration	0.14 (0.06, 17.4)	0.26 (0.05, 32.4)	0.45 (0.04, 66.6)
No immigration and dispersal	0.31 (0.23, 161.6)	0.41, (0.17, 109.4)	0.59 (0.07, 118.7)

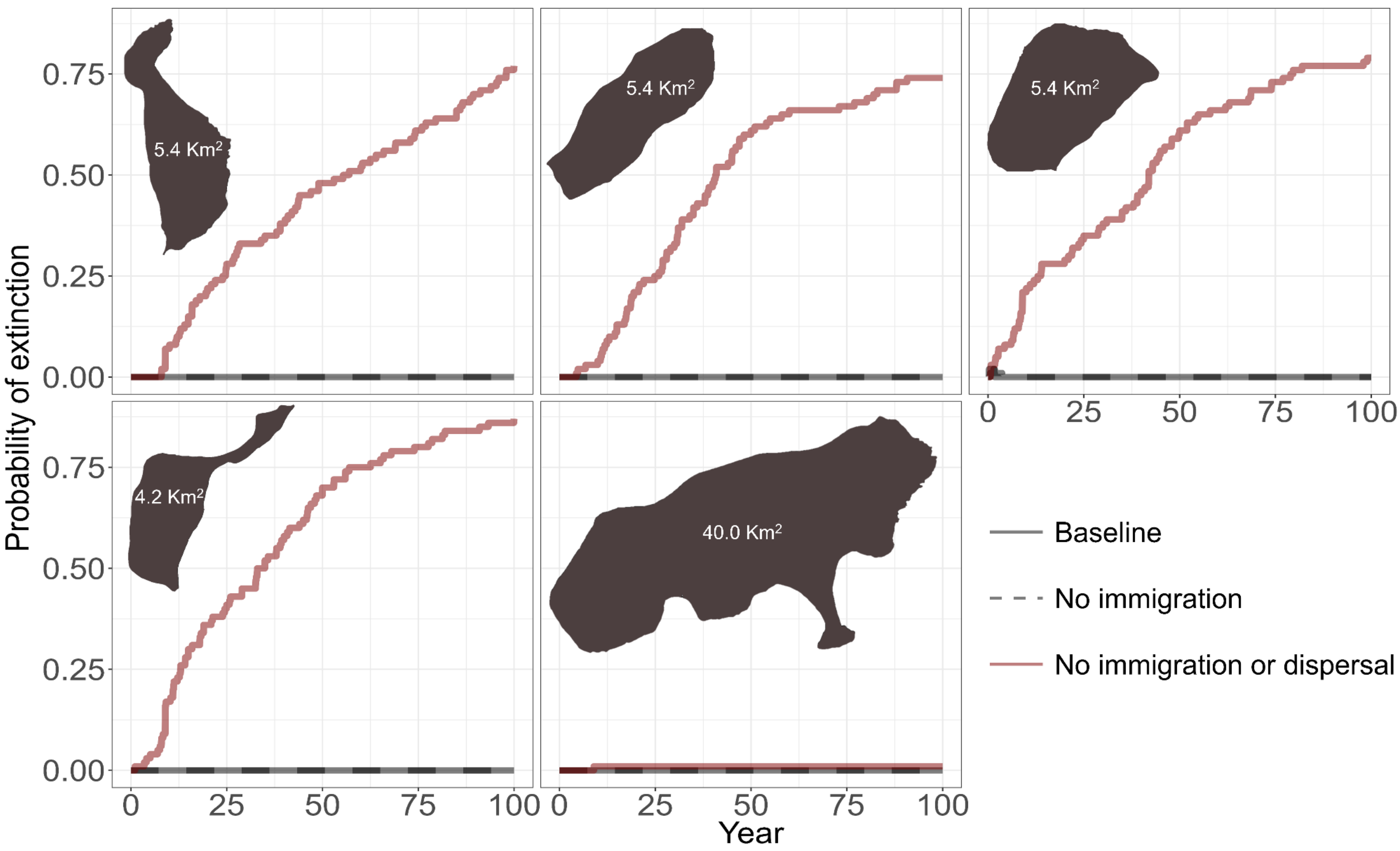
Figure 1: Core islands of the Apostle Islands archipelago with American marten (*Martes americana*) used to simulate the impact of changing ice conditions on genetic diversity (a). Ice observations from 1973 to 2022 within the islands by the daily percentage of ice cover from individual years (blue lines), averaged daily ice cover (black line), and average ice onset and off set (red lines) (b). Annual average ice cover from January 3rd to April 5th with trend line (blue line) from a time series decomposition accounting for annual variation (c). Percentage of ice cover data was obtained from the Great Lakes Environmental Research Laboratory part of the National Oceanic and Atmospheric Administration.

Figure 2: Projected observed heterozygosity and inbreeding from 100 replicates of a simulated individual based model of American martens on the Apostle Islands over 200 years. Changes in ice cover were simulated by reducing the mean or increasing the variance of the monthly baseline ice conditions (1998-2022) (a, b) and by reducing the mean or increasing the variance when immigration from the mainland was absent within the archipelago (c,d).

Figure 3: Projected probability of extinction (population size ≤ 1) by island within the Apostle Island archipelago from 100 replicates of a simulated individual based model of American martens on the Apostle Islands over 100 years. Baseline conditions (1998-2022) were compared to a scenario where either immigration from the mainland was absent or no immigration from the mainland or dispersal between the islands could occur.


a
American marten distribution
Core islands with martens
Ice grid
0
5
10 km
0
50
100 km
N
b
Ice Cover (%)
100
75
50
25
0
Jan
Apr
c
Average annual ice cover (%)
100
80
60
40
20
1980
1990
2000
2010
2020
Year


a
Observed heterozygosity
0.5
0.4
0.3
0.2
0 50 100 150 200
b
Inbreeding (F)
0.6
0.4
0.2
0.0
0 50 100 150 200
Baseline
20% Reduction
20% Increase
40% Reduction
40% Increase
No immigration or dispersal
c
Observed heterozygosity
0.5
0.4
0.3
0.2
0 50 100 150 200
Year
d
Inbreeding (F)
0.6
0.4
0.2
0.0
0 50 100 150 200
Year
No immigration
20% Reduction
20% Increase
40% Reduction
40% Increase
No immigration or dispersal


Probability of extinction
0.00
0.25
0.50
0.75
5.4 Km²
5.4 Km²
5.4 Km²
4.2 Km²
40.0 Km²
0
25
50
75
100
Year
Baseline
No immigration
No immigration or dispersal

Supporting Information

Matthew M Smith and Jonathon N Pauli. Connectivity maintains genetic diversity and population persistence within an archipelagic refugia even under declining lake ice

Overview, Design concepts, and Details

1. Purpose and patterns

The proximate purpose of this model is to estimate connectivity parameters within an archipelagic system (Apostle Islands, USA) for American martens (*Martes* americana) that most closely match observed data of population size, allelic richness, and observed heterozygosity. Connectivity parameters include the probability of migration from the mainland and the probability of dispersal of juveniles between islands. The ultimate purpose of the model is then to predict the effect of changing mean ice cover and variance on connectivity and the impact on population size, population persistence, and genetic diversity measures of allelic richness, heterozygosity, and inbreeding among the Apostle Islands.

2. Entities, state variables, and scales

The following entities are included in the model: agents representing adult martens, agents representing juvenile martens, grid cells/patches representing spatial-explicit islands within the archipelago, and the global environment tracks simulated time, monthly changes in ice cover, and stores variables that summarize the count and genetic diversity by island.

State variables for adult and juvenile martens were either informed from observed values or are emergent values from interactions between agents or spatial movement within the system.

Microsatellite values were selected based on observed frequencies from the founding population (Smith et al. 2021).

Table 1: Adult marten state variables

Variable name	Variable type and units	Description
Age	Integer; dynamic; year	Age of agent in years
Mom	Agent; static; text string	Unique ID of mother
Dad	Agent; static; text string	Unique ID of father
Sex	Categorical; static; Male (M) or Female (F)	Sex of marten
Migrant?	Categorical; static; Yes (Y) or No (N)	Marten that immigrated to the Apostle Islands from the mainland
MateID	Agent; dynamic; text string	For females, represents the ID of male mate that is selected
Microsatellites (Ma5, Ma8, Maa19, Gg3, Tt4, Mer041, Gg7, Ma14, Ma2, Mer022)	Integer; static; base pair length	Each microsatellite has two entries for each allele and represent the allele length in base pairs

Heterozygosity	Real number; static; proportion; 0 to 1	Proportion of heterozygote microsatellites
Recruited	Categorical; static; Yes (Y) or No (N)	Whether or not the marten was recruited into the island population when it was a juvenile
Dispersed?	Categorical; static; Yes (Y) or No (N)	Whether or not marten dispersed from another island when a juvenile
Island-og	Categorical; static; Cat, Manitou, Rocky, Otter, Stockton	Tracks the island they were born on or migrated to
Island-moved	Categorical; static; Cat, Manitou, Rocky, Otter, Stockton	Tracks island if they successfully dispersed
Island-current	Categorical; static; Cat, Manitou, Rocky, Otter, Stockton	Tracks the current island the marten is on – used for calculating summary of population size and genetic diversity on each island

Table 2: Juvenile marten state variables

Variable name	Variable type and units	Description
Age	Integer; dynamic; Can only be 1	Age of agent in years
Mom	Agent; static; text string	Unique ID of mother
Dad	Agent; static; text string	Unique ID of father
Sex	Categorical; static; Male (M) or Female (F)	Sex of marten
Migrant?	Categorical; static; Yes (Y) or No (N); Can only be "N"	Marten that immigrated to the Apostle Islands from the mainland
MateID	Agent; dynamic; text string; Not used for juveniles	For females, represents the ID of male mate that is selected
Microsatellites (Ma5, Ma8, Maa19, Gg3, Tt4, Mer041, Gg7, Ma14, Ma2, Mer022)	Integer; static; base pair length	Each microsatellite has two entries for each allele and represent the allele length in base pairs
Heterozygosity	Real number; static; proportion; 0 to 1	Proportion of heterozygote microsatellites
Recruited	Categorical; static; Yes (Y) or No (N)	Whether or not kit was recruited into the island population

Dispersed?	Categorical; dynamic; Yes (Y) or No (N)	Whether or not marten dispersed from another island when a juvenile
Island-og	Categorical; static; Cat, Manitou, Rocky, Otter, Stockton	Tracks the island they were born on or migrated to
Island-moved	Categorical; dynamic; Cat, Manitou, Rocky, Otter, Stockton	Tracks island if they successfully dispersed
Island-current	Categorical; dynamic; Cat, Manitou, Rocky, Otter, Stockton	Tracks the current island the marten is on – used for calculating summary of population size and genetic diversity on each island

Table 3: Patch state variables

Variable name	Variable type and units	Description
Island	Categorical; Cat, Manitou, Rocky, Otter, Stockton	Used to define patch belonging to each island
CC	Integer; >0; number of martens	Carrying capacity of each island based on island size

Table 4: Global environment state variables

Variable name	Variable type and units	Description

Parent1	Agent; dynamic; text string	Temporally stores father when creating juvenile martens if adult is available
Parent2	Agent; dynamic; text string	Temporally stores mother when creating juvenile martens if adult is available
Probability-of-ice	Percent; dynamic; numerical string; 12 values	Empirically observed percent of ice cover within archipelago for each month
Year	Integer; dynamic	Tracks year of simulation
Month	Integer; dynamic; 1 to 12	Tracks month of simulation
Ar-cat	Real number; dynamic	Stores the value of the average number of alleles on Cat Island
Ar-manitou	Real number; dynamic	Stores the value of the average number of alleles on Manitou Island
Ar-rocky	Real number; dynamic	Stores the value of the average number of alleles on Rocky Island
Ar-otter	Real number; dynamic	Stores the value of the average number of alleles on Otter Island

Ar-stockton	Real number; dynamic	Stores the value of the average number of alleles on Stockton Island
Count-cat	Integer; dynamic; ≥ 0	Stores the value of the number of martens on Cat Island
Count-manitou	Integer; dynamic; ≥ 0	Stores the value of the number of martens on Manitou Island
Count-rocky	Integer; dynamic; ≥ 0	Stores the value of the number of martens on Rocky Island
Count-otter	Integer; dynamic; ≥ 0	Stores the value of the number of martens on Otter Island
Count-stockton	Integer; dynamic; ≥ 0	Stores the value of the number of martens on Stockton Island
Ho-cat	Real number; dynamic; proportion; 0 to 1	Average heterozygosity for martens on Cat Island
Ho-manitou	Real number; dynamic; proportion; 0 to 1	Average heterozygosity for martens on Manitou Island

Ho-rocky	Real number; dynamic; proportion; 0 to 1	Average heterozygosity for martens on Rocky Island
Ho-otter	Real number; dynamic; proportion; 0 to 1	Average heterozygosity for martens on Otter Island
Ho-stockton	Real number; dynamic; proportion; 0 to 1	Average heterozygosity for martens on Stockton Island
Cat-martens	Agent-set; dynamic	Stores the agents (adults and juvenile martens) on Cat Island to calculate summary statistics.
Manitou-martens	Agent-set; dynamic	Stores the agents (adults and juvenile martens) on Manitou Island to calculate summary statistics.
Rocky-martens	Agent-set; dynamic	Stores the agents (adults and juvenile martens) on Rocky Island to calculate summary statistics.
Otter-martens	Agent-set; dynamic	Stores the agents (adults and juvenile martens) on Otter Island to calculate summary statistics.

Stockton-martens	Agent-set; dynamic	Stores the agents (adults and juvenile martens) on Stockton Island to calculate summary statistics.
Cat-geno-list	Integer; list; dynamic; base pair length	Stores observed alleles from all agents on Cat Island, used to calculate allelic richness
Manitou-geno-list	Integer; list; dynamic; base pair length	Stores observed alleles from all agents on Manitou Island, used to calculate allelic richness
Rocky-geno-list	Integer; list; dynamic; base pair length	Stores observed alleles from all agents on Rocky Island, used to calculate allelic richness
Otter-geno-list	Integer; list; dynamic; base pair length	Stores observed alleles from all agents on Otter Island, used to calculate allelic richness
Stockton-geno-list	Integer; list; dynamic; base pair length	Stores observed alleles from all agents on Stockton Island, used to calculate allelic richness

One time step represents one month, and simulations were run for 20 years based on an estimated year of marten colonization to the Apostle Islands (Smith et al. 2021). A monthly temporal scale was selected to simulate the life history of martens (e.g., delayed implantation, dispersal, and recruitment). The model is a two-dimensional and spatially explicit representation of 5 Apostle Islands (Cat, Manitou, Rocky, Otter, and Stockton) with 100 x 100 meter cells and a patch variable the identities the specific island.

3. Process overview and scheduling

The modeled processes and schedule were developed to follow the annual life cycle of martens and estimate parameters of survival, dispersal, and migration that most closely result in observed patterns of genetic diversity and population size. The Apostle Island archipelago is represented by an image file and two setup procedures are executed (setup-island and setup-cc) to define the state variable of island based on specific island name and define the state variable of carrying capacity (cc) that is inputted by the user. Two processes track population size and genetic diversity (island-count and calc-gen-div), four processes relate to adults (check-death, migrate, reproduce, and create-kits), and three process relate to juveniles (check-death, disperse, and recruit). For each time step (i.e., month), the environment executes the submodels: island-check, check-death, migrate, and disperse. Migration occurs from the mainland and dispersal only acts on juveniles within the archipelago. If the state variable of month equals four (i.e., April), the recruitment submodel is executed followed by cull-juveniles that removes juveniles not recruited into the population on each island, and new juveniles are born by executing the submodel create-kits. Additionally, adults age one year and we assumed senescence and ultimately death of adults would occur if they reached age 10 (Lacy and Clark 1999). If the state variable of month equals seven (i.e, July), the reproduction submodel is executed. At the end of each tick, the submodels of island-count and calc-gen-div are executed that update state variables that track population size (count-stockton, count-cat, count-manitou, count-otter, count-rocky), heterozygosity (ho-stockton, ho-cat, ho-manitou, ho-otter, ho-rocky), and allelic richness (ar-stockton, ar-cat, ar-manitou, ar-otter, ar-rocky) on each island. Also, the month increases by one and if the month is equal to 12, the month is reset to one. The creation of juveniles and reproduction are separate processes to model delayed implantation in this species. All actions occur in the same predetermined order:

1. The archipelago is spatially represented, and patches are assigned parameters using the procedures of setup-island and setup-cc.
2. Martens survive or die with different probabilities for adults and juveniles.
3. Migrate – potentially martens from the mainland migrate to the archipelago.
4. Disperse - potentially juveniles on the archipelago disperse to a new island.
5. If Month = 4, recruit juveniles then create kits, and adults age one year or die if age = 10.
6. If Month = 7, adult martens potentially find mates using the procedure reproduce.
7. Adults and juveniles on each island are counted using the procedure island-count.
8. Genetic diversity is estimated from adults and juveniles on each island using the procedure calc-gen-div.
9. Month increases by one and year is increased by one if month is equal to 12.
10. Simulation runs for 20 years.

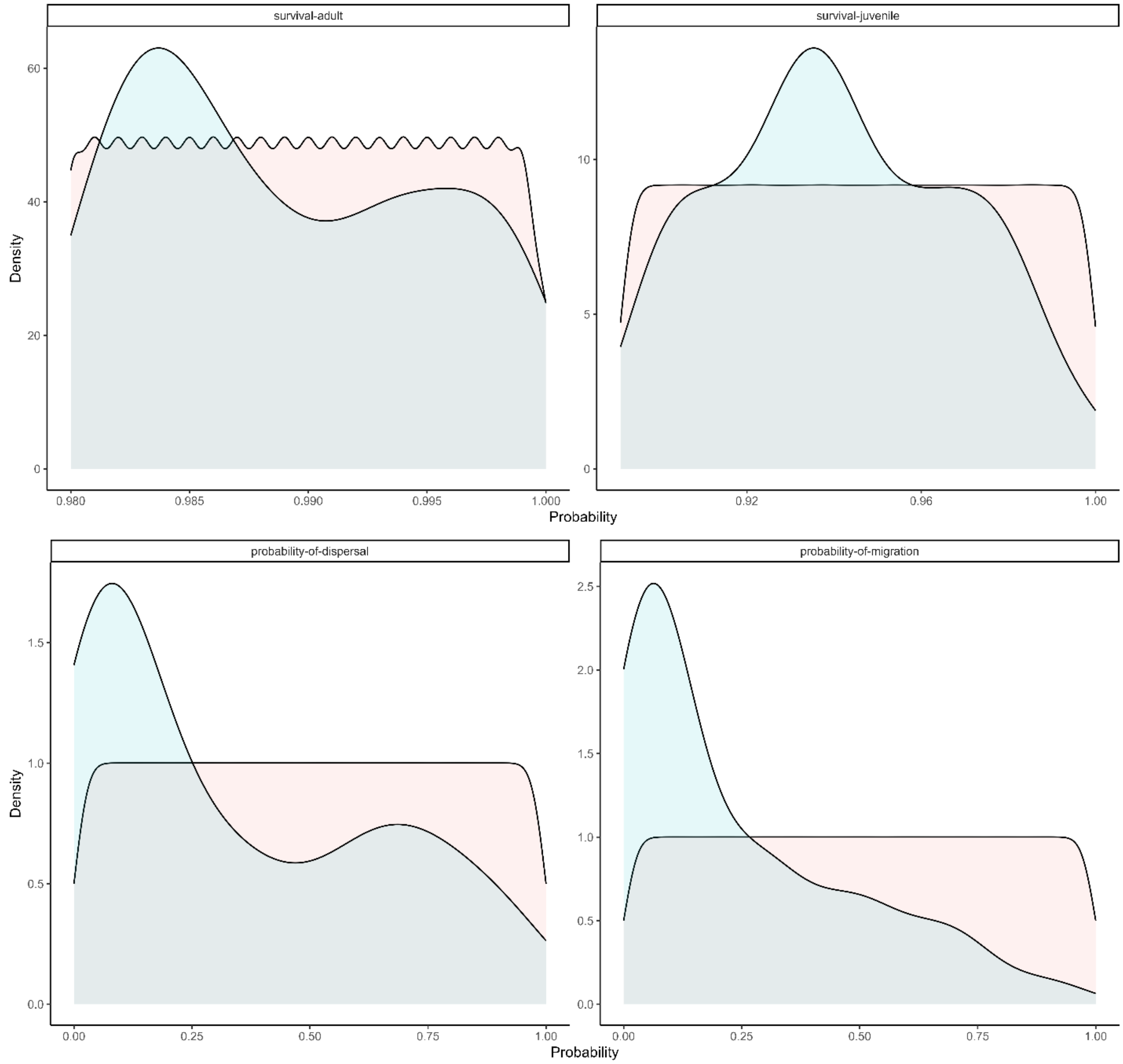


Figure S1: Prior (red) and posterior (blue) density of parameters from an individual-based model that simulated the colonization process of American martens to the Apostle Islands. An approximate Bayesian computation framework was used to estimate parameter values that mostly closely simulated observed patterns in population size and genetic diversity. Parameter included the probability of adult survival, probability of juvenile survival, the probability of dispersal between islands, and the probability of immigration from the mainland.

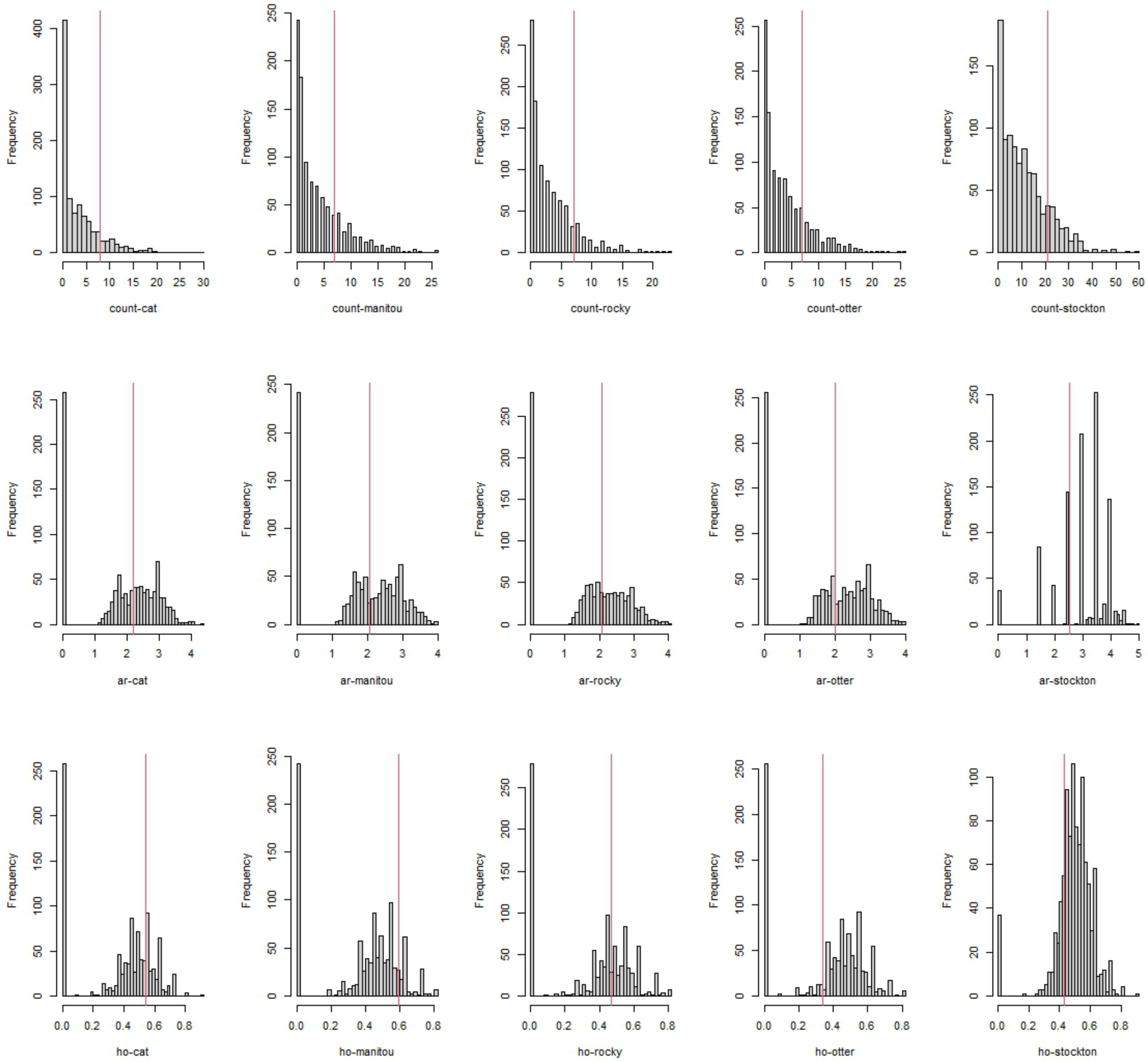


Figure S2: Posterior predictive check using 1000 repetitions from an individual-based model that simulated the colonization process of American martens to the Apostle Islands. Parameter values of probability of adult survival, probability of juvenile survival, the probability of dispersal between islands, and the probability of immigration from the mainland were inferred using an approximate Bayesian computation framework. Median values were used to estimate distributions of summary statistics and compared to observed values (red line). Summary statistics included the population size (count), number of alleles (ar), and observed heterozygosity (ho), on 5 islands (Cat, Manitou, Rocky, Otter, Stockton).

Predicting and prioritizing genetic diversity outcomes of animal translocations

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The problem

Environmental change is driving extinctions and isolating species globally; recovering and rescuing these populations has motivated conservation for over a century (Seddon et al 2014). Traditionally, recovery to self-sustaining populations have focused on habitat management approaches that ultimately increase the survival and reproduction of the at-risk population. However, genetic diversity is increasingly recognized as an integral component of long-term species recovery from past changes and to provide adaptive capacity to future change (Jamieson and Lacy 2012). Indeed, population declines, and isolation has reduced genetic diversity and increased inbreeding that escalates the extinction risk for threatened species (Forester et al. 2022).

Translocations, or the intentional movement of animals to repatriate extirpated or augment existing populations, have become a central tool for species recovery. Increasingly, translocations are viewed not only to bolster population size, but also genetic diversity. Indeed, translocations can improve fitness through the introduction of new genetic material when the recipient population is small or inbred and improve adaptive potential by increasing genetic diversity (Weeks et al. 2011; Whiteley et al. 2015). While increasing genetic diversity is often cited as a fundamental goal of translocations, the effectiveness is often not evaluated (but see Jackson et al. 2022).

Improving genetic diversity hinges on selecting an appropriate source population and identifying the correct number of individuals to be translocated; conservation practitioners, though, rarely have prior knowledge on the genetics of translocated individuals to inform either condition (Tracy et al. 2011). Even when known, the persistence of genetic diversity in the recipient population is often unexplored. By combining genetic data on the source with simulations to predict the rate of genetic loss, practitioners can improve both planning and outcomes of translocations for the maintenance of genetic diversity (Weiser et al. 2013; Gruber et al. 2019). Herein, we quantified the genetic diversity of translocated individuals, and then simulated how genetic diversity would erode over time under different scenarios: single translocation, additional augmentations, and rates of natural immigration.

Case study

Throughout their distributional range in the Great Lakes Region, Sharp-tailed grouse (*Tympanuchus phasianellus*) are declining in abundance and increasingly isolated. Small population sizes and limited gene flow put sharp-tailed grouse populations at increased risk of local extirpation. To mediate declines, a federal, state, and tribal partnership has begun to restore critical habitat and augment the contemporary population on the Moquah Barrens Wildlife Management Area in northwestern Wisconsin (Fig. S1). Concomitant with these goals was also the objective of increasing genetic diversity.

Over three years, 160 sharp-tailed grouse were translocated from a neighboring, but disjunct population in northwestern Minnesota. This source population exhibits high genetic diversity, making it an ideal source for the translocation (Roy et al. 2019). However, debate exists between minimizing the presence of strongly deleterious alleles (Kyriazis et al. 2021) or maximizing diversity of source populations (Ralls et al. 2020). Nevertheless, the general recommendation of choosing a source population that maximizes genetic diversity is well supported by empirical evidence and history of past augmentation outcomes (Frankham et al. 2015). Indeed, observed heterozygosity and number of alleles were similar between the source and translocated populations (Appendix S1). Simulations revealed that the genetic diversity, measured as retention of rare alleles, of the recipient population would erode rapidly if no further management actions were taken (Fig. 1a; Appendix S1). Augmentations at 10- or 25-year frequency increased the retention of genetic diversity but also eventually eroded due to small population size (Fig. 1a). However, only four migrants per year was enough to retain rare alleles (Fig. 1b). Increased connectivity was necessary to maintain genetic diversity and translocations alone, even at relatively high frequency, were subject to genetic loss without consistent natural immigration.

Discussion

Despite successful selection and release of translocated individuals, follow-up monitoring is essential to evaluate whether the diversity captured in the translocated population is incorporated into the extant population. Indeed, our findings show that the initial increase of genetic diversity quickly eroded with no further action and is likely common for many at-risk species (Jackson et al. 2022). Importantly, these simulations provide a reference and target for restoration efforts and increasing connectivity would minimize the frequency and intensity of additional augmentations and should be adopted more broadly in the planning and management of at-risk populations. For such isolated and small populations, which are typical for translocations not just here but elsewhere, future augmentations and maintaining connectivity through the planning of a recovery network (i.e., a natural metapopulations but emerging from human agency; Smith et al. 2021) is critical to meet the stated goals of increasing genetic diversity and population persistence. This case study highlights the importance of *a priori* assessment of the genetic makeup of translocated individuals and number to release as well as the erosion of genetic diversity to plan future augmentations and identify thresholds for connectivity.

While demographic monitoring post translocation is often emphasized in management plans and is important for short-term persistence (Fig. 1c), genetic diversity will play an important role in long-term persistence. With the increasing application of genomics in conservation, new opportunities are emerging to better assess the genetic benefits and risk from translocations and will be integral in future designs to evaluate sources and evolutionary potential among populations (Forester et al. 2022). In general, conservation practitioners can promote genetic diversity of translocations by 1. Sourcing individuals from a genetically diverse population; 2. Releasing a sufficient number that captures the genetic diversity of the source population; 3. Choosing a reintroduction site with connectivity to neighboring populations in the attempt to create a recovery network; 4. Evaluating the loss of genetic diversity through simulations to guide management plans; 5. Monitoring for genetic diversity following translocation. Translocations are essential tools to mediate the effects of environmental change and conservation practitioners should explicitly incorporate genetic diversity into management plans and evaluate alternative strategies, and ultimately adapt strategies following monitoring that promote the long-term persistence of genetic diversity.

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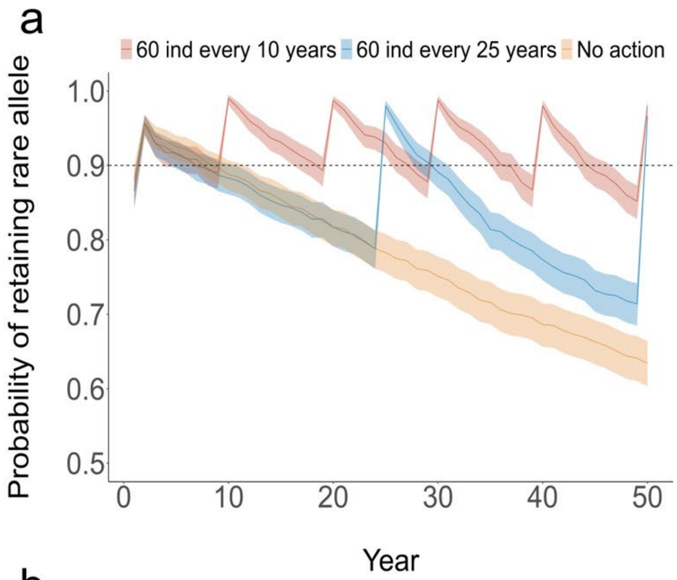
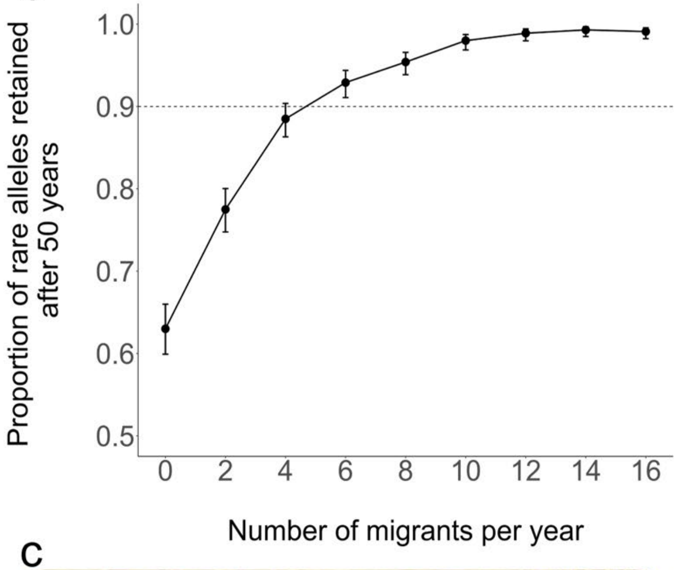
Figure 1: Simulated probability of retaining rare alleles (q = 0.05) following a translocation of sharp-tailed grouse (*Tympanuchus phasianellus*) to northern Wisconsin under different augmentation strategies (a) and dependent on the number of migrants per year (b). Image of sharp-tailed grouse wearing a VHF transmitter after translocation to monitor movement, survival, and habitat use (c).


a
60 ind every 10 years
60 ind every 25 years
No action
Probability of retaining rare allele
1.0
0.9
0.8
0.7
0.6
0.5
0
10
20
30
40
50
Year


b
Proportion of rare alleles retained after 50 years
1.0
0.9
0.8
0.7
0.6
0.5
0
2
4
6
8
10
12
14
16
Number of migrants per year


c