Landscape-mediated niche dynamics in North American carnivores

by

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Dissertation Abstract

Human-dominated landscapes are now ubiquitous, resulting in novel ecosystems with emergent community properties. The loss of predators has been a particularly pervasive consequence of this human expansion, and re-establishing lost trophic interactions is now a global conservation priority. The restoration of mammalian carnivores to modified landscapes has been proposed as a means to both preserve ecosystem functionality and promote biodiversity, but the mechanisms regulating these processes are poorly understood. For example, novel ecosystems provide novel prey and food subsidies that fundamentally alter carnivore foraging and predator-prey relationships, and modified landscapes can restructure niche space and enhance competitive interactions. Thus, ecologists have been unable to predict the functionality of carnivores in novel ecosystems, thereby limiting the potential of carnivore-mediated ecosystem restoration. My dissertation addresses these uncertainties in four chapters.

Chapter 1 assesses the dynamic history of carnivores in Isle Royale National Park and illustrates the impact of human disturbance on even remote carnivore communities. Isle Royale is one of the most pristine, well-studied island ecosystems in the world, yet little is known about the phylogenetic history of its mammals. I used non-invasive genetics and demographic models to show that recently rediscovered American martens (*Martes americana*) were historically extirpated, but naturally recolonized the island via an ice-bridge following a 76-year absence.

Chapter 2 explores the role of landscape composition and configuration in mediating carnivore coexistence. Carnivore restorations often target modified landscapes to restore lost trophic interactions, but land-use change has homogenized forest ecosystems, likely minimizing opportunities for niche partitioning. I used species distribution models to quantify the impact of spatial heterogeneity on the co-occurrence of American martens and fishers (*Pekania pennanti*).

I found that martens and fishers in human-dominated landscapes exhibited high niche overlap, and spatial heterogeneity had negative effects on co-occurrence. Conversely, niche overlap was low in preserved landscapes, and co-occurrence increased significantly with heterogeneity. These findings emphasize the importance of landscape heterogeneity for carnivore coexistence, and illustrate the complexities mediating carnivore restoration to human-dominated landscapes.

Chapter 3 examines the relative impact of exogenous versus endogenous drivers of carnivore foraging and functionality. Carnivore-mediated ecological restoration hinges on the transference of top-down forcing across ecosystems, but the retention of foraging characteristics – Eltonian niche conservatism – has received limited attention. I developed a novel stable isotope framework to quantify Eltonian niche conservatism and compared foraging plasticity in closely related carnivore species across a range of community and ecosystem contexts. I detected little niche conservatism, even among closely related carnivores in comparable landscapes. These results emphasize the context dependent nature of consumptive effects and suggest carnivore foraging and functionality are dynamic.

Lastly, Chapter 4 quantifies the impact of human-dominated landscapes on carnivore foraging and trophic structure. Human disturbance, including food subsidies, can fundamentally alter trophic interactions and dietary niches. Such dietary niche shifts have significant potential to increase niche overlap, competition, and interspecific killing in carnivore communities. I used stable isotope analyses to quantify resource consumption and trophic partitioning in 7 carnivore communities across a gradient of human disturbance. I found that consumption of human food subsidies, trophic niche width, and trophic niche overlap all increased with human disturbance. These results indicate that humans fundamentally alter resource niches and competitive overlap, likely destabilizing predator-prey interactions and carnivore coexistence in the Anthropocene.

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Dynamic colonization history in a rediscovered Isle Royale carnivore

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Abstract

Island ecosystems are globally threatened, and efforts to restore historical communities are widespread. Such conservation efforts should be informed by accurate assessments of historical community composition to establish appropriate restoration targets. Isle Royale National Park is one of the most researched island ecosystems in the world, yet little is actually known about the biogeographic history of most Isle Royale taxa. To address this uncertainty and inform restoration targets, we determined the phylogeographic history of American martens (*Martes americana*), a species rediscovered on Isle Royale 76 years after presumed extirpation. We characterized the genetic composition of martens throughout the Great Lakes region using nuclear and mitochondrial markers, identified the source of Isle Royale martens using genetic structure analyses, and used demographic bottleneck tests to test 3 competing colonization scenarios. Martens exhibited significant structure regionally, including a distinct Isle Royale cluster, but mitochondrial sequences revealed no monophyletic clades or evolutionarily significant units. Rather, martens were historically extirpated and recolonized Isle Royale from neighbouring Ontario, Canada in the late 20th century. These findings illustrate the underappreciated dynamics of island communities, underscore the importance of historical biogeography for establishing restoration baselines, and provide optimism for extirpated and declining Isle Royale vertebrates whose reintroductions have been widely debated.

Introduction

Island ecosystems, and the unique taxa they feature, have fascinated biologists since the inception of ecology and evolution (von Humboldt & Bonpland 1807; Darwin 1859; Wallace 1880). Due to their seeming simplicity, islands are often useful models to understand ecological interactions (Macarthur & Wilson 1963; McLaren & Peterson 1994) and the evolutionary histories of regional taxa (Cook *et al.* 2001). Moreover, islands have served as refugia in the face of global change throughout history (Fleming & Cook 2002; Graham *et al.* 2016), often resulting in endemic species or unique genetic lineages due to long-term isolation (Kier *et al.* 2009). Yet, contemporarily, islands are some of the most altered ecosystems (Wood *et al.* 2017) and are regularly subject to introduced species (Bellard *et al.* 2017), novel diseases (Wilmers *et al.* 2006), and overexploitation (Holdaway 2000). Consequently, extensive conservation programs have been established to protect island biodiversity (Campbell & Donlan 2005; Jones *et al.* 2016) and to restore departed island communities (Courchamp, Woodroffe & Roemer 2003; Hunter & Gibbs 2014). Historical community composition, though, is not always clear, leading to ambiguous restoration baselines and the potential mismanagement of native and invasive species (Pauli *et al.* 2015; West *et al.* 2017).

Isle Royale National Park is an isolated archipelago in the western reaches of Lake Superior, USA. A national park since 1931 and a designated wilderness area since 1976, Isle Royale is widely regarded as one of the most pristine island ecosystems in the world (Vucetich, Nelson & Peterson 2012; Radeloff *et al.* 2015). Moreover, Isle Royale is home to the longest running predator-prey study on record, resulting in a comprehensive understanding of wolf (*Canis lupus*)-moose (*Alces alce*s) interactions, and a deeper appreciation for paired population and trophic dynamics (Peterson, Page & Dodge 1984; McLaren & Peterson 1994; Bump, Peterson & Vucetich 2009). Recent declines in wolf abundance have also sparked widespread discussions on conservation ethics, wilderness management, and the restoration of island communities (Gore *et al.* 2011; Vucetich, Nelson & Peterson 2012; Mech *et al.* 2017). Despite this attention, little is actually known about the 17 other mammals that inhabit Isle Royale, and widespread species turnover throughout the 20th century has obscured historical community composition (Cochrane 2013). Indeed, historical assemblages of vertebrates have been constructed entirely from museum surveys and anecdotal accounts (Adams 1909; Mech 1966). Furthermore, lake ice formation, a primary mode of colonization to Isle Royale, has become increasingly stochastic due to regional climatic warming, potentially disrupting historical connectivity to the mainland (Licht *et al.* 2015). Thus, the restoration of Isle Royale fauna is confounded by uncertainties in both historical community composition and future colonization potential (Cochrane 2013). Nevertheless, the reintroduction of Isle Royale carnivores has garnered widespread consideration (Green 2016; Licht, Moen & Romanski 2017) and illuminated the need for *a priori* restoration baselines derived from phylogenetic histories of past and present community members (Cochrane 2013).

Prior to establishment as a National Park, Isle Royale was subject to significant anthropogenic disturbances at the turn of the 20th century that included the extirpation of Canada lynx (*Lynx canadensis*), woodland caribou (*Rangifer tarandus caribou*), and, presumably, American martens (*Martes americana*; hereafter martens) (Johnsson, Shelton & Jordan 1982). Though historically abundant on the island (Adams 1909), martens were valuable furbearers and trapped heavily until 1917 when the last recorded specimen was collected (Foster 1917). Following four decades of presumed absence, the National Park Service initiated a program to reintroduce martens from Ontario, Canada to Isle Royale in 1966; however, the translocation of martens to the island was never documented, though such a release cannot be completely discounted (Romanski & Belant 2008). A quarter century later marten tracks were observed, and in 1993 martens were once again confirmed on Isle Royale (Romanski & Belant 2008). Martens have since remained rare following this apparent 76-year absence, and the origins of this extant population are unknown.

Isle Royale has been isolated *c.* 11,000 years, resulting in unique lineages of several taxa (Kramm, Maki & Glime 1975; Kowal, Judziewicz & Edwards 2011). Like other historical community members (e.g. Isle Royale red squirrels [*Tamiasciurus hudsonicus regalis*]; Kramm, Maki & Glime 1975), martens could constitute an evolutionarily unique population. Throughout the Lake Superior Basin, however, martens have a dynamic history of extirpation and reintroduction that has resulted in a complex configuration of local populations with unique genetic structures (Williams & Scribner 2010; Grauer *et al.* 2017). Indeed, following widespread local extirpations, martens have since been reintroduced to Wisconsin and Michigan from source populations in Minnesota and Ontario, respectively, while Wisconsin also received translocated martens from Colorado now known to be non-native Pacific martens (*Martes caurina*; Dawson & Cook 2012) (Fig. 1a). Consequently, the management of Lake Superior martens, and Isle Royale in particular, is likely complicated by an amalgam of local and introduced lineages throughout the region.

Herein, we identified the source and colonization history of the recently rediscovered marten population on Isle Royale using population genetic and demographic analyses. We explored the phylogenetic history of martens on Isle Royale using nuclear and mitochondrial DNA from biological samples collected across the Lake Superior basin. Given the potential for endemism on Isle Royale and the complex genetic structure of marten populations regionally (Williams & Scribner 2010; Grauer *et al.* 2017), we then assessed the potential for Isle Royale martens as an evolutionarily significant unit (ESU; Moritz 1994, 1999). Finally, we used demographic bottleneck tests to assess three putative colonization scenarios: 1) an historic, presettlement colonization; 2) a successful 1966 reintroduction; and 3) a modern colonization consistent with the timing of rediscovery. Due to their historic prevalence, and the ability of martens to maintain cryptic populations for millennia (Pauli *et al.* 2015), we hypothesized that the extant marten population on Isle Royale stemmed from a historical colonization and presents an endemic evolutionary lineage. We predicted significant structure among nuclear markers, with martens on Isle Royale representing a distinct genetic cluster, and we expected reciprocal monophyly across mtDNA sequences for martens on Isle Royale.

Results

Microsatellite analyses

We genotyped a total of 230 unique individuals across 6 sampled populations of martens (Table 1). Despite isolation, martens on Isle Royale exhibited no evidence of inbreeding; however, allelic richness was considerably lower than all other locations, heterozygosity was the second lowest of all populations, and only 1 unique allele was present. Alternatively, martens from Colorado (i.e., *M. caurina*) exhibited the highest proportion of unique alleles, while martens in Wisconsin revealed high degrees of both allelic richness and private alleles despite being a reintroduced, state endangered species (Manlick *et al.* 2017). All populations exhibited deviations from HWE, and Isle Royale and Wisconsin each exhibited linkage disequilibrium (Table S1, Supporting Information).

Population structure

Across sites, pairwise F_{ST} (0.02-0.40) and G'_{ST} (0.01-0.45) ranged widely, with martens from Isle Royale and Colorado displaying the largest differences (> 0.1) from other populations (Fig. 2a).

Reintroduced populations did not diverge substantially from their source populations, as FCA illustrated 3 distinct population clusters: Colorado, Minnesota-Wisconsin, and Isle Royale-Michigan-Ontario (Fig. 1b). However, FCA revealed fine-scale structure in the latter group with Isle Royale further segregating from Michigan and Ontario martens, suggesting that martens on Isle Royale diverged from the closest geographic population in Ontario (Fig. 1c). AMOVA similarly detected significant structure among sites and indicated fine-scale structure with Isle Royale as a 4th distinct cluster (Table S2, Supporting Information).

Both the Bayesian and multivariate analyses of population structure identified 5 genetic clusters (Table S3, Supporting Information), and both classified martens from Isle Royale and Colorado as genetically unique populations (Fig. 2b,c). Conversely, the reintroduced populations in Michigan and Wisconsin exhibited considerable admixture with their respective source populations, Ontario and Minnesota, but no Lake Superior basin sites exhibited evidence of introduced alleles present in martens from Colorado (i.e., *M. caurina*). Structure analyses were consistent with and without the use of *M. caurina* as an outgroup (Fig. S1, Supporting Information).

mtDNA analyses

We successfully sequenced 137 individuals for the cytochrome *c* oxidase subunit I gene (COI) and 129 individuals for the cytochrome *b* gene (CytB). All sequenced scat samples were confirmed as martens via BLAST. All COI sequences included a section of 12 undetermined sites and were therefore concatenated to 174bp fragments for all subsequent analyses. Haplotype and nucleotide diversity were low to non-existent for COI, as multiple locations exhibited a single haplotype (Table 1). Conversely, CytB exhibited moderate diversity with 25 segregating sites compared to 4 in COI. Minnesota and Ontario martens presented the most CytB haplotypes, however, this relationship was driven by a large number of singletons (Fig. 3). In total, there were no fixed polymorphisms for any Lake Superior martens, and only Colorado martens (i.e., *M. caurina*) exhibited reciprocal monophyly (Fig. 3). Moreover, the majority of martens in the Lake Superior basin, including Isle Royale, were represented by single haplotype for both COI (n=110) and CytB (n=83) (Fig 3).

Demographic analyses

Program MIGRAINE (Leblois *et al.* 2014) detected a significant bottleneck in martens on Isle Royale, with an observed N_{ratio} of 0.0007 and a 95% confidence interval (0.00027-0.11) that did not overlap 1. Further, MIGRAINE estimated an historic effective population size (N_0) of 2947 (1208-14248) and a current effective population (N_1) of 2.05 (2.00 - ∞), resulting in an estimated bottleneck time of 0.50 (0.0041-1.22) generations. Similarly, the loss of heterozygosity test from the source population in Ontario estimated that N_e = 1.94 for Isle Royale martens, while tests in the program LDNe (Waples & Do 2008) estimated effective population sizes of 3.2 (2.2-7.6) and 257 (53-∞) for Isle Royale and Ontario, respectively.

Discussion

Martens on Isle Royale exhibited considerable differentiation in nuclear markers from other regional marten populations, but mitochondrial sequences revealed no reciprocally monophyletic marten lineages within the Lake Superior Basin. Rather, martens from Isle Royale overwhelmingly shared mtDNA haplotypes with other populations. Thus, contrary to our hypothesis and despite significant population structure in nuclear markers across the region, we found no evidence of ESUs in martens of the Lake Superior Basin. This incongruity between nuclear and mitochondrial analyses indicates that while extant martens on Isle Royale are a distinct and isolated population, their colonization of the island was recent. Demographic analyses confirmed that martens on Isle Royale were subject to a recent population change and detected a significant bottleneck. Moreover, all demographic analyses showed that martens on Isle Royale are a small cohort ($N_e \cong 2$) that derived from a much larger population of several hundred to thousands of individuals. This is consistent with our structure analyses showing that martens on Isle Royale were most closely related to individuals in Ontario, which is home to a large, panmictic marten population (Kyle & Strobeck 2003). Thus, we conclude that the rediscovered marten population on Isle Royale stemmed from a recent but cryptic colonization via mainland Ontario. Any apparent genetic differentiation in nuclear markers is likely the result of founder effects, and the low allelic richness, limited number of unique alleles, and reduced heterozygosity of Isle Royale relative to Ontario support this conclusion. Given the estimated effective population size of approximately 2 individuals, contemporary Isle Royale martens were likely founded by a pair of colonizing individuals or a fertilized female.

Assuming the extant marten population on Isle Royale was founded contemporarily by way of Ontario, we tested three plausible colonization scenarios. Given the low mutation rates of CytB and COI in vertebrates (Bradley & Baker 2001; Lavinia *et al.* 2016), it is possible that martens colonized Isle Royale within the last several hundred years and persisted undetected for much of the 20th century (Pauli *et al.* 2015). Secondly, martens could have been reintroduced to Isle Royale from Ontario *c.* 1966, again going undetected for several decades (Romanski & Belant 2008). Lastly, martens could have colonized Isle Royale in the late 20th century via Ontario, the closest mainland (35 km), possibly using an ice bridge across Lake Superior, as has occurred for other Isle Royale carnivores (Hedrick *et al.* 2014; Licht *et al.* 2015). Our MIGRAINE estimates indicate martens on Isle Royale experienced a significant bottleneck within the last generation (i.e. 5 years). While we know that extant martens have occupied Isle Royale for approximately 25 years (Romanski & Belant 2008), samples used in this analysis were primarily collected from 2006-2009, putting the timing of colonization within a decade of marten rediscovery. This estimate is consistent with our other analyses that suggest martens colonized Isle Royale recently and are still recovering from a significant population bottleneck. Moreover, given the prevalence of ecological research on Isle Royale in the 20th century(Mech 1966; Peterson 1995) it seems unlikely that martens would have gone undetected for decades following an earlier colonization event like the potential 1966 reintroduction. Thus, we postulate that martens were historically extirpated from Isle Royale but recolonized the island around the time of their rediscovery, *c.* 1991. Historical ice data shows numerous ice bridges connected Isle Royale to mainland Ontario in the 10 years preceding marten rediscovery (Licht *et al.* 2015), thereby making a natural colonization possible. It is worth noting, however, that martens are the most widely translocated carnivore in North America (Powell, Lewis & Slough 2012) and have a history of human-assisted island colonization – both sanctioned and unsanctioned (Pauli *et al.* 2015). Thus, human-assisted dispersal of martens to Isle Royale around the time of rediscovery cannot be precluded.

National Park Service policy aims to restore historical communities and ecosystem processes where appropriate, and the mammal community on Isle Royale appears to be an ideal candidate for reintroductions due to significant turnover in the last century (Licht, Moen & Romanski 2017). For instance, wolves, coyotes (*Canis latrans*), and martens have all colonized the island, while Canada lynx, coyotes, and martens were also extirpated at one point or another

(Mech 1966). The dominant herbivore, woodland caribou, was replaced by moose, and white-tailed deer (*Odocoileus virginianus*) were introduced but quickly extirpated. In addition, beavers (*Castor canadensis*) recolonized Isle Royale after apparent extirpation in the 19th century (Tanner & James 1830; Mech 1966), and foxes were likely introduced for fur farming (Rakestraw 1965; Mech 1966). This dynamic history of colonization and extinction in an ecosystem that has been protected for most of the last century complicates the baseline for restoring historical Isle Royale communities and interactions. Moreover, such dynamics, coupled with the lack of historical and prehistorical information regarding past Isle Royale communities, has precipitated questions about the necessity of reintroducing or augmenting mammal populations on the island (Cochrane 2013). Our data suggests that martens, one of the smaller mammals on Isle Royale, were historically extirpated but recolonized the island. Dispersal ability in mammals is strongly correlated with body mass (Sutherland *et al.* 2000), indicating that if martens did indeed immigrate to Isle Royale naturally, they were less likely to do so than other, larger-bodied carnivores. Moreover, ice bridges generally do not form until January (Assel 2003, 2005), months after the natal dispersal period in martens, and dispersal success is largely a function of available cover (Johnson *et al.* 2009), none of which is present over ice. Thus, if martens did naturally recolonize Isle Royale despite such barriers, the natural repatriation of larger carnivores may also be possible.

The frequency of ice bridges connecting Isle Royale to the mainland is decreasing due to climate change, thereby reducing the probability of natural immigration to the island for many species (Licht *et al.* 2015). This loss of gene flow will ultimately reduce genetic diversity in Isle Royale mammal populations, the effects of which are already evident in wolves (Räikkönen *et al.* 2009). Consequently, population augmentation will likely be necessary to maintain genetic diversity in most extant Isle Royale community members (i.e., genetic rescue; Hedrick *et al.* 2014) and for any potentially reintroduced species(Licht *et al.* 2015). It is therefore critical to understand the current genetic composition of other Isle Royale mammal populations in order to preserve potential endemic lineages or local adaptations (Frankham *et al.* 2011; Waller 2015), and to identify sources for potential translocations. We conducted the most thorough evolutionary assessment of an historical Isle Royale mammal to date and found that extant martens do not constitute a unique genetic lineage and could ultimately be augmented from a number of marten populations in the Lake Superior Basin with which they share haplotypes, though Ontario was identified as the most closely related population. Regardless, martens on Isle Royale possess reasonably high heterozygosity and maintain low inbreeding coefficients despite a significant bottleneck, indicating that direct genetic management is currently unnecessary. Previous studies, however, found that other Isle Royale mammals like red squirrels and deer mice (*Peromyscus maniculatus*) also appear unique, but these divergences have only been described morphologically (Kramm, Maki & Glime 1975) and via random amplifications of polymorphic DNA (RAPD; Vucetich *et al.* 2001), respectively. Our results show that population bottlenecks and founder effects can generate such putatively unique lineages, despite only recent divergence; thus, without a more complete assessment of evolutionary history, future management of these potentially endemic populations is uncertain. Furthermore, both red squirrels and deer mice, along with other Isle Royale mammals like snowshoe hares (*Lepus americanus*), have limited dispersal capabilities (Bowman, Jaeger & Fahrig 2002), and more thorough genetic assessments of these populations are needed to assess colonization, historical community baselines, and the potential for human-assisted dispersal.

Conclusions

Isle Royale National Park is a notable wilderness area with a pristine reputation and a storied history of ecological research. Yet, like many systems, Isle Royale has experienced significant anthropogenic change, and has a dynamic history of species colonization and extinction. Consequently, very little is known about the history of the island's vertebrate community as a whole. Our study revealed an unexpected and dynamic pattern of extinction and recolonization for a small-bodied carnivore and illustrates that even federally protected or historically pristine ecosystems have experienced more community turnover than previously appreciated. Given that anthropogenic disturbances have driven the turnover of fauna globally, identifying the biogeographic origins of extant species and documenting historical community composition are critical guideposts to establishing restoration baselines (Rick *et al.* 2014) and effectively managing both native and non-native species (Pauli *et al.* 2015; West *et al.* 2017). Our work also illustrates the importance of continued regional monitoring, the relevancy of historical surveys, and the need for genetic techniques to establish robust and defensible conservation targets. While often difficult to obtain, the combination of these approaches has proved particularly useful (Pauli *et al.* 2015), so we emphasize the importance of multiple, interdisciplinary stakeholders when establishing conservation and restoration programs. Finally, our findings show that martens, one of the least likely island colonizers, repatriated Isle Royale following extirpation, providing optimism for the natural recolonization of other extirpated or declining carnivore populations. Moreover, given that restoration initiatives often center around charismatic megafauna – species that generally possess the greatest dispersal power – conservationists are likely underrepresenting the natural colonization potential for most other taxa. Thus, future efforts aiming to re-establish island communities should first assess the colonization histories of smaller, more dispersal limited species, to inform and evaluate restoration efforts *a proiri*.

Methods

Sample collection and microsatellite analyses

To identify the source and colonization history of martens to Isle Royale, and to assess ESUs for the martens across the Lake Superior Basin, we analyzed biological samples from three distinct biogeographical regions (Fig. 1a). First, we collected scat samples on hiking trails across Isle Royale during summers from 2006-2008 and 2012-2013. Scats collected from 2006-2008 were stored in conical centrifuge tubes containing 95% ethanol and later dried, while scats from 2012-2013 were swabbed *a priori* using a cotton-tipped applicator to collect epithelial cells. We extracted DNA from all samples using commercially available kits (QIAGEN, Valencia, CA). Samples from 2006-2008 were identified as martens by Wildlife Genetics International (WGI; Nelson, BC, Canada) via sequencing of the 16S rRNA gene (Johnson & O'Brien 1997), while samples from 2012-2013 were identified using fragment analysis of control region segments (De Barba *et al.* 2014). Second, we sampled populations of martens on the mainland surrounding Lake Superior to capture regional genetic diversity and potential sources to Isle Royale. Specifically, we used existing genotypes from hair, scat, and tissue samples to characterize the reintroduced marten population in the Chequamegon National Forest of Wisconsin and existing genotypes from tissue samples to characterize its source population in the Superior National Forest of Minnesota (Fig. 1a) (Manlick *et al.* 2017). We then used muscle tissue from trapper harvested martens to characterize the reintroduced marten population in the Upper Peninsula of Michigan, as well as its source population in Ontario (Fig. 1a). Lastly, we used Pacific marten

(*Martes caurina*) muscle tissue from Colorado (Grauer *et al.* 2017) as an outgroup population to characterize the relative genetic diversity of martens in the Lake Superior basin and to assess the potential introduction of non-native alleles to the region. All sampling was approved by the University of Wisconsin Animal Care and Use Committee (A005239-A01) and conducted ethically under the guidelines established by the American Society of mammalogists(Sikes 2016).

We used a set of 14 polymorphic microsatellite loci to genotype samples, including Ma1, Ma2, Ma5, Ma7, Ma8, Ma11, Ma14, Ma19, Gg3, Gg7, and Tt4(Davis & Strobeck 1998), as well as Mer022, Mer041, and Mvis072 (Fleming, Ostrander & Cook 2002). Polymerase chain reactions were conducted following Manlick *et al.* (2017) analyzed on an ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, CA, U.S.A.), and scored using GeneMapper® (Applied Biosystems, V. 5.0). All samples were independently genotyped in duplicate to minimize potential genotyping errors (Taberlet *et al.* 1996), and genotypes in disagreement were successively re-scored via independent PCRs until genotypes could be confirmed or the sample was consumed. All unresolved scores (i.e. mismatching) were censored at the locus in question, and genotypes were screened for potential allelic dropout and null alleles in program CERVUS (Kalinowski, Taper & Marshall 2007) throughout the scoring process. We calculated an overall genotyping error rate of 0.066. Genotypes were combined across studies (Grauer *et al.* 2017; Manlick *et al.* 2017), therefore the number of loci analyzed varied by site (Table 1); however, sites limited to 8 or 9 loci contained the most polymorphic markers (Table S1, Supporting Information). Moreover, given the sensitivity of downstream analyses to missing data (e.g., multivariate analyses), all samples that failed to amplify at a minimum of 7 loci (50% genotyped) were discarded (Sackett *et al.* 2014).

Because all Isle Royale and some Wisconsin samples were collected noninvasively (see Manlick *et al.* 2017), we identified unique individuals prior to population genetic analyses. We used all available samples to first generate a genotype accumulation curve in the R package *poppr* (Kamvar, Brooks & Grünwald 2015) and, consistent with our genotyping procedure, determined that ≥ 7 markers were needed to identify unique individuals (Fig. S2, Supporting Information). We then performed an identity test across all samples using a maximum probability of identity threshold of 0.05 and the conservative estimator $P_{(ID)sib}$ in program CERVUS (Marshall *et al.* 1998; Kalinowski, Taper & Marshall 2007). All samples with $P_{(ID)sib} > 0.05$ were assumed to be the same individual and we consolidated them to a single multilocus genotype. Once samples were reduced to unique individuals, we tested all populations for deviations from Hardy-Weinberg Equilibrium (HWE) in *poppr* using permutation tests with 1000 iterations (Kamvar, Brooks & Grünwald 2015), and we assessed linkage disequilibrium in Genepop (Rousset 2008) using a sequential Bonferroni correction. Population metrics including observed and expected heterozygosity, allelic richness, private alleles, and inbreeding coefficients were calculated using the R packages *diversity* (Keenan *et al.* 2013) and *PopGenKit* (Paquette 2012).

Population structure

We quantified genetic structure between sampled populations by first calculating pairwise F_{ST} and the standardized metric G'_{ST} (Hedrick 2005) with 95% confidence intervals using 1000 permutations in *diversity* (Keenan *et al.* 2013). We then performed a three-dimensional factorial correspondence analysis (FCA) in GENETIX v. 4.05 (Belkhir *et al.* 2004) to capture variation among individuals and we visually identified population clusters. Finally, we implemented a series of hierarchical AMOVAs (Excoffier, Smouse & Quattro 1992) in *poppr* to first test for significant population structure when considering each sampled population separately, and then to explore the amount of variance explained by combining clustered populations identified via FCA.

To quantitatively assign individuals to genetic clusters and estimate the number of unique marten populations (*K*) within the Lake Superior basin we employed Bayesian clustering models in STRUCTURAMA 2.0 (Huelsenbeck, Andolfatto & Huelsenbeck 2011). Unlike most clustering algorithms, STRUCTURAMA does not assume a fixed number of populations and instead makes *K* a random variable to estimate the number of populations under a given Dirichlet process prior, the mean expected number of populations *E(K)*. We ran seven variations of this model with a prior *E(K)* ranging from 2 to 8 populations to test the sensitivity of model results to prior distributions. All models used a single MCMC chain with 10^6 generations sampled every 1,000 steps and an additional 10% burn-in. Using the estimated *K* that maximized likelihood, we then employed the classic Pritchard *et al.* (2000) model with admixture and correlated allele frequencies for 10^5 iterations with a 10% burn-in to assign individuals to genetic clusters.

Bayesian clustering models assume populations are in HWE and assign individuals to clusters that minimize disequilibrium; however, not all populations we analysed were in HWE (Table S1, Supporting Information; Manlick *et al.* 2017). To account for this, we also employed a discriminant analysis of principle components (DAPC) in the r package *adegenet* (Jombart 2008; Jombart, Devillard & Balloux 2010) to assign individuals to populations. DAPC is a multivariate statistical approach that does not assume HWE, but instead transforms genotypic data to principle components and assigns individuals to populations by maximizing variation between genetic clusters (see Jombart *et al.* 2010 for details). We calculated the number of principle components (*N*=12) via alpha-score optimization, identified the number of populations using *K*-means clustering and Bayesian Information Criterion, and then used DAPC to generate assignment probabilities for all individuals (Jombart, Devillard & Balloux 2010; Jombart 2012). Genetic structure diagrams were constructed for both the DAPC and STRUCTURAMA results and plotted using the R package *strataG* (Archer, Adams & Schneiders 2016).

Mitochondrial sequence analyses

To identify potential evolutionarily significant units and further quantify genetic variation among marten populations in the Lake Superior Basin, we amplified and sequenced fragments of the cytochrome *b* (CytB) and cytochrome *c* oxidase subunit I (COI) mtDNA genes. We sequenced all unique Isle Royale individuals and 20 randomly chosen individuals from each mainland population. All mainland samples were restricted to high-quality tissue samples; however, individuals from Isle Royale were identified from scat samples that also included potential prey DNA, thereby precluding the use of generalized mtDNA primers previously used to characterize martens (Stone, Flynn & Cook 2002). Consequently, we developed marten-specific primers and amplified a 370bp fragment of CytB and a 186bp fragment of COI (Methods S1, Table S4, Supporting Information). All PCR reactions used 3ul of template, 1uM of forward and reverse primers, 0.25 mM dNTPs, 200µM 10x Qiagen PCR buffer, additional $MgCl_2$ for total of 2.5mM, 2 mg/mL of BSA, and 5 units taq/µL. PCR conditions used an initial denature of 95°C for 3 min, followed by 40 cycles of 94°C for 30 s, 51°C for 20 s, and 72°C for 45 s, and finished with a final elongation of 72°C for 10 min. Fragments were sequenced in both the 5′ and 3′ directions on an ABI 3730xl capillary sequencer, chromatograms were visualized and cleaned using MEGA 7.0 (Kumar, Stecher & Tamura 2016), and sequences were aligned within MEGA 7.0 using the

MUSCLE algorithm (Edgar, Drive & Valley 2004). Sequences from martens sampled on Isle Royale (i.e., scat) were then entered into a GenBank nucleotide BLAST search to confirm species identity. All sequences were deposited in GenBank (accession nos. MH684021-MH684285).

We calculated haplotype and nucleotide diversity for CytB and COI in all sampled populations using the program POPART (Leigh & Bryant 2015). We then combined data for all samples successfully sequenced across both genes and assessed relatedness and monophyly among marten populations using a median-joining network developed in POPART.

Historical demography

To estimate the timing of colonization we assessed the demographic history of Isle Royale martens by characterizing temporal changes in effective population size using the single population with variable size (OnePopVarSize) model in program MIGRAINE v. 0.5.2 (Leblois *et al.* 2014). Migraine employs a class of importance sampling algorithms and a generalized stepwise-mutation model (GSM) for microsatellite loci to generate point estimates and 95% coverage confidence intervals for the scaled parameters ancestral population size ($2\theta = 2N_0\mu$), current population size ($2\theta = 2N_1\mu$), and time of the demographic change in generations ($T = T/2N_1$). Using these parameters, ancestral (N_0) and current (N_1) effective population sizes were estimated assuming a marten microsatellite mutation rate ($\mu = 3 \times 10^{-4}$)(Pauli *et al.* 2015) and then used to solve for T. We estimated an additional parameter, N_{ratio} (N_1/N_0), to quantify historical population expansion (>1) or contraction (<1), with significant demographic changes identified by estimates with 95% confidence intervals that did not overlap 1(Leblois *et al.* 2014). Because MIGRAINE is sensitive to the number of loci used (Leblois *et al.* 2014), we combined the aforementioned Isle Royale marten genotypes with additional loci independently genotyped by WGI for individual assignment for a previous study. Specifically, we used 27 individuals sampled on Isle Royale from 2006-2008 and combined 9 polymorphic loci used for structure analyses with 9 unique WGI loci for a total of 18 markers (Table S5, Supporting Information). All models were run using 3 replicates of 2000 points, with 3000 runs per point.

To further assess demographic variation of martens on Isle Royale we estimated the current effective population size (N_e) based on the loss of heterozygosity (Nei, Maruyama & R. Chakraborty 1975) and linkage disequilibrium (Waples & Do 2008). Given that the timing of colonization is not known, we employed a simplified loss of heterozygosity model and estimated N_e following $H_1 = H_0\left(1 - \frac{1}{2N_e}\right)$, where H_1 was the observed heterozygosity of the identified source population and H_0 was the observed heterozygosity of the Isle Royale population (Nei, Maruyama & R. Chakraborty 1975). Secondly, we used the linkage disequilibrium-based estimator of N_e in the program LDNe (Waples & Do 2008) to estimate effective population sizes for the source and Isle Royale populations. This approach assumes discrete generations and therefore cannot estimate N_e directly; thus we interpreted LDNe results as an estimate of the breeding population size (Robinson & Moyer 2013). We applied a random mating model, used the conservative, unbiased threshold of 0.05 for lowest allele frequency (P_{crit}; Waples & Do 2008, 2010), and calculated 95% CIs via permutation tests.

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Data availability

All data are available through the Dryad Digital Repository (doi:10.5061/dryad.m58q16m) and sequence data is available through GenBank (accession nos. MH684021- MH684285). All samples are housed in perpetuity at -80°C at the University of Wisconsin-Madison.

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Tables

Table 1. Diversity of 14 microsatellite loci and 2 mtDNA genes used to characterize American martens (*Martes americana*) across 5 Lake Superior basin sites and Colorado (*Martes caurina*, introduced to northern Wisconsin). Number of individuals genotyped (*N*), maximum number of loci genotyped (*L*), allelic richness (*Ra*), proportion of private alleles (*Pa*), observed heterozygosity (H_{Obs}), and Fisher's inbreeding coefficient (F_{IS}) were calculated for microsatellites, while number of individuals sequenced (*N*), number of haplotypes (*H*), haplotype diversity (*Hd*), and nucleotide diversity (π) were calculated for the cytochrome *b* (COI) and cytochrome *c* oxidase subunit I (CytB) sequences.

	Microsatellite diversity						COI (174bp)				CytB (370bp)			
Location	*N*	*L*	*Ra*	*Pa* (%)	H_{Obs}	F_{IS}	*N*	*H*	*Hd*	π	*N*	*H*	*Hd*	π
Colorado	29	9	5.33	32.65	0.45	0.13	20	2	0.44	0.003	20	3	0.42	0.002
Isle Royale	27	9	3.67	3.03	0.52	-0.02	39	1	0.00	0.00	31	3	0.13	0.0004
Michigan	30	8	5.73	0.00	0.67	-0.01	20	1	0.00	0.00	20	3	0.35	0.001
Minnesota	64	14	5.53	10.99	0.56	0.13	20	1	0.00	0.00	20	4	0.44	0.002
Ontario	30	8	6.28	0.00	0.70	-0.01	20	2	0.10	0.0006	20	7	0.64	0.004
Wisconsin	50	14	6.26	18.81	0.55	0.17	17	2	0.49	0.003	18	2	0.29	0.003

Figures

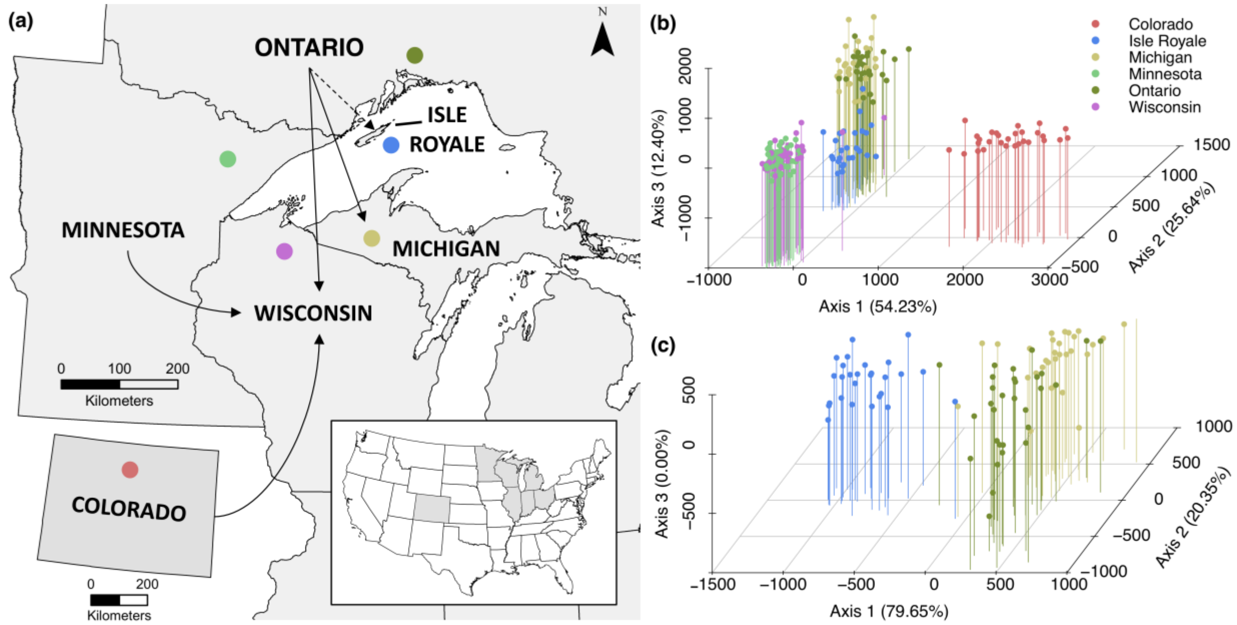

Figure 1. (a) Distribution of sampled sites in the Lake Superior basin, and the location of historical reintroductions (solid lines) as well as the potential reintroduction of martens to Isle Royale in 1966 (dashed line). Points and colours correspond to sampling locations and population clusters identified using factorial correspondence analysis (FCA) of microsatellite loci across all sites (b). Fine scale structure was detected, with Isle Royale segregating from Michigan and Ontario martens (c).

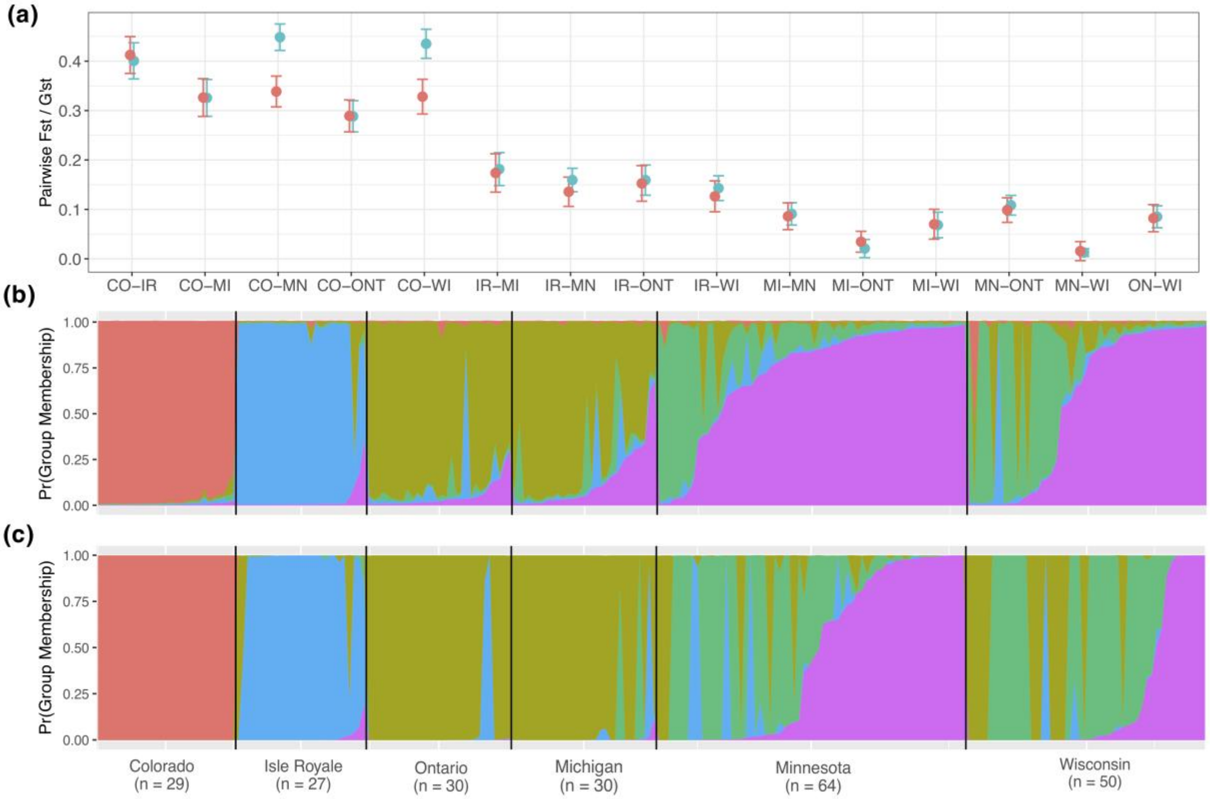

Figure 2. Population structure among microsatellites identified via pairwise F_{ST} (red) and G'_{ST} (blue) (a), Bayesian STRUCTURAMA analyses (b), and discriminant analysis of principle components (c). All methods identified Colorado (CO) and Isle Royale (IR) martens as distinct genetic clusters, while Michigan (MI), Minnesota (MN), Ontario (ONT), and Wisconsin (WI) exhibited more admixture.

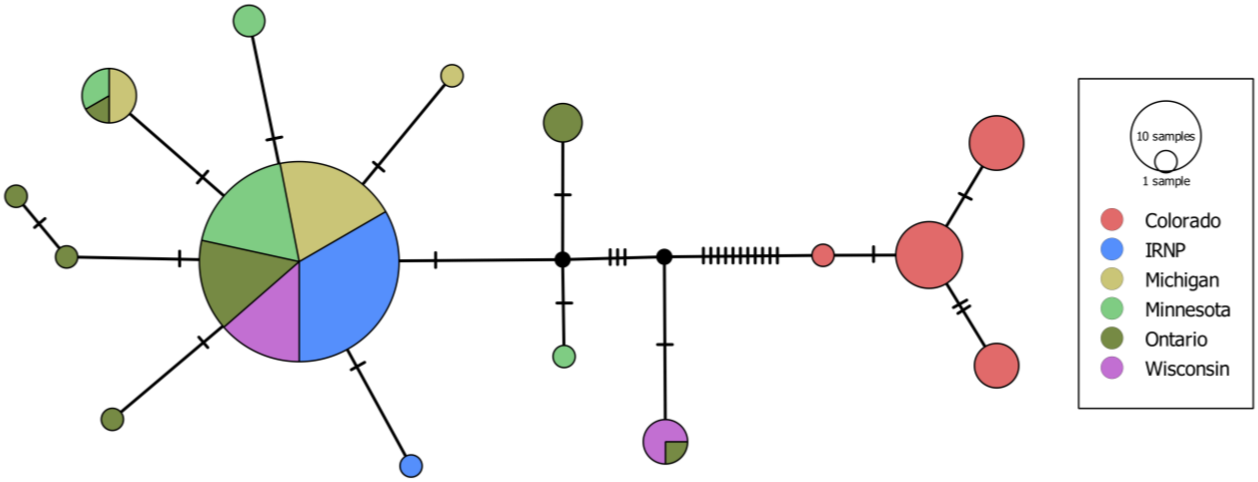

Figure 3. Median joining network for combined CytB and COI sequences. Tick marks indicate single nucleotide mutations. Colorado martens (*M. caurina*) were the only monophyletic group and Isle Royale (IRNP) was not distinct.

Supplementary Information

Methods S1, Table S1-S5, Figures S1-S2

Methods S1.

To develop marten-specific primers we first accessed complete 1140bp CytB American marten (*Martes americana*) sequences from Stone et al. (2002) and 600-658bp COI marten fragments from the Barcode of Life initiative (Adamowicz 2015). To account for prey sequences potentially present in marten scats we also accessed complete 1140bp CytB sequences for 50 deer mice (*Peromyscus maniculatus*), 50 red squirrels (*Tamiasciurus hudsonicus*), 5 snowshoe hares (*Lepus americanus*), and 8 moose (*Alces alces*), and we also used 600-658bp COI fragments from 20 deer mice, 20 red squirrels, 1 snowshoe hare, and 2 moose. All sequences were accessed via GenBank and aligned using the MUSCLE algorithm in MEGA7. For each gene, we used the program Primaclade (Gadberry et al. 2005) to identify conserved sequence pairs for marten primers. We then cross-checked all primer motifs with prey sequences and identified 2 primer pairs for each gene that minimized sequence overlap among martens and prey, particularly at the 3’ end. For all primers we assessed hairpins and self-dimers via OligoAnalyzer v. 3.1 (Integrated DNA Technologies), and then used Primer3 v. 0.4.0 (Untergasser et al. 2012) to confirm that primers matched known marten sequences. We then extracted DNA from 2 deer mice, 2 red squirrels, and 1 snowshoe hare collected by Carlson et al. (2014) and ran PCRs for all putative marten-specific primer pairs to test for cross amplification. PCR products were assessed via gel electrophoresis and primer pairs with the least non-specific amplification were selected for marten sequencing (Table S2).

Table S1. Summary of samples (N), number of alleles (k), polymorphic information content (PIC), observed heterozygosity (Ho), and expected heterozygosity (He) for all loci across sampled populations. Summary statistics in **bold** indicate loci that deviated from Hardy-Weinberg Equilibrium (α = 0.05) and statistics in *italics* indicate loci that exhibited linkage disequilibrium (α = 0.05; sequential Bonferroni correction).

	Summary (All)			Colorado			Isle Royale			Michigan			Minnesota			Ontario			Wisconsin		
Loci	N	k	PIC	k	Ho	He	k	Ho	He	k	Ho	He	k	Ho	He	k	Ho	He	k	Ho	He
Gg3	229	10	0.62	2	0.07	0.07	2	0.29	0.25	6	0.50	0.54	**8**	**0.56**	**0.65**	6	0.77	0.71	*8*	*0.60*	*0.59*
Gg7	229	9	0.77	**6**	**0.41**	**0.68**	4	0.36	0.32	6	0.77	0.73	8	0.70	0.79	7	0.80	0.80	*6*	*0.69*	*0.76*
Ma1	127	21	0.87	**10**	**0.74**	**0.79**	-	-	-	-	-	-	**10**	**0.70**	**0.83**	-	-	-	14	0.81	0.86
Ma11	201	7	0.54	-	-	-	2	0.50	0.50	3	0.40	0.39	5	0.52	0.60	2	0.31	0.27	***3***	***0.29***	***0.55***
Ma14	222	11	0.75	**6**	**0.54**	**0.71**	*4*	*0.63*	*0.75*	7	0.86	0.74	**7**	**0.57**	**0.67**	6	0.60	0.69	***7***	***0.55***	***0.68***
Ma19	97	5	0.71	-	-	-	-	-	-	-	-	-	5	0.71	0.77	-	-	-	*5*	*0.68*	*0.74*
Ma2	225	8	0.75	7	0.69	0.79	*4*	*0.69*	*0.70*	5	0.83	0.79	6	0.68	0.73	6	0.76	0.79	*7*	*0.71*	*0.73*
Ma5	219	11	0.77	7	0.66	0.61	6	0.62	0.67	5	0.60	0.70	**7**	**0.63**	**0.74**	**7**	**0.73**	**0.82**	6	0.77	0.73
Ma7	132	7	0.38	-	-	-	**3**	**0.33**	**0.35**	-	-	-	**4**	**0.36**	**0.41**	-	-	-	**6**	**0.28**	**0.43**
Ma8	193	10	0.77	-	-	-	*5*	*0.85*	*0.75*	**6**	**0.57**	**0.69**	**7**	**0.68**	**0.75**	7	0.80	0.83	8	0.70	0.80
Mer022	94	12	0.54	-	-	-	-	-	-	-	-	-	5	0.53	0.52	-	-	-	***7***	***0.41***	***0.60***
Mer041	140	7	0.50	4	0.29	0.57	-	-	-	-	-	-	4	0.38	0.46	-	-	-	***6***	***0.50***	***0.55***
Mvis072	225	21	0.76	4	0.30	0.39	3	0.40	0.46	9	0.87	0.82	11	0.72	0.73	10	0.87	0.83	***13***	***0.65***	***0.78***
Tt4	143	8	0.40	3	0.35	0.30	-	-	-	-	-	-	**4**	**0.05**	**0.11**	-	-	-	***5***	***0.08***	***0.20***
Overall	229	147	0.65	5.4	0.45	0.55	3.7	0.52	0.53	5.9	0.68	0.68	6.5	0.56	0.63	6.4	0.71	0.72	7.2	0.55	0.64

Table S2. Analysis of molecular variance (AMOVA) results quantifying percentage of variation explained by population clusters (n) identified using factorial correspondence analysis. All results were significant ($p<0.001$).

Covariance explained (%)	[1]Independent (n=6)	[2]FCA clusters (n=3)	[3]Isle Royale (n=4)
Between sites	9.00	9.06	10.47
Within sites	9.25	10.83	9.36
Within Samples	81.75	80.10	80.17

[1] All sites independent
[2] FCA clusters: Colorado, Isle Royale-Michigan-Ontario, and Minnesota-Wisconsin
[3] FCA clusters with Isle Royale separate: Colorado, Isle Royale, Michigan-Ontario, Minnesota-Wisconsin

Table S3. Assignment probabilities and likelihood of genetic clusters derived from STRUCTURAMA analysis of 6 marten populations in the Lake Superior basin and Colorado. Models were assigned prior probabilities ranging from 2 expected clusters [E(K) = 2] to 8 expected clusters [E(K) = 2]. Bold numbers indicate highest probability for each model and model with maximum likelihood. All but one model estimated 5 genetic clusters.

Clusters (K)	E(K) = 2	E(K) = 3	E(K) = 4	E(K) = 5	E(K) = 6	E(K) = 7	E(K) = 8
2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.22	0.05	0.01	0.00	0.01	0.00	0.00
4	**0.51**	0.36	0.24	0.16	0.15	0.09	0.08
5	0.25	**0.52**	**0.62**	**0.65**	**0.62**	**0.42**	**0.58**
6	0.01	0.07	0.12	0.18	0.22	0.41	0.32
7	0.00	0.00	0.00	0.01	0.01	0.08	0.02
8	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Likelihood	-5997.9	-5770.9	-5469.3	-5456.6	-5750.9	**-5441.0**	-5446.6

Table S4. Primers used to amplify CytB and COI fragments from marten scat.

Primer	Sequence (5’ to 3’)
Cytb_370F	CTTTTGAGGTGCGACCGTA
CytB_370R	GCGGAATATCATGCCTCG
COI_186F	ATAATTGGGGGCTTCGGA
COI_186R	CACTGGCAGGGATAAGAGTAGAA

Table S5. Summary of additional loci employed by WGI to genotype Isle Royale martens and used in MIGRAINE models.

†Locus	*N*	Alleles	H_O	H_E	PIC
Ma2	33	4	0.67	0.74	0.68
Ma7	33	2	0.36	0.34	0.28
Ma9	33	1	0.00	0.00	0.00
Ma10	33	3	0.64	0.68	0.59
Ma18	33	5	0.67	0.64	0.56
MP0055	33	3	0.55	0.58	0.49
MP0059	33	3	0.64	0.64	0.55
MP0085	33	3	0.64	0.51	0.39
MP0114	33	1	0.00	0.00	0.00
MP0175	13	1	0.00	0.00	0.00
MP0197	33	4	0.73	0.73	0.67
Mean	33	2.72	0.44	0.44	0.38

†Locus = microsatellite loci; *N* = sample size; Alleles = number of alleles detected; H_O = observed heterozygosity; H_E = expected heterozygosity; PIC = polymorphic information content

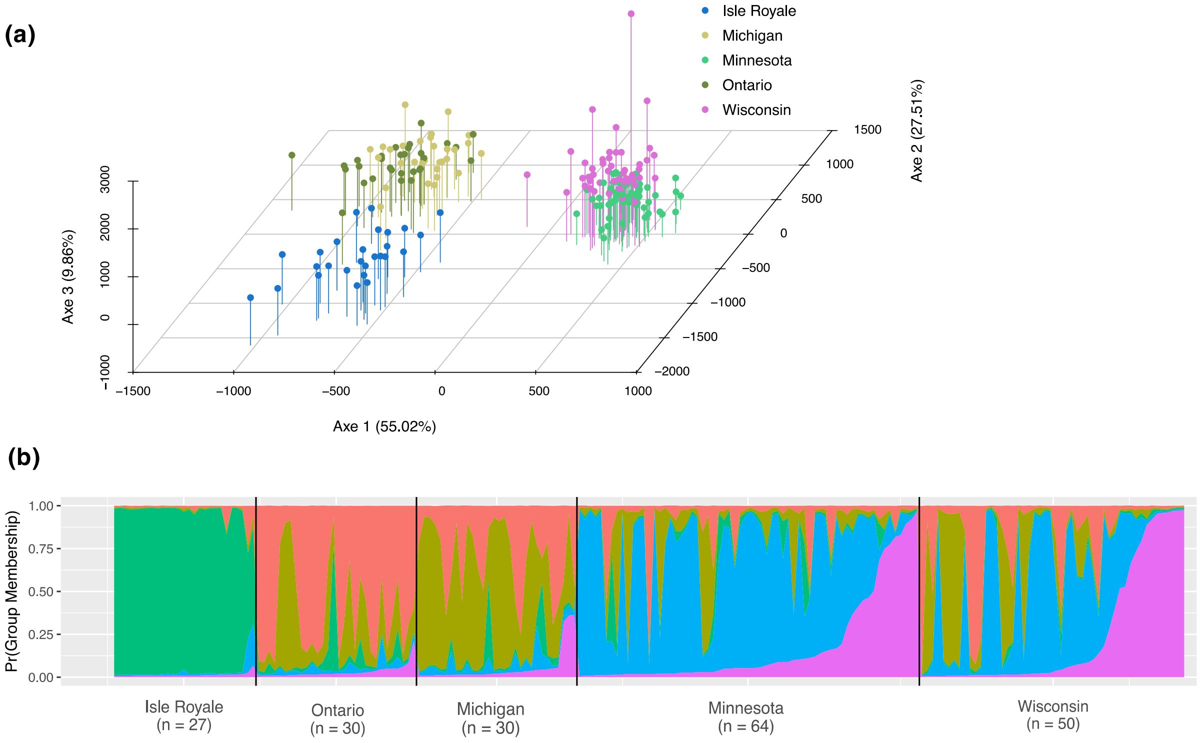

Fig S1. Genetic structure in microsatellite loci among Lake Superior Basin marten populations (i.e. no *Martes caurina*) using factorial correspondence analysis (a) and the Bayesian clustering algorithm STRUCTURAMA (b).

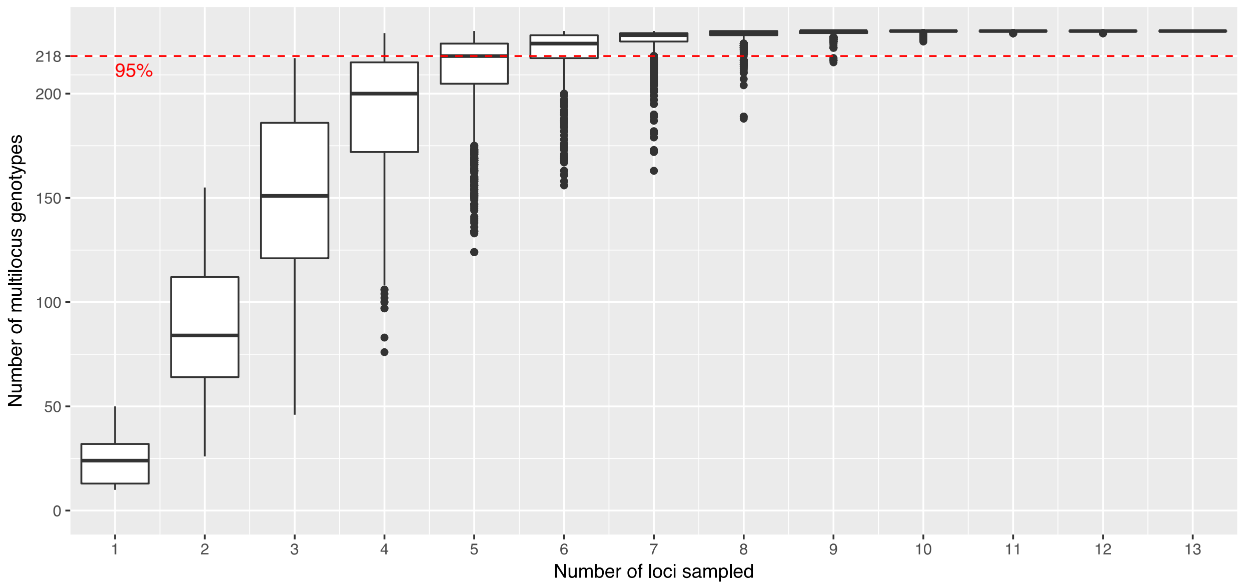

Figure S2. Genotype accumulation curve denoting number of loci needed to identify individuals. All analyses used individuals with ≥ 7 loci genotyped which captures >95% of the total multilocus genotypes observed.

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Can landscape heterogeneity promote carnivore coexistence in human-dominated landscapes?

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Abstract

Context: Interspecific competition can limit species distributions unless competitors partition niche space to enable coexistence. Landscape heterogeneity can facilitate niche partitioning and enable coexistence, but land-use change is restructuring terrestrial ecosystems with unknown consequences for species interactions.

Objectives: We tested the relationship between landscape heterogeneity and carnivore co-occurrence in natural and human-dominated ecosystems to assess the landscape-mediated impacts of anthropogenic change on coexistence.

Methods: We used boosted regression trees to model the distributions and co-occurrence of two competing forest carnivores, American martens and fishers, at two contrasting sites in the Great Lakes region, USA. We assessed the importance of climate and habitat variables for each species, measured spatial niche overlap, and quantified co-occurrence as a function of compositional (patch richness), configurational (landscape shape), and topographical (elevation range) heterogeneity per site.

Results: We observed significant differences in the effect of heterogeneity on co-occurrence between sites. The natural landscape exhibited little niche overlap and co-occurrence had a significant, positive relationship with heterogeneity. Conversely, the human-dominated site exhibited high niche overlap with variable effects of heterogeneity on co-occurrence. Elevation, snow pack, and development also had strong, contrasting effects on marten and fisher distributions, suggesting that differential use of habitat and anthropogenic features facilitates coexistence.

Conclusions: Heterogeneity can facilitate coexistence, but too much heterogeneity may undermine carnivore coexistence in human-dominated landscapes where habitat and space are limited. Moreover, future climate change will likely erode niche partitioning among martens and fishers, with particularly strong consequences for coexistence in human-dominated landscapes and at range boundaries.

Key words: ANCOVA, Chequamegon National Forest, Minnesota, Mustelid, Voyageurs National Park, Wisconsin

Introduction

Biotic interactions are important regulators of species' distributions (Peterson *et al.* 2011; Wisz *et al.* 2013). Interspecific competition, in particular, can govern the distribution of organisms when coexistence is unattainable (Bowers & Brown 1982; Erlinge & Sandell 1988; Wisz *et al.* 2013). To maintain stable coexistence, competitors must partition niche space by varying their use of space, time, or resources (Chase & Leibold 2003; Letten, Ke & Fukami 2017). Theory predicts that spatial heterogeneity can facilitate niche partitioning by providing additional niche axes, thereby enabling coexistence through interspecific variation in fitness, dispersal, or access to shared resources (Macarthur & Levins 1964; Chesson 2000). While this relationship is scale dependent (Chesson 2000; Amarasekare 2003), empirical evidence has shown that landscape heterogeneity can indeed promote coexistence (Menge & Menge 1974; Kotler & Brown 1988; Palmer 2003). However, land-use change is restructuring terrestrial ecosystems, with widespread consequences for landscape heterogeneity, competitive interactions, and species' distributions (Robertson *et al.* 2013; Gámez-Virués *et al.* 2015; Perović *et al.* 2015).

Mammalian carnivores exhibit strong agonistic interactions and their distributions are often regulated by interspecific competition (Donadio & Buskirk 2006; Fisher *et al.* 2013;

Santulli *et al.* 2014). Consequently, numerous coexistence mechanisms have been proposed, including spatial and temporal segregation, differential habitat and resource selection, behavioral avoidance, and intraguild predation (Manlick *et al.* 2017b). In natural systems, landscape heterogeneity can facilitate such mechanisms and promote coexistence (Durant 1998; Darimont, Paquet & Reimchen 2009; Fisher *et al.* 2013). Human-dominated landscapes, however, are now ubiquitous and simultaneously create heterogeneity in some niche axes while homogenizing others (McKinney & Lockwood 1999; Cardille & Lambois 2010; Radeloff *et al.* 2015). The effect of landscape heterogeneity on carnivore coexistence in these novel ecosystems is poorly understood (Manlick *et al.* 2017b), and excessive heterogeneity in human-dominated landscapes could inhibit competitor coexistence (Palmer 1992). Indeed, increasing evidence suggests that human agency is intensifying carnivore competition (Lewis *et al.* 2015; Cruz *et al.* 2018; Smith *et al.* 2018). At the same time, however, the restoration of carnivores to human-dominated landscapes is increasingly promoted as a means to restore ecosystem processes and lost species interactions (Chapron *et al.* 2014; Ripple *et al.* 2014), but the potential for increased interspecific competition among reintroduced species in these landscapes is rarely assessed (Manlick *et al.* 2017b).

American martens (*Martes americana*; hereafter, martens) and fishers (*Pekania pennanti*) are small-bodied forest carnivores and the most widely reintroduced carnivores in North America (Powell *et al.* 2012). Martens and fishers co-occur throughout the temperate regions of North America and are broadly associated with complex, old growth forests (Ruggiero *et al.* 1994). Both species exhibit similar habitat preferences and overlapping diets (Zielinski & Duncan 2004; Manlick *et al.* 2017b), often resulting in direct competition, particularly in modified landscapes at the southern extent of their distributional overlap where intraguild predation is common

(Krohn, Zielinski & Boone 1997; McCann, Zollner & Gilbert 2010). Sympatric populations often partition space, time, and habitat features, thereby minimizing competitive overlap (Fisher *et al.* 2013; McCann, Zollner & Gilbert 2017a; Zielinski, Tucker & Rennie 2017). In particular, differential use of habitat and snow features – stratified by elevation – likely enables coexistence throughout much of their range (Zielinski, Tucker & Rennie 2017). For instance, fishers utilize mixed cover types at low elevations throughout their range, while martens generally exploit deep, uncompressed snow in conifer forests via morphological adaptations that minimize foot loading (i.e., low body mass/foot surface area; Krohn et al. 1995; Fisher et al. 2013). Recent studies have hypothesized that landscape heterogeneity promotes these differences and may facilitate marten-fisher coexistence through increased niche partitioning (Fisher *et al.* 2013; Manlick *et al.* 2017b).

To test the influence of landscape heterogeneity on coexistence, we modeled the co-occurrence of martens and fishers in the Great Lakes region as a function of compositional, configurational, and topographic heterogeneity. Specifically, we estimated spatial niche overlap and the probability of co-occurrence for martens and fishers in two contrasting landscapes: the Chequamegon National Forest of Wisconsin, USA (hereafter, CNF) and Voyageurs National Park in northern Minnesota, USA (hereafter, VNP). Both sites occur within the historical range of martens and fishers and are characterized by mixed temperate forests and consistent snow cover. The CNF is characterized by human-dominated landscapes and widespread disturbance following European settlement. Both martens and fishers were reintroduced to the CNF in the late 20th century, and the area is now the southern boundary of marten-fisher overlap regionally. Despite decades of intensive management in the CNF, martens remain a state-endangered species (Manlick *et al.* 2017a) while fishers have expanded across the region (Pokallus & Pauli

2015). Conversely, VNP has seen considerably less ecological change (Goring *et al.* 2016; Goring & Williams 2017), being a federally protected National Park since 1975. Moreover, regional surveys show substantially higher ratios of marten to fisher abundance in the VNP area compared to the CNF (Erb 2015; Manlick *et al.* 2017b; Woodford 2017). Thus, the CNF and VNP provide a valuable comparison to test the effects of landscape heterogeneity on co-occurrence in natural versus human-dominated systems. We hypothesized that niche overlap would be higher in the modified landscapes of CNF than in the preserved VNP, but we predicted that the probability of co-occurrence in both sites would increase with landscape heterogeneity.

Methods

Study sites

The CNF is a multi-use forest dominated by deciduous forest and woody wetlands, with evergreen and mixed forest interspersed (Fig. 1a; Table 1). Anthropogenic disturbance has heavily altered CNF forests, and historically conifer-dominated systems are now comprised largely of mixed hardwoods (e.g., sugar maple [*Acer saccharum*], yellow birch [*Betula alleghaniensis*], and aspen [*Populus* spp.]; Rhemtulla et al., 2007; Schulte et al., 2007). These novel CNF forests have reduced heterogeneity, as forests of large, structurally complex trees have been replaced by smaller trees, increased stem densities, and reduced total basal areas (Rhemtulla, Mladenoff & Clayton 2009; Goring *et al.* 2016). Meanwhile, VNP is dominated by five large lakes with evenly distributed deciduous, evergreen, and mixed forests, as well as woody wetlands (Fig. 1b; Table 1). While VNP has also seen changes in forest composition, including deciduous forests replacing conifers (mainly *Populus* spp.; Goring et al., 2015; Paulson et al., 2016), the CNF has seen continued human pressure and now contains an order of magnitude more developed lands than VNP (Table 1). Though both systems are characterized by cold winters with consistent snow cover, VNP typically maintains 1.5 times more snow pack than the CNF (i.e., snow-water equivalent; Table 1). Our study focused on the Great Divide District of the CNF (1,851 km^2) and the entirety of VNP plus state and federal forests bordering the southern boundary of the park (1,642 km^2).

Sampling

In the CNF, we surveyed winter snow tracks (November-April) along 153 km of maintained forest roads from 2001 to 2014 following Manlick et al. (2017b). All surveys occurred a minimum of 2 activity periods (i.e., dusk and dawn) after snowfall to ensure opportunities for animal movement, and we repeated surveys up to 4 times per winter. We georeferenced all tracks that bisected surveyed roads (Fig. 1a, b), and we identified marten and fisher tracks using a combination of morphology, behavior, and straddle width (Manlick *et al.* 2017b; McCann, Zollner & Gilbert 2017b). Tracks separated by >500 m were assumed to be separate detections (Manlick *et al.* 2017b). In VNP, we deployed camera traps from 2007-2017, resulting in 298 unique sampling locations and >25,000 trap nights. Camera deployment ranged from 1-210 days ($\bar{x}$ = 60.02) and species observations were identified visually by VNP staff. Unique detections of martens and fishers were defined as images captured >30 minutes from a previous observation. All detections were limited to snow-on season (October-April) for comparison to CNF snow-track surveys (Fig. 1c, d). All sampling adhered to the ethical guidelines established by the American Society of Mammalogists (Sikes 2016).

Species distribution modeling

We modeled marten and fisher distributions in CNF and VNP using presence-absence data from each species as response variables. In the CNF, we used all marten and fisher track detections from 2001-2014 as presences. For absences, we subdivided the 153 km of surveyed roads into 1 km transects and identified all transects where martens and fishers were never detected. Using repeated surveys from 2013-2014 (Manlick *et al.* 2017b), we calculated the per-survey detection probability for martens and fishers as 0.20 and 0.12, respectively. For each species, every transect without a detection from 2001-2014 (minimum of 10 surveys) was deemed unoccupied and we randomly generated a point along each unoccupied transect to be used as absences (Fig. 1a, b). For VNP, every camera trap detection of martens and fishers from October-April was used to compile presences. We then calculated daily detection probabilities of 0.11 and 0.07 for martens and fishers, respectively, and restricted absences to sites that were active ≥14 days without ever detecting a marten or fisher (Fig. 1c, d).

We modeled marten and fisher distributions using 20 predictor variables to capture the effects of climate (e.g., temperature, snow-water equivalent), elevation, and land cover composition (e.g., % cover) and configuration (e.g., edge density, largest patch index) on marten and fisher occurrence (Table 1). Specifically, we used the USGS National Elevation dataset (30×30 m; Gesch et al., 2002) to quantify topography and the 2011 National Land Cover Database (NLCD, 30×30 m; Wickham et al., 2013) to quantify land cover variables. All land cover composition and configuration variables were calculated in the program FRAGSTATS (McGarigal *et al.* 2002). We used the R package *daymetr* (Hufkens *et al.* 2018) to calculate climate variables from 30-year means (1985-2015) based on Daymet interpolated climate surfaces (1×1 km; Thornton et al., 2012) limited to October-April. To assess scale-dependency, we quantified predictors within 1, 5, and 10 km^2 of all locations. We then gridded CNF and VNP and calculated variables in 1, 5, and 10 km^2 cells to predict marten and fisher distributions across each study area.

We modeled species distributions and estimated relative variable importance for martens and fishers at each site using Boosted Regression Trees (BRTs) in the R package *dismo* (Elith, Leathwick & Hastie 2008; Hijmans *et al.* 2013). BRTs are a machine learning approach that combines large numbers of simple regression trees through boosting techniques to maximize predictive performance (Elith, Leathwick & Hastie 2008). This approach allowed us to assess the relative importance of variables for each species while also incorporating nonlinear relationships and complex interactions between variables. Moreover, unlike classical regression approaches, BRTs can account for correlation in detections and variables and they do not require a top model for accurate prediction (Elith, Leathwick & Hastie 2008) – all issues that have plagued the use of snow-track data in species distribution modeling (Manlick *et al.* 2017b). We used a bagging fraction of 0.5, a tree complexity of 5 (i.e., up to 5-way interactions), and a learning rate ranging from 0.001-0.0001 to ensure >1,000 trees (per Elith et al. 2008). All models were fit using 10-fold cross validation via the 'gbm.step' function in *dismo*, and predictive performance was assessed using area under the receiver operating curve (AUC). Models were then used to predict the probability of marten [p(marten)] and fisher [p(fisher)] occurrence across CNF and VNP at the 1, 5, and 10 km^2 resolutions. Lastly, we used the 'hetcor' function in the R package *polycor* (Fox 2016) to assess the directional relationship between the spatial predictors and species occurrences modeled by BRTs.

Co-occurrence, overlap, and heterogeneity

We calculated the probability of marten-fisher co-occurrence [p(co-occur)] as p(marten)×p(fisher) for each cell at each resolution in both CNF and VNP. We also estimated the realized spatial overlap of martens and fishers in CNF and VNP at each scale by calculating the similarity of species distributions. Specifically, we used the Expected Shared Presences (ESP) of each species following Godsoe (2014) and Godsoe & Case (2015) where $\mathrm{ESP} = \frac{2\sum_j P_{1j}P_{2j}}{\sum_i (P_{1i}+P_{2i})}$, j is each cell, and P_{1j} and P_{2j} are p(marten) and p(fisher) in each cell, respectively. This metric ranges from 0 (no overlap) to 1 (complete overlap) and calculates a generalized Sørensen similarity of two species geographic distributions (Godsoe 2014).

To test the relationship between marten-fisher co-occurrence and landscape heterogeneity in each study site, we modeled p(co-occur) at each scale as a function of three independent heterogeneity metrics to capture variability in landscape composition, landscape configuration, and topographic complexity. Specifically, we quantified patch richness (i.e., the number of land cover classes in each cell) to measure compositional heterogeneity and landscape shape index (LSI; i.e., patch aggregation and complexity) to capture the heterogeneity of land cover configuration in each cell. All land cover metrics were calculated in FRAGSTATS. Topographic heterogeneity was measured as the range of elevation in each cell using the National Elevation dataset. We combined data from both sites and normalized all covariates to range from 0-1. We used ANCOVAs to test for differences in the relationship between landscape heterogeneity and co-occurrence by site (i.e., site × heterogeneity interactions) and for differences in intercepts (i.e., variation in mean co-occurrence by site). If significant interactions were not detected, we removed interaction terms and used more parsimonious additive models to test for differences in intercepts. Lastly, we used simple linear regressions to explore the independent relationship between co-occurrence and landscape heterogeneity within each site. All models adhered to the assumptions of linear regression.

Results

We detected 128 marten and 249 fisher presences in the CNF from 2001-2014. Along the 153 km of surveyed roads, 91 transects had no marten detections and were used to generate marten absences, compared to only 39 transects without a fisher detection (Fig. 1a, b). In VNP, we detected marten presence at 61 camera locations and fisher presence at 73 locations, resulting in 152 and 137 absences for martens and fishers, respectively (Fig. 1c, d). Predictive performance of BRTs was high for all models (all AUC > 0.94).

Variable importance from BRTs revealed that elevation was the strongest predictor for martens in the CNF, with a positive relationship at all scales (Fig. 2a-c). Marten detections further exhibited a strong, positive interaction between elevation and snow-water equivalent (i.e., snow pack) at all scales (Appendix S1). In addition, martens responded positively to large patches of contiguous land cover at the finest resolution (1 km^2) but showed contrasting responses to large patches and high proportions of specific land cover types at coarser scales (Fig. 2a-c, Appendix S1). Conversely, elevation and snow had a negative effect on fisher occurrences in the CNF at all scales, with particularly strong effects at the finest scale (Fig. 2a-c; Appendix S1). Notably, the strongest indicator of fisher occurrence at the intermediate resolution (5 km^2) was human development, while avoidance of wetlands and water bodies appeared to drive fisher distribution at the largest scale. In total, martens and fishers showed contrasting responses to the most influential variables at all scales (e.g., elevation, snow, development). Nevertheless, predicted fisher occurrence was nearly ubiquitous across the study area, while martens were restricted to isolated pockets (Fig. 3a, b). Consequently, predicted co-occurrence was high for all cells occupied by martens (Fig. 3c), resulting in an ESP (i.e., distribution overlap) of 0.59, 0.51, and 0.52 for the 1, 5, and 10 km^2 scales, respectively.

In VNP, variable importance for martens and fishers was similar to the CNF. Specifically, snow-water equivalent was the primary driver of fisher occurrence, exhibiting strong negative effects at all scales (Fig. 2d-f). Interestingly, martens also displayed a negative overall relationship with snow (Fig. 2d-f), though this response was largely driven by strong, negative associations at the highest snow depths (Appendix S2). Moreover, martens did not exhibit strong associations with any particular variables but responded positively to a number of different land cover types, including evergreen forest, shrubland, and woody wetlands. In total, detections of both species were associated with a diversity of cover types, resulting in patchy distributions of both species across VNP (Fig. 3d, e). Consequently, predicted co-occurrence was low across the park (Fig. 3f) and ESP estimated a distributional overlap of 0.37, 0.37, and 0.36 for the 1, 5, and 10 km^2 scales, respectively.

The relationship between co-occurrence and landscape heterogeneity differed significantly between CNF and VNP for all metrics at the finest scale (1 km^2), but the significance of these interactions decreased at coarser resolutions (Table 2, Fig. 4). However, the effect of patch richness (i.e., composition) was consistently different between sites, with less co-occurrence in the CNF as patch richness increased. Models also detected significant differences in intercepts for all metrics at all scales, indicating mean co-occurrence was consistently higher in the CNF than VNP (Table 2, Fig. 4). Furthermore, co-occurrence increased significantly with all heterogeneity metrics at all scales in VNP, while heterogeneity was largely insignificant to co-occurrence in the CNF (Fig. 4). Co-occurrence in the CNF did, however, increase significantly with topography (i.e., elevation range) at the finest scale and with complex landscape configurations (i.e., LSI) at the larger scales (Fig. 4).

Discussion

Landscape heterogeneity is predicted to limit niche overlap and facilitate competitor coexistence. We explicitly tested this prediction using sympatric populations of martens and fishers in the contrasting landscapes of VNP and CNF. We detected little niche overlap in VNP and found that co-occurrence increased significantly with all forms of landscape heterogeneity. Conversely, we observed high niche overlap and variable impacts of landscape heterogeneity on co-occurrence in the human-dominated landscape of CNF, with co-occurrence actually decreasing as a function of patch richness across scales. These results support the hypothesized relationship between landscape heterogeneity and coexistence but also imply a tipping point at which landscape complexity inhibits coexistence (*sensu* Palmer 1992). For instance, we observed positive responses of co-occurrence to complex topography and landscape configurations in both the CNF and VNP, particularly at the coarser scales, but we also detected consistently negative effects of patch richness on co-occurrence in the CNF where richness is correlated with development and agriculture ($r > 0.6$). This suggests that while complex topography and patch configuration may promote coexistence, variation in the underlying land cover composition that regulates habitat availability could undermine such facilitation. Human-dominated landscapes present such challenges *en masse*, as novel land cover like development and agriculture are increasingly prevalent. For instance, edge density, development, and agriculture were all higher in the CNF while large patches of contiguous forest were more common in VNP, particularly for preferred habitats like mixed and evergreen forest that were consistent drivers of marten and fisher distribution. Ultimately, our results show that human-dominated landscapes present a challenge in balancing the positive effects of landscape heterogeneity on competitor coexistence while also maintaining adequate habitat and resources.

Our BRT models revealed that elevation and snow were significant drivers of marten and fisher distribution in both the CNF and VNP, with contrasting effects on each species. For example, the interaction between elevation and snow pack had a strong positive effect on marten distribution in the CNF at all scales, while both elevation and snow pack restricted fisher occurrences. Likewise, elevation had a positive impact on marten distribution in VNP, while snow pack was the primary driver of fisher occurrence at all scales, largely restricting detections to sites with < 40 kg/m^2 (i.e., mean snow-water equivalent; Table 1, Appendix S2). Sites with >40 kg/m^2 snow pack, however, were notably rare in the CNF, likely contributing to the ubiquitous presence of fishers in the study area. Ultimately, these results are consistent with the positive effect of topographical complexity on coexistence, and with previous research illustrating the differential impact of snow on martens and fishers in montane systems (e.g., Krohn et al. 1995; Krohn et al. 1997; Zielinski et al. 2017). Thus, our findings support the hypothesis that elevation and snow mediate the distributions and coexistence of martens and fishers, even at relatively low elevations.

Fishers in the CNF selected for low intensity development, land cover driven by an extensive road network that further reduces snowpack and likely facilitates the movement of fishers and other mesopredators (Whiteman & Buskirk 2013; Manlick *et al.* 2017b; Zuckerberg & Pauli 2018). Interestingly, VNP has some of the lowest road densities in the country, while the CNF approximates mean road density across the United States (Riiters & Wickham 2003; Girvetz *et al.* 2007). This suggests that road-snow interactions in the CNF are broadly representative of the potential impact motorized corridors can have on habitat- and snow-mediated competition. Indeed, previous research has shown that species with high foot loads like fishers and canids exploit compacted snow along motorized corridors, to the potential detriment of snow-adapted prey and competitors (Bayne, Boutin & Moses 2008; Whittington *et al.* 2011; Gese, Dowd & Aubry 2013; Whiteman & Buskirk 2013). Our results support these studies and indicate that development in human-dominated landscapes can support less snow adapted species (e.g., fishers) and erode niche partitioning with snow adapted competitors (e.g., martens). Furthermore, future climate projections estimate significant declines in snow pack for both the CNF and VNP by the end of the 21st century (Notaro *et al.* 2010, 2014). Such climate changes will favor fishers and other southerly distributed mesocarnivores, likely exacerbating competition with martens regionally (Manlick *et al.* 2017b; Zielinski, Tucker & Rennie 2017) or even driving martens to regional extirpation (Carroll 2007; Lawler, Safford & Girvetz 2012).

We estimated niche overlap between martens and fishers at the southern extent of their sympatry in the CNF and over 250 km north in VNP. At our southern site in the CNF, we detected > 1.5 times more niche overlap than in the more northerly VNP, and mean co-occurrence was significantly higher in the CNF at all scales. Range boundary dynamics could have contributed to this observed niche overlap and may have influenced the differential impacts of heterogeneity on co-occurrence observed in the CNF. For example, populations at range boundaries often maintain sparse distributions (Brown 1984), with species capable of exploiting anthropogenic landscapes exhibiting the highest population densities (Channell & Lomolino 2000). We observed similar patterns, including a patchy distribution of martens and the widespread occurrence of fishers selecting for human development in the CNF. Moreover, populations at range boundaries often utilize suboptimal habitat (Lawton 1993), and may even increase niche breadth in the absence of preferred resources (Zielinski & Duncan 2004; Oliver *et al.* 2009). Our models revealed that both martens and fishers used atypical habitat, including shrubs, wetlands, and development. Consequently, these boundary characteristics may have contributed to the widespread distribution of fishers and the high degree of niche overlap with martens in the CNF. As noted, landscape heterogeneity can help minimize such overlap, but this often occurs via the spatial partitioning of resources (Fisher *et al.* 2013). Thus, we suggest that landscape heterogeneity may have weaker effects on co-occurrence at range boundaries where distributions are constrained and space is limiting, and our results support this hypothesis. Given the high probability of fisher occurrence across the CNF, however, co-occurrence (i.e., p(marten)×p(fisher)) was often a reflection of marten distribution. Thus, our modeled responses of co-occurrence to landscape heterogeneity may have been more indicative of marten habitat selection. Nonetheless, such dynamics are likely prevalent at range boundaries and in anthropogenic landscapes where dominant, more generalist species (e.g., fishers) are widespread and can competitively exclude subordinate species by exploiting a wider degree of resources (Peers, Thornton & Murray 2013). Future studies should continue to explore this relationship between niche breadth and land-use change across species distributions in order to further assess the impact of human-dominated landscapes on coexistence at range boundaries.

Our models clearly illustrate the variable effects of landscape heterogeneity on co-occurrence and niche overlap for these species across landscapes, but there are important limitations to consider. First, because our BRTs did not account for imperfect detection it was essential to correctly identify presences and absences given that pseudoabsences and “background” data can overestimate niche overlap (i.e., ESP; Godsoe 2014). In VNP we used daily detection probabilities to set a conservative threshold and assign absences to camera stations; however, the CNF did not have fixed survey locations so we randomly generated absences along transect segments without detections during the entire survey period. It is possible that CNF models thus utilized informed pseudoabsences which could have inflated niche overlap estimates; however, given our survey-level detection probabilities (Manlick *et al.* 2017b) it is unlikely that martens and fishers went undetected when present over the 14-year survey period. Second, both species distribution models and our regression analyses only incorporated remotely sensed data on climate and land cover variables. These variables relied on coarse cover type classifications, and previous research has shown that both martens and fishers select for fine-scale habitat features across scales (Buskirk & Powell 1994; Shirk, Raphael & Cushman 2014; McCann, Zollner & Gilbert 2014). Moreover, our data captured variation in land cover composition and configuration, but not the underlying structural complexity that is important for both martens and fishers (Buskirk & Powell 1994; McCann, Zollner & Gilbert 2014). Thus, it is possible that martens and fishers both select for and partition fine-scale habitats or structural complexity that were not captured in our analyses. Future studies could incorporate increasingly available LiDAR data to assess the partitioning of these additional niche axes (Joyce *et al.* 2019). Lastly, species must partition space, time, or resources to facilitate co-existence, and our results indicate that martens and fishers in VNP partition space and habitat features (e.g., snow) while animals in the CNF do not. Thus, martens and fishers may partition other niche axes to enable long-term coexistence (McCann, Zollner & Gilbert 2017a), though Manlick et al. (2017b) observed high spatial, temporal, and dietary overlap. Heterogeneity in fine-scale habitats, forest structure, or prey are thus likely to facilitate co-occurrence. Moreover, interactions between resources (e.g., habitat and prey) could also generate environmental heterogeneity, and future research should explore the dynamics of resource availability to assess the mechanisms underlying such heterogeneity.

We revealed potential costs of landscape heterogeneity for carnivore coexistence in human-dominated landscapes, where increased landscape heterogeneity may be conflated with fragmentation and anthropogenic development. Furthermore, our results suggest human-dominated landscapes can favor species able to exploit these novel landscapes (e.g., fishers), further increasing niche overlap and reducing the potential for coexistence. This is consistent with recent studies illustrating the adverse effects of human agency on carnivore niche partitioning (Lewis *et al.* 2015; Smith *et al.* 2018). Nevertheless, carnivore reintroductions are advocated as a potential mechanism to restore ecosystem processes and restructure existing carnivore communities (Ripple *et al.* 2011, 2014; Chapron *et al.* 2014), with restoration programs often targeting modified landscapes like the CNF (Navarro & Pereira 2015). We show that interspecific competition is likely among reintroduced carnivores in human-dominated landscapes and that landscape heterogeneity will not facilitate coexistence, particularly at range boundaries. Thus, we encourage wildlife managers to consider competitive interactions when establishing future carnivore reintroduction programs.

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Data accessibility

All data is archived in the Data Dryad digital repository (accession pending).

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Tables

Table 1. Means (SD) of variables used in boosted regression trees for martens (*Martes americana*) and fishers (*Pekania pennanti*) in the Chequamegon National Forest (CNF) and Voyageurs National Park (VNP) at 1, 5, and 10 km^2 scales.

	1 km^2		5 km^2		10 km^2	
Variable	CNF (*N* = 1976)	VNP (*N*=1762)	CNF (*N*=410)	VNP (*N*=378)	CNF (*N*=217)	VNP (*N*=206)
Elevation (m)	438.95 (20.47)	357.75 (17.63)	439.02 (19.61)	357.82 (17.04)	438.01 (21.36)	357.67 (17.18)
Maximum temperature (°C)	2.42 (0.20)	1.00 (0.14)	2.42 (0.2)	1.00 (0.14)	2.42 (0.2)	1.01 (0.14)
Minimum temperature (°C)	-8.94 (0.12)	-11.02 (0.11)	-8.94 (0.11)	-11.02 (0.1)	-8.93 (0.12)	-11.02 (0.09)
Snow-water equivalent (kg/m^2)	24.89 (5.31)	39.85 (4.79)	25.11 (5.6)	39.84 (4.69)	25.19 (5.86)	39.98 (4.67)
Edge density	148.23 (49.31)	130.61 (66.88)	150.62 (36.13)	128.78 (59.84)	150.59 (32.25)	123.98 (61.07)
Largest patch index (LPI)	43.19 (20.78)	47.90 (25.79)	32.44 (18.47)	39.65 (24.91)	28.64 (17.18)	38.37 (26.5)
Deciduous forest (%)	36.05 (23.63)	15.58 (16.91)	36.28 (18.96)	15.41 (14.21)	37.24 (17.83)	15.08 (13.65)
Deciduous forest LPI	28.23 (24.61)	10.34 (14.75)	22.84 (20.17)	7.95 (11.47)	20.79 (19.13)	6.68 (9.75)
Development (%)	2.95 (3.42)	0.17 (0.67)	3.02 (2.19)	0.18 (0.48)	2.99 (1.76)	0.18 (0.43)
Development LPI	2.40 (3.07)	0.13 (0.54)	2.03 (1.89)	0.10 (0.28)	1.76 (1.47)	0.09 (0.22)
Evergreen forest (%)	9.14 (10.39)	10.63 (13.66)	9.06 (8.14)	10.10 (10.81)	8.83 (7.06)	9.48 (9.71)
Evergreen forest LPI	5.02 (7.60)	6.58 (10.79)	2.96 (4.29)	4.04 (6.08)	2.22 (3.03)	3.01 (4.42)
Mixed forest (%)	11.66 (8.74)	19.21 (15.99)	11.63 (6.72)	18.36 (13.5)	11.52 (5.97)	17.43 (12.21)
Mixed forest LPI	5.23 (5.63)	12.07 (13.57)	2.84 (3.1)	8.31 (9.33)	2.05 (2.25)	6.75 (7.27)
Shrub (%)	5.49 (5.87)	2.93 (6.11)	5.42 (4.18)	2.96 (4.61)	5.45 (3.84)	2.98 (4.28)
Shrub LPI	2.37 (3.65)	1.87 (4.52)	1.26 (1.75)	1.19 (2.36)	0.92 (1.13)	0.91 (1.64)
Water (%)	4.65 (12.28)	22.37 (32.04)	4.81 (9.71)	21.08 (26.92)	4.56 (7.77)	19.28 (24.07)
Water LPI	4.26 (11.94)	21.59 (31.99)	3.91 (9.26)	19.75 (26.98)	3.27 (6.86)	17.61 (24.13)
Woody wetland (%)	28.32 (20.39)	19.09 (22.26)	28.00 (16.00)	19.01 (19.98)	27.50 (14.92)	18.29 (18.47)
Woody wetland LPI	21.13 (20.19)	14.54 (22.03)	15.91 (14.97)	11.88 (19.65)	13.71 (12.77)	10.38 (17.4)

Table 2. Means (SD) of heterogeneity variables and significance (*p*) of ANCOVAs used to test the relationship between heterogeneity and co-occurrence of martens (*Martes americana*) and fishers (*Pekania pennanti*) in the Chequamegon National Forest (CNF) and Voyageurs National Park (VNP) at 1, 5, and 10 km^2 scales. Significant differences (bold) in slope indicate an interaction between site and heterogeneity, while significant differences in intercepts indicate variation in mean co-occurrence by site.

	1 km^2				5 km^2				10 km^2			
Heterogeneity	CNF	VNP	Slope	Intercept	CNF	VNP	Slope	Intercept	CNF	VNP	Slope	Intercept
Landscape shape	4.75 (1.23)	4.26 (1.67)	< **0.001**	< **0.001**	9.42 (2.01)	8.20 (3.34)	0.505	< **0.001**	12.96 (2.55)	10.80 (4.83)	0.388	< **0.001**
Patch richness	6.55 (1.24)	5.88 (2.00)	< **0.001**	< **0.001**	8.44 (1.21)	7.65 (2.14)	< **0.001**	< **0.001**	9.22 (1.29)	8.16 (2.51)	**0.006**	< **0.001**
Topography	30.87 (16.16)	26.90 (18.67)	0.203	< **0.001**	44.89 (23.74)	39.07 (22.89)	0.207	< **0.001**	53.60 (29.21)	43.90 (25.69)	**0.004**	< **0.001**

Figures

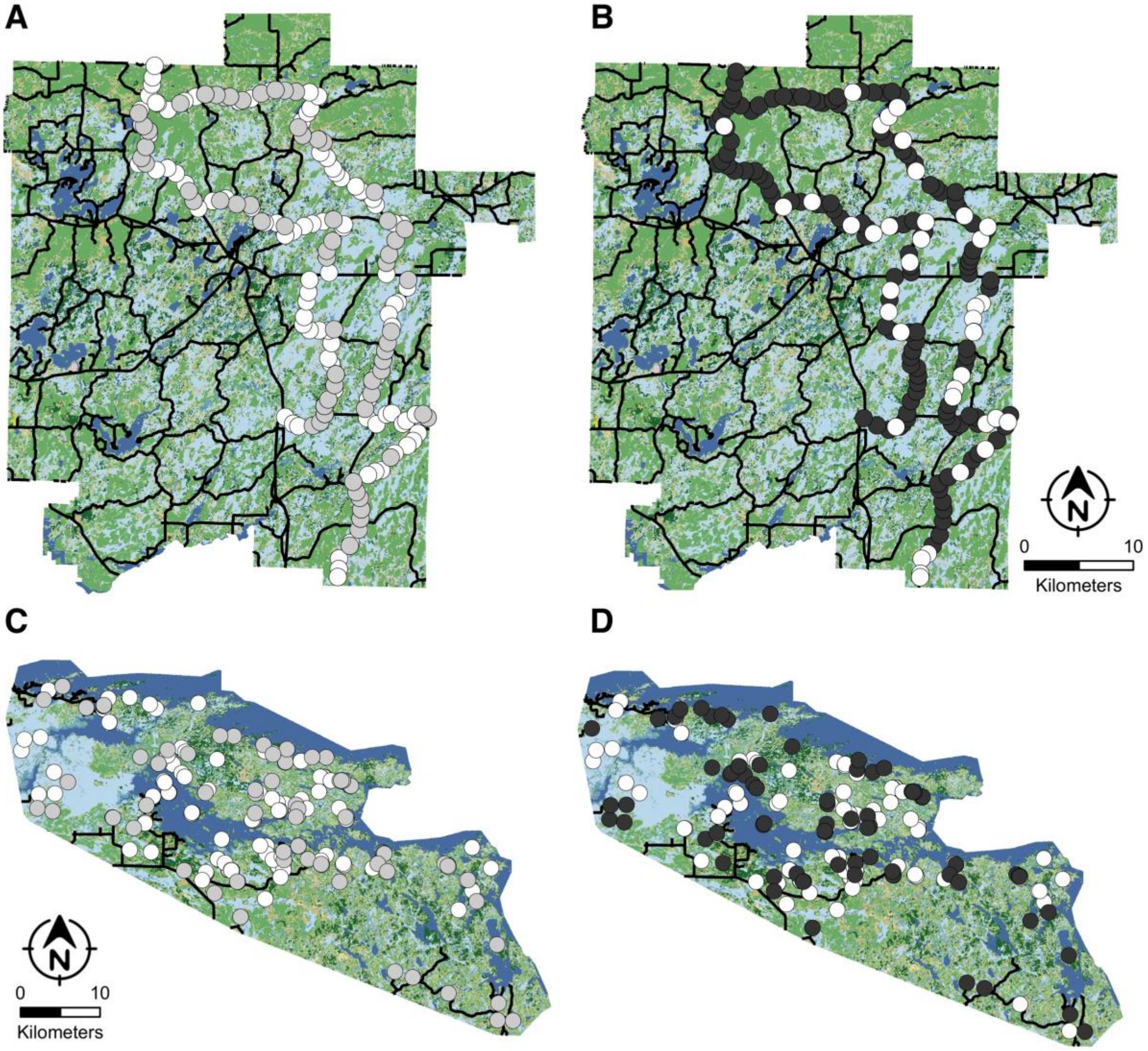

Figure 1. Presences (gray-black) and absences (white) of martens (a, c) and fishers (b, d) in the Chequamegon National Forest (top) and Voyageurs National Park (bottom). Background raster illustrate underlying land cover from NLCD 2011 and dark lines denote maintained roads.

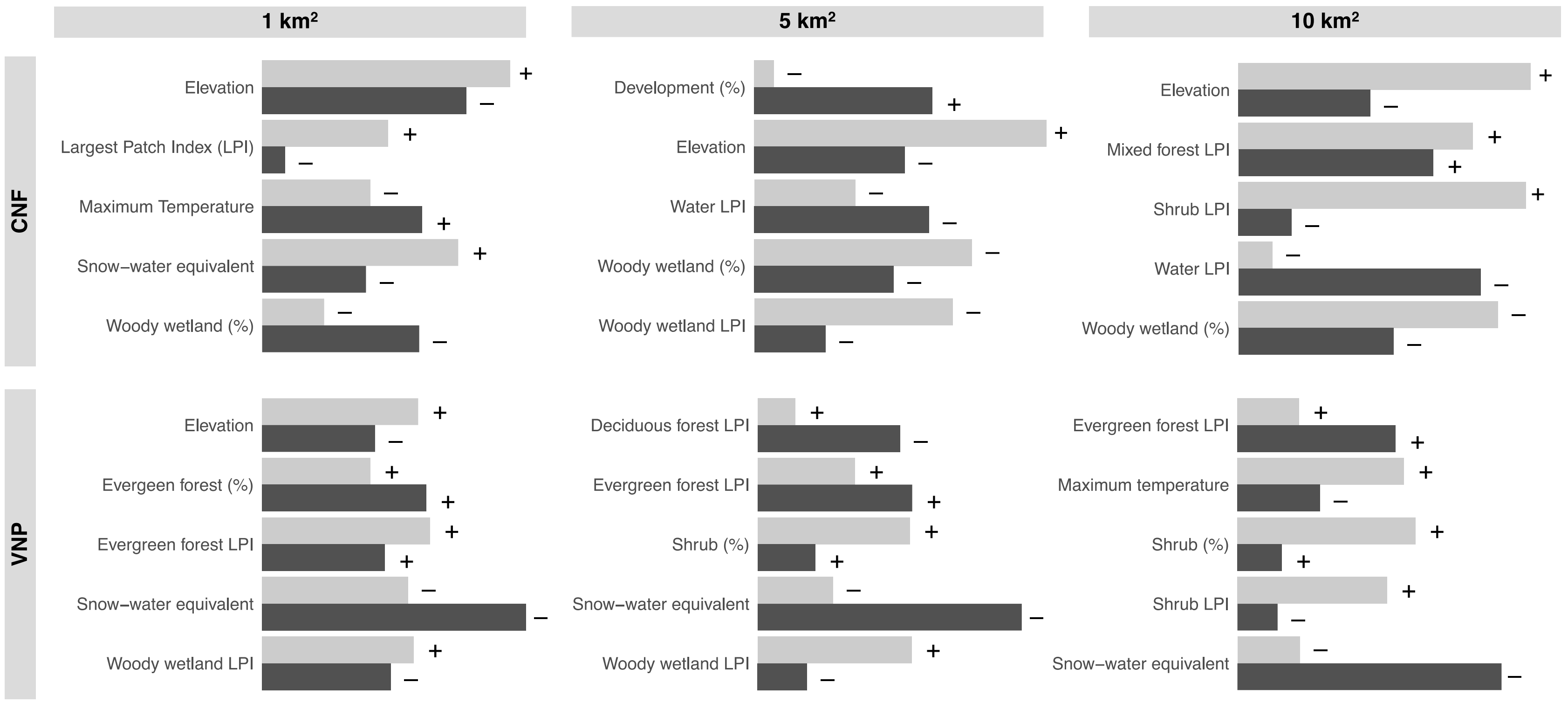

Figure 2. Relative influence of the five most important variables from boosted regression trees for martens (light grey) and fishers (dark grey) in the Chequamegon National Forest (a-c) and Voyageurs National Park (d-f) at the 1 km^2, 5 km^2, and 10 km^2 scales. Pluses indicate positive relationships and minuses indicate negative associations between species and variables.

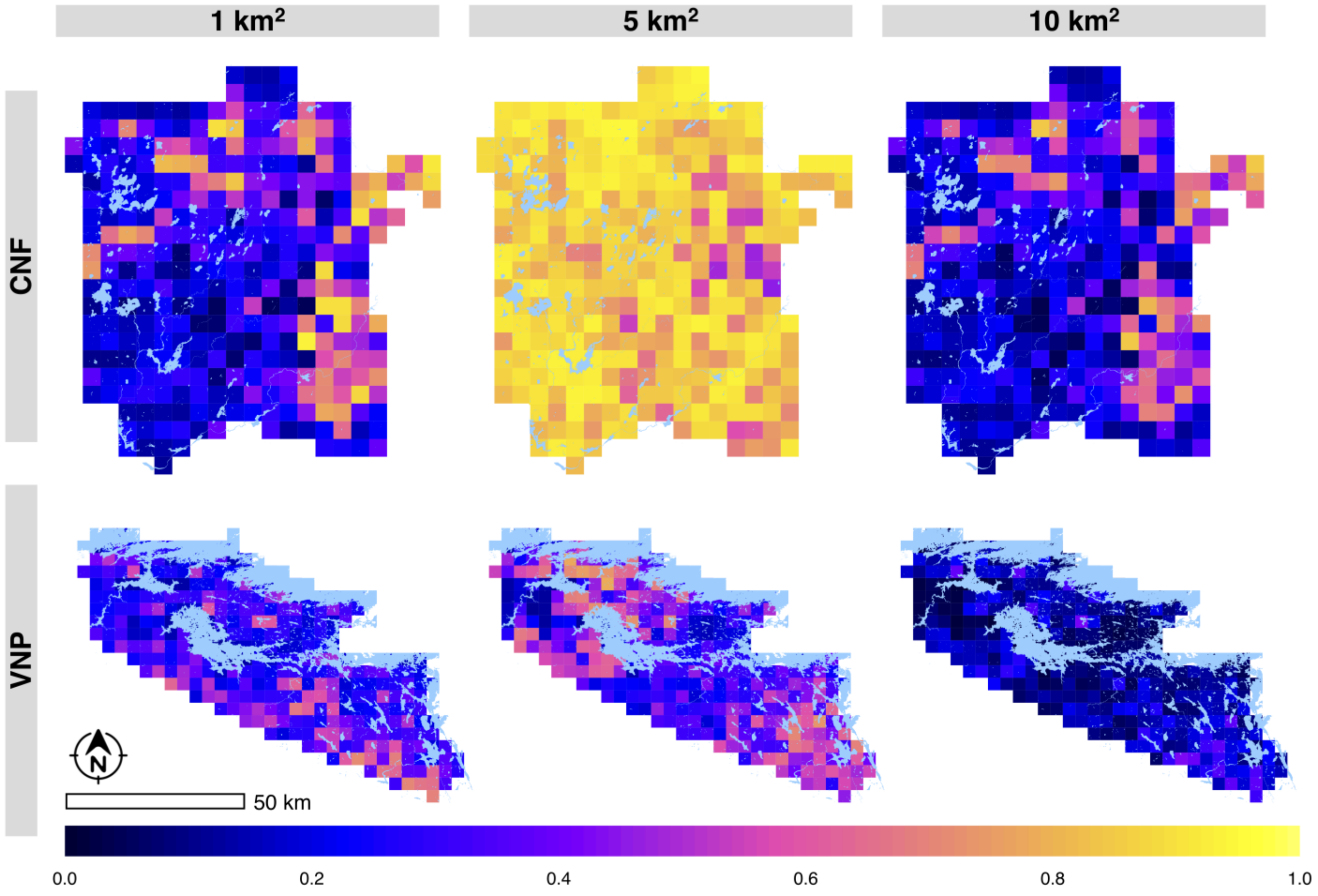

Figure 3. Predicted probability of marten occurrence (A), fisher occurrence (B) and co-occurrence (C) in the Chequamegon National Forest, and probability of marten occurrence (D), fisher occurrence (E) and co-occurrence (F) in Voyageurs National Park at the 5 km^2 scale.

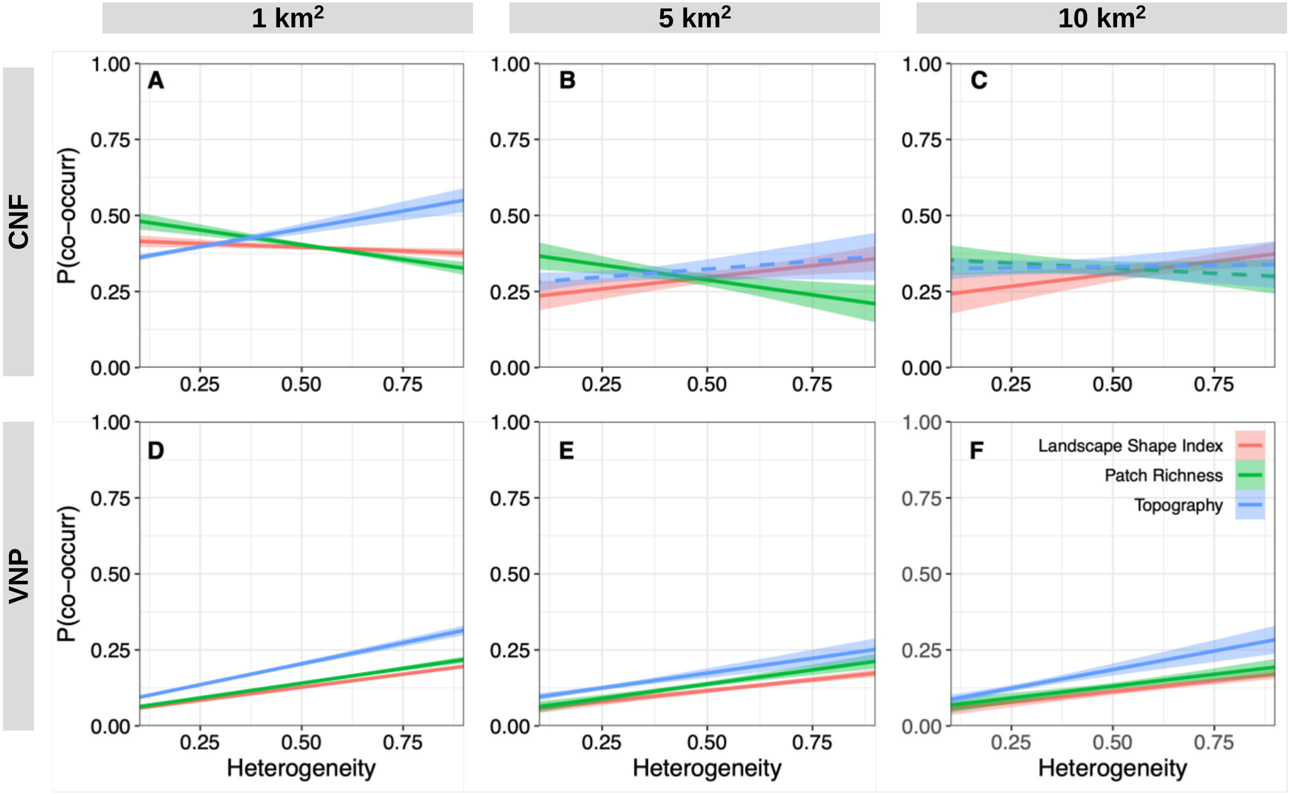

Figure 4. Relationship between landscape heterogeneity and probability of marten-fisher co-occurrence in the Chequamegon National Forest (top, A-C) and Voyageurs National Park (bottom, D-F) at the 1 km^2, 5 km^2, and 10 km^2 scales. Solid lines denote significant relationships, dashed lines denote non-significant relationships, and shaded ribbons illustrate 95% confidence intervals.

Supporting Information

Appendix 1. Fitted relationships illustrating the effect of spatial predictors on marten and fisher detections in the CNF at all scales (Figs S1-S6), and the interactive effect of elevation and snow-water equivalent (SWE) on marten occurrence in the CNF (Fig. S7).

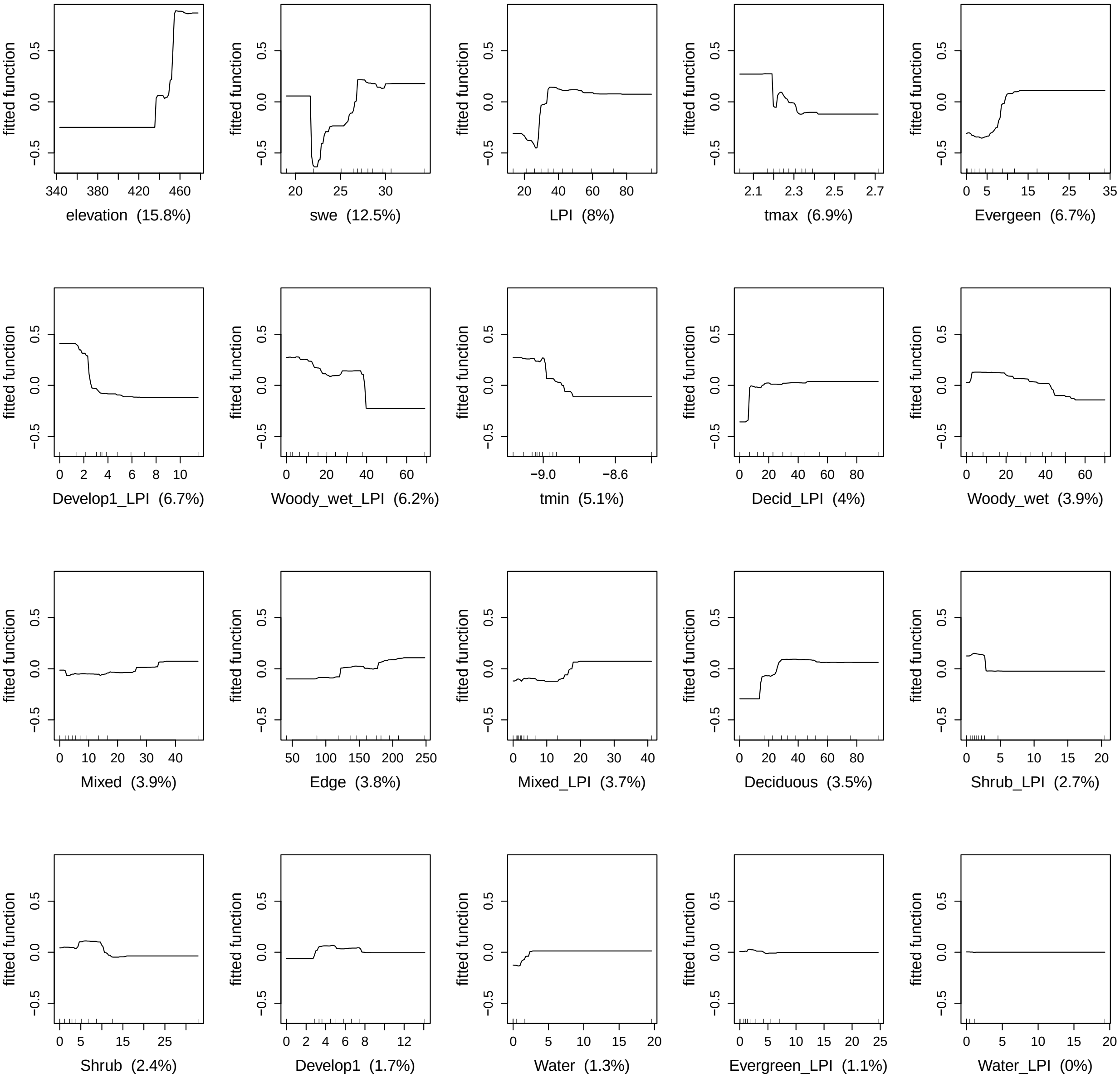

Figure S1. Fitted functions for CNF martens at the 1 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

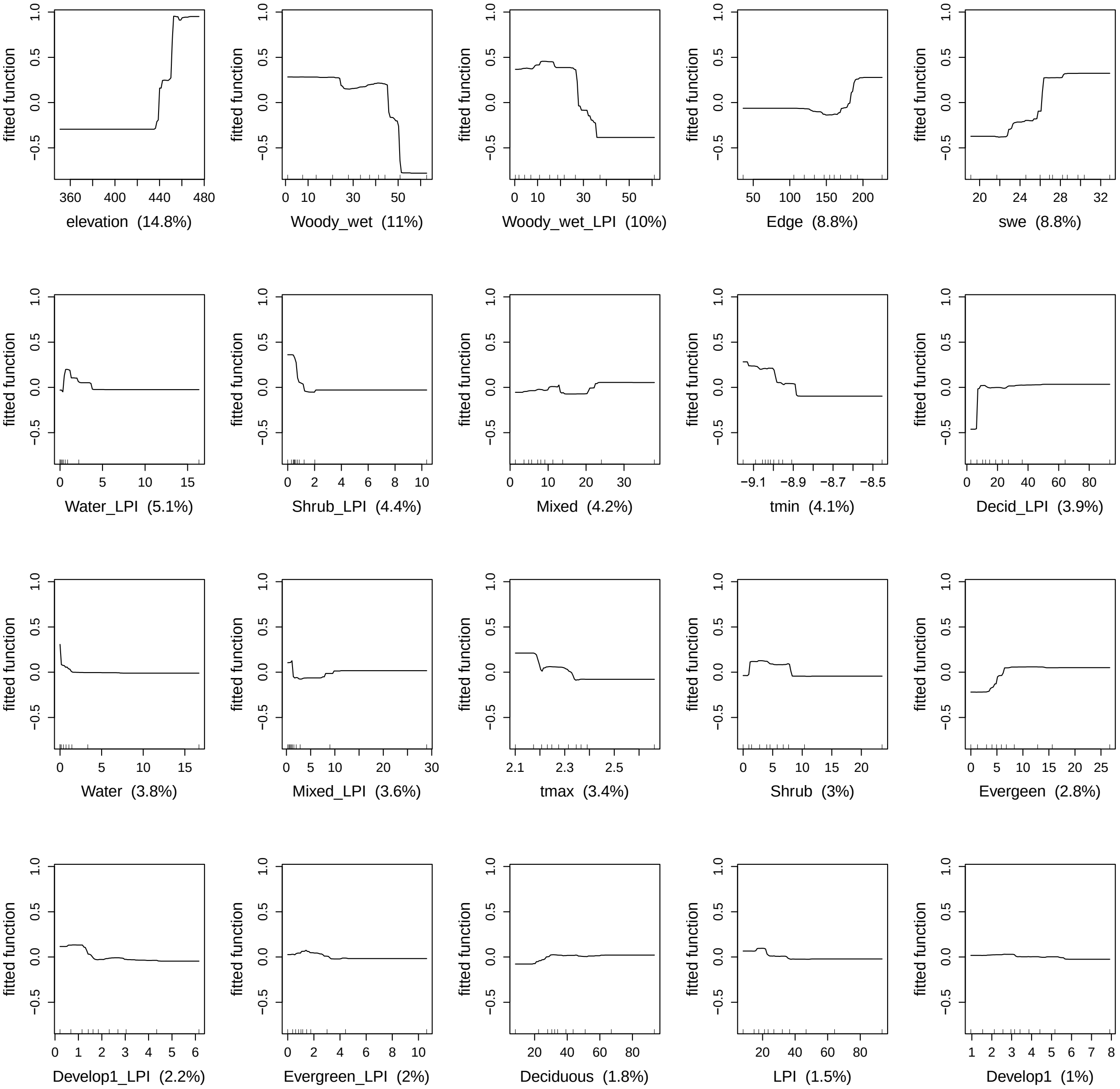

Figure S2. Fitted functions for CNF martens at the 5 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

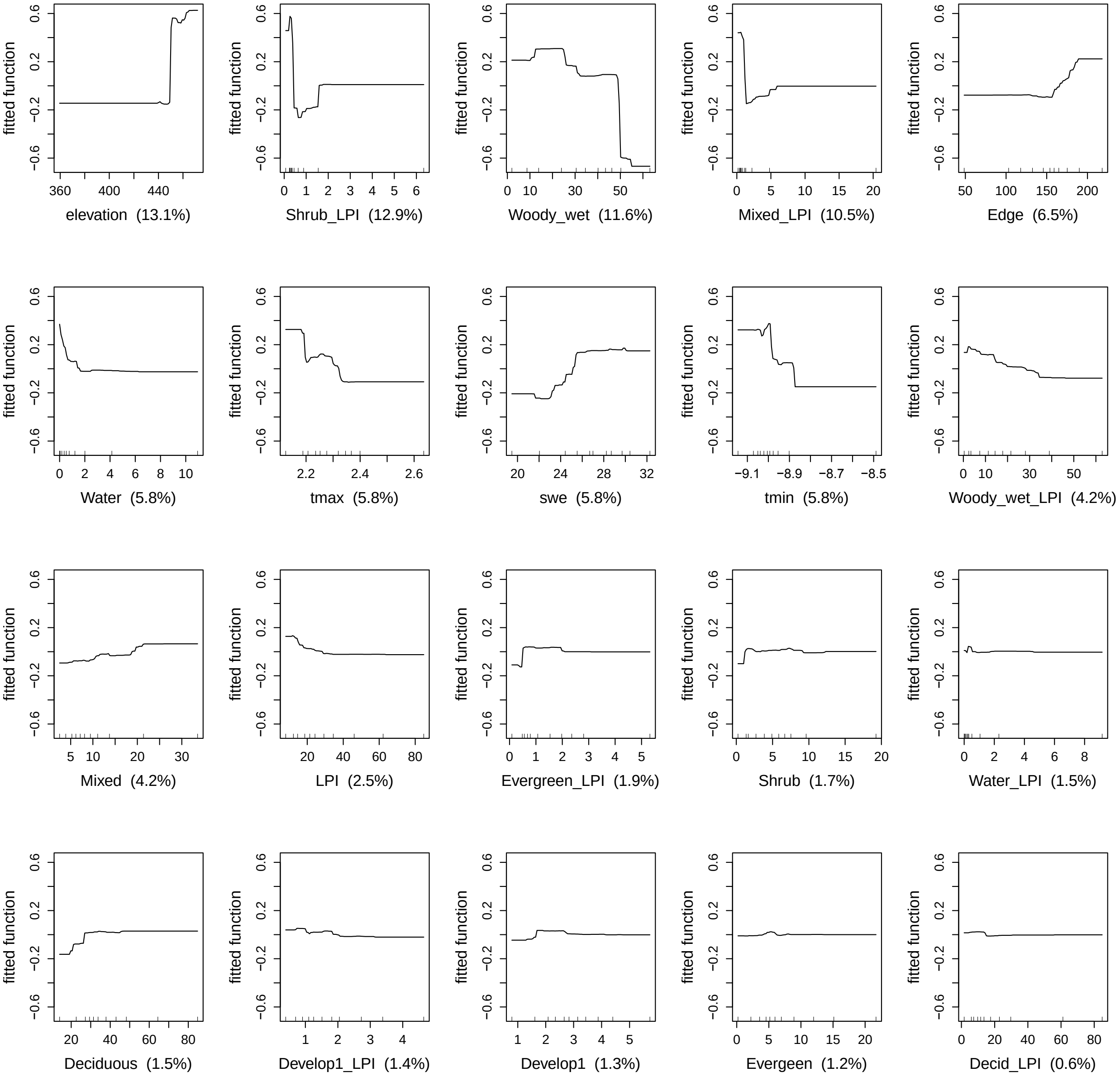

Figure S3. Fitted functions for CNF martens at the 10 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

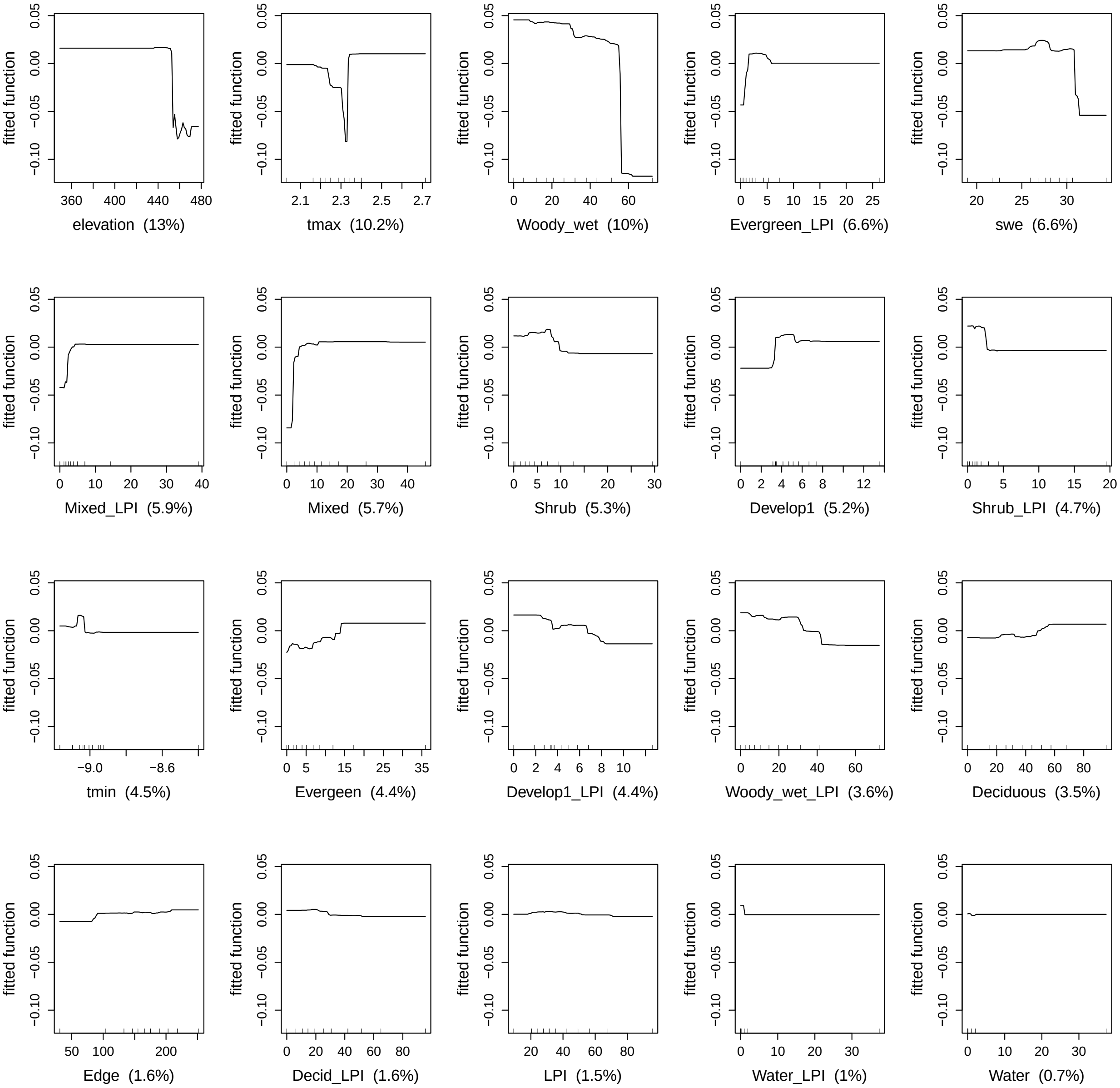

Figure S4. Fitted functions for CNF fishers at the 1 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

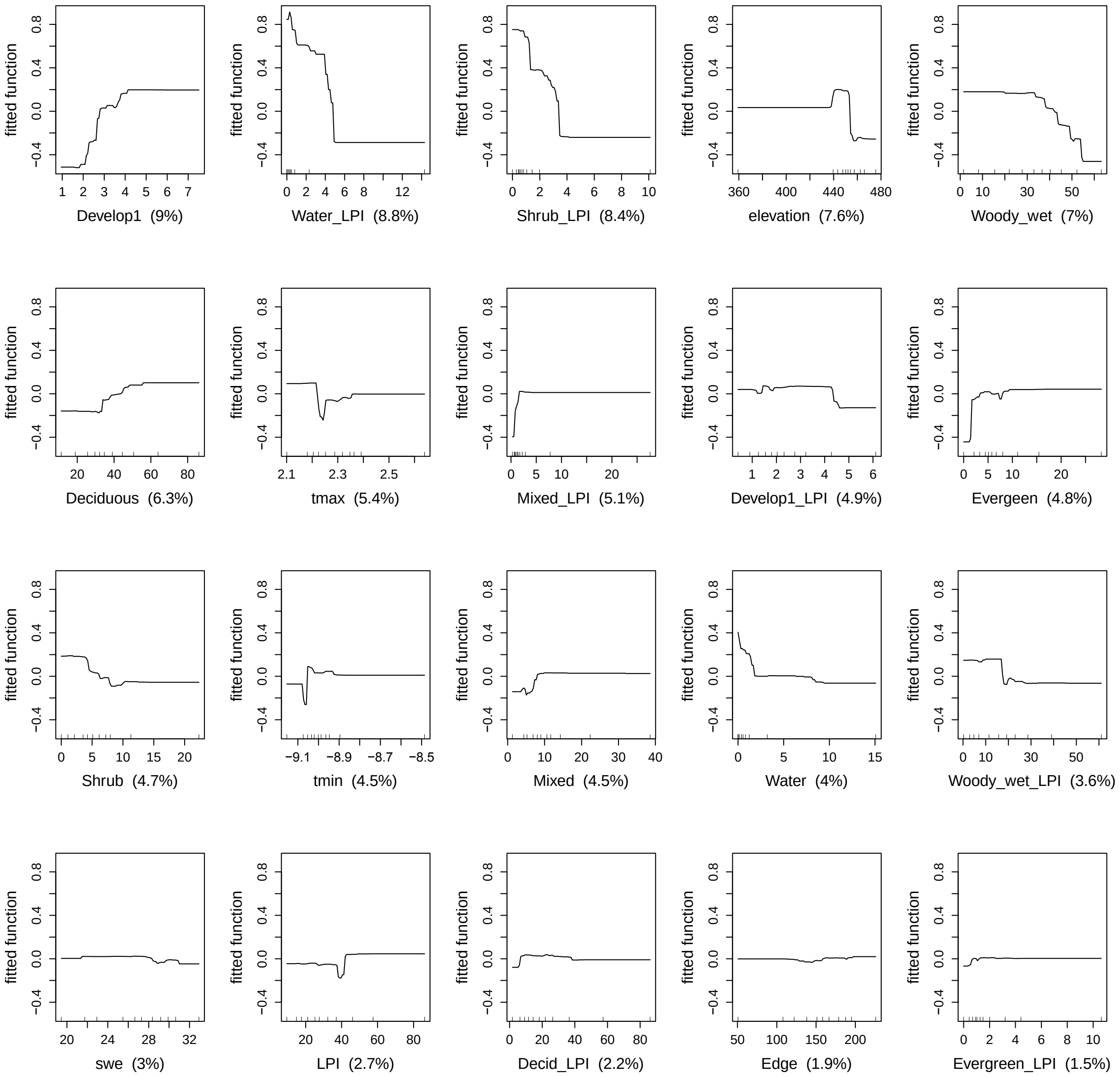

Figure S5. Fitted functions for CNF fishers at the 5 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

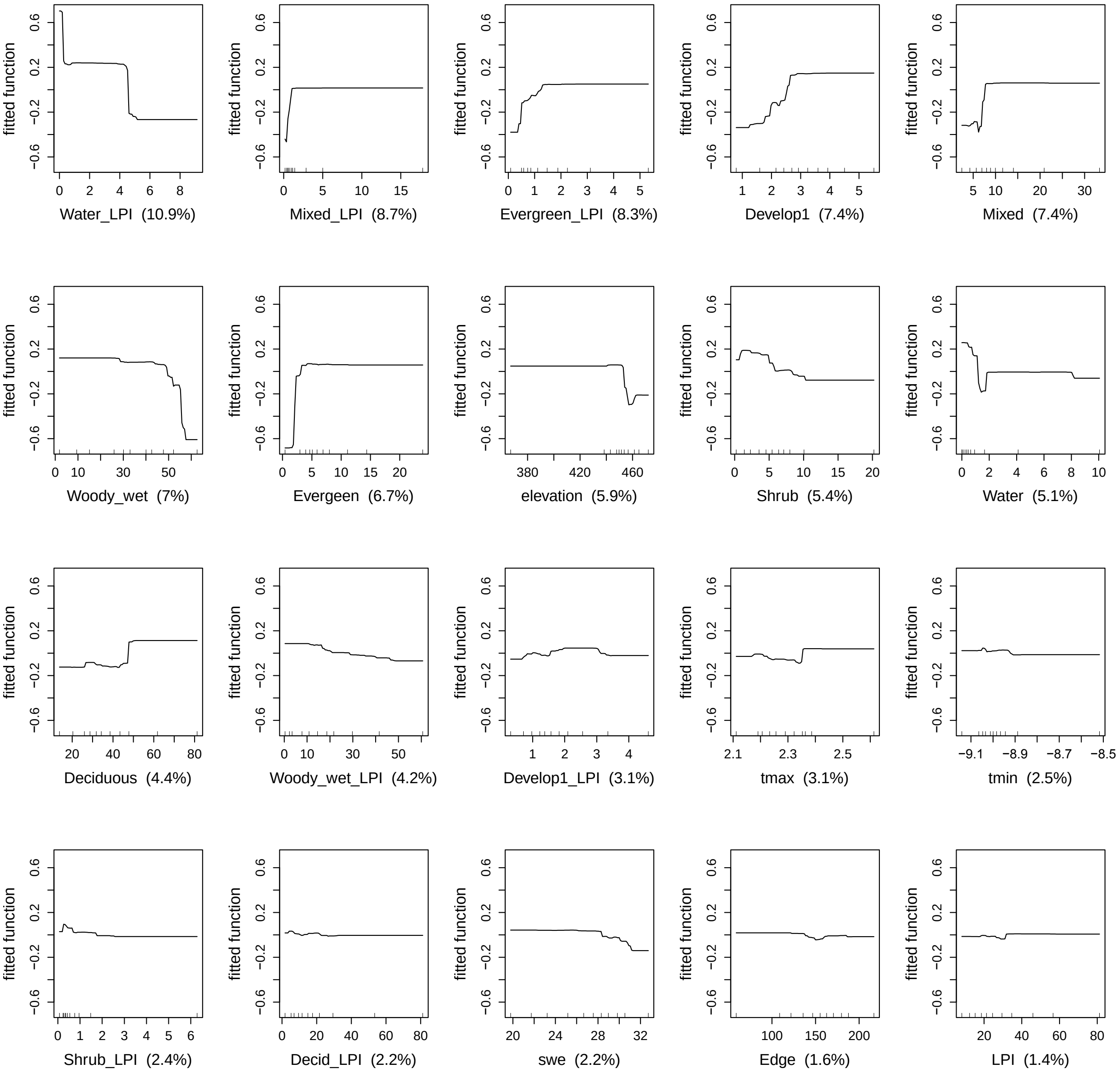

Figure S6. Fitted functions for CNF fishers at the 10 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

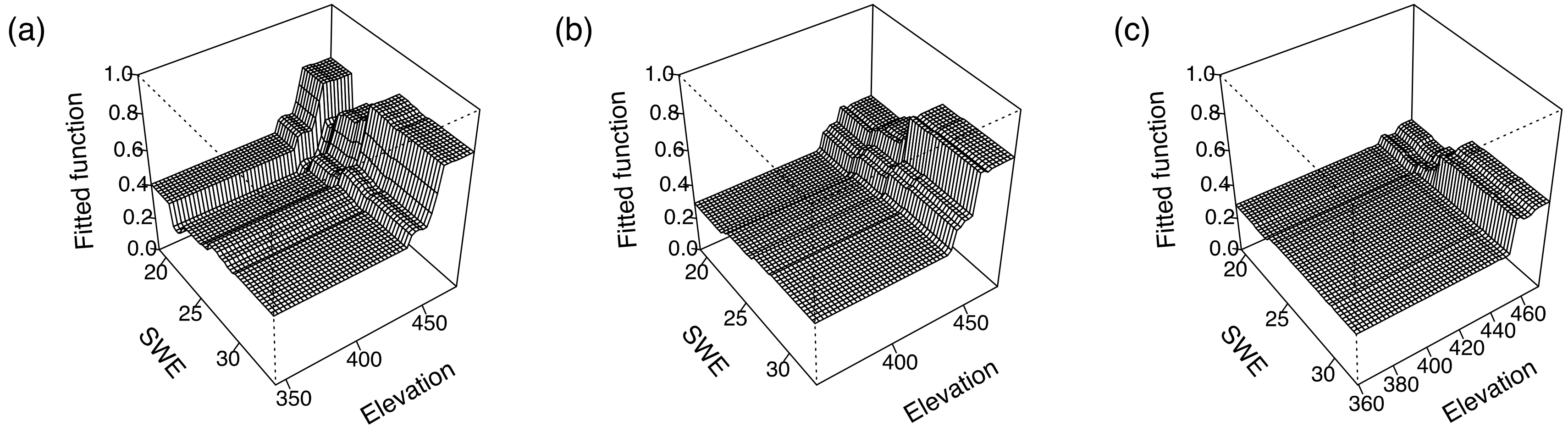

Figure S7. Fitted interaction between elevation (m), snow-water equivalent (in.), and marten occurrence (fitted function) in the CNF at the 1, 5, and 10 km^2 resolutions (a-c). High elevation (>450 m), high snow pack (>25 in.) sites yielded the highest probability of marten occurrence.

Appendix 2. Fitted relationships illustrating the effect of spatial predictors on marten and fisher detections in VNP at all scales (Figs S1-S6).

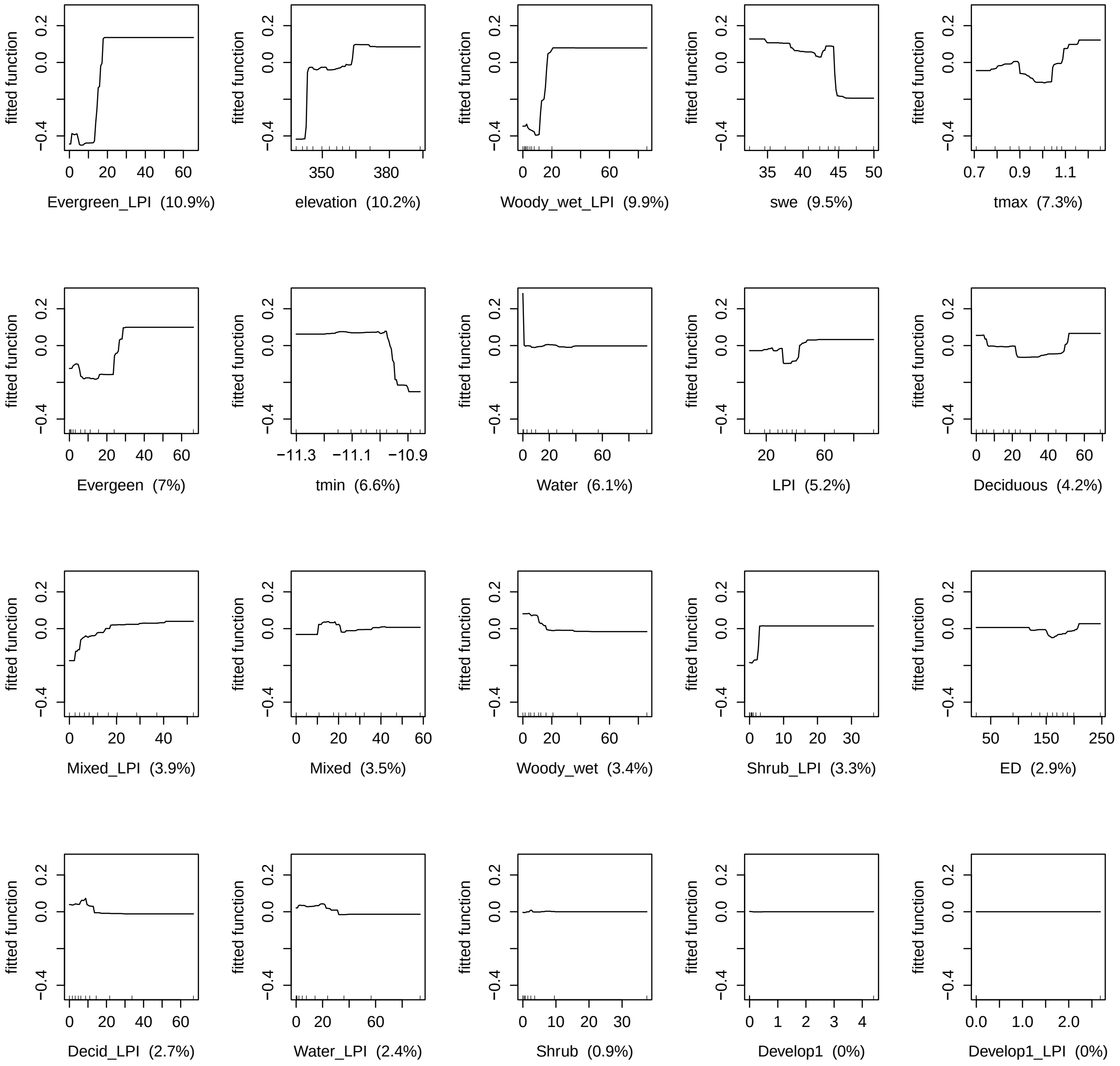

Figure S1. Fitted functions for VNP martens at the 1 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

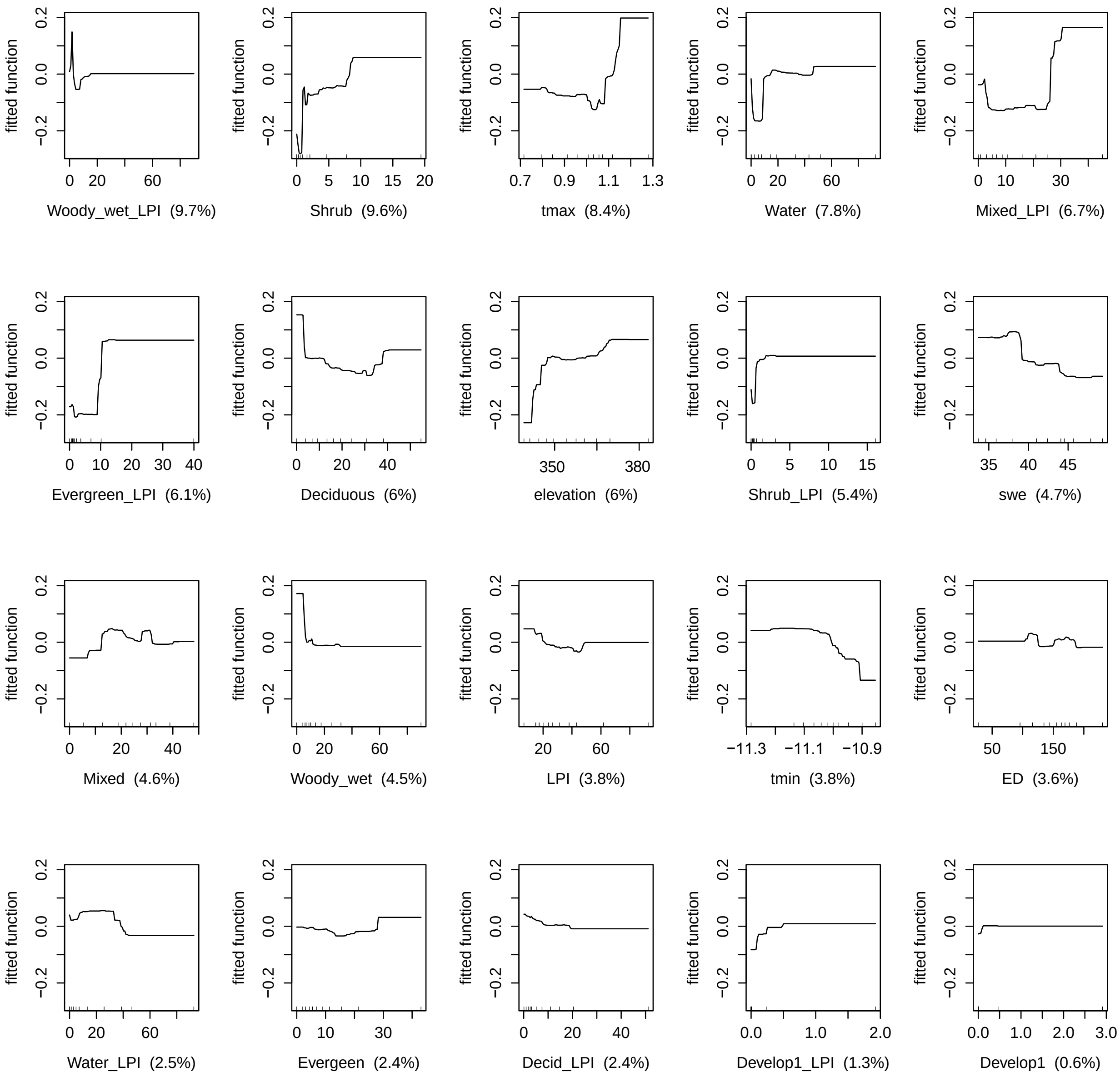

Figure S2. Fitted functions for VNP martens at the 5 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

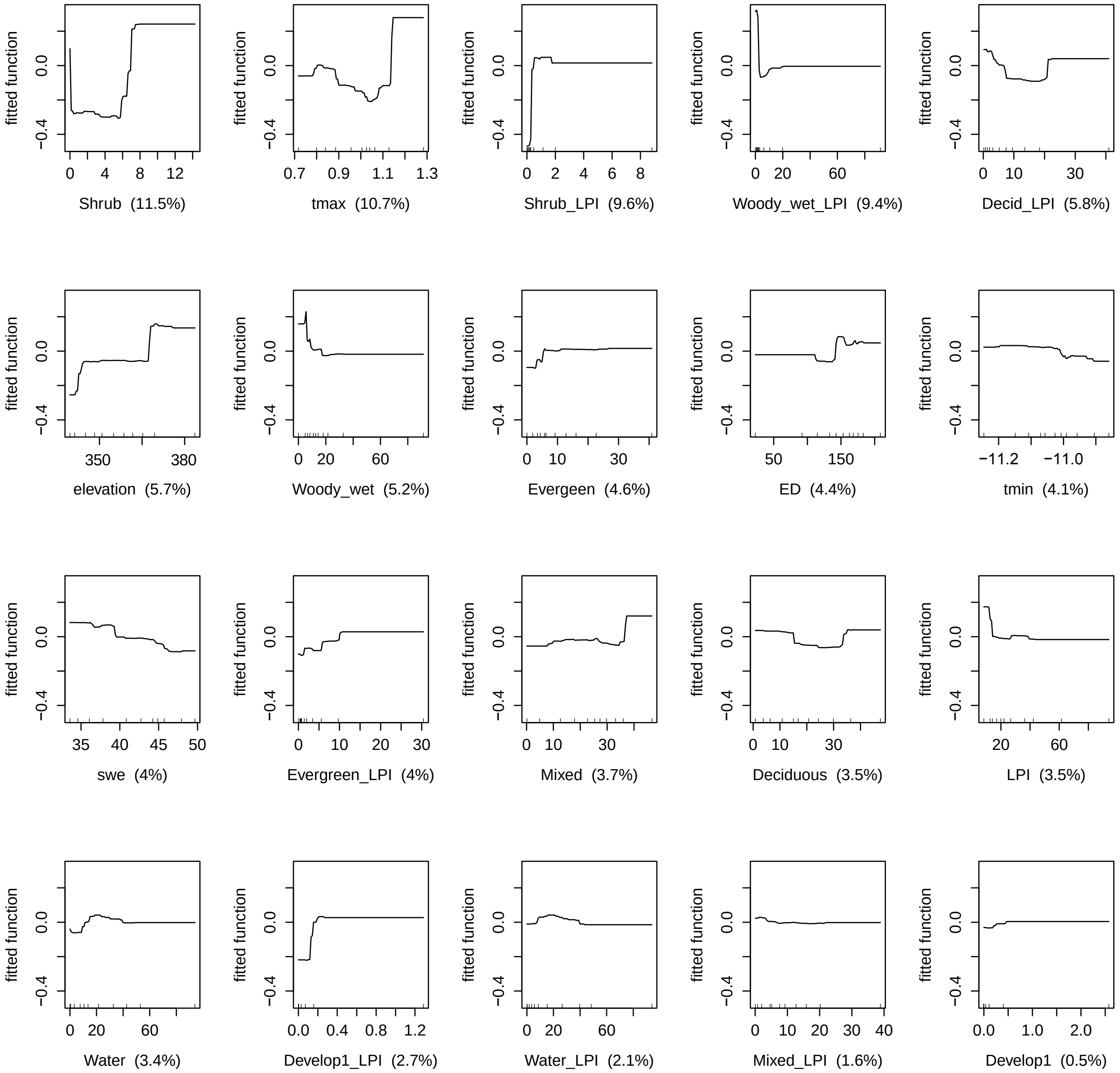

Figure S3. Fitted functions for VNP martens at the 10 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

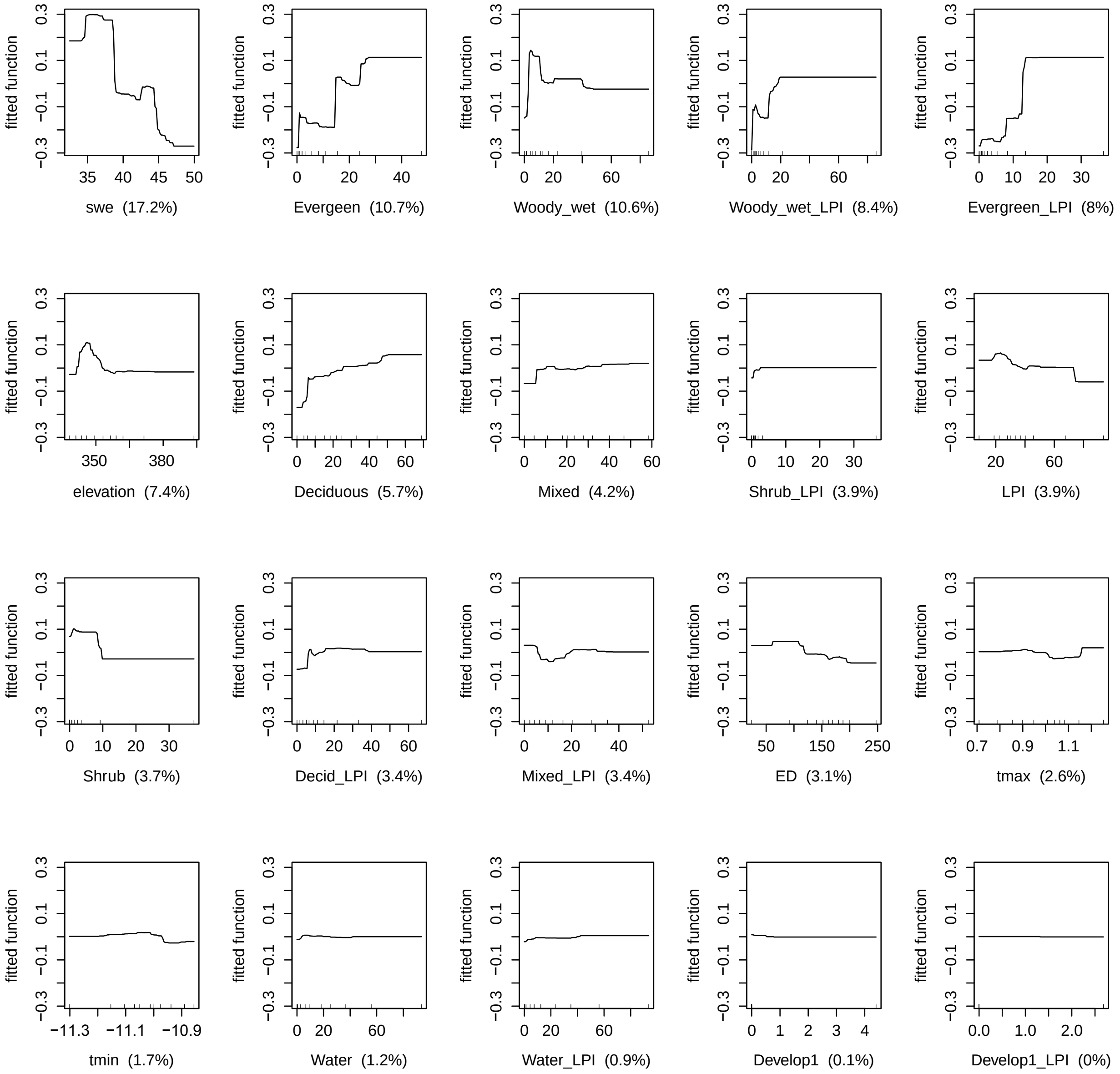

Figure S4. Fitted functions for VNP fishers at the 1 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

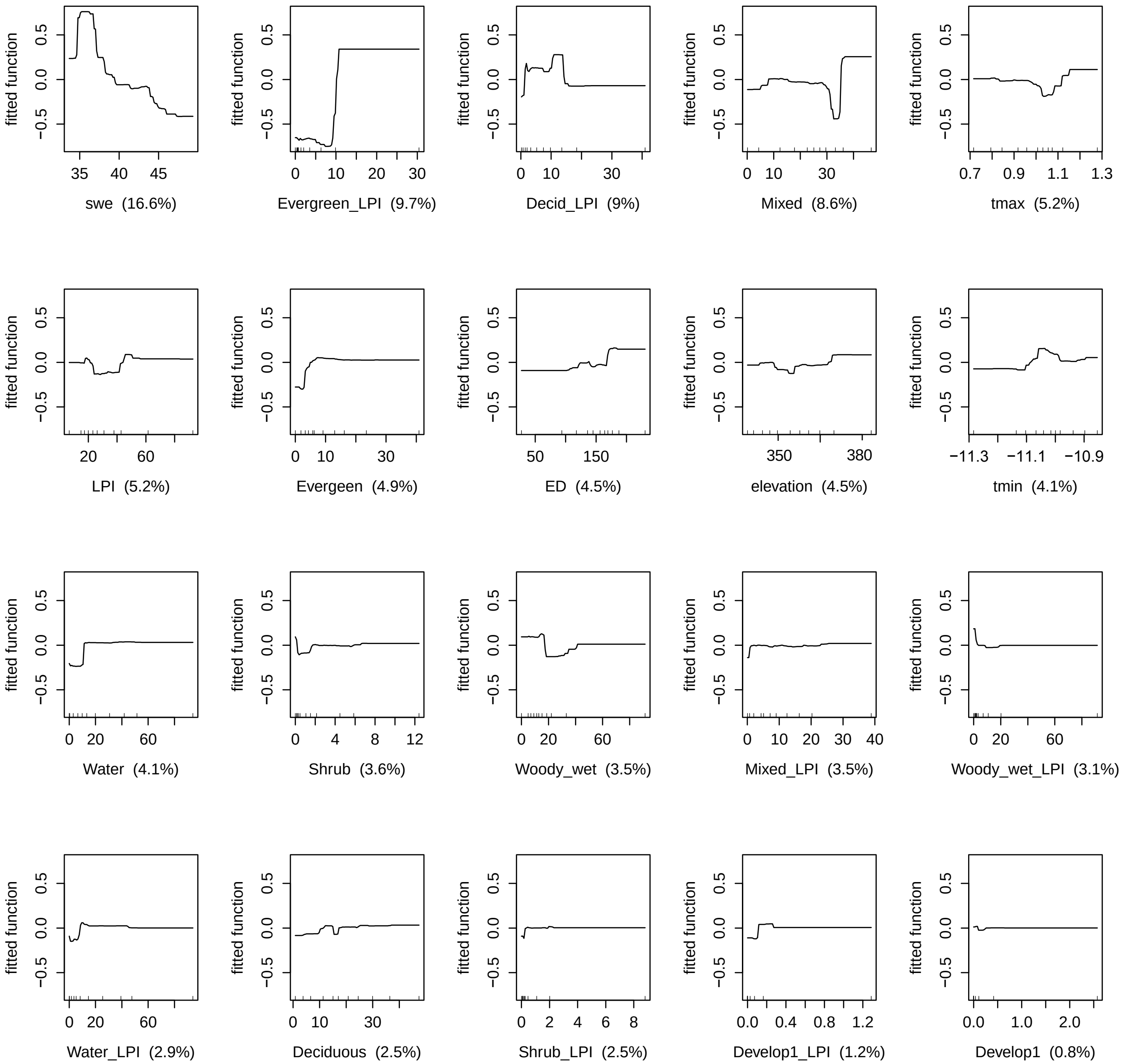

Figure S5. Fitted functions for VNP fishers at the 5 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

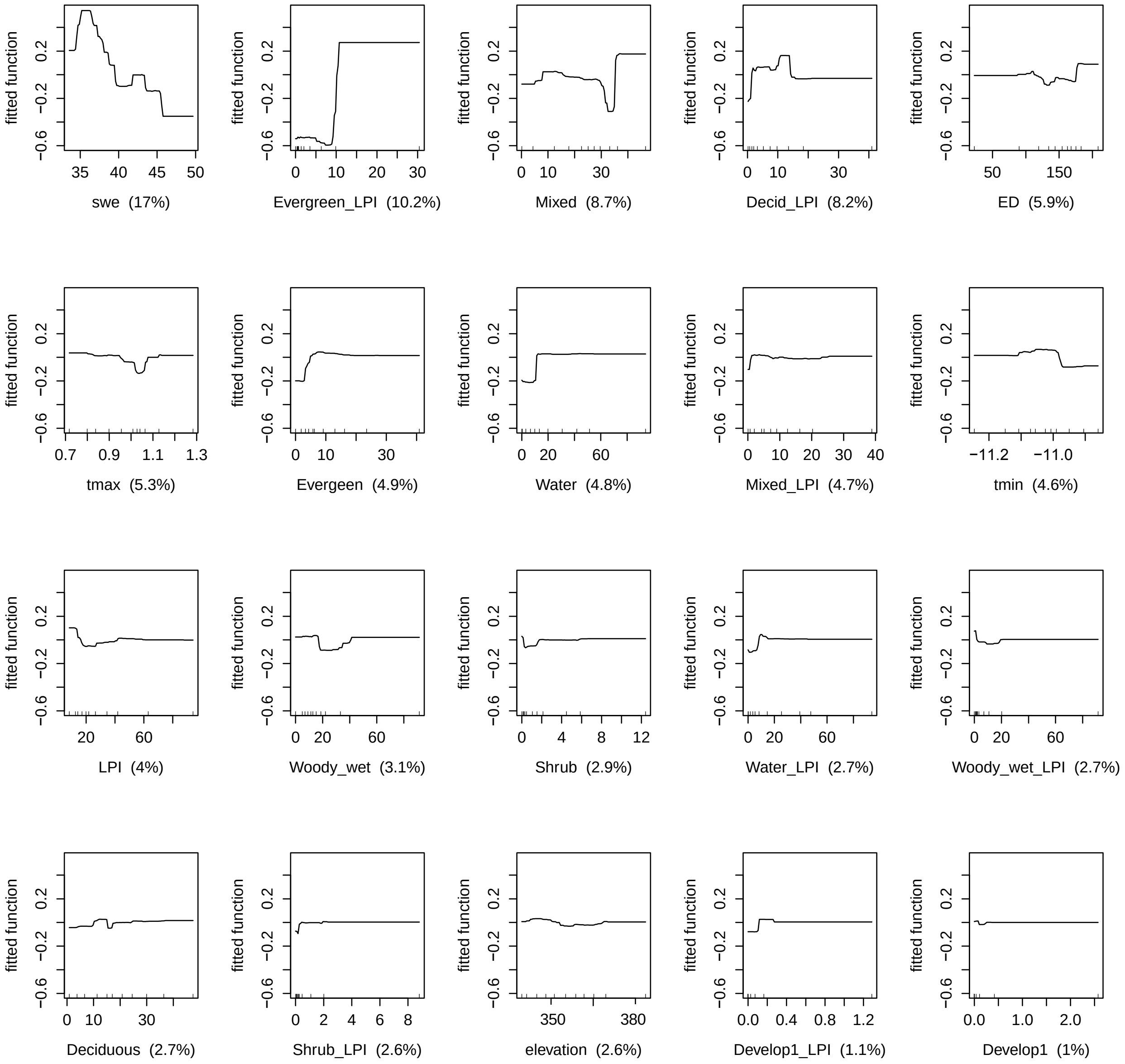

Figure S6. Fitted functions for VNP fishers at the 10 km^2 scale. The x-axes denote the 20 spatial predictors with relative influence (%) on marten occurrences, and the y-axes illustrate fitted function with positive relationships > 0 and negative relationships < 0.

Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations

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Abstract

1. Niche conservatism – the retention of ecological traits across space and time – is an emerging topic of interest because it can predict responses to global change. The conservation of Grinnellian niche characteristics, like species-habitat associations, has received widespread attention, but the conservation of Eltonian traits such as consumer-resource interactions remains poorly understood.
2. The inability to quantify Eltonian niches through space and time has historically limited the assessment of Eltonian niche conservatism and the dynamics of foraging across populations. Consequently, the relative influence of endogenous factors like phylogeny versus exogenous features like environmental context has rarely been addressed.
3. We tested Eltonian niche conservatism using a paired design to compare foraging among four populations of American (*Martes americana*) and Pacific martens (*Martes caurina*), morphologically and ecologically similar sister taxa that are allopatrically distributed throughout western North America. We developed a three-stage isotopic framework and then quantified dietary niche overlap between the sister species and paired island-mainland sites to assess the relative influence of endogenous (i.e., species) versus exogenous (i.e., environment) factors on Eltonian niches. First, we calculated pairwise dietary overlap in scaled δ-space using standard ellipses. We then estimated proportional diets ("p-space") for individuals using isotopic mixing models and developed a novel utilization distribution overlap approach to quantify proportional dietary overlap. Lastly, we estimated population-level proportional diets and quantified the differential use of functional prey groups across sites.

4. We detected no pairwise overlap of dietary niches in δ-space, and distributions of individual diets in p-space revealed little overlap in core diets across populations. All pairwise comparisons of individuals revealed significant differences in diet, and population-level comparisons detected contrasting use of functional prey groups.
5. We developed a multi-faceted isotopic framework to quantify Eltonian niches and found limited evidence of Eltonian niche conservatism across carnivore populations. Our findings are consistent with the growing recognition of dietary plasticity in consumers and suggest that consumer-resource dynamics are largely driven by exogenous environmental factors like land cover and community composition. These results illustrate the context-dependent nature of foraging and indicate consumer functionality can be dynamic.

Keywords: Alaska, British Columbia, foraging, functional roles, *Martes*, niche conservatism, predator restoration

Introduction

Ecologists have long been fascinated by trait differences across populations and species (MacArthur 1972). As one of the most influential concepts in ecology, niche theory has been central to identifying causes of ecological divergence among taxa (Chase & Leibold 2003). More recently, the retention of ecological traits across space and time – niche conservatism – has emerged as a primary interest of ecologists (Wiens & Graham 2005). Niche conservatism helps explain the structure of biodiversity gradients (Allen & Gillooly 2006; Buckley *et al.* 2010) and improves predictions of species' responses to global change (Pearman *et al.* 2008; Cooper, Freckleton & Jetz 2011) and species invasions (Wiens & Graham 2005). Moreover, niche conservatism is a fundamental assumption of many species distribution models used to map Grinellian niches, the non-interactive, environmental aspects of a species' range (Grinnell 1917). Consequently, Grinellian niches have been the primary focus of ecological niche conservatism and a renewed interest in species-habitat associations (Peterson et al., 2011). Similarly, Phylogenetic niche conservatism, or the retention of ancestral ecological traits among related taxa, has also received widespread attention, shedding light on community assembly and the adaptability of species across systems (Losos 2008; Cooper, Freckleton & Jetz 2011). Meanwhile, biotic interactions have remained a cornerstone of ecology (Chase & Leibold 2003), yet the conservation of consumer-resource dynamics defined by the Eltonian niche (Elton 1927) has remained relatively understudied (Olalla-Tárraga *et al.* 2016; Rosado *et al.* 2016). Given the importance of such trophic dynamics for ecological processes (Estes *et al.* 2011), understanding the role of Eltonian niche conservatism and the capacity for adaptability will be key to both preserving and restoring ecosystem functions in the face of continuing global change.

Re-establishing trophic interactions has become a global ecological priority (Dobson *et al.* 2006; Estes *et al.* 2011), and the restoration of predators has been proposed to both preserve ecosystem functionality (Ritchie *et al.* 2012) and promote biodiversity (Terborgh 2015). In particular, the re-establishment of mammalian carnivores is increasingly promoted to restore ecosystem functionality, largely through the transference of consumer-resource dynamics and top-down forcing (Ritchie *et al.* 2012; Ripple *et al.* 2014). Restoring these functional relationships among consumers, however, remains challenging (Fraser *et al.* 2015), mostly due to the dynamic nature of foraging ecology and the inability to quantify trophic interactions through space and time. Indeed, such predator-driven ecological restoration hinges on Eltonian niche conservatism and the preservation of consumer-resource dynamics, but these processes remain poorly understood.

Eltonian niche conservatism is governed by foraging ecology, which is generally a function of climate, land cover, and biotic interactions (Stephens, Brown & Ydenberg 2007). At the site level, climate often determines primary productivity, land cover composition, and species richness (MacArthur 1972; Chapin III, Matson & Vitousek 2011), which in turn regulates resource availability. At the individual level, climate and land cover influence activity levels by altering foraging rates and metabolic costs (Kearney, Shine & Porter 2009). Similarly, biotic interactions like predation and competition interact with climate and land cover to modify resource accessibility and alter foraging dynamics (Darimont, Paquet & Reimchen 2009). Given the number of exogenous factors influencing foraging ecology across scales, the conservation of Eltonian niches has been unsurprisingly both supported (Böhning-Gaese & Oberrath 1999) and contested (Olalla-Tárraga *et al.* 2016).

While Grinellian and phylogenetic niche conservatism have been widely observed in mammals (Peterson, Soberón & Sánchez-Cordero 1999; Cooper, Freckleton & Jetz 2011; Olalla-Tárraga *et al.* 2011), idiosyncratic patterns of divergence and conservatism have been observed across carnivore clades, including felids, canids, and mustelids (Buckley *et al.* 2010; Diniz-Filho *et al.* 2010). Nevertheless, Grinellian niche axes are correlated with resource availability, suggesting that Eltonian niches are also conserved in both space and time (Soberón 2007). Indeed, Olalla-Tárraga et al. (2016) observed Eltonian niche conservatism in mammals at broad phylogenetic scales; however, carnivores exhibited the weakest response of all mammalian orders and limited dietary information led to contrasting conclusions. Recent fine-scale analyses have similarly revealed remarkable foraging plasticity among carnivore species (Darimont, Paquet & Reimchen 2009; Newsome *et al.* 2015), suggesting exogenous drivers like land cover and competition may regulate Eltonian niches rather than phylogeny. Consequently, functional roles coupled to foraging may be similarly dynamic, with important consequences for ecological processes across ecosystems.

To assess Eltonian niche conservatism, we examined the diets of two generalist and closely related carnivores in northwestern North America: American (*Martes americana)* and Pacific martens (*M. caurina*). These mustelids are recently diverged sister taxa that possess comparable morphological and ecological characteristics and occupy similar land cover types across western North America (Dawson *et al.* 2017). Though isolated for millennia, both species occur throughout the Pacific Northwest, with American martens predominating in mainland populations to the north and Pacific martens occupying coastal regions to the south (Dawson *et al.* 2017). In addition, complex colonization histories have led to sporadic distributions of both species throughout the archipelagic systems of Alaska and British Columbia (Pauli *et al.* 2015). Like many North American carnivores, both marten species are forest habitat specialists but dietary generalists (Martin 1994). Moreover, both species are sensitive to land-use change and regularly compete with other carnivores, both of which are hypothesized to affect foraging dynamics (Manlick *et al.* 2017; Zielinski, Tucker & Rennie 2017).

To quantify Eltonian niche conservatism in American and Pacific martens we developed a novel stable isotope framework. Measuring Eltonian niches has long troubled ecologists and the inability to accurately assess biotic interactions like foraging across space and time has resulted in the Eltonian shortfall (Rosado *et al.* 2016) and limited estimates of Eltonian niche conservatism (Olalla-Tárraga *et al.* 2016). However, stable isotope analyses have emerged as an ideal tool to quantify Eltonian niches because they measure the assimilation of resources in consumer tissues and capture biotic interactions that are mediated by foraging (Newsome *et al.* 2007; Larson, Olden & Usio 2010; Comte, Cucherousset & Olden 2016). Herein, we use stable isotope analyses to assess differences in foraging across species and environmental context by estimating the diets of American and Pacific martens on mainland and island sites in the Pacific Northwest of North America that differ in biotic interactions (i.e. carnivore richness), dominant land cover, and level of human disturbance (Fig. 1). Specifically, we developed a three-stage isotopic framework that compared Eltonian niches across populations by calculating: 1) pairwise dietary overlap in isotopic δ-space; 2) individual diets using isotopic mixing models and pairwise niche overlap using a novel implementation of utilization distribution overlap indices in proportional dietary space; and 3) pairwise differences in the proportional use of functional prey groups using population-level diets from isotopic mixing models.

Materials and Methods

Study areas

We compared diets of American and Pacific marten populations in a 2×2 paired design of mainland and island sites (Fig. 1). Mainland populations included Misty Fjords National Monument, Alaska (hereafter, Mainland *americana*) and Oregon Dunes National Recreation Area (hereafter, Mainland *caurina*). Island populations included Prince of Wales Island, Alaska (hereafter, Island *americana*) and Haida Gwaii Islands (formerly Queen Charlotte Islands; hereafter, Island *caurina*). All populations were coastal, and potential exogenous drivers of foraging such as prey, competitors, and land cover composition were similar across sites (Supporting Information, Tables S1-S2). Prey groups were largely conserved across sites, and each population had access to 5 primary prey known to support martens: small mammals, birds, deer, berries, and marine-derived resources (Martin 1994). Conversely, carnivore richness, which has the potential to mediate foraging through competitive interactions, did differ by location and was higher at mainland than island sites (Fig. 1; Supporting Information, Table S1), enabling inferences on biotically mediated foraging differences across populations. Estimates of prey availability and predator abundance data were not available for this study. Mainland *americana*, Island *americana*, and Island *caurina* sites are composed of temperate, coastal rainforests characterized by dense, old-growth forest. The southern-most site, Mainland *caurina*, features sand dunes and wetlands bounded by ericaceous shrubs with a broader landscape dominated by xeric conifer forests. However, the dominant land cover at the Mainland *caurina* site was impervious surfaces (Fig. 1), indicating substantial human impacts.

Sampling

We collected all hair samples from martens within 2 km of the coast to ensure every individual had access to the same primary prey groups. Samples were collected in fall and winter using active capture techniques (Moriarty *et al.* 2016) and trapper harvested samples (Pauli *et al.* 2015) (Supporting Information, Table S2). Hair is an inert tissue that represents diet over the period it was synthesized, and peak marten hair growth occurs from July through October (Pauli *et al.* 2009). Therefore, our samples represent the assimilated diets of martens in autumn. Prey samples were collected opportunistically from each site or derived from the literature (Supporting Information, Table S2). In total, we sampled all primary prey groups (small mammals, birds, deer, berries, and marine-derived resources) at each site. All sampling adhered to the ethical guidelines established by the American Society of Mammalogists (Sikes 2016), was approved by the University of Wyoming and USDA Forest Service's Institute for Animal Care and Use

Committee (USFS 2015-002), and was permitted by the Oregon Department of Fish and Wildlife (ODFW 119-15), Alaska Department of Fish and Game (ADFG 06-016) and British Columbia Ministry of the Environment.

Stable isotope analyses

Marten and prey hair samples were rinsed 3× with a 2:1 chloroform:methanol solution to remove surface contaminants, homogenized with surgical scissors, and dried at 56°C for a minimum of 72 h. Similarly, all vegetation, marine, and tissue samples were rinsed 3× with a 2:1 chloroform:methanol solution and dried at 56°C for 72 h, but samples were subsequently homogenized with either a ball mill mixer or mortar and pestle. Samples were weighed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis on a Costech 4010 elemental analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V mass spectrometer at the University of New Mexico Center for Stable Isotopes. Results were calculated as parts per mil (‰) ratios relative to the international standards Vienna Peedee Belemnite (C) and atmospheric nitrogen (N).

To assess isotopic niche overlap in δ-space and identify the comparability of isoscapes, we employed a multi-response permutation procedure (MRPP) using 10,000 iterations in the R package *vegan* (Oksanen *et al.* 2013) to test for differences in means and variances among functional prey groups. Because raw δ values of prey groups differed significantly across all sites, and comparisons across variable isoscapes can be misleading (Newsome *et al.* 2012), we trophically-corrected all marten isotopic signatures ($\delta^{13}C = -2.6$; $\delta^{15}N = -3.4$; *Vulpes vulpes*; Roth and Hobson 2000) and scaled them to their respective mixing spaces, resulting in a unitless, multidimensional isoscape that enabled inter-population comparisons (see Cucherousset & Villéger 2015 for details). To assess dietary niche overlap between sites, we calculated isotopic niches for each population using standard ellipses corrected for sample size (SEA_C) and quantified SEA_C overlap in δ-space using the R package SIAR (Parnell *et al.* 2010). We then employed a MRPP in using 10,000 iterations to test for pairwise differences in the means of scaled isotopic values between marten populations.

To estimate the proportional dietary contributions for each population we first identified prey groups using a K nearest-neighbour randomization test (Rosing, Ben-David & Barry 1998) to differentiate prey items within each site, and we then compared across locations to identify the finest resolution of prey groups consistent across sites. This resulted in three isotopically distinct (all pairwise $P < 0.05$) functional prey groups that were available to martens in each population: berries, marine-derived resources, and terrestrial vertebrates. Isotopic signatures of songbirds, deer, and small mammals were indistinguishable from one another and aggregated to comprise the terrestrial vertebrates group. Likewise, salmon, crabs, and intertidal mollusks dominated marine-derived prey, while berries segregated as a single group. We estimated dietary proportions using Bayesian-based isotopic mixing models in SIAR (Parnell *et al.* 2010), and we estimated individual diets using the ‘siarsolomcmcv4’ model and population-level diets using the ‘siarmcmcdirichletv4’ model. All models incorporated concentration dependence using the mean elemental concentrations for each prey group, were corrected for trophic enrichment of marten samples (as above; Roth & Hobson 2000), and incorporated only uniform prior distributions. Each model ran 200,000 iterations, with an additional 25% burn-in, and was sampled 10,000 times.

To quantify dietary overlap in p-space, we used mean dietary proportions estimated for each individual and employed an isometric log-ratio transformation to convert compositional diets into Cartesian coordinates suitable for multivariate analyses (Egozcue *et al.* 2003). Using the transformed dietary estimates we generated 50% and 95% kernel density estimates of dietary distributions for each population and then calculated proportional overlap of diets and the pairwise utilization distribution overlap index (UDOI; *sensu* Fieberg and Kochanny 2005) in dietary p-space using the R package *adehabitatHR* (Calenge & Fortmann-Roe 2013). With this framework, 50% UDOIs represent the overlap of "core" diets, while 95% UDOIs represent overlap of "available" dietary resources for each population (Fieberg & Kochanny 2005). Estimates of overlap range from zero (no overlap) to one (complete overlap) and are akin to the Hurlbert index of niche overlap (Fieberg & Kochanny 2005). We then tested for significant differences in proportional diets between populations using the transformed diet estimates and pairwise MRPPs with 10,000 iterations.

Lastly, we assessed pairwise differences in functional prey groups using the posterior distributions of population-level diets estimated in SIAR. Following Hopkins et al. (2014), we extracted the marginal posterior distributions for each diet item per site and calculated the probability that populations consumed different proportions of functional prey groups. For each comparison we created two new distributions, $Y = X1_{ij} – X2_{ik}$ and $Z = X2_{ik} – X1_{ij}$, where $X1_{ij}$ is the marginal posterior distribution for diet item *i* in population *j* and $X2_{ik}$ is the marginal posterior distribution for diet item *i* in population *k*. To identify significant differences in prey use between sites we then calculated the two-sided probability that the difference between marginal posterior distributions Y and Z was less than zero, given by $P(Y < 0) + P(Z > 0)$ (see Hopkins et al., 2014 for details). This test is analogous to a t-test and significance was assessed at $\alpha = 0.05$, 0.01, and 0.001.

Results

We sampled 158 American martens, 65 Pacific martens, and 296 prey items across all 4 sites (Table 1). Using scaled isotopic values, we detected no overlap in SEA_C between any pairwise comparisons in δ-space (Fig. 2). Similarly, permutation tests detected significant differences ($P < 0.05$) in scaled isotopic signatures for all comparisons (Fig. 2).

Utilization distribution overlap indices revealed little to no overlap in core diets (0.0 – 0.10, 50% UDOI; Table 2, Fig. 3), but high overlap in available diets (95% UDOI) for *M. americana* and island populations (Table 2). Moreover, percent overlap of dietary distributions in p-space was high (> 50%) for the majority of comparisons (Table 2). Nevertheless, pairwise MRPPs detected significant differences in the distribution of individual diets for all pairwise comparisons (Fig. 3).

Proportional diets of individuals and populations indicated that, in general, mainland marten populations exhibited specialized diets dominated by terrestrial vertebrates, while island populations exhibited generalist tendencies with evenly distributed use of prey groups (Table 1, Figs 3-4). Pairwise comparisons of prey use across populations were widely idiosyncratic, but we detected more significant differences in prey use between species than between island and mainland sites (Fig. 4). We detected little divergence in use of terrestrial vertebrates (all populations ≥30% use), and both mainland populations exhibited > 50% reliance on this resource (Table 2, Fig. 3). All populations displayed ≥ 30% use of marine-derived resources, except for Mainland *caurina* where the limited use of marine prey (12%) drove all significant differences among comparisons, including the only significant difference between *M. caurina* populations (Fig. 3). Likewise, the consumption of berries was highly variable (9.8-36.2%) and exhibited significant differences in 3 of 4 pairwise comparisons, including the only significant difference in *M. americana* populations.

Discussion

We employed a series of stable isotope analyses to quantify Eltonian niches across marten populations in the Pacific Northwest and our analyses revealed little dietary niche overlap across populations. We detected no overlap in isotopic δ-space, limited overlap of core diets in p-space, and highly variable use of functional prey groups across populations. All analyses detected significant differences between populations. These findings suggest that martens in the Pacific Northwest exhibit little Eltonian niche conservatism across either species or sites. Our study is one of few to explicitly assess Eltonian niche conservatism, and the first to assess fine-scale Eltonian niches as a function of endogenous vs. exogenous drivers (Larson, Olden & Usio 2010; Comte, Cucherousset & Olden 2016; Olalla-Tárraga *et al.* 2016). Nevertheless, our results are consistent with recent studies illustrating the plasticity of mammalian dietary niches (Terry, Guerre & Taylor 2017) and the lack of niche conservatism among carnivores in particular (Buckley *et al.* 2010; Diniz-Filho *et al.* 2010).

Eltonian niches are notoriously difficult to quantify (Rosado *et al.* 2016), and qualitative measures of dietary breadth have previously led to contrasting evidence of Eltonian niche conservatism in mammals (Olalla-Tárraga *et al.* 2016). We developed an isotopic framework using complimentary analyses of isotopic δ-space and dietary p-space to clearly illustrate the variable nature of foraging across carnivore populations. Numerous studies assess isotopic niche overlap in δ-space or calculate proportional diets, but few combine these approaches to quantitatively assess diet variability. Moreover, quantifiable metrics of dietary *overlap* in p-space are nascent (Newsome *et al.* 2007; Parnell *et al.* 2010). Our approach quantifies overlap in both isotopic niches and dietary proportions, and it can be used to quantify dietary differences between populations or species through space and time. Indeed, while we implemented this framework to assess dietary overlap and measure Eltonian niche conservatism across four populations with similar environmental contexts, analogous approaches could be used to quantify niche overlap in competitors, shifts in diets through time, or foraging dynamics following anthropogenic disturbance.

While our approach employed three complimentary analyses, each has important limitations. For example, when comparing isotopic signatures of consumers in δ-space across ecosystems, dietary relationships can be skewed by isoscape variability (Newsome *et al.* 2012). We accounted for such differences in isoscapes by standardizing each population to its own isotopic mixing space (Cucherousset & Villéger 2015), but this assumes all prey species are accounted for and that the total isotopic variability of the site has been captured. Despite our extensive prey sampling, it is unlikely that we captured the entire isotopic landscape. However, transforming isotopic signatures to p-space via mixing models removes the potential scaling discrepancies present in δ-space (Newsome *et al.* 2007). Moreover, mixing models allowed us to estimate proportional diets for martens and then determine p-space overlap using a novel UDOI approach traditionally used to quantify spatial overlap. Analogous to home range analyses, dietary overlap from UDOI may be sensitive to sample sizes and the parameters defining kernel density estimates (Erran & Powell 1996; Fieberg & Kochanny 2005), but this approach allows for quantitative estimates of p-space overlap via methods familiar to most ecologists. Similarly, quantifying the differential use of prey via posterior distribution overlap provides a clear and tractable analytical approach analogous to a t-test. Nevertheless, these analyses rely on mixing models with important constraints. For instance, our functional prey groups exhibited considerable linearity at each site, resulting in negative correlations between posterior probabilities of dietary proportions for both individual and population-level diet estimates (Supporting Information, Figs S1-S2). This means there were multiple solutions to each mixing model, though there was little variation in posterior probabilities for most models (Fig. 4) suggesting dietary estimates were consistent despite collinearity in prey isotope signatures. It is worth noting, however, that model uncertainty and variation in posterior probabilities could reduce power to detect differences in diets between populations. Additionally, trophic discrimination factors can influence estimates from mixing models (Phillips *et al.* 2014), and species-specific discrimination factors were unavailable for this study. However, our applied enrichment factor has been widely used to estimate carnivore diets (Yeakel *et al.* 2009; Darimont, Paquet & Reimchen 2009; Carlson *et al.* 2014) and falls within the predicted range for martens (Healy *et al.* 2018). Despite these nuances, we implemented three independent approaches to quantify dietary overlap and observed equivalent results, thereby reinforcing our conclusions and the power of these complimentary analyses. Ultimately, this framework provides a blueprint for future ecologists to quantitatively test dietary differences in space and time.

We found limited evidence for Eltonian niche conservatism and pairwise diet comparisons revealed tradeoffs in the use of resources across populations. For instance, all individuals were sampled within 2 km of the Pacific coast, yet Mainland *caurina* martens displayed a significantly lower use of marine resources compared to other sites but compensated with the highest consumption of berries. Unlike the other locations, vegetation in the Mainland *caurina* site typically does not extend to the shoreline, and allochthonous marine resources (e.g. salmon) have been severely depleted (Nehlsen, Williams & Lichatowich 1991). Thus, Mainland *caurina* individuals were confined to vegetated areas (Linnell *et al.* 2018) and access to marine resources was likely limited to inlets and seasonal flooding. Moreover, the 13 Mainland *caurina* individuals sampled constitute up to a quarter of all individuals in this isolated population (Linnell *et al.* 2018), but the area harbors over a dozen competing carnivores that could have also prevented access to marine resources. Indeed, while mainland populations generally relied on terrestrial vertebrates, island populations exhibited more generalist diets, likely due to lower carnivore richness and reduced interspecific competition for alternative resources (*sensu* Darimont et al., 2009). Island *caurina*, the site with the lowest carnivore richness, displayed nearly uniform dietary proportions, while both mainland sites exhibited high carnivore richness and skewed dietary proportions in martens (Table 2, Fig. 3). These results indicate that exogenous environmental factors like prey availability (e.g. allochthonous resources) and competition may have a stronger influence on foraging ecology than phylogeny, with landscape composition likely mediating foraging through competition, resource availability, and access to resources. Our work aimed to quantify dietary overlap and niche conservatism, and therefore did not explicitly quantify underlying environmental factors like competition, prey availability, or fine-scale habitat use that influence carnivore foraging. Nevertheless, pairwise overlap of individual diet distributions and 95% UDOIs indicated that the dietary space “available” to each population was similar, with > 50% overlap in both metrics observed for the majority of comparisons (Table 2). Future studies should further assess the relationship between landscapes, prey availability, and competition in order to test the relative strengths of these drivers on foraging and dietary niche plasticity.

While we detected significant differences in diets across populations, we also found that marten diets differed more between species (*M. americana* vs. *M. caurina*) than between environmental contexts (islands vs. mainland). These results suggest that the Eltonian niches of martens could in part be conserved phylogenetically. For example, island populations differed in their use of berries and terrestrial vertebrates, while mainland populations differed in use of berries and marine prey. Conversely, *M. americana* diets differed only in the use of berries and *M. caurina* diets differed only in use of marine prey, though uncertainty in the mainland *caurina* diet estimates may have limited our power to detect such differences. Nevertheless, we observed significant differences in the use of functional prey groups across all comparisons and this variation could have considerable implications for the functional roles of carnivores across ecosystems. Indeed, given the ability of martens to disperse seeds (Willson 1993) and marine-derived nutrients (Ben-David, Hanley & Schell 1998), as well as regulate disease and invasive species through small mammal predation (Hofmeester *et al.* 2017; Sheehy *et al.* 2018), such differences in population-level diets could translate to important differences in functional roles across sites. Moreover, limited isotopic variability and knowledge on prey availability required the use of highly generalized prey groups for our analyses, but martens across their distributions have been shown to specialize on a wide range of species including cricetids (e.g., mice, voles), snowshoe hares (*Lepus americanus*), and even deer (Raine 1987; Zielinski & Duncan 2004; Carlson *et al.* 2014). While we detected extensive use of terrestrial vertebrates, it is possible that martens across our sampled populations further differed in their use of specific prey items. Likewise, seasonal and inter-annual variation in resources, along with increases in anthropogenic subsidies, can have similar effects on foraging (Ben-David, Flynn & Schell 1997; Newsome *et al.* 2015), indicating that the functional roles of carnivores are likely regulated by exogenous environmental factors rather than endogenous, phylogenetic constraints.

Ecologists have historically viewed carnivores, including martens, as habitat and resource specialists (Rosenzweig 1966), but the global recovery of carnivores across diverse landscapes has questioned this paradigm (Pauli, Donadio & Lambertucci 2018). We observed highly variable diets across marten populations, and our findings are consistent with recent studies illustrating widespread dietary plasticity among carnivores across ecosystems (Davis *et al.* 2015; Newsome *et al.* 2015; Smith, Wang & Wilmers 2016). For example, cougars (*Puma concolor*) in the Intermountain West have exhibited isotopic niche shifts from historical specialization to contemporary semi-generalization following changes in land use (Moss *et al.* 2016), while even highly specialized carnivores like black-footed ferrets (*Mustela nigripes*) have demonstrated surprising levels of dietary plasticity (Brickner *et al.* 2014). Moreover, our results reinforce the growing body of literature showing that exogenous factors like resource availability and competition regulate foraging ecology and niche plasticity in both apex and mesopredators (Darimont, Paquet & Reimchen 2009; Newsome *et al.* 2015; Smith, Wang & Wilmers 2016). Nevertheless, ecologists often assume that the functional roles of carnivores are conserved across ecosystems and clades. Consequently, the restoration of carnivores has been promoted as a means to re-establish trophic relationships and lost functional roles (Ripple *et al.* 2014), and many efforts target carnivore recovery with the explicit goal of resurrecting lost trophic relationships (Donlan 2005) or interactions observed in different landscapes (Ripple *et al.* 2011). However, such strategies are contingent upon Eltonian niche conservatism and trophic stationarity, and our results suggest that Eltonian niches and functional roles are not conserved, even among closely related species in comparable ecosystems. Consequently, these findings suggest that foraging dynamics and the realized functional roles of carnivores may not be transferable across ecosystems, presenting additional complexity to calls for carnivore-driven restoration efforts.

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Data Accessibility

All isotopic signatures are available at https://figshare.com/articles/Manlick_et_al_2018_FigShare_xlsx/7252994.

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Tables

Table 1. Mean estimated dietary proportions of functional prey groups for each sampled marten population (with 95% confidence intervals).

Site	Prey group	Dietary Proportion (%)
Island *americana* (*n* = 98)	Berries (*n* = 45)	25.2 (20.5-29.9)
	Marine-derived (*n* = 25)	32.5 (28.9-36.1)
	Terrestrial vertebrates (*n* = 37)	42.4 (36.5-48.3)
Mainland *americana* (*n* = 55)	Berries (*n* = 21)	9.8 (2.7-16.7)
	Marine-derived (*n* = 7)	38.3 (28.8-47.1)
	Terrestrial vertebrates (*n* = 34)	51.9 (40.1-64.7)
Island *caurina* (*n* = 52)	Berries (*n* = 20)	34.8 (28.3-41.2)
	Marine-derived (*n* = 5)	34.9 (31.4-38.5)
	Terrestrial vertebrates (*n* = 17)	30.3 (22.5-38.7)
Mainland *caurina* (*n* = 13)	Berries (*n* = 14)	36.2 (14.9-52.6)
	Marine-derived (*n* = 3)	12.1 (0.0-26.4)
	Terrestrial vertebrates (*n* = 55)	51.7 (22.5-81.5)

Table 2. Estimated Eltonian niche overlap of marten populations in proportional dietary space via utilization distribution overlap indices for core dietary space (50% UDOI) and available dietary space (95% UDOI). In addition, total overlap of 95% kernel density diet estimates (percent overlap) was estimated for Island *americana* (IA), Mainland *americana* (MA), Island *caurina* (IC), and Mainland *caurina* (MC) populations. IA/MA arrangement indicates the percent of Island *americana* diets overlapping Mainland *americana* diets followed by the percent of Mainland *americana* diets overlapping Island *americana* diets, with codification maintained for all comparisons.

Comparison	50% UDOI	95% UDOI	Percent overlap
Americana (IA/MA)	0.07	0.73	87.4/61.7
Caurina (IC/MC)	0.00	0.03	12.8/52.3
Island (IA/IC)	0.10	0.96	66.3/89.5
Mainland (MA/MC)	0.00	0.08	12.8/100

Figures

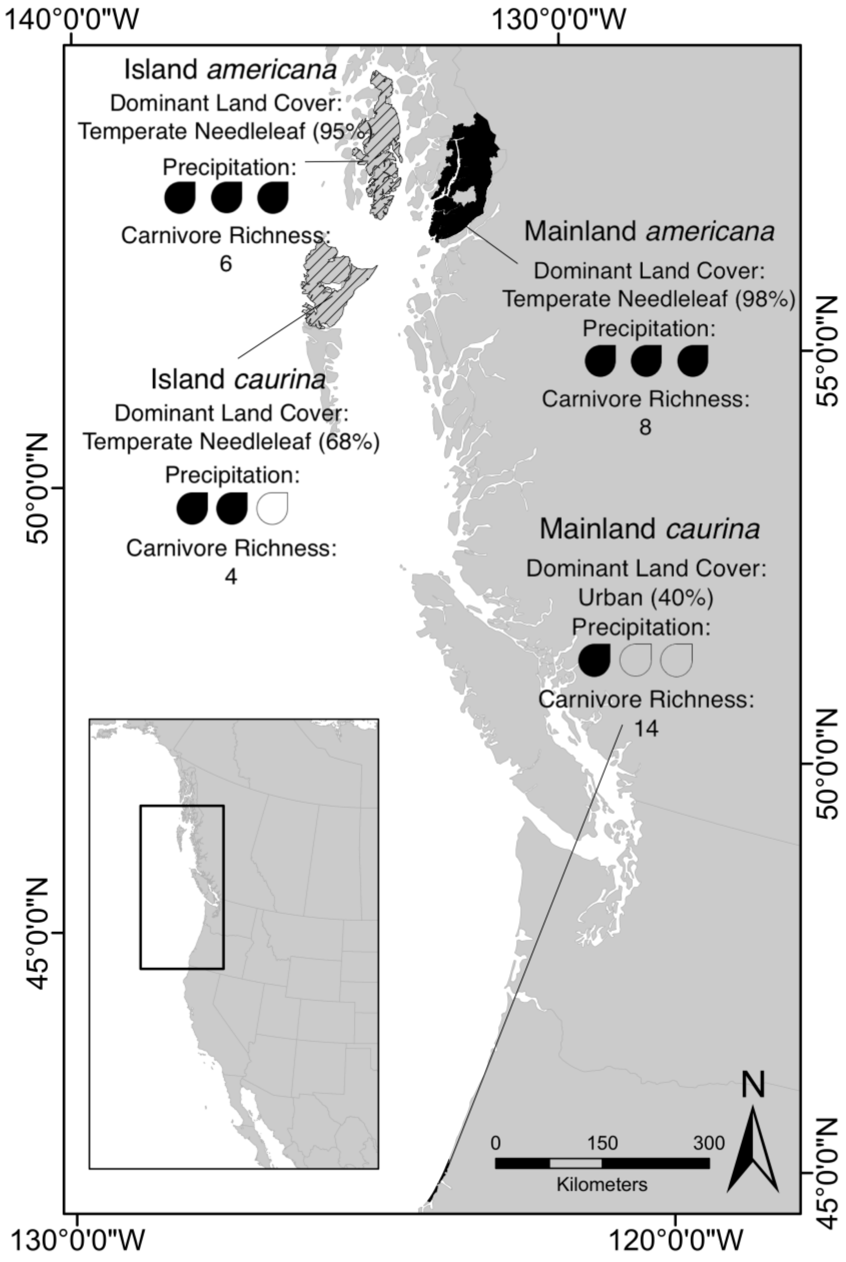

Figure 1. Comparison between mainland and island species of marten, including dominant land cover, precipitation level, and carnivore richness values. Cross-hatched regions show where *Martes americana* is present, while black regions show where *M. caurina* is present. Three raindrops indicate high levels of precipitation (>170 mm/month) and one raindrop indicates low levels of precipitation (<140 mm/month). Carnivore richness is measured by the number of carnivores present in the area.

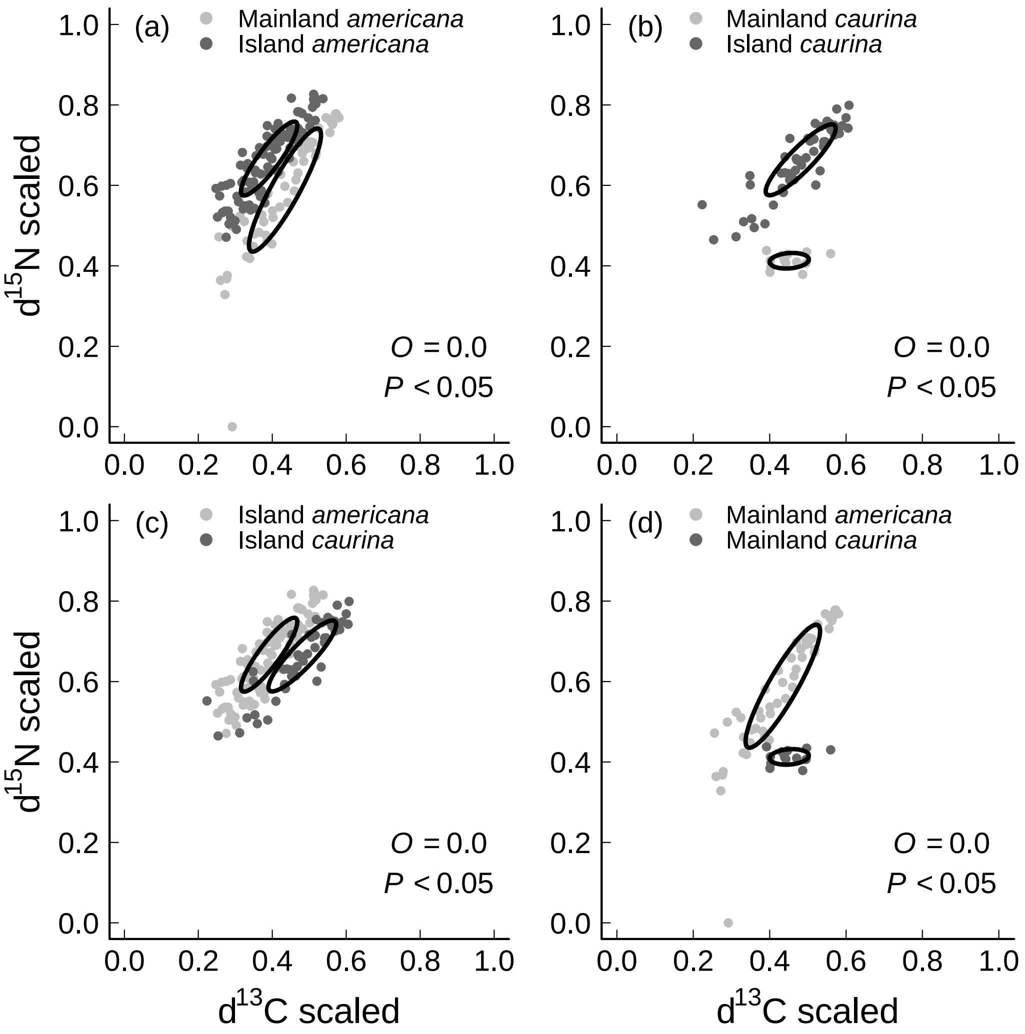

Figure 2. Niche overlap in corrected δ-space for *Martes americana* (a), *M. caurina* (b), island martens (c), and mainland martens (d) from 4 study sites in northwestern North America. Pairwise isotopic niche overlap (*O*) among standard ellipses corrected for small sample size (SEA_C; black) was zero for all comparisons. *P*-values indicate significance of a multi-response permutation procedure (MRPP) comparing the distribution of individuals in corrected δ-space.

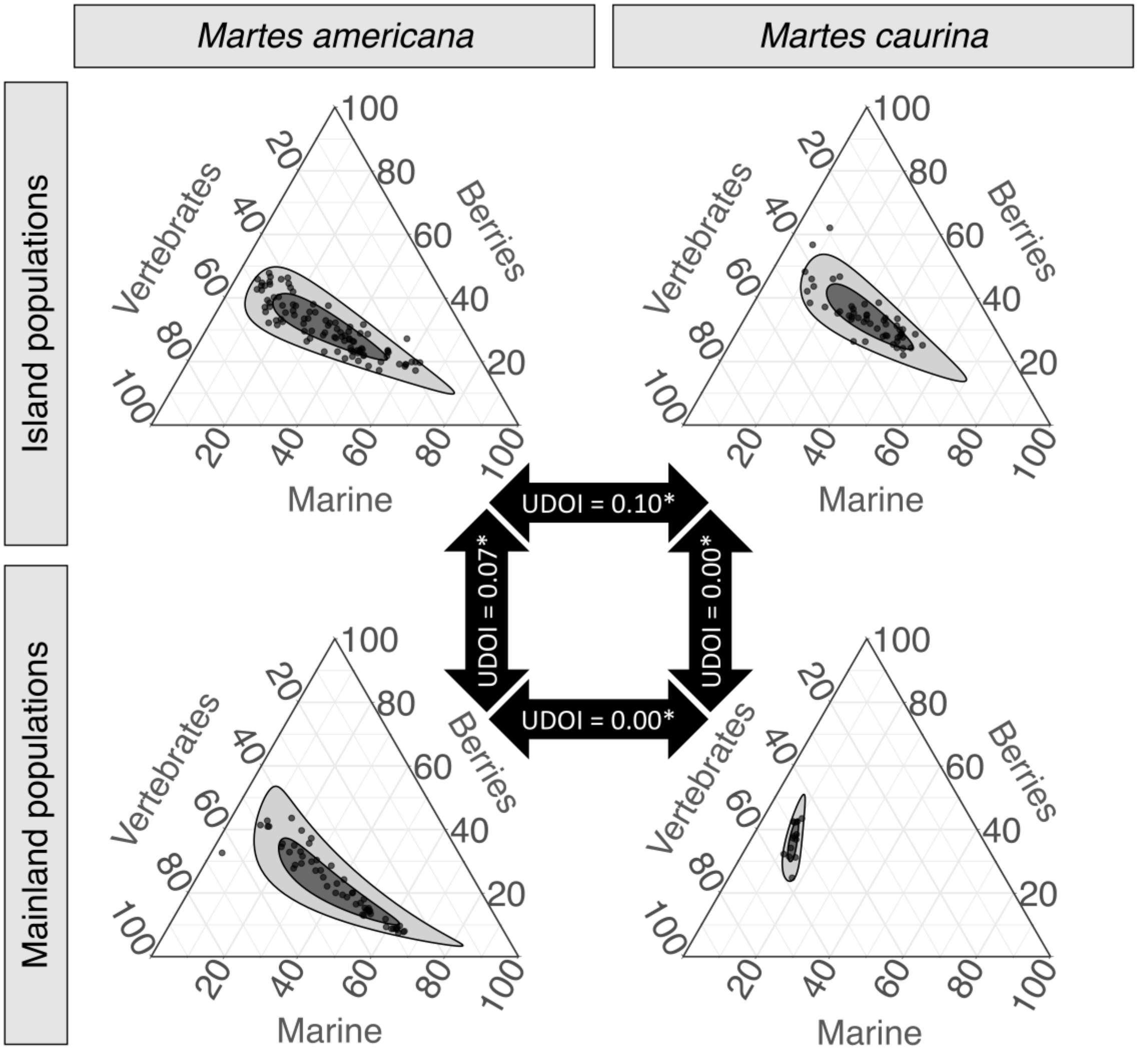

Figure 3. Ternary plots of proportional dietary space for *Martes americana* and *M. caurina* populations using individual dietary estimates from isotopic mixing models. Axes denote proportion (%) of each functional prey group estimated for each population, points denote estimated individual diets, dark grey polygons denote 50% confidence intervals for the population, and light grey polygons denote 95% confidence intervals for the population. Inset arrows show pairwise utilization distribution overlap indices of core diets (50% UDOI) ranging from no overlap (0.0) to complete overlap (1.0), and asterisks indicate significance ($\alpha = 0.05$) of a multi-response permutation procedure (MRPP) comparing the distribution of estimated proportional diets for individuals.

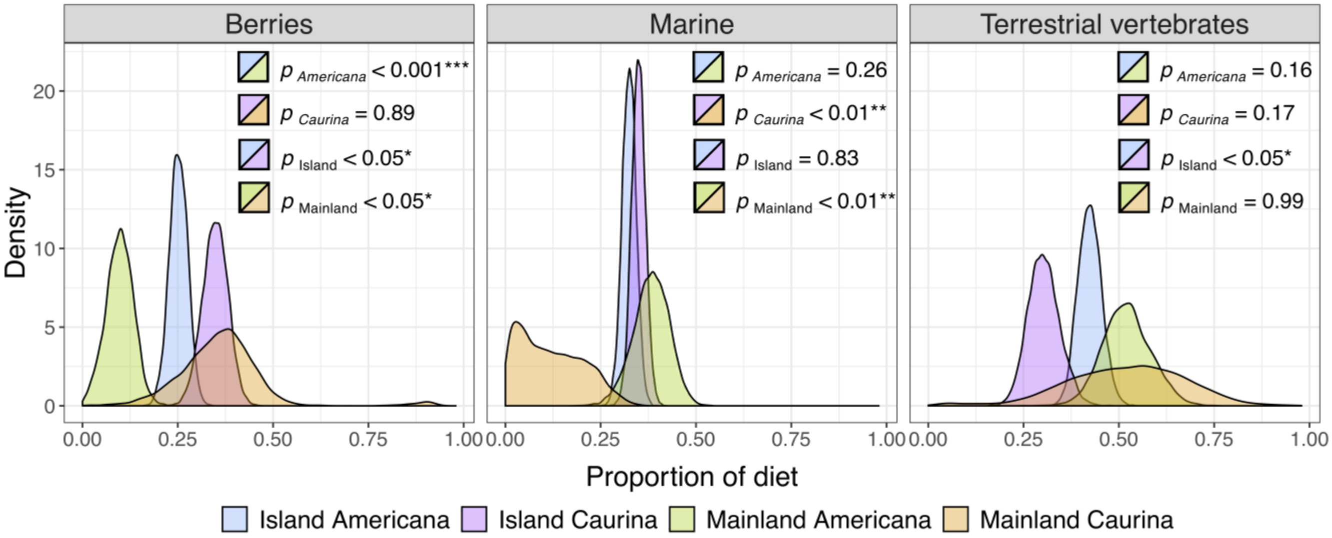

Figure 4. Posterior distributions of berries, marine-derived resources, and terrestrial vertebrates estimated for sampled American (*Martes americana*) and Pacific (*M. caurina*) populations using Bayesian-based isotopic mixing models. Inset p-values denote results of t-tests quantifying differences in posterior distributions between mainland and island *M. americana* ($P_{Americana}$), mainland and island *M. caurina* ($P_{Caurina}$), island *M. americana* and island *M. caurina* (P_{Island}), and mainland *M. americana* and *M. caurina* ($P_{Mainland}$). Significance was assessed at $\alpha = 0.05$ (*), 0.01 (**), and 0.001 (***).

Supporting Information

Appendix S1, Tables S1-S2, Figures S1-S2

Appendix S1: Study sites

Mainland *americana*, Island *americana*, and Island *caurina* sites are composed of temperate, coastal rainforests characterized by dense, old-growth forest dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Alaska cedar (*Cupressus nootkatensis*) and Sitka spruce (*Picea sitchensis*). Each site has a thick understory dominated by devil's club (*Oplopanax horridus*), evergreen huckleberry (*Vaccinium ovatum*), and skunk cabbage (*Lysichiton americanus*). The southern-most site, Mainland *caurina*, features sand dunes and wetlands bounded by ericaceous shrubs such as salal (*Gautheria shallon*), evergreen huckleberry (*Vaccinium ovatum*), and Pacific rhododendron (*Rhododendron macrophyllum*), with a broader landscape dominated by lodgepole pine (*Pinus contorta*) and late-successional Sitka spruce, and Douglas fir (*Pseudotsuga menziesii)* forests. The dominant land cover at the Mainland *caurina* site was urban (i.e., impervious surfaces; Fig. 1), indicating significant human impacts. Sites also differed abiotically along climactic gradients (Fig. 1; Supporting Information, Table S1). Nevertheless, available prey was largely conserved across sites, with berries (e.g., blueberry [*Vaccinium cyanococcus*], devil's club [*Oplopanax horridus*], and salmonberry [*Rubus spectabilis*]), small mammals (*Microtus* spp., *Zapus* spp., *Aplodontia* spp., *Neotamias* spp., *Neotoma* spp., *Sorex* spp., *Peromyscus* spp., and *Tamiasciurus* spp.), birds (*Passeriformes* spp.), deer (*Odocoileus hemionus*), and marine species (Salmonids [*Oncorhynchus* spp.] and intertidal crustaceans [*Cancridae* spp., *Pteriomorpha* spp.]) available at each (Supporting Information, Table S2).

Table S1. Comparisons between island and mainland geography and between species of martens, including land cover, climate, competitors, and level of human disturbance variations. Climate dataset aggregated from 1987-2016 at 1km resolution for each site based on each marten sampling locations (Grechka *et al.* 2016).

		Island *americana*	Mainland *americana*
Climate	Annual Temperature (℃)	5.6	4.1
	Elevation (m)	82.8	96.8
	Precipitation (mm/month)	170.5	177.4
	Relative Humidity (%)	79.9	78.8
	Soil Moisture (mm/month)	407.9	405.2
	Wetness Index (days/month)	18.1	17.9
Land cover (%)	Temperate Needleleaf	95.4	98
	Mixed Forest	1.2	2.8
	Temperate Shrubland	2.5	-
Carnivore Richness		Black bear	Black bear
		Wolf	Brown bear
		Mink	Wolf
		River otter	Mink
		Ermine	River otter
			Ermine
			Fisher
Human Disturbance		Low	Low

		Island *caurina*	Mainland *caurina*
Climate	Annual Temperature (℃)	8.3	11.2
	Elevation (m)	30.4	21.9
	Precipitation (mm/month)	140.1	100.6
	Relative Humidity (%)	83	78.7
	Soil Moisture (mm/month)	281.7	339.4
	Wetness Index (days/month)	18.8	12.3

Land cover (%)	Temperate Needleleaf	68	15.1
	Mixed Forest	33	-
	Temperate Grassland	-	3
	Temperate Shrubland	1	-
	Wetland	-	36.9
	Urban	-	40.6
	Barren Land	-	4.4
Carnivore Richness		Black bear	Black bear
		River otter	River otter
		Ermine	Ermine
		Raccoon	Raccoon
			Gray Foxes
			Coyote
			Virginia opossum
			Fisher
			Long-tailed weasel
			Mink
			Spotted skunk
			Striped skunk
			Puma
			Bobcat
Human Disturbance		Low	High

Table S2. All species sampled for stable isotope analysis, including number of individuals (N), year sampled, and citation if isotopic data was retrieved from the literature.

Site	Group	Species	N	Year	Citation
Mainland *americana*		American marten (*Martes americana*)	60	2008	Pauli et al., 2015
	Terrestrial	Southern red-backed vole (*Myodes gapperi*)	11	2008	
		Northwestern deer mouse (*Peromyscus keeni*)	8	2008	
		Cinereus shrew (*Sorex cinereus*)	5	2008	
		Woodpecker (Picidae)	4	2008	
		Thrush (Turdidae)	4	2008	
		Tree swallow (*Tachycineta bicolor*)	1	2008	
		Deer (*Odocoileus hemionus sitkensis)*	1	2008	
	Berries	Alaskan blueberry (*Vaccinium alaskaense*)	6	2008	
		Red huckleberry (*Vaccinium parvifolium*)	5	2008	
		Black raspberry (*Rubus leucodermis*)	3	2008	
		Devil’s club (*Oplopanax horridus*)	4	2008	
		Salmonberry (*Rubus spectabilis*)	3	2008	
	Marine	Dungeness crab (*Metacarcinus magister*)	1	2008	
		Pink Salmon (*Oncorhynchus gorbuscha*)	5	2008	
		California mussel (*Mytilus californianus*)	1	2008	
Island *americana*		American marten (*Martes americana*)	98	2006	Pauli et al., 2015
	Terrestrial	Northwestern deer mouse (*Peromyscus keeni*)	21	2006	

		Mule deer (*Odocoileus hemionus*)	7	2016	
		Northern flying squirrel (*Glaucomys sabrinus*)	5	2006	
		Shrew (*Sorex cinereus*)	4	2006	
	Berries	Blueberry (*Vaccinium*)	10	2006	Flaherty et al., 2010
		Devil's club (*Oplopanax horridus*)	10	2006	Flaherty et al., 2010
		Salmonberry (*Rubus spectabilis*)	10	2006	Flaherty et al., 2010
		Russian current (*Ribes*)	7	2006	Flaherty et al., 2010
		Muskeg berry	6	2006	Flaherty et al., 2010
		Elderberry (*Sambucus*)	2	2006	Flaherty et al., 2010
	Marine	Pink salmon (*Oncorhynchus gorbuscha*)	8	2006	
		Dog salmon (*Oncorhynchus keta*)	4	2006	
		Silver salmon (*Oncorhynchus kisutch*)	4	2006	
		Pacific oyster (*Crassostrea gigas*)	1	2006	
		Rock crab (*Cancer productus*)	1	2006	
		Purple shore crab (*Hemigrapsus nudus*)	1	2006	
		California mussel (*Mytilus californianus*)	1	2006	
		Butter clam (*Saxidomus gigantea*)	1	2006	
		Neck clam (*Mercenaria mercenaria*)	1	2006	
		Horse clam (*Tresus nuttallii*)	1	2006	
Island *caurina*		Pacific marten (*Martes caurina*)	52	2008	(Pauli *et al.* 2015)
	Terrestrial	Northwestern deer mouse (*Peromyscus keeni*)	10	2008	

		Dusky shrew (*Sorex monticolus*)	4	2008	
		Red Squirrel (*Tamiasciurus hudsonicus*)	2	2008	
		Mule deer (*Odocoileus hemionus*)	1	2008	
	Berries	Blueberry (*Vaccinium ovalifolium*)	5	2008	
		Raspberry (*Rubus leucodermis*)	1	2008	
		Thimbleberry (*Rubus parviflorus*)	1	2008	
		Salmonberry (*Rubus spectabilis*)	1	2008	
	Marine	Dungeness crab (*Metacarcinus magister*)	1	2008	
		Unidentified marine	4	2008	
Mainland *caurina*		Pacific marten (*Martes caurina*)	13	2015	(Linnell *et al.* 2018)
	Terrestrial	Vagrant shrew (*Sorex vagrans*)	8	2004, 2015	
		Mountain beaver (*Aplodontia rufa*)	7	2015	
		Townsend’s chipmunk (*Neotamias townsendii*)	6	2015	
		Deer mouse (*Peromyscus maniculatus*)	4	2004, 2015	
		Douglas squirrel (*Tamiasciurus douglasii*)	4	2015	
		Bushy-tailed woodrat (*Neotoma cinerea*)	4	2015	
		Creeping vole (*Microtus oregoni*)	3	2015	
		Jumping mouse (*Zapus trinotatus*)	1	2011	
		Bushy-tailed woodrat (*Neotoma fuscipes*)	1	2015	
		Dark-eyed Junco (*Junco hyermalis*)	2	-	

	Fox sparrow (*Passerella iliaca*)	2	2008
	Varied thrush (*Ixoreus naevius*)	2	-
	Swainson’s thrush (*Catharus ustulatus*)	2	2005, 2008
	Hermit thrush (*Catharus guttatus*)	1	2005
	Killdeer (*Charadrius vociferus*)	1	2009
	American robin (*Turdus migratorius*)	1	-
	Palm Warbler (*Steophaga palmarum*)	1	-
	Bushtit (*Psaltriparus minimus*)	1	2009
	American goldfinch (*Spinus tristis*)	1	2011
	Red-breasted nuthatch (*Sitta canadensis*)	1	2005
	Red-winged blackbird (*Agelaius phoeniceus*)	1	2010
	Golden-crowned kinglet (*Regulus satrapa*)	1	2015
Berries	Cascara (*Rhamnus purshiana*)	2	2016
	Salmonberry (*Rubus spectabilis*)	2	2016
	Salal (*Gaultheria shallon*)	2	2016
	Evergreen huckleberry (*Vaccinium ovatum*)	2	2016
	Black twinberry (*Lonicera involucrata*)	1	2016
	Red-flowering currant (*Ribes sanguineum*)	1	2016
	Pacific crab apple (*Malus fusca*)	1	2016
	Coastal strawberry (*Fragaria chiloensis*)	1	2016
	Thimbleberry (*Rubus parviflorus*)	1	2016

Marine	Purple shore crab (*Hemigrapsus nudus*)	1	2017
	Gooseneck barnacles (*Pollicipes pollicipes*)	1	2017
	Blue mussel (*Mytilus edulis*)	1	2017
	Dungeness crab (*Metacarcinus magister*)	2	2017

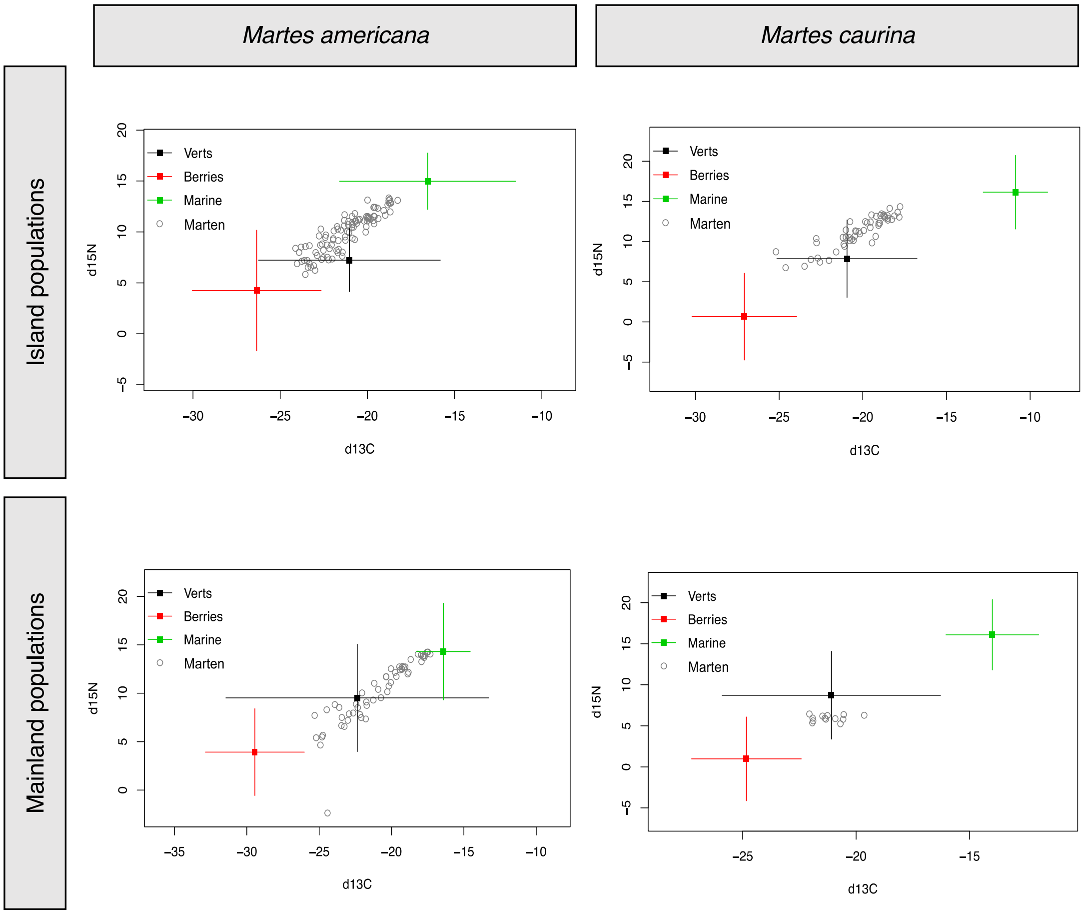

Figure S1. Mixing space for marten populations analyzed.

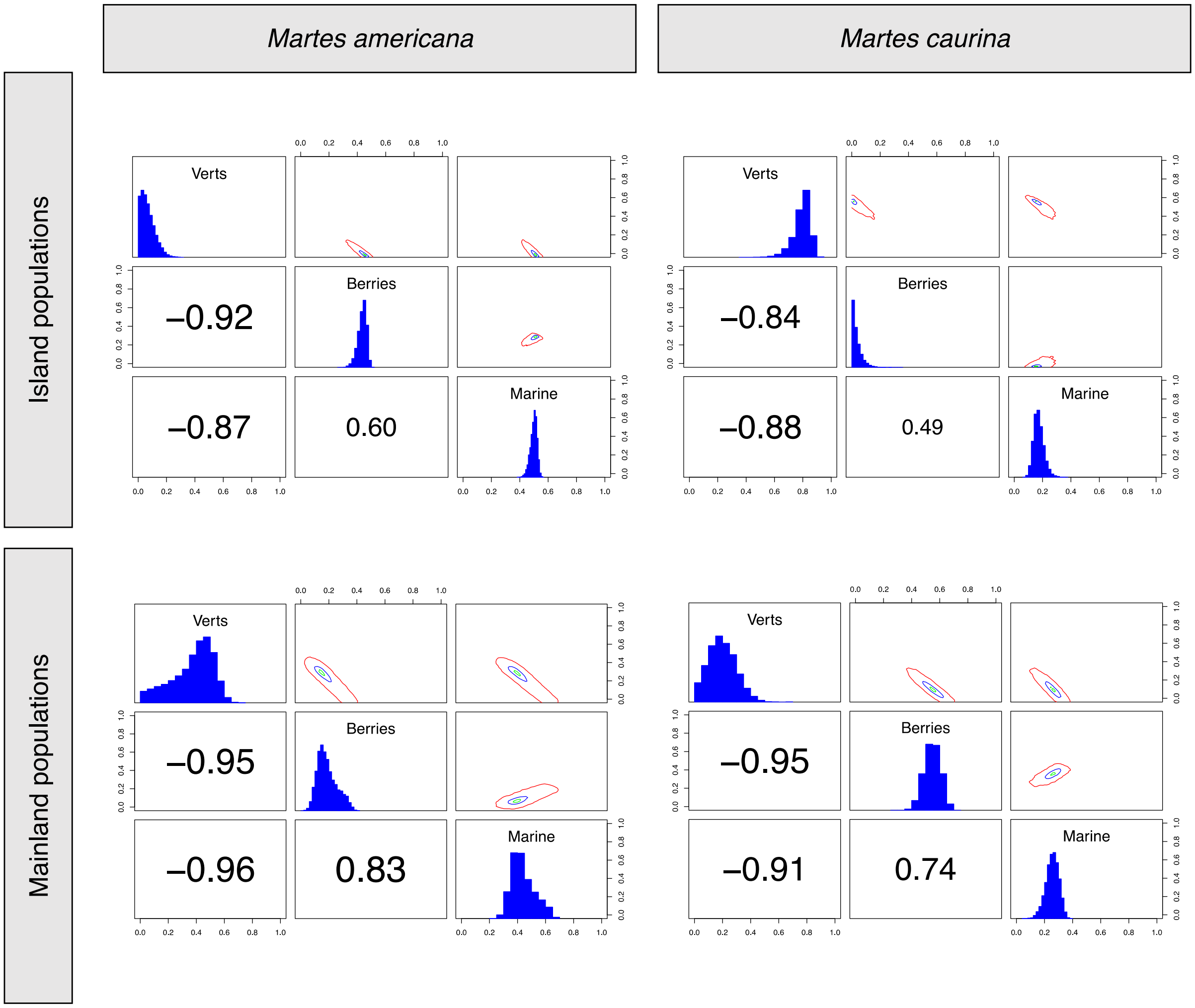

Figure S2. Diagnostic matrix plots for each mixing model illustrating correlations in posterior probabilities of dietary proportions.

Supporting References

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Human disturbance increases niche overlap in North American carnivores

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Abstract

Animal foraging and competition are defined by the partitioning of three primary niche axes: space, time, and resources. Human disturbance is rapidly altering the spatiotemporal distributions of animals, but the impact of humans on resource consumption and partitioning across communities is poorly understood. We assessed resource consumption and trophic partitioning along a gradient of human disturbance using stable isotope analyses of 684 carnivores from 7 communities in North America. We found that consumption of human food subsidies, trophic niche width, and trophic niche overlap all increased with human footprint, indicating humans fundamentally alter resource niches and competitive interactions in terrestrial carnivores. Given that food subsidies increase human-carnivore conflict and that trophic overlap is the primary driver of interspecific killing among carnivores, our results suggest humans destabilize carnivore communities by increasing the probability of conflict with humans and among competitors.

Introduction

Human development has restructured terrestrial ecosystems with widespread consequences for biotic interactions and ecosystem function (Foley *et al.* 2005; Estes *et al.* 2011). This expanding human footprint has shifted the realized niches of many animals by restricting movement (Tucker *et al.* 2018) and temporal partitioning (Gaynor *et al.* 2018). Similarly, human-dominated landscapes can shift resource consumption and alter the functional roles of consumers via modified predation rates (Smith, Wang & Wilmers 2015) and decoupled predator-prey relationships (Rodewald, Kearns & Shustack 2011). Moreover, dietary niche partitioning is a principle driver of competition and coexistence in ecological communities (Rosenzweig 1966; Pianka 1974). To date, however, the influence of human disturbance on resource consumption has been almost entirely restricted to single-species analyses at local scales, and the consequences for trophic interactions and niche partitioning among communities remains poorly understood.

Human disturbances have systematically extirpated apex predators and disrupted trophic interactions (Estes *et al.* 2011; Ripple *et al.* 2014). Re-establishing trophic complexity is now a conservation priority (Duffy *et al.* 2007; Dobson *et al.* 2009), and the restoration of mammalian carnivores to modified landscapes is increasingly identified as a means to restore top-down forces (Ripple *et al.* 2014). Maintaining functional carnivore guilds in such landscapes is nevertheless challenging due to shifting realized niches and novel biotic interactions (Moss *et al.* 2016; Smith, Wang & Wilmers 2016). For example, human presence can temporally displace carnivores and increase competition for prey (Smith *et al.* 2018), altered resource availability can trigger ecological traps (Moss, Alldredge & Pauli 2016; Lamb *et al.* 2017), and the consumption of human food subsidies exacerbates both interspecific competition and human-wildlife conflict (Hopkins *et al.* 2014; Murray *et al.* 2015a; Newsome *et al.* 2015a). Quantifying the influence of humans on trophic interactions is therefore critical to understanding both the ecological and societal impact of carnivores in the Anthropocene.

To quantify human impacts on carnivore trophic interactions and niche partitioning we used δ^{13}C and δ^{15}N stable isotope analyses of 684 individuals from 7 sites in the Great Lakes Region of the eastern United States (Fig. 1; Tables S1-S2, Supporting Information). We targeted sites across a gradient of human disturbance and sampled 7 sympatric apex and mesocarnivores, including gray wolves (*Canis lupis;* hereafter, wolves), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), red foxes (*Vulpes Vulpes*), gray foxes (*Urocyon cinereoargenteus*), fishers (*Pekania pennanti*) and American martens (*Martes americana*). Because stable isotope analyses are sensitive at broad scales (Newsome *et al.* 2012), we restricted our analysis to sites within the temperate broadleaf and mixed forest biome of the eastern United States (Olson *et al.* 2001). One of the most altered biomes on the planet (Hannah, Carr & Lankerani 1995; Hoekstra *et al.* 2005), this region is notable for its recovered carnivore communities, high carnivore richness, and spectrum of human disturbance – indeed, our sites ranged from federally protected national parks to urban and exurban landscapes (Table S1, Fig. S1, Supporting Information). Moreover, the region is defined by C_3 primary production, enabling the assessment human food consumption by carnivores via the analysis of $\delta^{13}C$ values (Newsome *et al.* 2015b; Kirby, Macfarland & Pauli 2017).

We modeled trophic structure as a function of the human footprint index (Gossner *et al.* 2016) at 3 biological levels – individuals, populations, and communities. We used Bayesian hierarchical mixed-effects models to quantify responses in individual consumption of human food ($\delta^{13}C$, $\delta^{15}N$; ‰), trophic niche width per population (SEAc; ‰), and pairwise trophic niche overlap within each community (O; ‰). All models accounted for sample size and spatial extent, and we included additional covariates (e.g., carnivore richness, body mass) known to influence trophic structure. For each response variable we developed a suite of *a priori* models, identified top models using leave-one-out cross-validation (Vehtari, Gelman & Gabry 2017), and interpreted effect sizes to assess the influence of human disturbance on trophic interactions from individuals to communities.

Results and Discussion

We found that $\delta^{13}C$, $\delta^{15}N$, trophic niche width, and trophic niche overlap all increased with human footprint, but the average magnitude and response varied by carnivore species. These results indicate that human disturbance is altering trophic structure in carnivores across multiple levels of biological organization with potential impacts for population and community dynamics.

Individuals

We found that δ^{13}C (median (β) = 0.13, 95% Credible Interval (CI) = 0.02-0.24) and δ^{15}N (β = 0.03, CI = -0.02-0.08) values increased with human footprint, revealing significant increases in the use of human food subsidies disturbed landscapes (Fig. 2). Our best fit model for δ^{13}C included random slopes and intercepts for species and site (Table S3, Supporting Information), indicating that mean δ^{13}C values and the response to human footprint varied by species and location (Fig. 2A). The best fit δ^{15}N model also found that mean δ^{15}N values and the response to human footprint varied by species (Fig. 2B), but only mean δ^{15}N values varied by location (Table S4, Supporting Information). Many local studies have documented such elevated δ^{13}C and δ^{15}N values in carnivores due to the integration of human food subsidies (Newsome *et al.* 2015b; Moss *et al.* 2016; Kirby, Macfarland & Pauli 2017), with wide-ranging consequences for individual survival (Murray *et al.* 2015b; Moss, Alldredge & Pauli 2016), space use (Newsome *et al.* 2015b), interspecific killing (Moss *et al.* 2016), and human-wildlife conflict (Hopkins *et al.* 2014; Murray *et al.* 2015a; Kirby, Alldredge & Pauli 2016). We detected elevated δ^{13}C and δ^{15}N values in both mesocarnivores and apex predators across sites, indicating that human subsidies pervade terrestrial food webs, but we also observed substantial plasticity among this predator guild. For instance, strict carnivores like bobcats exhibited low average consumption of human food subsidies but strong responses to human footprint ($\delta^{13}C_{\mathrm{Intercept}}$ = -24.78‰; β = 0.16), while generalists like red foxes showed elevated use of human foods across sites with weaker responses to disturbance ($\delta^{13}C_{\mathrm{Intercept}}$ = -22.72‰, β = 0.10). Nevertheless, all species, including apex predators like wolves, exhibited strong dietary responses to human disturbance at the individual level. These results illustrate the pervasive impacts of human presence on terrestrial consumers and suggest the continued expansion of human activities will alter carnivore foraging and increase human-wildlife conflict in the Anthropocene.

Populations

Trophic niche width increased as a function of human footprint ($\beta = 0.93$, CI = 0.02-1.80) for all carnivores, but average niche width varied by species (Fig. 3A-B). This trophic niche expansion indicates a broader incorporation of dietary resources by carnivores in human-dominated landscapes, likely via the consumption of human food subsidies, domestic livestock, and synanthropic wildlife (e.g., feral cats [*Felis catus*], Virginia opossum [*Didelphis virginiana*]; Newsome *et al.* 2015b; Moss *et al.* 2016; Smith *et al.* 2018). In addition to human footprint, our top model revealed a strong relationship between carnivore richness ($\beta = 2.10$, CI= 0.32-3.97) and trophic niche width, but little effect of sample size ($\beta = -0.09$, CI = -0.37-0.20; Table S5, Supporting Information). While carnivore richness and competition can structure foraging (Manlick *et al.* 2019), the number of carnivores at each site was strongly correlated with site area (see Methods), a known driver of isotopic niche width (Reddin *et al.* 2018). Consequently, the apparent influence of carnivore richness is likely conflated with site area and represents underlying isotopic variability in the landscape. Nevertheless, our top model accounted for these differences and still detected trophic niche expansion, suggesting strong dietary plasticity and adaptability across this carnivore guild.

Communities

Trophic niche expansion and dietary plasticity can have profound effects on competitive interactions, and we found that pairwise niche overlap between carnivore species increased significantly with human footprint ($\beta = 0.07$, CI = 0.01-0.13; Fig. 3C-D). Species nevertheless varied in their degree of overlap, with bobcats ($\beta_0^{offset} = 0.94$), red foxes ($\beta_0^{offset} = 0.39$), and coyotes ($\beta_0^{offset} = 0.33$) exhibiting the greatest overlap with competitors (Fig. 3C-D). Moreover, while our top model found little influence of sample size ratio (i.e., differences in sample size between species; $\beta = -0.05$, CI = -0.25-0.16), we detected a significant effect of carnivore richness on niche overlap ($\beta = 0.20$, CI = 0.09-0.32; Table S6, Supporting Information). Similar to niche width, carnivore richness was conflated with site area, but diffuse competition in diverse carnivore communities likely contributed to the observed impact of richness on pairwise niche overlap (Pianka 1974). Carnivores also exhibit direct interspecific effects (Palomares & Caro 1999), and trophic niche overlap is a fundamental driver of competition (Schoener 1974), coexistence (Périquet, Fritz & Revilla 2014), and interspecific killing (Fedriani *et al.* 2000; Donadio & Buskirk 2006). Our results show that human disturbance increases dietary overlap in both apex and mesocarnivores, likely destabilizing carnivore communities through heightened agonistic interactions (Donadio & Buskirk 2006). Interestingly, smaller competitors like martens ($\beta_0^{offset} = -0.27$) and gray foxes ($\beta_0^{offset} = -0.69$) exhibited considerably lower overlap on average, suggesting subordinate species may also shift their realized trophic niches to minimize competitive overlap, with unknown impacts on life history traits or population viability.

Conclusions

Human disturbance has drastically altered the spatial and temporal niches of animals (Gaynor *et al.* 2018; Tucker *et al.* 2018). We show that human disturbance also modifies arguably the most fundamental niche axis, resource use. Indeed, we found that carnivores incorporate significantly more food subsidies in human-dominated landscapes, leading to trophic niche expansion and increased trophic niche within carnivore communities. These results illustrate the widespread impact of humans on trophic interactions via resource subsidies, suggesting that carnivore competition will escalate with the growing human footprint (Newsome *et al.* 2015a). Trophic niche dynamics, in particular, often regulate competition and coexistence in carnivores, leading to morphological and dietary divergence within carnivore guilds (Dayan & Simberloff 1994; Davies *et al.* 2007). Our data suggest that carnivore diets are highly plastic and increasingly subsidized by human foods, potentially undermining millennia of selective forces that have facilitated historical coexistence. Furthermore, the dynamic trophic interactions observed across ecosystems suggest that predator-prey interactions and the top-down functional roles of carnivores likely vary across human-dominated landscapes. Ultimately, these findings suggest that the probability of human-carnivore conflict and interspecific killing among carnivores increases with human disturbance (Donadio & Buskirk 2006; Newsome *et al.* 2015a), likely destabilizing predator-prey interactions and carnivore coexistence in the Anthropocene.

Methods

Sites and samples

We quantified the influence of human disturbance on carnivore trophic structure via hierarchical sampling of carnivore species across 7 sites in the Great Lakes region (Fig. 1). Sites were defined using state-level land and furbearer management units, and we quantified human disturbance as the mean human footprint index (Venter *et al.* 2016) per site. The human footprint index incorporated multiple aspects of disturbance, including agricultural and developed land, roads and railways, human population density, and night-time lights (Venter *et al.* 2016). In total, sites ranged across a >3.5-fold increase in human disturbance (Table S1, Supporting Information). Within each site we collected biological samples (hair and/or bone) of carnivores for stable isotope analysis via direct sampling of carnivore tissues (e.g., trapper harvest, depredation harvest, collared animals, known-fate mortality) or archived biological collections, and we supplemented sampling with published isotopic values from the literature (Warsen 2012; Warsen, Frair & Teece 2014; Carlson *et al.* 2014; Manlick *et al.* 2017; Table S2, Supporting Information). In total, we sampled 7 competing carnivore species, gray wolves (*Canis lupis; N* = 102; wolves), coyotes (*Canis latrans; N* = 111), bobcats (*Lynx rufus; N* = 101), red foxes (*Vulpes Vulpes; N* = 82), gray foxes (*Urocyon cinereoargenteus; N* = 26), fishers (*Pekania pennanti; N* = 174) and American martens (*Martes americana; N* = 88; martens). Sites varied in community composition and sample sizes (Fig. 1; Table S2, Supporting Information). For all samples we identified harvest or sampling location to the finest resolution possible (e.g., county, township, management unit), and we recorded harvest date and sex when available (Table S2, Supporting Information; archived data).

Stable isotope analyses

We quantified carnivore trophic structure using δ^{13}C and δ^{15}N stable isotope analyses. Stable isotopes in animal tissues reflect the flow of energy through communities, with δ^{13}C capturing the diversity of basal resources in a system and δ^{15}N describing trophic position (Post 2002). Patterns in consumer stable isotope values (e.g., δ^{13}C and δ^{15}N) thus allow for the multi-dimensional quantification of habitat and resource use known as the isotopic or trophic niche (Newsome *et al.* 2007; Layman *et al.* 2012). Accordingly, stable isotope analyses have become a common tool to quantify the impact of human disturbance on trophic interactions and consumer niche dynamics (Layman *et al.* 2007; Newsome *et al.* 2015b; Pool *et al.* 2015; Moss *et al.* 2016). We used hair and bone samples to quantify the trophic niches of carnivores across study sites. Hair samples were rinsed 3 times with a 2:1 chloroform-methanol solution to remove surface contaminants before being homogenized and dried for 72 hours at 56°C (Manlick *et al.* 2019). Bone samples were demineralized in 0.5N hydrochloric acid at 4°C for a minimum of 24 hours and the remaining bone collagen was lipid-extracted via immersion in 2:1 chloroform-methanol solution for a minimum of 72 hours (Kirby, Macfarland & Pauli 2017). Bone collagen samples were then rinsed with deionized water to remove solvents, dried for 72 hours at 56°C, and homogenized homogenized with either a ball mill mixer or mortar and pestle. All samples were weighed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis at the University of New Mexico Center for Stable Isotopes using a Costech 4010 elemental analyzer (Costech, Valenicia, CA) coupled to a Thermo Scientific Delta V mass spectrometer (Thermo Scientific, Bremen, Germany). Isotopic ratios were quantified as parts per mil [‰] relative to the international standards Vienna Peedee Belemnite (C) and atmospheric Nitrogen (N).

Hair is a metabolically inert tissue and reflects the assimilated diet of an individual over the temporal period that the hair was synthesized (Pauli *et al.* 2009). All harvested and non-invasively collected samples were acquired after the annual molt (~June-October) during fall and winter trapping seasons (Table S2, Supporting Information; archived data); therefore, all isotopic signatures from hair represent trophic relationships from late summer through fall. Conversely, bone collagen integrates continuously, represents multiple years of assimilated diet, and turns over at a different rate, potentially resulting in divergent isotopic signatures between hair and bone collagen within a single individual (Bearhop *et al.* 2004). We used bone collagen from gray wolf museum specimens to capture the trophic niche of wolves at one site (Table S2, Supporting Information; archived data), but we detected no significant differences between paired bone collagen and hair samples using two independent datasets (Table S7, Supporting Information). Thus, all bone collagen isotopic signatures were retained in downstream analyses.

Trophic niche dynamics

For consumers, the trophic niche defined by $\delta^{13}C$ and $\delta^{15}N$ values ultimately represents the consumption of prey and the potential impact of a species on its community or environment (i.e. the Eltonian niche; Manlick *et al.* 2019). Consequently, shifts in consumer trophic niches largely reflect either niche collapse due to limited prey availability (Layman *et al.* 2007; Manlick *et al.* 2017) or niche expansion following increased food subsidies (Newsome *et al.* 2015b; Moss *et al.* 2016). Human disturbance has been shown to drastically increase food subsidies (Oro *et al.* 2013; Kirby, Alldredge & Pauli 2016), with likely consequences for community trophic structure. To assess the impact of human disturbance on carnivore trophic structure, we used Bayesian hierarchical mixed-effects models and a leave-one-out model selection framework to analyze stable isotope signatures at three levels: individuals, populations, and communities.

Individuals – To quantify individual responses to human disturbance, we subset our data to include all individuals with a known county of origin ($N = 597$), calculated mean human footprint per county, and modeled $\delta^{13}C$ and $\delta^{15}N$ values as a function of human footprint. We developed a suite of 10 *a priori* models incorporating site and species as random effects (Tables S3-S4, Supporting Information), including a fully varying model with random slopes and intercepts for both site and species, two null models varying only by site or species (i.e., “intercept only”), and all subsets in between. All site-level random effects included a nested county grouping to account for repeated measures within sites. In all of our study sites C_3 photosynthetic plants predominate and are easily distinguishable via $\delta^{13}C$ values (−28 to −22 ‰; Farquhar, Ehleringer & Hubick 1989; Newsome *et al.* 2015). Conversely, human food subsidies in the United States, including agricultural residuals and human refuse, are largely defined by C_4 photosynthetic plants like corn (Jahren & Kraft 2008; Kirby, Macfarland & Pauli 2017) with distinct $\delta^{13}C$ signatures (−12 to −14 ‰; Farquhar, Ehleringer & Hubick 1989) that permeate terrestrial food webs via animal consumption (Newsome *et al.* 2010; Hopkins *et al.* 2014; Kirby, Alldredge & Pauli 2016). Similarly, domestic animals and synanthropic wildlife commonly found in urban carnivore diets also exhibit elevated $\delta^{15}N$ values (Newsome *et al.* 2015b; Moss *et al.* 2016). Thus, we predicted that both $\delta^{13}C$ and $\delta^{15}N$ values would increase with human footprint.

Populations – To assess species-level responses to human disturbance, we first estimated trophic niche width for each species at each site (i.e., population; $N = 38$) using 95% standard ellipses corrected for small sample size (SEAc) via the r package SIBER (Jackson *et al.* 2011). We excluded all populations with < 5 samples ($\bar{x} = 17.71$) following SIBER recommendations (Jackson *et al.* 2011). We then modeled SEAc (‰) for each population as a function of human footprint including species as a random effect. Secondly, because community composition can also regulate the trophic niches of carnivores (Darimont, Paquet & Reimchen 2009; Manlick *et al.* 2019), we also included carnivore richness as a predictor of $SEAc_{95}$. Carnivore richness was correlated with site area ($r = 0.88$, $p < 0.001$), a strong predictor of isotopic niche width (Reddin *et al.* 2018), but uncorrelated with human footprint ($r = -0.11$, $p = 0.49$). Thus, we retained carnivore richness to capture both community and scale effects on niche width, and denoted richness for each site as the total number of terrestrial carnivore species (order *Carnivora*) present, as estimated by local natural resource agencies. Despite the unbiased nature of standard ellipses (Jackson *et al.* 2011), we also included sample size as a predictor of SEAc to account for any potential differences in niche width due to unequal sampling. We developed 8 candidate models to test the response of trophic niche width to human footprint, including a full model with all predictors and species-level responses to human footprint (i.e., random slopes and intercepts), a null model with only a species-level random effect, and subsets with varying predictors and random effect structures (Table S5, Supporting Information). Because both human footprint and carnivore richness are site-level continuous variables, we did not include site as a random effect to minimize covariance within model parameters. We predicted that SEAc (i.e., trophic niche width) would increase with human footprint.

Communities – We quantified community-level responses to human disturbance by estimating trophic niche overlap between all species pairs within each site (*N* = 176). We estimated niche overlap for each species as $O_{ij} = \frac{o_{ij}}{SEAc_i}$, where *i* indicates the species of interest, *j* indicates the competing species, o_{ij} indicates the area of SEAc overlap between competitors (‰), and $SEAc_i$ indicates the total trophic niche area for the species of interest (‰). The resultant metric (O_{ij}) represents the proportion of a given species' trophic niche overlapped by a potential competitor and ranges from 0 (no overlap) to 1 (complete overlap). We calculated O_{ij} for both species in all species pairs. We then modeled O_{ij} as a function of human footprint including species as a random effect to assess differences in trophic niche overlap by species. We again included carnivore richness as a covariate to account for community and scale effects on trophic niches, and we also included the sample size ratio between each species pair to account for potential differences in proportional overlap due to unequal sample sizes. Given that diet overlap in carnivores is often a function of body size difference (BSD), we estimated BSD for all pairwise species comparisons following Donadio & Buskirk (2006). For each species, we estimated mean body mass (kg) using published values from the literature and cataloged biological specimens on VertNet (Constable *et al.* 2010; Table S8, Supporting Information). All populations and individuals used to estimate body mass were restricted to the Great Lakes region, and we estimated mean body mass for midwestern and northeastern coyotes separately due to the significant differences in body mass between regions (Way 2007). In total, we developed a suite of 12 candidate models to quantify the impact of human footprint on pairwise niche overlap, including a full model with all predictors and species-level responses to human footprint (i.e., random slopes and intercepts), a null model with only a species-level random effect, and subsets with varying predictors and random effect structures (Table S6, Supporting Information). Because human footprint and carnivore richness are site-level continuous variables, we did not include site as a random effect to minimize covariance within model parameters. We predicted that O_{ij} would increase with human footprint.

Statistical procedures – Models were implemented in the r package *rstanarm* v. 2.18.2 (Stan Development Team 2016). The *rstanarm* package utilizes a Hamiltonian Markov chain Monte Carlo sampling algorithm that efficiently samples parameter space to provide robust inferences on ecological processes (Monnahan, Thorson & Branch 2017). We used the default, weakly informative priors for all models – Normal (0, 10) on intercepts, Normal (0, 2.5) on coefficients – and predictors were centered and scaled internally by *rstanarm* to have a mean of 0 and standard deviation of 1. Models of $\delta^{13}C$, $\delta^{15}N$, and SEAc held continuous and unbounded response variables and used linear mixed-effect regressions with Gaussian likelihood distributions. Conversely, O_{ij} required a bounded distribution (0,1) and we therefore used beta-regression with a Beta likelihood distribution and logit link. Beta-regressions do not, however, permit boundary values (0 or 1) which were present in our data. We therefore transformed O_{ij} data following Smithson & Verkuilen (2006) using the equation $\frac{y*(n-1)+0.5}{n}$, where y was the O_{ij} value and n was sample size, effectively limiting data to (0.005, 0.995). We set proposal acceptance probability to a minimum of 0.95 (max 0.995) to avoid divergent transitions while maximizing model efficiency. Models ran 4 chains with 2,000 iterations, with the first 1,000 iterations discarded as burn-in. All models exhibited convergence (all $\hat{R} = 1.0$) and effective posterior sample sizes exceeded 1000 in all cases. Lastly, we visually inspected model diagnostics (e.g., autocorrelation, trace plots) using the r package *shinystan* (Gabry 2017). We compared multiple models for each analysis by estimating the expected log predictive density (ELPD) for each model using the approximate leave-one-out cross-validation procedure in the r package *loo* v. 2.1.0 (Vehtari, Gelman & Gabry 2017; Vehtari *et al.* 2019). We used a Pareto *K* threshold of 0.7 to account for the impact of potential outliers and selected top models via comparison of ELPD, with top ranked models exhibiting the highest ELPD values.

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Data accessibility

All data used in this study is available in supplementary files and the Figshare online data repository (DOI:10.6084/m9.figshare.8006750).

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Figures

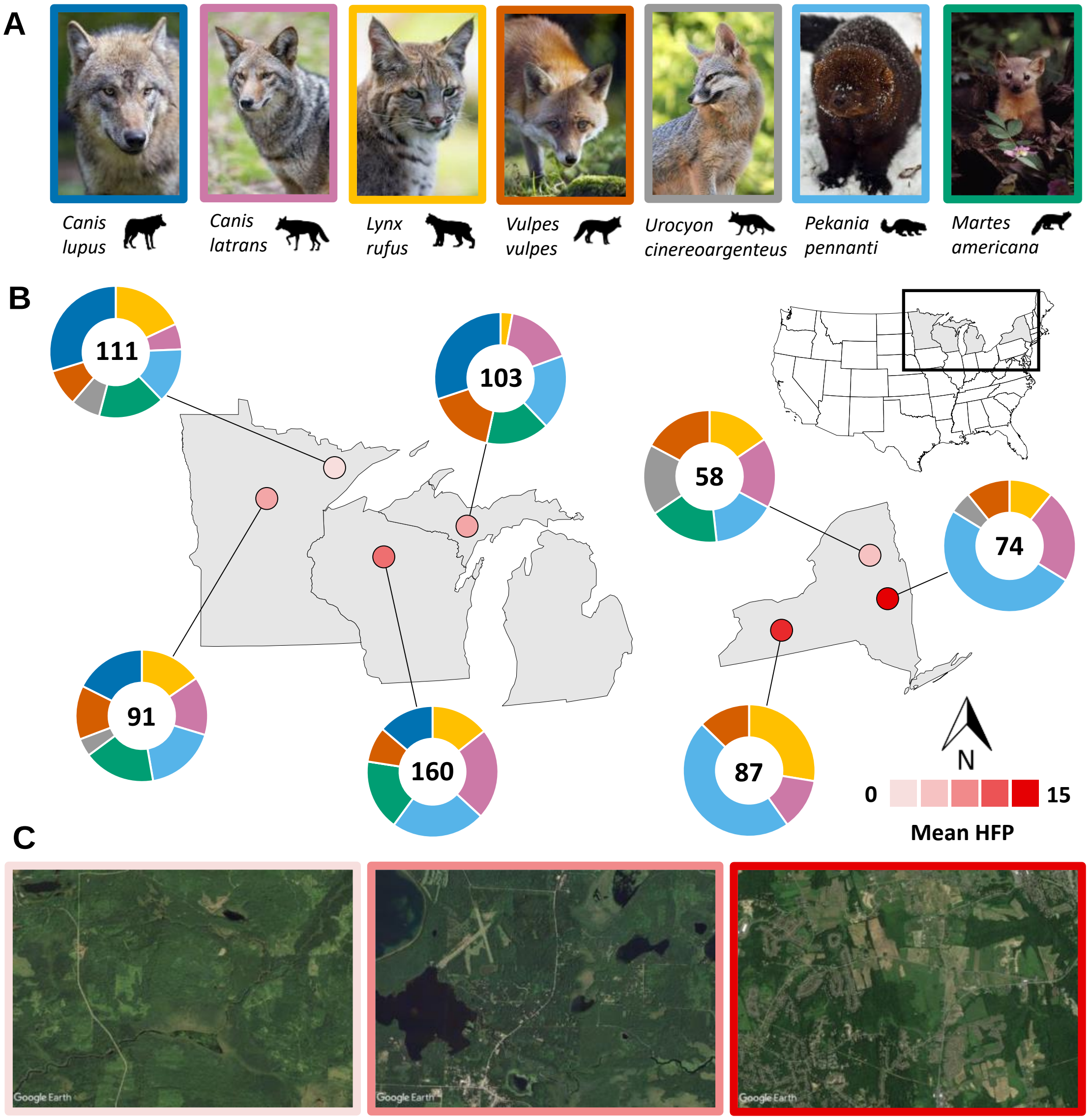

Fig. 1. Distribution of samples from 7 sites across gradient of human footprint. (**A**) Sampled carnivore species: gray wolves (*Canis lupis*, dark blue), coyotes (*Canis latrans*, violet), bobcats (*Lynx rufus*, yellow), red foxes (*Vulpes vulpes*, orange), gray foxes (*Urocyon cinereoargenteus*, gray), fishers (*Pekania pennanti*, light blue), American martens (*Martes americana*, green). (**B**) Donut plots with sample size (center) and proportion of species sampled per site, red points illustrating mean human footprint (HFP) per site and inset map with location of sites in the Great Lakes region, USA. (**C**) Example landscapes from sites with low (HFP=3.66; Superior National Forest, MN), medium (HFP=6.05; Chequamegon-Nicolet National Forest, WI), and high (HFP=13.20; Greater Albany, NY) human impacts. Photo credit, left to right: Tambako the Jaguar/Flickr, Tambako the Jaguar/Flickr, Tambako the Jaguar/Flickr, Tambako the Jaguar/Flickr, Renee Grayson/Flickr, ForestWander/Creative Commons, United States Fish and Wildlife Service/Public Domain.

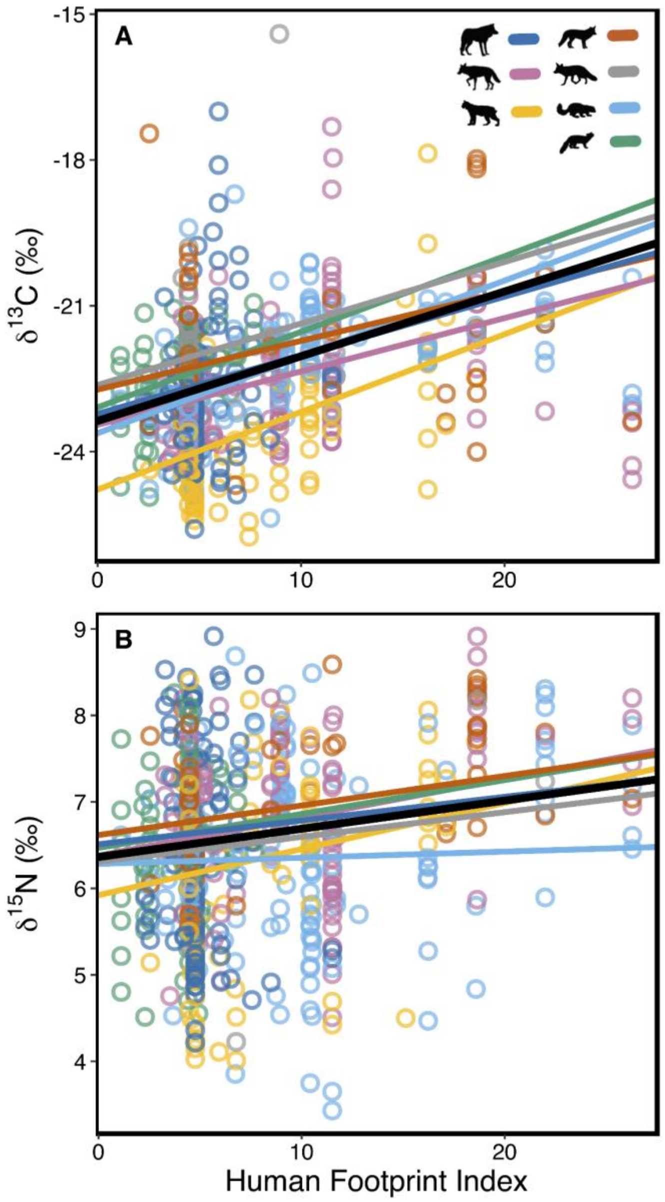

Fig. 2. Individual responses to human footprint. Response of $\delta^{13}C$ (**A**) and $\delta^{15}N$ (**B**) values to human footprint for gray wolves (dark blue), coyotes (violet), bobcats (yellow), red foxes (orange), gray foxes (gray), fishers (light blue), and American martens (green). Black line indicates global response to human footprint. All lines represent median slopes and intercepts from Bayesian mixed-effects model with random slopes and intercepts varying by species and site.

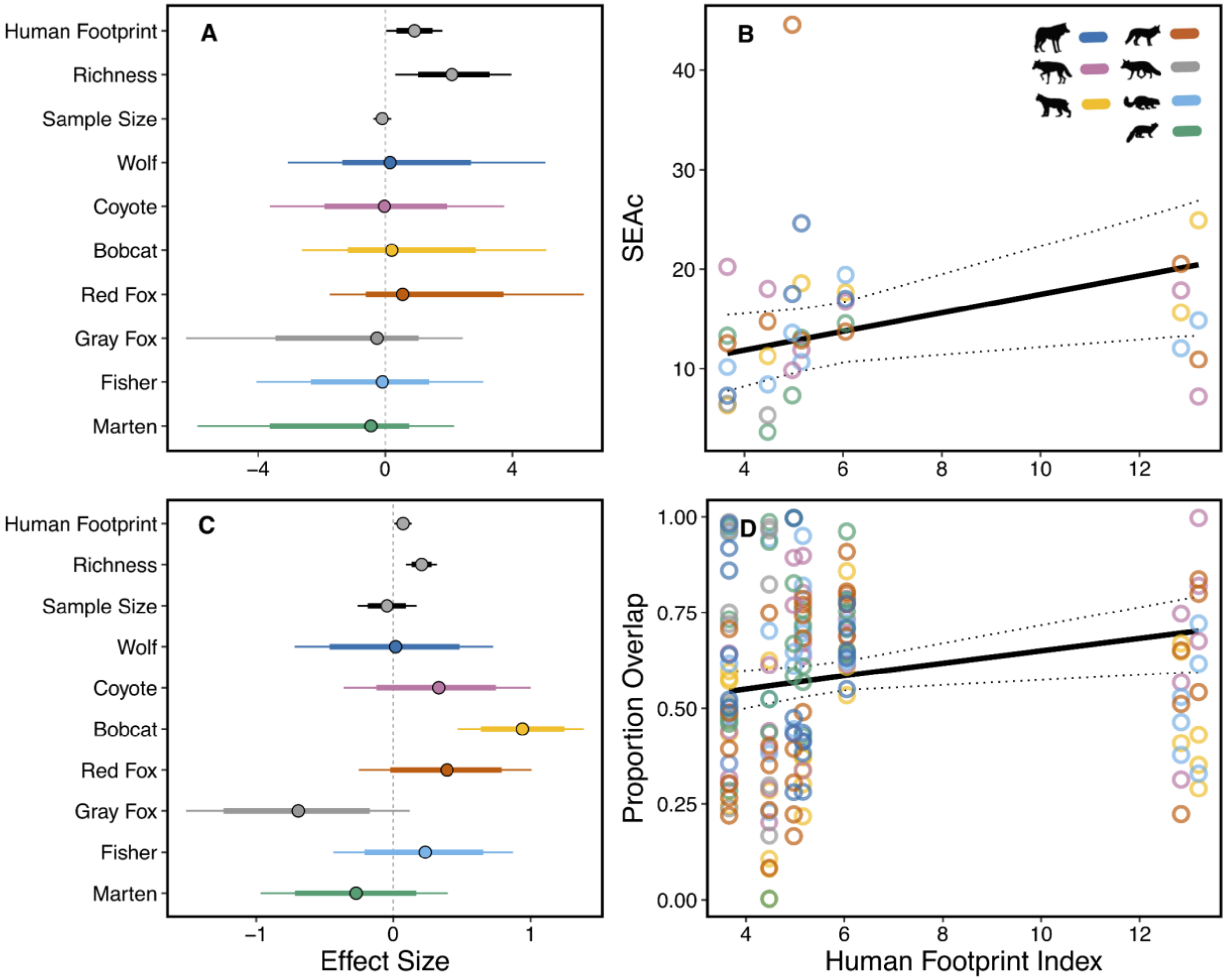

Fig. 3. Population and community responses to human footprint. (**A**) Effect sizes for top Bayesian mixed-effects model of trophic niche width (SEAc), including fixed (regression coefficients, black) and random effects (intercept offset, color by species). (**B**) Predicted response of trophic niche width (SEAc) to human footprint across species. Black line indicates median response and dotted lines denote 95% credible interval. (**C**) Effect sizes for top Bayesian mixed-effects model of pairwise niche overlap, including fixed (regression coefficients, black) and random effects (intercept offset, color by species). (**D**) Predicted response of pairwise niche overlap to human footprint across species. Black line indicates median response and dotted lines denote 95% credible interval.

Supporting Information

Tables S1-S8, Figures S1

Table 1. Sites sampled in the Great Lakes region and the local management unit(s) used to delineate site boundaries. Covariates for each site included human footprint index (HFI), site area (km^2), and terrestrial carnivore richness (Richness).

Site	State	Management unit(s)	HFI	Area (km^2)	Richness
Adirondack Park	New York	Adirondack Park Forest Preserve	4.47	20,849.25	11
Albany	New York	NY Dept. of Environmental Conservation Region 4	13.20	17,405.44	10
Chequamegon-Nicolet National Forest	Wisconsin	WI Dept. of Natural Resources North Zone, Fisher zones A-D	6.05	49,991.89	14
Chippewa National Forest	Minnesota	South Furbearer Zone	5.16	29,536.29	13
Finger Lakes	New York	NY Dept. of Environmental Conservation Region 8	12.84	13,453.9	10
Superior National Forest	Minnesota	North Furbearer Zone, Voyageurs National Park	3.66	25,898.67	12
Upper Peninsula	Michigan	MI Dept. of Natural Resources Zone 1	4.97	38,773.03	15

Table S2. Species sampled at each site, sample size per site (*N*), mean δ^{13}C and δ^{15}N values per species, temporal sampling window (Years), source of samples, agencies and organizations providing samples (Contributors), and reference for literature-derived values. Full data set available at https://figshare.com/s/95576b5b87b46bbe2b55, DOI: 10.6084/m9.figshare.8006750.

Site	**Species**	***N***	**δ^{13}C**	**δ^{15}N**	**Source**	**Contributors**	**Reference**
Adirondack Park	Bobcat	9	-24.37	6.27	Trapper harvested	SUNY-ESF	Warsen 2012; Warsen, Frair & Teece 2014
	Coyote	10	-22.66	6.77			
	Fisher	9	-22.59	6.54			
	Gray Fox	10	-21.82	6.57			
	Marten	10	-21.66	7.44			
	Red Fox	10	-21.24	6.80			
Albany	Bobcat	8	-23.19	6.95	Trapper harvested	New York DEC Region 4	-
	Coyote	17	-23.35	7.40			
	Fisher	37	-21.91	7.07			
	Gray Fox	4	-20.29	6.89			
	Red Fox	8	-22.43	7.16			
Chequamegon-Nicolet National Forest	Bobcat	23	-22.55	5.33	Trapper harvested, Museum specimen, noninvasive hair snare, Mortality	UW-Madison Museum of Zoology, Great Lakes Indian Fish and Wildlife Commission, WI DNR, USDA APHIS	Carlson *et al.* 2014; Manlick *et al.* 2017
	Coyote	36	-21.74	6.21			
	Fisher	36	-22.28	5.76			
	Marten	28	-22.10	6.13			
	Red Fox	14	-21.87	6.39			
	Wolf	22	-21.96	6.22			
Chippewa National Forest	Bobcat	14	-24.62	5.96	Trapper harvested, Depredation harvest	MN DNR, USDA APHIS	-
	Coyote	13	-22.32	7.00			
	Fisher	16	-23.72	6.32			
	Gray Fox	4	-22.43	5.74			
	Marten	16	-22.87	6.47			
	Red Fox	12	-23.07	6.92			
	Wolf	16	-21.20	6.94			
	Bobcat	24	-22.64	6.89			-

Finger Lakes	Coyote	12	-21.16	7.88	Trapper harvested	New York DEC Region 8	
	Fisher	41	-21.54	6.02			
	Gray Fox	1	-20.75	8.17			
	Red Fox	11	-20.98	7.78			
Superior National Forest	Bobcat	20	-24.59	5.02	Trapper harvested, Depredation harvest, collared animals	MN DNR, USDA APHIS, Voyageurs National Park	-
	Coyote	7	-23.52	6.06			
	Fisher	15	-23.72	6.17			
	Gray Fox	8	-22.88	5.90			
	Marten	18	-23.29	6.24			
	Red Fox	10	-22.60	6.40			
	Wolf	33	-23.55	5.46			
Upper Peninsula	Bobcat	3	-24.60	5.95	Trapper harvested, museum specimens, collared animals	MI DNR, Northern Michigan University Museum of Zoology, North American Fur Auctions, Groenwald Fur and Wool Co.	-
	Coyote	17	-23.36	6.57			
	Fisher	19	-22.91	6.35			
	Marten	16	-22.25	6.74			
	Red Fox	17	-21.68	7.37			
	Wolf	31	-22.88	7.57			

Table S3. Hypotheses and model structure for Bayesian mixed-effects models of $\delta^{13}C$ (‰) values. Models were ranked using expected log predictive density (ELPD) and selected (ΔELPD) using approximate leave-one-out cross-validation. Human footprint index (HFI) was included as a fixed effect, and random effects included species and site, with a nested effect of county to account for pseudoreplication in HFI at the county level. Top model is represented in bold.

Model	**Hypothesis**	**ELPD**	**ΔELPD**
HFI + (HFI | Species) + (HFI | Site/County)	**$\delta^{13}C$ values driven by HFI, but mean (int) and response to HFI (slope) vary by species and site (Global)**	**-901.4**	**0.0**
HFI + (HFI | Species) + (1 | Site/County)	δ13C values driven by HFI, but mean (int) varies by species and site and response to HFI (slope) varies by species	-903.3	-1.8
HFI + (1 | Species) + (HFI | Site/County)	δ13C values driven by HFI, but mean (int) varies by species and site and response to HFI (slope) varies by site	-904.2	-2.8
HFI + (1 | Species) + (1 | Site/County)	δ13C values driven by HFI, but mean (int) varies by species and site	-906.8	-5.4
HFI + (HFI | Species)	δ13C values driven by HFI, but mean (int) and response to HFI (slope) varies by species	-982.2	-80.8
HFI + (HFI | Site/County)	δ13C values driven by HFI, but mean (int) and response to HFI (slope) varies by site	-957.6	-56.2
HFI + (1 | Species)	δ13C values driven by HFI, but mean (int) varies by Species	-986.4	-84.9
HFI + (1 | Site/County)	δ13C values driven by HFI, but mean (int) varies by Site	-959.4	-58.0
1 + (1 | Species)	Mean δ13C values (int) varies by Species, but not related to HFI (Null)	-1021.8	-120.4
1 + (1 | Site/County)	Mean δ13C values (int) varies by Site, but not related to HFI (Null)	-958.9	-57.5

Table S4. Hypotheses and model structure for Bayesian mixed-effects models of δ^{15}N (‰) values. Models were ranked using expected log predictive density (ELPD) and selected (ΔELPD) using approximate leave-one-out cross-validation. Human footprint index (HFI) was included as a fixed effect, and random effects included species and site, with a nested effect of county to account for pseudoreplication in HFI at the county level. Top model is represented in bold.

Model	**Hypothesis**	**ELPD**	**ΔELPD**
HFI + (HFI | Species) + (HFI | Site/County)	δ^{15}N values driven by HFI, but mean (int) and response to HFI (slope) vary by species and site (Global)	-761.3	-0.3
HFI + (HFI | Species) + (1 | Site/County)	**δ^{15}N values driven by HFI, but mean (int) varies by species and site and response to HFI (slope) varies by species**	**-761.0**	**0.0**
HFI + (1 | Species) + (HFI | Site/County)	δ^{15}N values driven by HFI, but mean (int) varies by species and site and response to HFI (slope) varies by site	-763.5	-2.5
HFI + (1 | Species) + (1 | Site/County)	δ^{15}N values driven by HFI, but mean (int) varies by species and site	-761.7	-0.8
HFI + (HFI | Species)	δ^{15}N values driven by HFI, but mean (int) and response to HFI (slope) varies by species	-843.1	-82.1
HFI + (HFI | Site/County)	δ^{15}N values driven by HFI, but mean (int) and response to HFI (slope) varies by site	-778.2	-17.3
HFI + (1 | Species)	δ^{15}N values driven by HFI, but mean (int) varies by species	-842.7	-81.7
HFI + (1 | Site/County)	δ^{15}N values driven by HFI, but mean (int) varies by site	-777.5	-16.6
1 + (1 | Species)	Mean δ^{15}N values (int) varies by species, but not related to HFI (Null)	-860.3	-99.3
1 + (1 | Site/County)	Mean δ^{15}N values (int) varies by site, but not related to HFI (Null)	-777.4	-16.4

Table S5. Hypotheses and model structure for Bayesian mixed-effects models of trophic niche width, SEAc (‰). Models were ranked using expected log predictive density (ELPD) and selected (ΔELPD) using approximate leave-one-out cross-validation. Human footprint index (HFI), terrestrial carnivore richness (Richness), and sample size (Sample) were included as fixed effects, with species as a random effect. Top model is represented in bold.

Model	Hypothesis	ELPD	ΔELPD
HFI + Richness + Sample + (HFI | Species)	SEAc is driven by HFI, carnivore richness, and sample size, but mean (int) and response to HFI (slope) vary by species (Global)	-133.5	-0.8
HFI + Richness + Sample + (1 | Species)	**SEAc is driven by HFI, carnivore richness, and sample size, but mean SEAc (int) varies by species**	**-132.7**	**0.0**
HFI + Sample + (HFI | Species)	SEAc is driven by HFI and sample size, but mean (int) and response to HFI (slope) vary by species	-136.0	-3.4
HFI + Sample + (1 | Species)	SEAc is driven by HFI and sample size, but mean (int) varies by species	-135.5	-2.8
Richness + Sample + (1 | Species)	SEAc is driven by carnivore richness and sample size but mean (int) varies by species	-133.7	-1.1
Richness + (1 | Species)	SEAc is driven by carnivore richness but mean (int) varies by species	-133.5	-0.9
Sample + (1 | Species)	SEAc is driven by sample size but mean (int) varies by species	-133.9	-1.2
1 + (1 | Species)	Mean SEAc differs by species but is not related to HFI, carnivore richness, or sample size (Null)	-132.9	-0.2

Table S6. Hypotheses and model structure for Bayesian mixed-effects models of pairwise niche overlap (proportion of overlapping SEAc; O_{ij}). Models were ranked using expected log predictive density (ELPD) and selected (ΔELPD) using approximate leave-one-out cross-validation. Human footprint index (HFI), terrestrial carnivore richness (Richness), body size difference (BSD), and sample size ratio (Ratio) were included as fixed effects, with species as a random effect. Top model is represented in bold.

Model	**Hypothesis**	**ELPD**	**ΔELPD**
HFI + Richness + BSD + Ratio + (HFI | Species)	Niche overlap driven by HFI, Richness, BSD, and Ratio, but mean overlap (int) & response to HFI (slope) varies by species (Global)	6.4	-0.7
HFI + Richness + BSD + Ratio + (1 | Species)	Niche overlap is driven by HFI, Richness, BSD, and Ratio, but mean overlap (int) varies by species	6.0	-1.1
HFI + BSD + Ratio + (HFI | Species)	Niche overlap driven by HFI, BSD, and Ratio, but mean overlap (int) and response to HFI (slope) varies by species	0.5	-6.6
HFI + BSD + Ratio + (1 | Species)	Niche overlap is driven by HFI, BSD, and Ratio, but mean overlap (int) varies by species	0.6	-6.5
HFI + Richness + Ratio + (HFI | Species)	Niche overlap is driven by HFI, Richness, and Ratio, but mean overlap (int) & response to HFI (slope) varies by species	7.0	-0.1
HFI + Richness + Ratio + (1 | Species)	**Niche overlap is driven by HFI, Richness, and Ratio, but mean (int) varies by species**	**7.1**	**0.0**
HFI + Ratio + (HFI | Species)	Niche overlap is driven by HFI and Ratio, but mean (int) & response to HFI (slope) vary by species	1.8	-5.3
HFI + Ratio + (1 | Species)	Niche overlap is driven by HFI and Ratio, but mean (int) varies by species	1.7	-5.4
Richness + Ratio + (1 | Species)	Niche overlap is driven by Richness and Ratio, but mean (int) varies by species	5.8	-1.3
BSD + Ratio + (1 | Species)	Niche overlap is driven by BSD and Ratio, but mean (int) varies by species	1.6	-5.5
Ratio + (1 | Species)	Niche overlap is driven by Ratio, but mean (int) varies by species	2.6	-4.5
1 + (1 | Species)	Mean overlap varies by species but is not related to HFI, Richness, Ratio, or BSD (Null)	3.7	-3.4

Table S7. Comparison of $\delta^{13}C$ and $\delta^{15}N$ values from hair and bone via paired t-tests.

Reference	**Location**	***N***	**Value**	**Hair (SD)**	**Bone (SD)**	**T**	***p***
This study	Wisconsin	6	$\delta^{13}C$	-21.57 (2.20)	-21.32 (0.88)	-0.34	0.75
		6	$\delta^{15}N$	6.59 (1.19)	6.74 (0.85)	-0.45	0.67
Fox-Dobbs *et al.* 2007	Minnesota	18	$\delta^{13}C$	-22.85 (0.70)	-22.50 (0.93)	1.80	0.09
		18	$\delta^{15}N$	6.46 (0.79)	6.73 (0.72)	1.60	0.13

Table S8. Mean body mass (kg) by species, including locality, sample size (*N*), sex and age classes, and source (citation). Species include bobcats (*Lynx rufus*), coyotes (*Canis latrans*), fishers (*Pekania pennanti*), gray foxes (*Urocyon cinereoargenteus*), American martens (*Martes americana*), red foxes (*Vulpes vulpes*), gray wolves (*Canis lupis*). Coyotes were assessed regionally (Northeast vs. Midwest) due to differences in body size across range (Way 2007).

Species	**Location**	***N***	**Mass (kg)**	**Class**	**Citation**
Bobcat	Maine	46	12.30	Male	Litvaitis, Clark & Hunt 1986
	Maine	63	7.20	Female	Litvaitis, Clark & Hunt 1986
	Minnesota	2	9.75	Female	Kapfer 2014
	New Hampshire	17	11.20	Juv Male	Litvaitis, Stevens & Mautz 1984
	New Hampshire	13	6.60	Juv Female	Litvaitis, Stevens & Mautz 1984
	New Hampshire	12	13.30	Ad Male	Litvaitis, Stevens & Mautz 1984
	New Hampshire	24	7.40	Ad Female	Litvaitis, Stevens & Mautz 1984
	Vermont	14	12.16	All	Donovan *et al.* 2011
	Wisconsin	11	13.70	Male	Lovallo & Anderson 1996
	Wisconsin	8	9.70	Female	Lovallo & Anderson 1996
	All		**9.77**		
Coyote (Northeast)	Cape Cod, Massachussets	18	17.90		Way 2007
	Cape Cod, Massachussets	17	16.00		
	Maine	37	15.90		
	Maine	28	15.80		
	Maine	22	14.50		
	Maine	20	13.70		
	New Hampshire	15	20.40		
	New Hampshire	13	17.90		
	Rhode Island	21	16.60		
	Rhode Island	15	15.30		
	Vermont	10	17.80		
	Vermont	7	16.60		
	W. Massachussets	24	16.90		
	W. Massachussets	18	14.50		
	All		**16.21**		
Coyote (Midwest)	Michigan	3	15.49		Vertnet Specimens
	Ontario, CAN	15	13.70		Schmitz & Lavigne 1987
	Quebec, CAN	7	13.73		Messier & Barrette 1982
	Wisconsin	3	9.73		Huegel & Rongstad 1985
	All		**13.47**		

Fisher	Connecticut	8	4.07	Male	Kilpatrick & Rego 1994
	Connecticut	12	2.24	Female	Kilpatrick & Rego 1994
	Maine	51	4.49	Male	Powell 1979
	Maine	44	2.35	Female	Powell 1979
	Minnesota	34	3.98	Male	Powell 1979
	Minnesota	13	2.25	Female	Powell 1979
	Minnesota	9	4.04	Male	Powell 1979
	Minnesota	6	2.22	Female	Powell 1979
	Minnesota	50	3.89	Male	Powell 1979
	Minnesota	38	2.20	Female	Powell 1979
	New Hampshire	39	4.30	Male	Powell 1979
	New Hampshire	21	2.14	Female	Powell 1979
	New Hampshire	50	3.30	Male	Giuliano, Litvaitis & Stevens 1989
	New Hampshire	82	1.60	Female	Giuliano, Litvaitis & Stevens 1989
	New York	26	3.71	Male	Powell 1979
	New York	41	2.06	Female	Powell 1979
	Ontario, CAN	147	3.95	Male	Powell 1979
	Ontario, CAN	154	2.11	Female	Powell 1979
	Quebec, CAN	37	4.70	Male	Renard, Lavoie & Larivière 2008
	Quebec, CAN	40	2.40	Female	Renard, Lavoie & Larivière 2008
	UP, Michigan	15	3.48	Male	Powell 1979
	UP, Michigan	10	2.22	Female	Powell 1979
	Wisconsin	22	3.40	All	Wright 1999
	All		**3.05**		
Gray Fox	Iowa	1	4.00		Vertnet Specimens
	Massachussets	2	4.75		
	Michigan	2	4.49		
	New Hampshire	1	4.80		
	New York	5	2.83		
	Rhode Island	5	4.11		
	All		**3.87**		
Marten	Labrador, CAN	5	1.31	Ad Male	Smith & Schaefer 2002
	Labrador, CAN	8	1.18	Juv Male	Smith & Schaefer 2002
	Labrador, CAN	6	0.85	Ad Fem	Smith & Schaefer 2002
	Labrador, CAN	8	0.80	Juv Fem	Smith & Schaefer 2002
	Maine	14	0.77	Male	Katnik, Harrison & Hodgman 1994
	Maine	14	0.52	Female	Katnik, Harrison & Hodgman 1994
	Maine	8	0.71	All	Buskirk & McDonald 1989
	Minnesota	84	1.01	Male	J. Woodford, WI DNR; pers. comm.
	Minnesota	90	0.66	Female	J. Woodford, WI DNR; pers. comm.

	Minnesota	4	0.80	All	Buskirk & McDonald 1989
	New York	9	0.69	All	Buskirk & McDonald 1989
	UP, Michigan	25	1.03	Male	Spriggs 2015
	UP, Michigan	22	0.68	Female	Spriggs 2015
	Wisconsin	39	0.80	All	Wright 1999
	Wisconsin	42	0.92	Male	J. Woodford, WI DNR; pers. comm.
	Wisconsin	18	0.62	Female	J. Woodford, WI DNR; pers. comm.
	Wisconsin	10	1.10	Male	Gilbert *et al.* 2009
	Wisconsin	6	0.74	Female	Gilbert *et al.* 2009
	All		**0.83**		
Red fox	Illinois	14	5.25	Adult	Storm *et al.* 1976
	Illinois	32	4.82	Subadult	Storm *et al.* 1976
	Illinois	13	4.13	Adult	Storm *et al.* 1976
	Illinois	24	3.99	Subadult	Storm *et al.* 1976
	Iowa	19	4.82	Adult	Storm *et al.* 1976
	Iowa	87	4.65	Subadult	Storm *et al.* 1976
	Iowa	22	3.94	Adult	Storm *et al.* 1976
	Iowa	68	3.72	Subadult	Storm *et al.* 1976
	Ontario, CAN	37	4.10	Male	Voigt 1987
	Ontario, CAN	37	3.40	Female	Voigt 1987
	Indiana	47	5.25	Male	Hoffman & Kirkpatrick 1954
	Indiana	52	4.21	Female	Hoffman & Kirkpatrick 1954
	Quebec, CAN	29	3.68	All	Lefebvre *et al.* 1999
	New York	3	4.67		Vertnet specimens
	Pennsylvania	1	5.13		Vertnet specimen
	Massachussets	1	4.40		Vertnet specimen
	Connecticut	1	3.30		Vertnet specimen
	Rhode Island	2	5.25		Vertnet specimens
	All		**4.29**		
Wolf	UP, Michigan	42	28.01	All	Vertnet Specimens
	Minnesota	32	26.30	Female	Mech & Paul 2008
	Minnesota	36	30.60	Male	Mech & Paul 2008
	Minnesota	197	27.97	Female	Mech & Paul 2008
	Minnesota	177	34.31	Male	Mech & Paul 2008
	Minnesota	187	28.62	Female	Mech & Paul 2008
	Minnesota	173	33.97	Male	Mech & Paul 2008
	Minnesota	263	28.35	Female	Mech & Paul 2008
	Minnesota	282	34.64	Male	Mech & Paul 2008
	Minnesota	177	29.28	Female	Mech & Paul 2008

Minnesota	217	35.34	Male	Mech & Paul 2008
Minnesota	94	30.01	Female	Mech & Paul 2008
Minnesota	121	35.94	Male	Mech & Paul 2008
Wisconsin	9	29.38	All	UW-Madison Museum of Zoology
Ontario, CAN	13	20.70	All	Schmitz & Lavigne 1987
Ontario, CAN	20	25.50	All	Schmitz & Lavigne 1987
All		**31.48**		

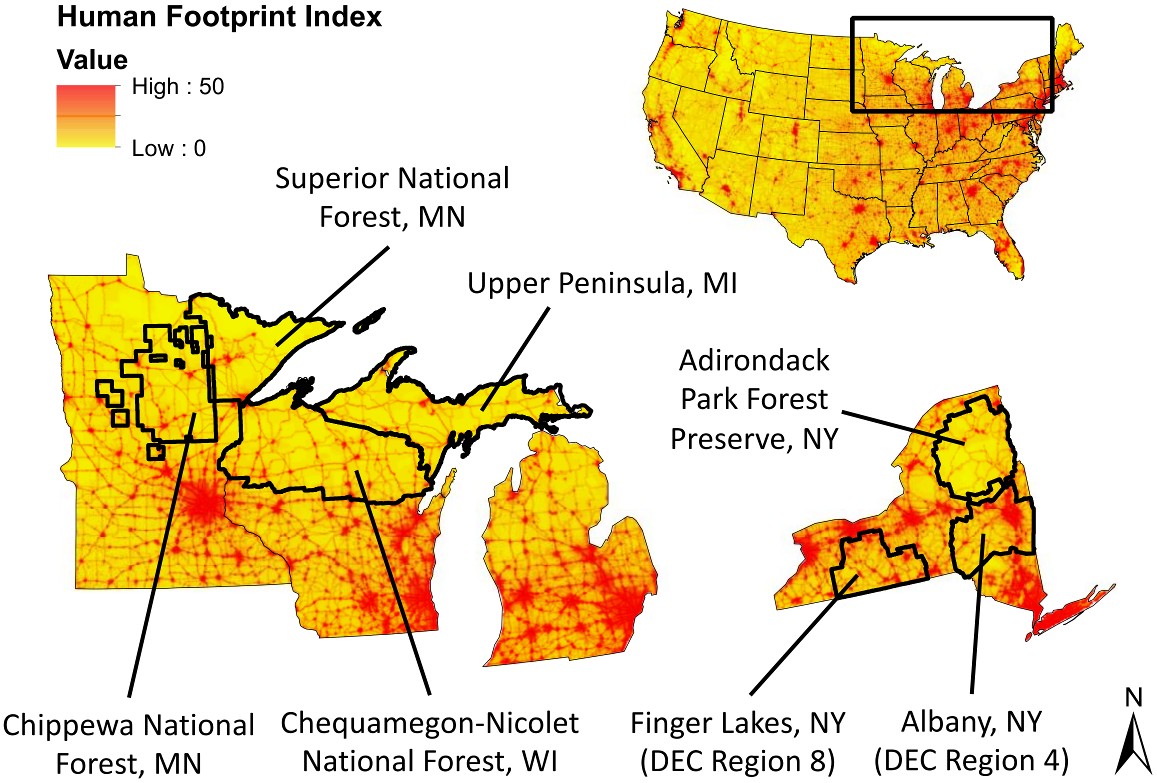

Figure S1. Distribution and boundaries (black polygons) of sites. Background raster illustrates human footprint index and inset map denotes location of sites in the continental United States.

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