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RESEARCH ARTICLE

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Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations

Philip J. Manlick[1] | Shelby M. Petersen[1] | Katie M. Moriarty[2] | Jonathan N. Pauli[1]

[1]Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin

[2]Pacific Northwest Research Station, USDA Forest Service, Olympia, Washington

Correspondence
Philip J. Manlick
Email: pmanlick@wisc.edu

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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 martens *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.

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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

1 | 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 (Cooper, Freckleton, & Jetz, 2011; Pearman, Guisan, Broennimann, & Randin, 2008) and species invasions (Wiens & Graham, 2005). Moreover, niche conservatism is a fundamental assumption of many species distribution models used to map Grinnellian niches, the non-interactive, environmental aspects of a species' range (Grinnell, 1917). Consequently, Grinnellian 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 (Cooper et al., 2011; Losos, 2008). 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, González-Suárez, Bernardo-Madrid, Revilla, & Villalobos, 2016; Rosado, Figueiredo, de Mattos, & Grelle, 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 (Ripple et al., 2014; Ritchie et al., 2012). 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 (Chapin, Matson, & Vitousek, 2011; MacArthur, 1972), 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 Grinnellian and phylogenetic niche conservatism have been widely observed in mammals (Cooper et al., 2011; Olalla-Tárraga et al., 2011; Peterson, Soberón, & Sánchez-Cordero, 1999), idiosyncratic patterns of divergence and conservatism have been observed across carnivore clades, including felids, canids and mustelids (Buckley et al., 2010; Diniz-Filho, Terribile, Da Cruz, & Vieira, 2010). Nevertheless, Grinnellian 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 et al., 2009; Newsome, Garbe, Wilson, & Gehrt, 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 martens *Martes americana* and Pacific martens *Martes 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, Woodford, Zuckerberg, & Pauli, 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 (Comte, Cucherousset, & Olden, 2016; Larson, Olden, & Usio, 2010; Newsome, Martinez del Rio, Bearhop, & Phillips, 2007). 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 (Figure 1). Specifically, we developed a three-stage isotopic framework that compared Eltonian niches across populations by calculating: (a) pairwise dietary overlap in isotopic δ-space; (b) individual diets using isotopic mixing models and pairwise niche overlap using a novel implementation of utilization distribution overlap indices in proportional dietary space; and (c) pairwise differences in the proportional use of functional prey groups using population-level diets from isotopic mixing models.

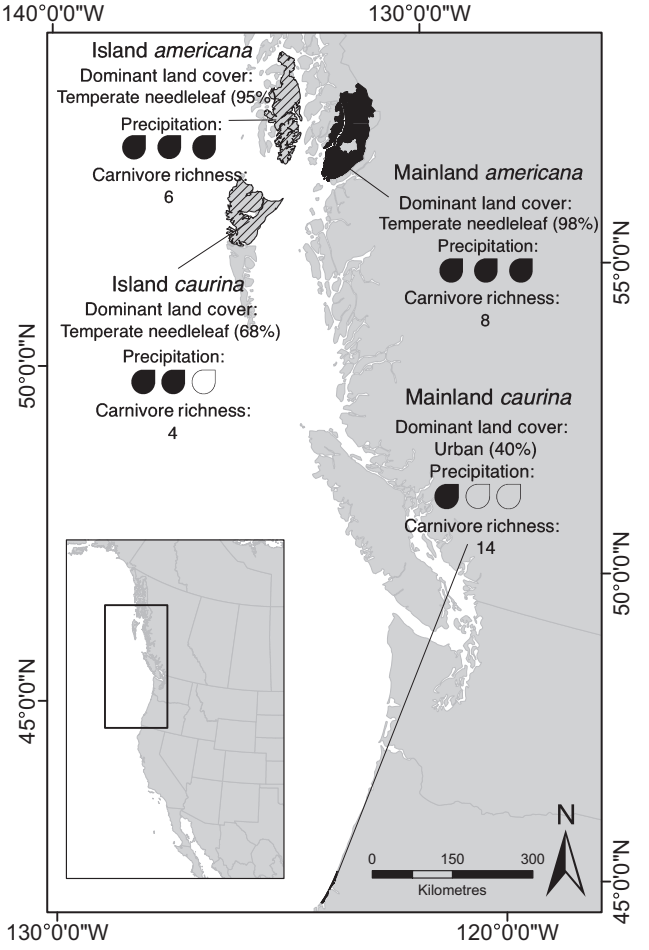

FIGURE 1 Comparison of mainland and island sites, including dominant land cover, precipitation level and carnivore richness values. Cross-hatched regions illustrate *Martes americana* presence, while black regions illustrate *Martes caurina* presence. Three raindrops indicate high levels of precipitation (>170 mm/month), and one raindrop indicates low levels of precipitation (<140 mm/month). Carnivore richness indicates the number of carnivores present at each site

2 | MATERIALS AND METHODS

2.1 | Study areas

We compared diets of American and Pacific marten populations in a 2 × 2 paired design of mainland and island sites (Figure 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 (Tables S1 and S2, Supporting Information). Prey groups were largely conserved across sites, and each population had access to five 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 (Figure 1; Table S1, Supporting Information), 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 southernmost 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 (Figure 1), indicating substantial human impacts.

2.2 | 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, Bailey, Smythe, & Verschuyl, 2016) and trapper harvested samples (Pauli et al., 2015) (Table S2, Supporting Information). 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, Ben-David, Buskirk, DePue, & Smith, 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 (Table S2, Supporting Information). 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.

2.3 | 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 hr. Similarly, all vegetation, marine and tissue samples were rinsed 3× with a 2:1 chloroform:methanol solution and dried at 56°C for 72 hr, but samples were subsequently homogenized with either a ball mill mixer or a mortar and pestle. Samples were weighed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis on a Costech 4010 elemental analyser (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 to 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, Yeakel, Wheatley, & Tinker, 2012), we trophically corrected all marten isotopic signatures ($\delta^{13}C = -2.6$; $\delta^{15}N = -3.4$; *Vulpes vulpes*; Roth & 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, Inger, Bearhop, & Jackson, 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 vertebrate group. Likewise, salmon, crabs and intertidal molluscs 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, Pawlowsky-Glahn, Mateu-Figueras, & Barceló-Vidal, 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 & Kochanny, 2005) in dietary p-space using the R package ADEHABITATHR (Calenge, 2006). 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, Koch, Ferguson, and Kalinowski (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.

3 | RESULTS

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

Utilization distribution overlap indices revealed little to no overlap in core diets (0.0–0.10, 50% UDOI; Table 2, Figure 3), but high overlap in available diets (95% UDOI) for *M. americana* and island populations (Table 2). Moreover, per cent 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 (Figure 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, Figures 3 and 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 (Figure 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, Figure 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 (Figure 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.

TABLE 1 Estimated mean proportional contribution of each functional prey group to sampled marten populations (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)

4 | 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 versus exogenous drivers (Comte et al., 2016; Larson et al., 2010; 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

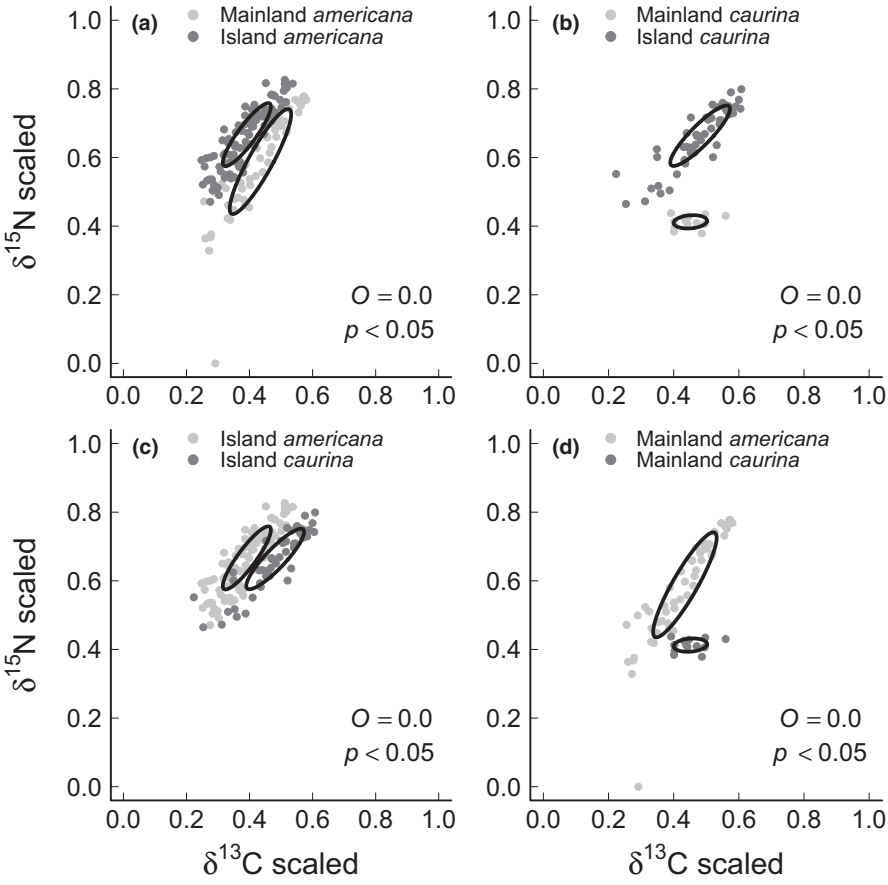

FIGURE 2 Niche overlap in corrected δ-space for *Martes americana* (a), *Martes caurina* (b), island martens (c) and mainland martens (d) from four study sites in northwestern North America. Pairwise isotopic niche overlap (*O*) among standard ellipses corrected for small sample size (SEA_C; black) was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

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 (Figures S1 and S2, Supporting Information). This means there were multiple solutions to each mixing model, though there was little variation in posterior probabilities for most models (Figure 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 (Carlson et al., 2014; Darimont et al., 2009; Yeakel et al., 2009) 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,

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 (per cent overlap) was estimated for Island *americana* (IA), Mainland *americana* (MA), Island *caurina* (IC) and Mainland *caurina* (MC) populations. IA/MA arrangement indicates the per cent of Island *americana* diets overlapping Mainland *americana* diets followed by the per cent of Mainland *americana* diets overlapping Island *americana* diets, with codification maintained for all comparisons

Comparison	50% UDOI	95% UDOI	Per cent 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

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 trade-offs 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, Moriarty, Green, & Levi, 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 harbours 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, Figure 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

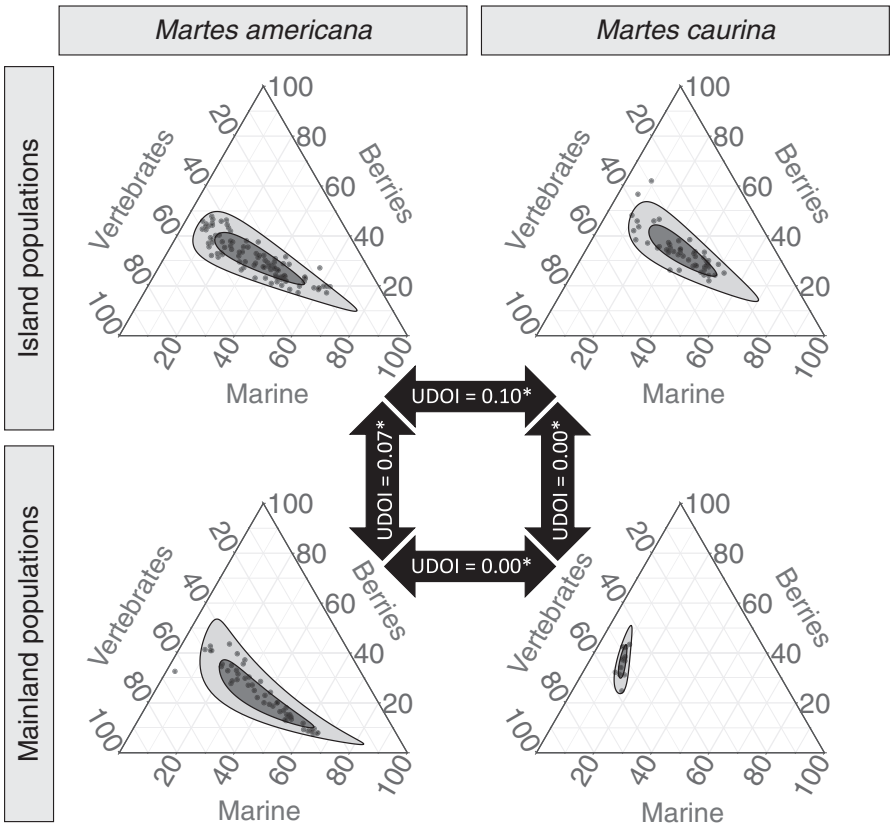

FIGURE 3 Ternary plots of proportional dietary space for *Martes americana* and *Martes caurina* populations using individual dietary estimates from isotopic mixing models. Axes denote proportion (%) of each functional prey group estimated for each population, points denote estimated individual diets, 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

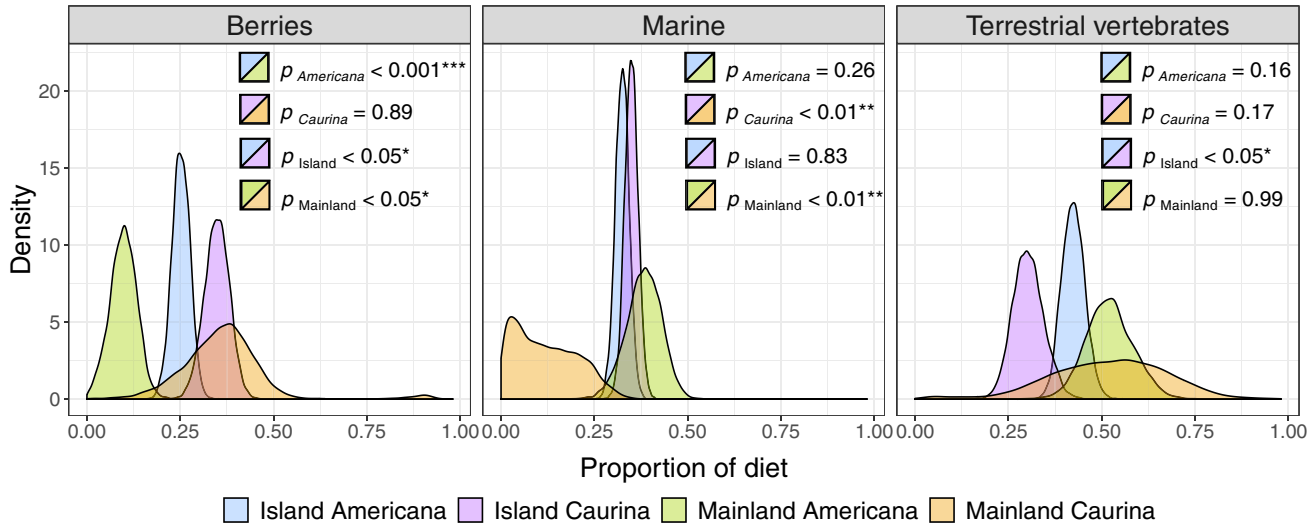

FIGURE 4 Posterior distributions of berries, marine-derived resources and terrestrial vertebrates estimated for sampled American (*Martes americana*) and Pacific (*Martes caurina*) populations using Bayesian-based isotopic mixing models. Inset *p*-values denote results of *t* tests quantifying differences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

to resources. Our work aimed to quantify dietary overlap and niche conservatism and therefore did not explicitly quantify underlying environmental factors such as 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 the use of berries and marine prey. Conversely, *M. americana* diets differed only in the use of berries and *M. caurina* diets differed only in the 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, Sutherland, O'Reilly, & Lambin, 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 (Carlson et al., 2014; Raine, 1987; Zielinski & Duncan, 2004). 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, Alldredge, Logan, & Pauli, 2016), while even highly specialized carnivores like black-footed ferrets *Mustela nigripes* have demonstrated surprising levels of dietary plasticity (Brickner, Grenier, Crosier, & Pauli, 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 et al., 2009; Newsome et al., 2015; Smith et al.,

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, Wirsing, Beschta, & Buskirk, 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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AUTHORS' CONTRIBUTIONS

All authors developed the ideas and designed the study; K.M.M. and J.N.P. collected biological samples; S.M.P. processed isotopic data, and P.J.M. performed statistical analyses. P.J.M. and S.M.P. wrote the manuscript, and all authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All isotopic signatures are available at https://figshare.com/articles/Manlick_et_al_2018_FigSahre_xlsx/7252994.

ORCID

Philip J. Manlick https://orcid.org/0000-0001-9143-9446

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SUPPORTING INFORMATION

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

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