Dietary partitioning of fishers and martens in a rapidly changing landscape

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ARTICLE INFO

ABSTRACT

Niche partitioning is critical for the stable coexistence of competing species that share limited resources. Yet, niches are dynamic, especially in the face of rapid environmental change. Carnivores exhibit particularly strong forms of competition and are differentially affected by change. Fishers (*Pekania pennanti*) and martens (*Martes caurina*) are two species of carnivores that overlap in space, time, and resources. In the Sierra Nevada of California, these two species share habitats that are undergoing a sudden restructuring due to drought and the subsequent mortality of more than half of all trees. Using a long-term dataset from across the affected region of the Sierra Nevada, we quantified the diet, as well as dietary niche overlap and niche shift of fishers and martens during summer months before, during, and after these disturbances and as a function of spatial overlap. The summer diet of fishers and martens did not appear to be affected by change in live forest canopy and tree mortality. While fisher diet was unaffected by elevation, martens exhibited an increasing reliance on vertebrate prey at higher elevations. Our results suggest that during summer months the diet of fishers is highly diverse, even including fungi and insects, but the diet of martens is less diverse and more reliant on vertebrate prey. These different consumption patterns — which were largely unaffected by changing environmental conditions, except elevation — have led to unexpectedly low overlap in trophic niche space during the timeframe measured. Our findings demonstrate that the coexistence of martens and fishers regionally is likely facilitated, in part, through partitioning along the trophic niche axis. If drought conditions persist and lead to continued or increasingly reduced snowpack and altered vegetation, future research should assess how niche partitioning of fishers, martens, and other members of the broader carnivore community will endure.

1. Introduction

Understanding processes that define species coexistence is central to understanding community dynamics and in predicting species responses to environmental change (Amarasekare, 2003; HilleRisLambers et al., 2012). The niche concept is a useful framework to identify the range of needs and tolerances of individual organisms across biotic and abiotic axes (Carscadden et al., 2020), and to explore niche overlap and competitive interactions (Polis et al., 1989; Amarasekare, 2003; Costa-Pereira et al., 2018). Indeed, niche partitioning is a principle mechanism by which competing species can exhibit stable co-existence (Linnell and Strand, 2000; Levine and HilleRisLambers, 2009). Species typically partition along at least one of three primary niche axes: spatial, temporal, and trophic (Amarasekare, 2003; Carscadden et al., 2020). Species limit spatial and temporal overlap with competitors by adjusting how they occupy a landscape (Zhong et al., 2016; Schirmer et al., 2019) or when they are active (Adams and Thibault, 2006; Dini-Andreote et al., 2014). When changes to the use of space and time are unavailable or simply infeasible, species can partition resources such as food for competitive coexistence (Schmidt et al., 2011; Manlick and Pauli, 2020), which can induce wide-ranging consequences on individual fitness and community dynamics (Costa et al., 2008; Kartzinel et al., 2015; Manlick et al., 2019). Niche overlap in carnivores can lead to agonistic interactions that are particularly consequential, as phenotypic adaptations within this guild are evolved toward causing physical harm or direct mortality (Donadio and Buskirk, 2006). To avoid or reduce interference and encounters with larger competitors, smaller carnivores will often vary how they exploit land covers, timing of activity, or dietary resources (Berger et al., 2008; Elmhagen et al., 2010; Rodriguez Curras et al., 2022).

Martens (*Martes caurina*) and fishers (*Pekania pennanti)* are small carnivores (0.9 kg and 3.8 kg, respectively) in the subfamily Guloninae that exhibit wide overlap in their spatial, temporal, and trophic niche (Aubry et al., 2012). They are generally associated with similar forest and prey types (Zielinski et al., 1997; Pauli et al., 2022) and their use of habitat and space has been shown to be strongly influenced by the presence of the other species (Fisher et al., 2013; Sweitzer and Furnas, 2016). Martens are smaller and more vulnerable to antagonistic interactions with fishers, thus, martens typically exhibit reductions in distribution, abundance and vital rates when fishers are present (Sweitzer and Furnas, 2016; Zielinski et al., 2017; Jensen and Humphries, 2019). To avoid competition and conflict with larger-bodied competitors, martens will adjust their spatial, temporal and dietary niche space (Rosenzweig, 1966; Zielinski and Duncan, 2004; Manlick et al., 2017). In particular, martens will occupy higher elevational sites that feature deep, persistent, and powdery snowpack for much of the year, which due to their low foot loading (body mass: total foot area), has enabled martens to successfully exploit snowy environments (Raine, 1987; Harrison et al., 2004; Manlick and Pauli, 2020). Primary prey for fishers in much of North America are porcupines (*Erethizon dorsatum*) and snowshoe hares (*Lepus americanus*), along with a broad array of small mammal species (Powell, 1982; Martin, 1994; LaPoint et al., 2015). Martens forage on a narrower guild of smaller mammalian prey items (Microtinae, red squirrels [*Tamiasciurus hudsonicus*]; (Zielinski et al., 1983; Thompson and Colgan, 1990; Jensen and Humphries, 2019). Martens exhibit a broadening dietary niche when preferred prey becomes less common (Thompson and Colgan, 1990), and their population density and distribution are negatively affected with increased reliance on secondary, less profitable, or high-risk prey (Carlson et al., 2014). Deep snow and structurally complex vegetation may moderate competitive interactions by providing a refuge for subordinate predators such as marten (Finke and Denno, 2002; Jensen and Humphries, 2019). Nevertheless, recent research has shown that the presence of martens can also induce notable shifts in the dietary niche of fisher away from smaller-bodied prey, presumably due to the increased foraging efficiency of martens on these smaller shared prey items (Smith et al., 2023).

In the southern Sierra Nevada mountains of the United States, fishers and martens co-occur at a regional scale, and are associated with similar forested land cover characteristics and prey (Zielinski and Duncan, 2004; Thompson et al., 2011; Slauson and Zielinski, 2019). They are often parapatric, with martens occupying higher elevations, but precipitation and topography provide enough spatial niche differentiation in some locations to allow for spatial overlap (Fig. 1) (Zielinski et al., 2017). Fishers in the southern Sierra Nevada are federally endangered (USFWS, 2020), while martens are designated a sensitive species by the US Forest Service (Zielinski et al., 2017). At least seasonally, fishers in this region consume fungi, lizards, and insects (Zielinski et al., 1999; Smith et al., 2022; Kuntze et al., 2024), which are atypical items that can supplant small mammal prey, and whose consumption can potentially lead to lower fitness and reproductive rates (Green et al., 2018b). Previous analysis of scat samples in the southern Sierra Nevada has shown surprisingly diverse diets for martens at lower elevations as well as fishers, with both species showing similar patterns in the items selected and their ranked importance (Zielinski and Duncan, 2004). These findings indicate that there is dietary overlap between the two species, although an explicit analysis of proportional diet as a function of spatial overlap, habitat and elevation is lacking (Zielinski and Duncan, 2004).

The potential effect that elevation, precipitation, and habitat have on dietary overlap has been particularly relevant recently, as the southern Sierra Nevada experienced historically low snowpack from 2012 to 2015 (Asner et al., 2016). This led to severe drought conditions unseen in the last 1200 years (Griffin and Anchukaitis, 2014; Asner et al., 2016), which contributed to a tree mortality event that killed over 55 % of all trees in the region (Byer and Jin, 2017). In addition to reducing the diversity and volume of primary producers on the landscape, events like
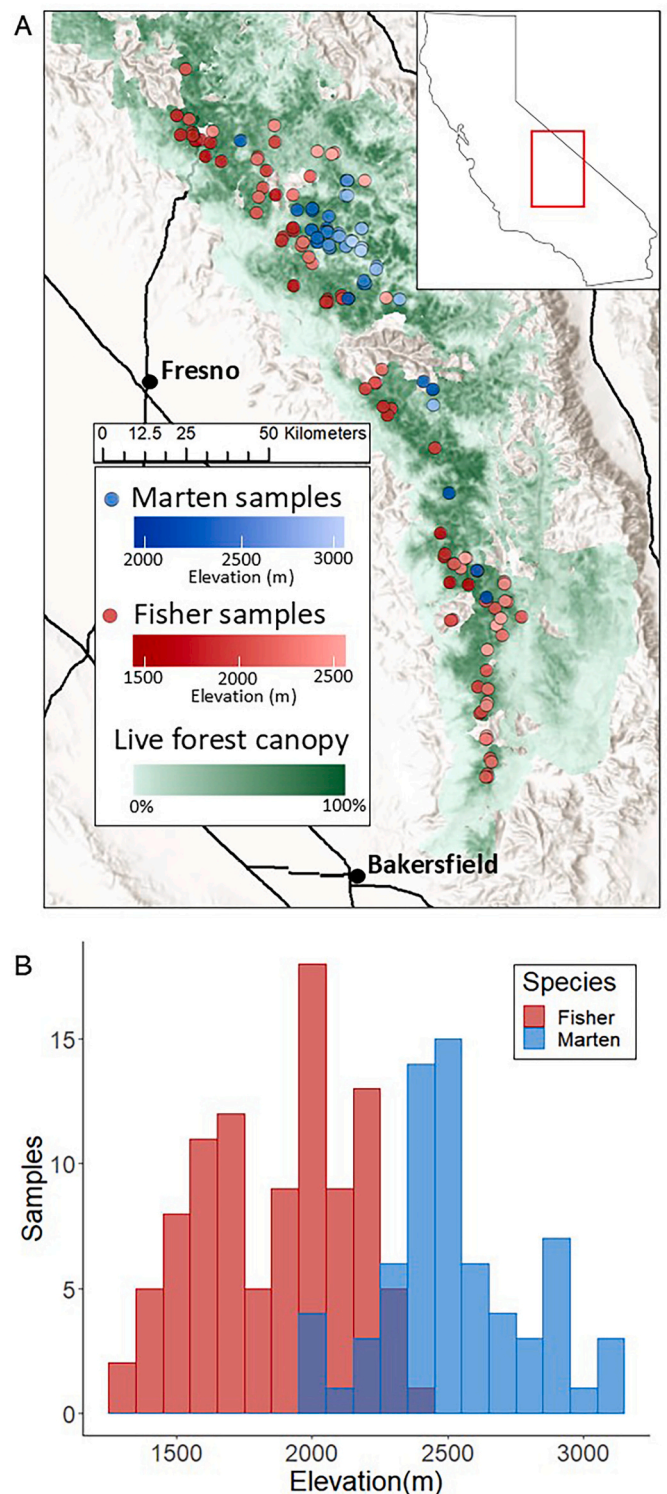

Fig. 1. A) Locations of fisher (*Pekania pennanti*) and marten (*Martes caurina*) hair samples collected from 2006 to 2018 in Sierra Nevada, USA, againsta background of live forest canopy as of 2015. B) Elevational distribution (meters) of fisher and marten hair samples. Color should be used in print.

this could re-sculpt the foraging strategies of carnivores (Hunter and Price, 1992; Morton et al., 1995; Sperry and Weatherhead, 2008), including fishers and martens (Jensen et al., 2012). Examination of fisher diets from before and after drought and tree mortality have shown corresponding shifts in consumption patterns, particularly in regards to mammalian and plant food items (Pilgrim et al., 2023). Understanding

any dietary changes for both species in response to this recent environmental change is important to understanding underlying shifts in community structure and resource overlap. Resource limitation and competition can both have critical impacts on the conservation of these two threatened species facing a rapidly changing natural system (Elmhagen and Rushton, 2007; Ritchie and Johnson, 2009; Elmhagen et al., 2010).

To quantify the diet and niche differentiation between fishers and martens in the southern Sierra Nevada and their response to ongoing habitat changes, we analyzed consumption patterns of these species from years before, during, and after tree mortality. We conducted stomach content analysis of fishers collected between 2008 and 2017 and analyzed stable isotope ratios in hair samples collected from both species between May and September from 2006 to 2018.

2. Material and methods

2.1. Study area

Our work was conducted on Sierra and Sequoia National Forest land in the Sierra Nevada Mountains of California (Fig. 1). Sampling locations were mid-slope (2122 m average, 1274–3065 m range) in mixed oak (*Quercus spp.*), fir (*Abies spp.*), and pine (*Pinus spp.*) forests. Some important food items available for mid-sized consumers include small to medium vertebrate species (sciurids, cricetids, passerines, lagomorphs, squamates), fungi, wasps, and hard (acorns, pine nuts) and soft mast (berries) (Zielinski and Duncan, 2004; Smith et al., 2022). The region experiences dry summers, and most annual precipitation falls as snow in the winter months (Zielinski et al., 2004). From 2012 to 2015, precipitation levels in the southern Sierra Nevada fell from its historical average of 108 cm per year to an average of 29 cm per year, leading to historically severe drought conditions (Minnich, 2007; Griffin and Anchukaitis, 2014; Stephens et al., 2018). This contributed to a large-scale tree mortality event during which more than 55 % of all trees in the region died (Byer and Jin, 2017; Stephens et al., 2018).

2.2. Sample collection and analysis

Stomach content analysis was conducted on fisher mortality specimens ($n = 45$) collected during population monitoring in the Sierra Nevada and western US (Sierra Nevada Adaptive Management Project (SNAMP), the USFS Kings River Fisher Project (KRFP), the Stirling CA Reintroduction, the Hoopa Valley Reservation) as well as opportunistic specimens (Supplemental Table 6). Live animal procedures were approved by the University of California, Davis, (IACUC Protocol No. 16551), and carcass collection and examination approved by CDFW state scientific collecting and salvage permits (#SC-7304). Available stomach sample contents were separated from individuals during necropsies, placed in sterile whirl packs, and stored in a —20C freezer until analyzed (Gabriel et al., 2015). Individual stomach contents were thawed, visually separated, and individually weighed to the nearest hundred mg, prey were identified to their nearest identifiable taxonomical level, separated to that taxonomical level, and weighed to generate the percent of overall stomach mass present.

We conducted our stable isotope analyses using all available fisher ($n = 113$) and marten ($n = 70$) hair samples collected as part of the U.S. Forest Service Sierra Nevada Carnivore Monitoring Program (Zielinski et al., 2013). Hair snaring devices were affixed to baited remote camera and track-collection survey stations with planned revisits within seven days during summer months (May – September) of 2006–2009 and 2011–2018 (2006: $n = 11$; 2007: $n = 13$; 2008: $n = 10$; 2009: $n = 6$; 2011: $n = 9$; 2012: $n = 22$; 2013: $n = 12$; 2014: $n = 15$; 2015: $n = 32$; 2016: $n = 9$; 2017: $n = 27$; 2018: $n = 17$; Supplemental table 1). Given that fishers and martens molt from August to October, hair samples represent the period of consumption and isotopic incorporation from the months preceding this period (June–September) of the year prior to

sample collection) (Pauli et al., 2009). We limited pseudoreplication primarily through multi-locus genotyping of samples (see Tucker et al., 2017) to confirm that we were sampling from distinct individuals within a season. When genotyping was unsuccessful, we restricted samples ($n = 39$) to those that were > 11 km (fisher) or > 5 km (marten) from the nearest neighboring sampling site from that year (>95 % of home ranges are <11 km (fishers) and 5 km (martens) in diameter, respectively; Zielinski et al., 2004, 2005; Davis et al., 2007). Two marten samples were collected from the Inyo National Forest, which is outside our ability to estimate co-occurring fisher occupancy and to categorize land cover estimates and, thus, were excluded from analyses.

To calculate stable isotopes of potential food sources, we collected samples ($n = 303$; Supplemental table 2a) from items reported as >5 % of fisher or marten diet in previous Sierra Nevada analyses (Grenfell and Fasenfest, 1979; Zielinski et al., 1983; Zielinski and Duncan, 2004; Golightly et al., 2006; Slauson and Zielinski, 2019). We collected fungi; seeds, berries and nuts of plants; insects; and hair, feathers, and scales from vertebrates. We live-trapped small mammals with Sherman (5 × 6 × 17 cm, H.B. Sherman Traps Inc., Tallahassee, FL) and Havahart (model 0745; Woodstream Corp., Lititz, PA) trapping grids (IACUC #A006193). To avoid sampling animals that have consumed human food (Kirby et al., 2016), all trapping was done >200 m away from any buildings, roads, or campgrounds. After capturing small mammals, a clump of hair was cut from their lower back to be used in analysis and to serve as a mark to prevent re-sampling of the same individual. We also identified and collected small mammal hair samples when they were left at our carnivore monitoring camera or track stations ($n = 14$) (Taylor and Raphael, 1988). For small mammal species that we did not trap we obtained samples from museum specimens ($n = 39$; Supplemental table 3).

We removed surface oils by washing with 2:1 chloroform: methanol and then homogenized samples before drying them for 72 h at 55 °C (Pauli et al., 2009). Insect, plant, and fungi samples were dried for 72 h at 55 °C, after which we use a laboratory mixer mill (Mixer Mill MM200, Restch Inc. Newton, PA, USA) to homogenize (Kirby et al., 2016). We then placed the samples into tin combustion capsules for weighing, and analyzed them (>10 % in duplicate) with a Carlo Erba 1110 Elemental Analyzer coupled to a Thermo Delta Plus XP IRMS. Our results were calibrated with internal laboratory standards and reported as per mil (parts per thousand [‰]) ratios relative to the international standards of Peedee Belemnite (PDB; $\delta^{13}C$) and atmospheric nitrogen (AIR; $\delta^{15}N$).

2.3. Statistical analyses

To examine the isotopic niches of martens and fishers we used the standard ellipse area corrected for small sample size (SEAc) (R package *SIBER*; Jackson et al., 2011). We used SEAc values for each species to compare niche width size, and used the overlap between the underlying 95 % prediction ellipses as a metric of isotopic niche similarity.

We estimated the proportional diet of fishers and martens using Bayesian based mixing models in the package MixSIAR (Stock et al., 2018). We placed forage items into relevant categories *a priori* (vertebrates, plants, fungi, and insects), and used a K nearest-neighbor analysis (Rosing et al., 1998) to confirm that each category was isotopically unique. Martens and fishers consume different vertebrate prey from each other (Zielinski and Duncan, 2004), and so we, thus, excluded prey that are not consumed (Philips et al., 2014). Consequently, martens and fishers possessed slightly different prey species in the vertebrate category (Supplemental Table 6), and subsequent analyses were conducted using these groupings. We accounted for trophic enrichment between forage items and consumer tissue by correcting our prey data ($\delta^{13}C \pm sd$: 2.6 ‰ ± 0.09; $\delta^{15}N \pm sd$: 3.4 ‰ ± 1.2) (Roth and Hobson, 2000). Precipitation rates and elevation can influence natural abundances of nitrogen isotopes (Averill and Finzi, 2011; Ma et al., 2012; Xiao et al., 2012), so we compared the isotopes of prey from a latitudinal precipitation gradient (Zielinski et al., 2017) and from high (>2145 m) and low

elevation (<2145 m) classes. We did not detect any differences between areas with differing elevations or rates of precipitation ($p > 0.05$; K-means cluster analysis).

To account for variation in carbon and nitrogen concentrations between prey samples, we factored in elemental concentrations of each item based on laboratory results and from literature (Hopkins and Ferguson, 2012). We accounted for the digestibility of carbon and nitrogen in each forage item (Phillips and Koch, 2002) by correcting the isotopic mixing space using concentration dependence in MixSIAR (Stock et al., 2018). We calculated digestibility for each item using laboratory derived values from the literature to the most precise taxonomic classification level available (Phillips and Koch, 2002). We used MixSIAR to calculate posterior probability densities of proportional contributions from our forage categories to groupings of fishers and martens. For each model, we specified a uniform ("uninformative") prior and ran three Markov chains (length = 300,000; burn-in = 200,000; thinning rate = 100). We considered Gelman-Rubin diagnostic (R) values <1.05 to indicate model convergence.

To explore the effects of drought and tree mortality on marten and fisher diet, we used existing fractional land cover maps developed from satellite-based mNDVI (modified Normalized Difference Vegetation Index; Liu and Huete, 1995) quantifications to estimate proportional land cover by category (live forest canopy, tree mortality, shrub, bare ground) in each year from 2014 to 2018 (30 m pixel resolution; McGregor, 2021). Canopy metrics from survey years preceding 2015 (2006–2014) use the values from 2014, as this is the earliest year this information is available and only relatively minor changes in cover (*e.g.* background mortality, fire, management) are known to have occurred (Rollins, 2009). To understand the impacts of tree mortality, we used an average neighborhood value of standing live-forest canopy and tree mortality at sampling sites. We created moving window values for both the mean of live forest canopy cover and tree mortality over 1km^2 (sampling scale for local overlapping martens and fishers; Spencer et al., 2011, Zielinski et al., 2013) and then extracted it as a continuous value for each corresponding hair sample by collection site and year. We also grouped samples categorically as either before tree mortality (2006–2015) or after (2017–2018), based on the peak of the event in 2016.

We used co-occurrence probabilities to estimate how interspecies overlap influenced the diet of fishers and martens. To account for potential partitioning between species, we estimated the likelihood that a fisher or marten would have overlapped the other species in the location and season of its sampling. Using the detections from US Forest Service population monitoring (Zielinski et al., 2013) we compiled values from previously developed multi-season, single-species dynamic occupancy models. Initial rates of occupancy were calculated by incorporating site detections of the target species with detection probabilities based on device type (camera, track box, hair snare) and spatial covariates (canopy cover, snow depth, precipitation, minimum temperature) for each year. Subsequent occupancy was informed by within-season detections and site persistence and colonization metrics informed by device type, spatial covariates, and prior-season detections for each year. The model was fit using Markov chain Monte Carlo (MCMC) methods of JAGS v. 4.2.0 (Plummer, 2003), and convergence was assessed by examining trace plots and R values (Gelman et al., 2013). We then created moving window values of the mean occupancy estimate over 1km^2. We used this moving window value to estimate a continuous value of the probability of occupancy of the opposing species at the sampling locations within the same season.

We explored a simple suite of *a priori* models (null, species co-occurrence, % live forest canopy, and elevation in meters) in MixSIAR and evaluated model fit using an approximate leave-one-out (LOOic) cross-validation (Stock et al., 2018). We specified error structure for all models and considered Gelman–Rubin diagnostic values <1.05 to indicate model convergence (Stock et al., 2018). Covariates with significant influence (w_i > null) on diet were then modeled continuously against

proportional input of prey categories. Any prey category that never exceeded 10 % of proportional dietary input at any point along a linear model was excluded (Stock et al., 2018), and the linear model produced with the remaining categories. As sexual dimorphism can impact ecological interactions for fishers and martens, we first explored differences in the diet for males and females of each species, and planned to restrict our subsequent analyses by sex if appropriate.

2.4. Theory and calculation

While stomach content analysis is subject to limitations due to differential digestive rates of prey materials, it can provide important context for dietary selection, and has not been conducted on fishers and martens in this portion of their range. Stable isotope analysis is complementary, as it overcomes limitations in live sample differences in prey digestibility and detection rates to accurately estimate proportionality, providing key data on the relative presence and volume of different prey classes within diets.

We hypothesized that the diets of fishers and martens would exhibit a high degree of overlap in general, and that increased species co-occurrence and lower proportions of live forest canopy cover will compress trophic niche space. Specifically, we predicted that the consumption of vertebrate prey by martens would decrease in areas of higher overlap with fishers because of increased competition. We also predicted that lower levels of live forest canopy and increased tree mortality would result in smaller dietary niches for both marten and fisher as a result of a simplification of these forested ecosystems. We hypothesized that elevational gradients would also mediate dietary overlap, and predicted that marten specialization on vertebrate prey would be greatest at the highest elevations and be more generalized at lower elevations, where prey is more diverse and competition is increased.

2.5. Results

Necropsies of 45 fishers collected from the Sierra Nevada and other locations in the western US revealed a diversity of prey items (Supplemental Table 6). Several fishers had full stomachs containing only fungi, insects, and plant material, equal to or greater in volume of other individuals with satiated stomachs containing small mammals (Fig. 2). Stomach content analysis confirms direct and significant consumption of these atypical diet items as the majority of diet in 29 % of stomachs analyzed. Multiple fisher had sympatric mesocarnivores (striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale gracilis*), and ringtails (*Bassariscus astutus*) in stomach contents, although martens were not detected (Supplemental Table 1).

The overall isotopic niche of martens (SEAc = 4.47 ‰^{2}; $n = 68$) was larger than that of fishers (SEAc = 3.40 ‰^{2}; $n = 101$) in the southern Sierra Nevada mountains (Fig. 3) during summer months. The isotopic niche space of fishers overlapped 74 % with that of martens, while 51 % of the isotopic niche space of martens overlapped with that of fishers. We did not detect an effect of sex, for either species (male fishers: $n = 35$; female fishers: $n = 40$; male martens: $n = 33$; female: $n = 9$), on diet (Supplemental Table 5, Supplemental Fig. 2). Martens primarily consumed vertebrates, regardless of tree mortality, making up an estimated 71 % of their overall diet in the Southern Sierra Nevada (Table 1). This proportion appeared to have declined in the years following tree mortality, although credible intervals overlapped. Insects and plants made up relatively low proportions of their diet, and fungi was the least consumed item (Table 1). The diet of martens contrasts to that of fishers, where fungi constituted nearly half of fisher diet (42 %) and vertebrates (15 %) were the least consumed item (Table 1).

We found no support for the influence of fisher occupancy, live forest canopy cover, or tree mortality on the diet of martens, as the null model outperformed these predictor variables (Table 2). Instead, we found support for elevation ($w_i = 0.826$, Table 2) driving the diet of martens.
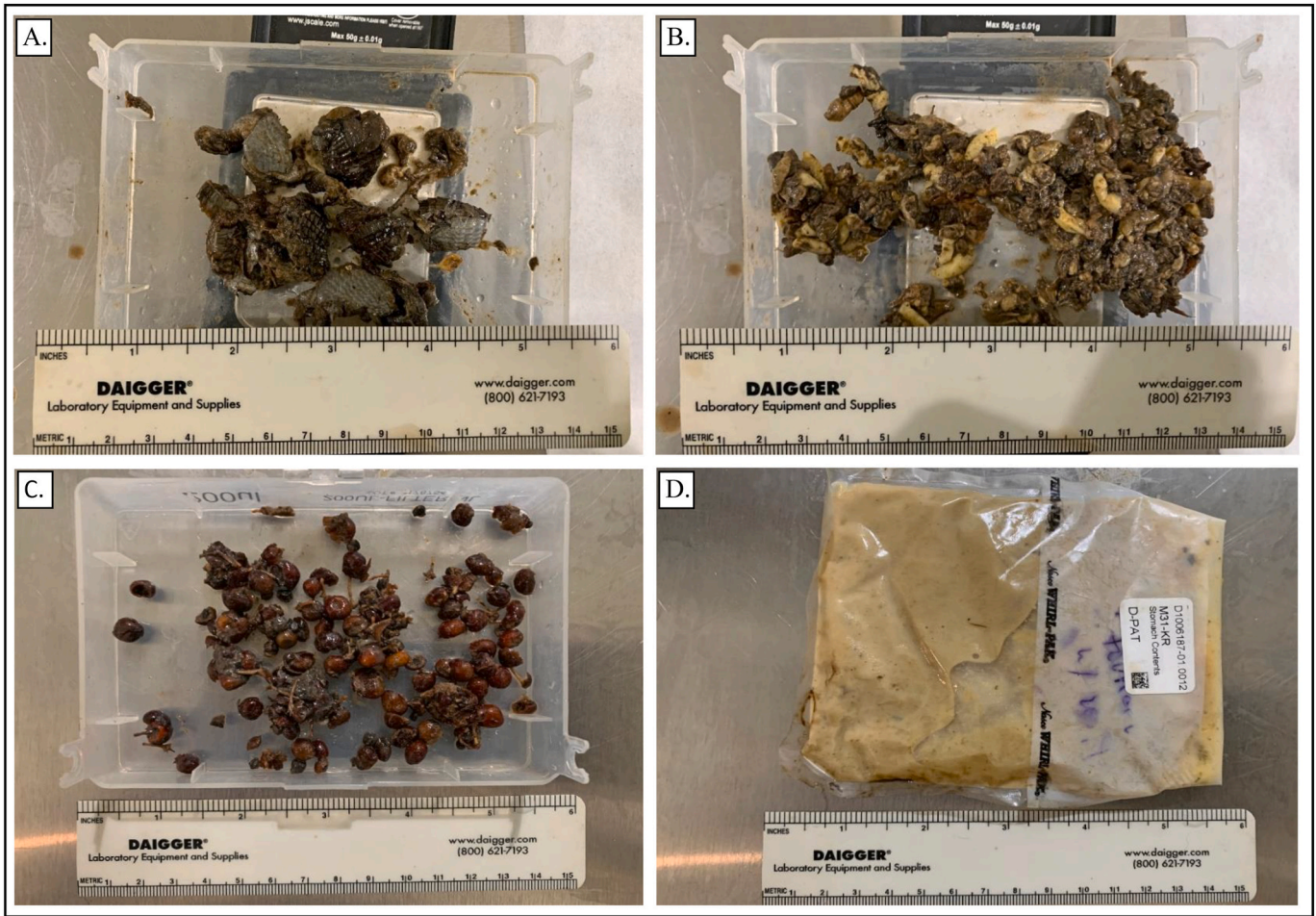
Fig. 2. Items collected from the stomachs of necropsied fishers collected from the Sierra Nevada and northern California, USA, between 2008 and 2017, from Supplemental Table 6. A.) *Elgaria* from individual 15, B.)*Vespidae* larvae from individual 18, C.) *Arctostaphylos* mast from individual 23, and D.) fungi slurry from individual 22. Color should be used in print.
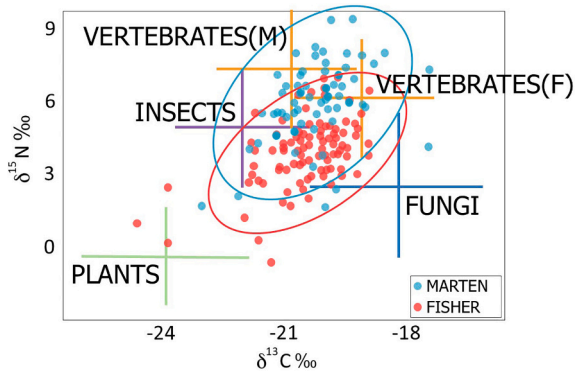

Fig. 3. Isotopic biplot displaying the alignment of fishers (*Pekania pennanti*), martens (*Martes caurina*), and their dietary prey groupings adjusted for dietary discrimination. Fisher (F) and marten (M) vertebrate prey are depicted separately given the groupings' differing composition and isotope values. Overlaid on individual consumer points are standard error ellipses (SEAc). Color should be used in print.

Marten consumption of vertebrates and insects were particularly correlated to elevation (1951–2421 m [elevational overlap with fisher]: $n = 26$; 2428–3066 m [outside of fisher elevational range]: $n = 44$), with insects decreasing (0.77[0.04–0.94] to 0.01[0.001–0.25]) and vertebrates increasing (0.08[0.01–0.50] to 0.79[0.52–0.93]) as elevation

Table 1

Estimated proportional dietary contributions (95 % credibility intervals) for martens (*Martes caurina)* and fishers (*Pekania pennanti*) in the Southern Sierra Nevada from 2006 to 2018 before and after a major tree mortality event that peaked in 2016.

Dietary Source	Martens before tree mortality (2006–2015) ($n = 45$)	Martens after tree mortality (2017–2018) ($n = 20$)	Fishers before tree Mortality (2006–2015) ($n = 85$)	Fishers after tree mortality (2017–2018) ($n = 24$)
Fungi	0.03 (0.01–0.10)	0.08 (0.01–0.24)	0.42 (0.31–0.54)	0.42 (0.29–0.55)
Vertebrates	0.86 (0.69–0.88)	0.62 (0.44–0.82)	0.15 (0.03–0.26)	0.11 (0.03–0.19)
Plants	0.06 (0.01–0.16)	0.09 (0.01–0.22)	0.13 (0.03–0.27)	0.33 (0.17–0.49)
Insects	0.06 (0.01–0.21)	0.21 (0.01–0.44)	0.29 (0.05–0.51)	0.14 (0.02–0.36)

increases (Fig. 4). In contrast to martens, the proportional diet of fishers was largely unaffected by environmental context; we found most support for the null model ($w_i = 0.412$, Table 3), which outperformed elevation, overlap with martens, proportion of tree mortality, and live forest canopy cover (Table 3).

Table 2

Definition and ranking of covariates included in isotopic mixing models to quantify marten (*Martes caurina*) diet in relation to elevation, canopy, and fisher (*Pekania pennanti*) occupancy, as sampled from 2006 to 2018 in the southern Sierra Nevada Mountains. "LOO" abbreviates leave-one-out cross validation results, where lower values indicate higher predictive capability.

| Covariate(s)	Definition	LOOic	Weight
Elevation	Elevation (m) above sea level where the marten was sampled	149.7	0.826
Null	No covariate included	156.6	0.100
Fisher occupancy	Average estimate of fisher occupancy for the 1km^2 surrounding the location where the marten was sampled	159.5	0.034
Tree Mortality	Average estimate of standing dead canopy for the 1km^2 area surrounding where the marten was sampled	159.8	0.032
Canopy	Average estimate of live forest canopy for the 1km^2 area surrounding where the marten was sampled	160.7	0.009
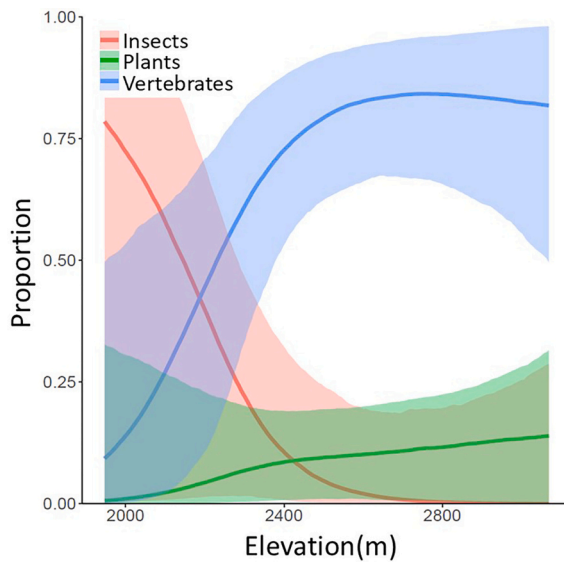
Fig. 4. Proportional dietary estimates and 95 % credible intervals from isotope mixing models for the response of martens (*Martes caurina*) to variation in elevation, as sampled from 2006 to 2018 in the southern Sierra Nevada Mountains. Color should be used in print.

Table 3

Definition and ranking of covariates included in isotopic mixing models to quantify fisher (*Pekania pennanti*) diet in relation to elevation, canopy, and marten (*Martes caurina*) occupancy, as sampled from 2006 to 2018 in the southern Sierra Nevada Mountains. "LOO" abbreviates leave-one-out cross validation results, where lower values indicate higher predictive capability.

Covariate(s)	Definition	LOOic	Weight
Null	No covariate included	183.1	0.412
Marten occupancy	Average estimate of marten occupancy for the 1km^2 surrounding the location where the fisher was sampled	183.3	0.367
Elevation	Elevation (m) above sea level where the fisher was sampled	184.3	0.123
Canopy	Average estimate of live forest canopy for the 1km^2 area surrounding where the fisher was sampled	184.9	0.059
Tree Mortality	Average estimate of standing dead canopy for the 1km^2 area surrounding where the fisher was sampled	185.9	0.040

2.6. Discussion

Our results reveal that martens and fishers in the southern Sierra Nevadas exhibited divergent summer diets and limited trophic niche overlap, regardless of interspecies co-occurrence or forest conditions. This is in contrast to previous literature from this region and the western United States, which has typically found diets to be largely or entirely overlapped (Pauli et al., 2022). In our study, martens consumed mostly small vertebrates, as expected from what they generally consume across their distributional range (Ben-David et al., 1997; Jensen et al., 2012). In contrast, fishers incorporated a wide range of food items, including non-trivial amounts of fungi and insects, into their diet during the summer. Fungi and insect consumption had been shown previously in the Southern Sierra Nevada population (Zielinski et al., 1999; Smith et al., 2022), but it is generally assumed that vertebrate prey is the dominant class of prey consumed by fishers in this region, or that consumption of atypical prey is incidental. While our analysis focused on diet during the summer, it would be interesting to determine whether diet shifts and possible dietary differentiation between these two carnivores would increase in other seasons. The data from necropsy were from animals collected throughout the year, but only represented a snapshot of prey consumption at time of death. The stomach contents for some individual fishers we examined were filled with fungi and insects. Notably, proportions of fungi, plant material and insects were unlikely to be derived secondarily by fishers consuming vertebrate prey that initially consumed these materials. Species like flying squirrel with fungi, or small mammals with plant and/or insects were not detected, despite the longer retention of hair or bone material in stomachs *versus* soft material. This evidence supports the idea that these alternative prey items are intentionally, not incidentally, consumed. Trophic niche overlap between these fisher and marten was smaller than expected, indicating a reduction in interference competition between fishers and martens, at least seasonally, creating sufficient trophic niche space when these species do co-occur.

Given the degree and scale of changes in forest composition throughout our study area, it would be reasonable to predict that some prey species would be reduced or even eliminated from the local landscape and unavailable to predators. Unfortunately, reliable estimates of prey availability before and after the forest change in this region are unavailable, limiting our ability to evaluate any shifts in prey availability due to changing forest conditions. Regardless, we did not find that either tree mortality or canopy cover influenced the diet of either martens or fishers. Some of this attenuated response of diet to change is likely the result of martens and fishers selecting against canopy loss within their home ranges. Indeed, our sampling sites for fishers exhibited 29 % canopy loss and sampling sites for martens had only 10 % canopy loss, compared to the regional average canopy loss of 55 %. In particular, martens likely exhibited a weak change in diet in response to forest die-off because they primarily inhabit elevations above the most significant tree mortality, and were able to continue targeting the vertebrate prey that they prefer. On the other hand, fishers which experienced more tree mortality, appeared to buffer dramatic shifts in their diet due to the overall dietary diversity to begin with. It is also possible that dietary changes were simply not realized at the time of our sampling. Indeed, the effect of perturbations like drought and tree mortality on primary production, fungal, and vertebrate consumers, can be lagged by multiple years (Fryxell et al., 1991; Schickmann et al., 2012; Watts et al., 2020).

Recent research that analyzed fisher scat with DNA metabarcoding from a study site within this region detected changes in frequency of consumption of before and after tree mortality (Pilgrim et al., 2023). Most notably, frequency of mammal consumption fell from 82 % to 49 %, while plant consumption rose from 19 % to 46 %. DNA metabarcoding has high taxonomic resolution, and is able to identify whether a particular species was consumed, but is limited in estimating proportional and assimilated diet. Our isotopic analysis for diet had reduced

taxonomic resolution in our prey groups, but provided a robust estimate of overall assimilated diet for both martens and fishers. Interestingly, another isotopic analysis of fishers from the same study site found proportional diets that were generally between our two works (Kuntze et al., 2024). Kuntze et al. reported that 25 % of the diet of fishers were fungi while 28 % of their diet was vertebrates. Future work that combine metabarcoding (for taxonomic resolution) and the analysis of stable isotopes (for assimilated diet) would help to clarify the dietary shifts from environmental perturbations and dietary overlap between competing species.

In the limited instances of overlap for both fishers and martens, the presence of the opposing species was not an important predictor of dietary input. Given the divergence seen in their diets — with martens being vertebrate specialists and fishers having a diverse diet that includes a significant amount of non-vertebrate food sources — it is not particularly surprising that co-occurrence was unimportant. While our work shows clear partitioning and little reciprocal effect of competitor presence on the diet of martens or fishers, the timeframe of our data (May–October) could miss important seasonal variation in competition. The Sierra Nevada Mountains are also home to many other competing carnivores, such as ringtails, gray foxes (*Urocyon cinereoargenteus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and mountain lions (*Puma concolor*) (Zielinski et al., 2005). A carnivore community that features more diversity can increase competitive effects and subsequent dietary niche displacement (Thompson and Gese, 2007; Green et al., 2018a). While martens and fishers were expected to exhibit the greatest competition and conflict, the lack of an effect might be understood to mean that their diets have diverged historically. Any adjacent dietary niche space occupied by the remaining carnivore community has not been investigated and it is unknown if their diets are linked to drought changes, historical divergence or elevational or another landscape variables. The fact that we detected fishers with similar-sized meso-carnivores in stomach samples, yet no martens, minimizes the potential concern regarding the potential for direct predation of martens by fisher even if further overlap were to occur. As bobcats are the primary predator of fishers, and occasionally predate martens (Wengert et al., 2014), monitoring whether antagonistic interactions with bobcats increases for martens with further changes in climate and loss of snowpack is a line of future inquiry. Quantifying the diet for the entire community throughout the year could better inform the ultimate resource partitioning occurring in the Sierra Nevada and potentially reveal if other species of carnivorans were immediately affected by the tree mortality event.

We found that martens exhibited strong associations with prey consumption as a function of elevation. At lower elevations, insects make up an increasing proportion of marten diet. In this regard, the diet of martens becomes more like fishers when focusing on areas where the two species overlap in space. Habitats at lower elevation contain more complex and abundant insect communities compared to those upslope (Hodkinson, 2005), suggesting that martens will take advantage of this food resource when it is available. Marten consumption of vertebrate prey was greatest at higher elevations. This stands to reason, as marten out-compete other regional carnivore species for vertebrate consumption in higher-elevation landscapes that disproportionately feature snow for most of the year (Ben-David et al., 1997; Zielinski et al., 2017; Jensen and Humphries, 2019). Increased consumption of small mammals has been tied to increased reproduction and population densities for martens (Thompson and Colgan, 1987), making the availability of this dietary niche space important in their conservation and management. Continued declines in snowpack and simplification of forested systems by disturbance could have significant impacts on the stability and robustness of small mammals as a prey source (Thompson and Colgan, 1987; Bowman et al., 2006; Andruskiw et al., 2008). In the Kern Plateau, a drier and higher elevation site adjacent to our current study system, fishers primarily consume vertebrates (Smith et al., 2022) and there are no records of martens occurring (Zielinski et al., 2017), even though the

elevation profiles found there are more typical of martens. Precipitation (which principally falls as snow) on the Kern Plateau is lower compared to the rest of southern Sierras, which then could support carnivores with heavier footload, such as fishers (Zielinski et al., 2017). It is possible that fisher are able to occupy a more preferable and nutritionally dense trophic niche of small vertebrates (rather than fungi) and exclude the smaller bodied and subordinate martens. Given projected changes in climate for the Sierra Nevada (Zielinski et al., 2017), species dynamics on the Kern Plateau might serve as an analog for changes to this community in future scenarios where precipitation is chronically lower.

2.7. Conclusions

The threat of shifting climate and related biotic interactions has the potential to destabilize fisher and marten populations and decouple them from their spatial, temporal, and trophic niche axes. Our work suggests that fisher and marten occupy different trophic niche axes, and this relationship is resilient, at least through the time period sampled, to acute changes in their habitat due to tree mortality. Martens are able to isolate their own trophic niche at higher elevations. However, if declines in annual snow continue, fishers may be able to occupy and eventually exclude martens from higher elevation habitat.

Ethics statement

CRediT authorship contribution statement

G. Bradley Smith: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jody M. Tucker:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Mourad Gabriel:** Writing – review & editing, Validation, Resources, Methodology, Investigation. **Greta Wengert:** Writing – review & editing, Validation, Methodology, Investigation. **Jonathan N. Pauli:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

contributions of isotopic results from prey items from B. Hobart from the University of Wisconsin. We also thank the American Society of Mammalogists for their support through a grant-in-aid of research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2024.e00375.

References

Adams, R.A., Thibault, K.M., 2006. Temporal resource partitioning by bats at water holes. J. Zool. 270, 466–472.

Amarasekare, P., 2003. Competitive coexistence in spatially structured environments: A synthesis. Ecol. Lett. 6, 1109–1122.

Andruskiw, M., Fryxell, J.M., Thompson, I.D., Baker, J.A., 2008. Habitat-mediated variation in predation risk by the American marten. Ecology 89, 2273–2280.

Asner, G.P., Brodrick, P.G., Anderson, C.B., Vaughn, N., Knapp, D.E., Martin, R.E., 2016. Progressive forest canopy water loss during the 2012–2015 California drought. Proc. Natl. Acad. Sci. 113, E249–E255.

Aubry, K.B., Zielinski, W.J., Raphael, M.G., Proulx, G., Buskirk, S.W. (Eds.), 2012. Biology and Conservation of Martens, Sables, and Fishers. Cornell University Press. Ithaca, New York, USA.

Averill, C., Finzi, A., 2011. Increasing plant use of organic nitrogen with elevation is reflected in nitrogen uptake rates and ecosystem δ15N. Ecology 92, 883–891.

Ben-David, M., Flynn, R.W., Schell, D.M., 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. Oecologia 111, 280–291.

Berger, K.M., Gese, E.M., Berger, J., 2008. Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. Ecology 89, 818–828.

Bowman, J., Donovan, D., Rosatte, R.C., 2006. Numerical response of fishers to synchronous prey dynamics. J. Mammal. 87, 480–484.

Byer, S., Jin, Y., 2017. Detecting drought-induced tree mortality in Sierra Nevada forests with time series of satellite data. Remote Sens. (Basel) 9, 929.

Carlson, J.E., Gilbert, J.H., Pokallus, J.W., Manlick, P.J., Moss, W.E., Pauli, J.N., 2014. Potential role of prey in the recovery of American martens to Wisconsin. J. Wildl. Manag. 78, 1499–1504.

Carscadden, K.A., Emery, N.C., Arnillas, Carlos A., Cadotte, M.W., Afkhami, M.E., Gravel, D., Livingstone, S.W., Wiens, J.J., 2020. Niche breadth: causes and consequences for ecology, evolution, and conservation. Q. Rev. Biol. 95, 179–214.

Costa, G.C., Vitt, L.J., Pianka, E.R., Mesquita, D.O., Colli, G.R., 2008. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. Glob. Ecol. Biogeogr. 17, 670–677.

Costa-Pereira, R., Rudolf, V.H.W., Souza, F.L., Araújo, M.S., 2018. Drivers of individual niche variation in coexisting species. Journal of Animal Ecology 87, 1452–1464.

Davis, F.W., Seo, C., Zielinski, W.J., 2007. Regional variation in home-range-scale habitat models for fisher (*Martes pennanti*) in California. Ecol. Appl. 17, 2195–2213.

Dini-Andreote, F., De Cássia Pereira, M., Silva, E., Triadó-Margarit, X., Casamayor, E.O., Van Elsas, J.D., Salles, J.F., 2014. Dynamics of bacterial community succession in a salt marsh chronosequence: evidences for temporal niche partitioning. ISME J. 8, 1989–2001.

Donadio, E., Buskirk, S.W., 2006. Diet, morphology, and interspecific killing in Carnivora. Am. Nat. 167, 524–536.

Elmhagen, B., Rushton, S.P., 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol. Lett. 10, 197–206.

Elmhagen, B., Ludwig, G., Rushton, S.P., Helle, P., Lindén, H., 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity: gradients. J. Animal Ecol. 79, 785–794.

Finke, D.L., Denno, R.F., 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology 83, 643–652.

Fisher, J.T., Anholt, B., Bradbury, S., Wheatley, M., Volpe, J.P., 2013. Spatial segregation of sympatric marten and fishers: the influence of landscapes and species-scapes. Ecography 36, 240–248.

Fryxell, J.M., Hussell, D.J.T., Lambert, A.B., Smith, P.C., 1991. Time lags and population fluctuations in white-tailed deer. The Journal of Wildlife Management 55, 377–385.

Gabriel, M.W., Woods, L.W., Wengert, G.M., Stephenson, N., Higley, J.M., Thompson, C., Matthews, S.M., Sweitzer, R.A., Purcell, K., Barrett, R.H., Keller, S.M., 2015. Patterns of natural and human-caused mortality factors of a rare forest carnivore, the fisher (Pekania pennanti) in California. PloS One 10 (11), e0140640.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B. (Eds.), 2013. Bayesian data analysis, 3rd edition. Chapman & Hall/CRC. Boca Raton, Florida, USA.

Golightly, R.T., Penland, T.F., Zielinski, W.J., Higley, J.M., 2006. Fisher Diet in the Klamath/North Coast Bioregion. MS Thesis.. Humboldt State University.

Green, D.S., Matthews, S.M., Swiers, R.C., Callas, R.L., Scott Yaeger, J., Farber, S.L., Schwartz, M.K., Powell, R.A., 2018a. Dynamic occupancy modelling reveals a hierarchy of competition among fishers, grey foxes and ringtails. Journal of Animal Ecology 87, 813–824.

Green, R.E., Purcell, K.L., Thompson, C.M., Kelt, D.A., Wittmer, H.U., 2018b. Reproductive parameters of the fisher (Pekania pennanti) in the southern Sierra Nevada, California. J. Mammal. 99, 537–553.

Grenfell, W.E., Fasenfest, M., 1979. Winter food habits of fishers, Martes pennanti, in northwestern California. California Fish and Game 65, 186–189.

Griffin, D., Anchukaitis, K.J., 2014. How unusual is the 2012-2014 California drought? Geophys. Res. Lett. 41, 9017–9023.

Harrison, D.J., Fuller, A.K., Proulx, G., 2004. Martens and Fishers (martes) in Human-Altered Environments: An International Perspective. Martens and Fishers (Martes) in Human-Altered Environments: An International Perspective. Springer Science & Business Media, Berlin, Germany.

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M., 2012. Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst. 43, 227–248.

Hodkinson, I.D., 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biol. Rev. Camb. Philos. Soc. 80, 489–513.

Hopkins, J.B., Ferguson, J.M., 2012. Estimating the diets of animals using stable isotopes and a comprehensive Bayesian mixing model. PloS One 7, e28478.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., A. C. P. and S. B. Andrew L. Jackson, Richard Inger., 2011. Comparing isotopic niche widths among and within communities: SIBER — stable isotope Bayesian ellipses in R. J. Anim. Ecol. 80, 595–602.

Jensen, P.G., Humphries, M.M., 2019. Abiotic conditions mediate intraguild interactions between mammalian carnivores. Journal of Animal Ecology 88, 1305–1318.

Jensen, P.G., Demers, C.L., McNulty, S.A., Jakubas, W.J., Humphries, M.M., 2012. Marten and fisher responses to fluctuations in prey populations and mast crops in the northern hardwood forest. Journal of Wildlife Management 76, 489–502.

Kartzinel, T.R., Chen, P.A., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., Rubenstein, D.I., Wang, W., Pringle, R.M., 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proc. Natl. Acad. Sci. U. S. A. 112, 8019–8024.

Kirby, R., Alldredge, M.W., Pauli, J.N., 2016. The diet of black bears tracks the human footprint across a rapidly developing landscape. Biol. Conserv. 200, 51–59.

Kuntze, C., Peery, M.Z., Green, R.E., Purcell, K.L., Pauli, J.N., 2024. Sex and age mediate the effects of rapid environmental change for a forest carnivore, the Fisher (Pekania pennanti). J. Mammal. 105, 13–25.

LaPoint, S.D., Belant, J.L., Kays, R.W., 2015. Mesopredator release facilitates range expansion in fisher. Anim. Conserv. 18, 50–61.

Levine, J.M., HilleRisLambers, J., 2009. The importance of niches for the maintenance of species diversity. Nature 461, 254–257.

Linnell, J.D.C., Strand, O., 2000. Interference interactions, co-existence and conservation of mammalian carnivores John D. C. Linnell; Olav Strand. Diversity and Distributions 6, 169–176.

Liu, H.Q., Huete, A., 1995. Feedback based modification of the NDVI to minimize canopy background and atmospheric noise. IEEE Trans. Geosci. Remote Sens. 33, 457–465.

Ma, J.Y., Sun, W., Liu, X.N., Chen, F.H., 2012. Variation in the stable carbon and nitrogen isotope composition of plants and soil along a precipitation gradient in northern China. PloS One 7, e51894.

Manlick, P.J., Pauli, J.N., 2020. Human disturbance increases trophic niche overlap in terrestrial carnivore communities. Proc. Natl. Acad. Sci. 117, 26842–26848.

Manlick, P.J., Woodford, J.E., Zuckerberg, B., Pauli, J.N., 2017. Niche compression intensifies competition between reintroduced American martens (Martes americana) and fishers (Pekania pennanti). J. Mammal. 98 (3), 690–702.

Manlick, P.J., Petersen, S.M., Moriarty, K.M., Pauli, J.N., 2019. Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations. Funct. Ecol. 33, 335–345.

Martin, S.K., 1994. Feeding ecology of American martens and fishers. In: Buskirk, S.W., Harestad, A., Raphael, M., Powell, R.A. (Eds.), Cornell University Press, Martens, sables, and fishers: biology and conservation. Ithaca, New York, pp. 297–315.

McGregor, E. L. (2021). Land Cover Classification (5-meter) - Kings River Fisher Project 2014–2018 (Version 1) [Data set]. Oregon State University. https://doi.org/https://doi.org/10.7267/J9602723W.

Minnich, R.A., 2007. Climate, Paleoclimate, and Paleovegetation. In: Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California. University of California Press, Berkeley, CA, pp. 43–70.

Pauli, J.N., Ben-David, M., Buskirk, S.W., DePue, J.E., Smith, W.P., 2009. An isotopic technique to mark mid-sized vertebrates non-invasively. J. Zool. 278, 141–148.

Pauli, J.N., Manlick, P.J., Tucker, J.M., Smith, G.B., Jensen, P.G., Fisher, J.T., 2022. Competitive overlap between martens (Martes americana and Martes caurina) and fishers (Pekania pennanti): a rangewide perspective and synthesis. Mammal Rev. 52, 392–409.

Phillips, D.L., Koch, P.L., 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia 130, 114–125.

Pilgrim, K.L., Green, R.E., Purcell, K.L., Wilcox, T.M., Mcgregor, E.L., Gelason, L.E., Wasser, S.K., 2023. Shifts in fisher (*Pekania pennanti*) diet in response to climate-induced tree mortality in California assessed with DNA metabarcoding. Journal for Nature Conservation 73, 126408.

Plummer, M., 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd international workshop on distributed statistical computing 125, 10, pp. 1–10.

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20, 297–330.

Powell, R.A., 1982. The Fisher: Life History, Ecology, and Behavior. University of Minnesota Press.

Raine, R.M., 1987. Winter food habits and foraging behaviour of fishers (Martes pennanti) and martens (Martes americana) in southeastern Manitoba. Can. J. Zool. 65, 745–747.

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12, 982–998.

Rodriguez Curras, M., Donadio, E., Middleton, A.D., Pauli, J.N., 2022. Carnivore niche partitioning in a human landscape. Am. Nat. 199, 00.

Rollins, M.G., 2009. LANDFIRE: A nationally consistent vegetation, wildland fire, and fuel assessment. Int. J. Wildland Fire 18, 235–249.

Rosenzweig, M.L., 1966. Community structure in sympatric Carnivora. J. Mammal. 47, 602–612.

Rosing, M.N., Ben-David, M., Barry, R.P., 1998. Analysis of stable isotope data: a K nearest-neighbors randomiztion test. Journal of Wildife Management 62, 380–388.

Roth, J.D., Hobson, K.A., 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. Can. J. Zool. 78, 848–852.

Schickmann, S., Urban, A., Kräutler, K., Nopp-Mayr, U., Hackländer, K., 2012. The interrelationship of mycophagous small mammals and ectomycorrhizal fungi in primeval, disturbed and managed central European mountainous forests. Oecologia 170, 395–409.

Schirmer, A., Herde, A., Eccard, J.A., Dammhahn, M., 2019. Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. Oecologia 189, 647–660.

Schmidt, S.N., Harvey, C.J., Vander Zanden, M.J., 2011. Historical and contemporary trophic niche partitioning among Laurentian Great Lakes coregonines. Ecol. Appl. 21, 888–896.

Slauson, K.M., Zielinski, W.J., 2019. Diets of denning female Pacific martens vary with the developmental stage of their kits. Ecol. Evol. 9, 5963–5974.

Smith, G.B., Tucker, J.M., Pauli, J.N., 2022. Habitat and drought influence the diet of an unexpected mycophagist: fishers in the Sierra Nevada, California. J. Mammal. 103, 328–338.

Smith, M.M., Erb, J.D., Pauli, J.N., 2023. Reciprocated competition between two forest carnivores drives dietary specialization. J. Anim. Ecol. 92, 1695–1706.

Spencer, W., Rustigian-Romsos, H., Strittholt, J., Scheller, R., Zielinski, W., Truex, R., 2011. Using occupancy and population models to assess habitat conservation opportunities for an isolated carnivore population. Biol. Conserv. 144, 788–803.

Sperry, J.H., Weatherhead, P.J., 2008. Prey-mediated effects of drought on condition and survival of a terrestrial snake. Ecology 89, 2770–2776.

Stephens, S.L., Collins, B.M., Fettig, C.J., Finney, M.A., Hoffman, C.M., Knapp, E.E., North, M.P., Safford, H., Wayman, R.B., 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. BioScience 68, 77–88.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., Semmens, B.X., 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6, e5096.

Sweitzer, R.A., Furnas, B.J., 2016. Data from camera surveys identifying co-occurrence and occupancy linkages between fishers (Pekania pennanti), rodent prey, mesocarnivores, and larger predators in mixed-conifer forests. Data Brief 6, 783–792.

Taylor, C.A., Raphael, M.G., 1988. Identification of mammal tracks from sooted track stations in the Pacific northwest. Calif. Fish and Game 74, 4–15.

Thompson, I.D., Colgan, P.W., 1987. Numerical responses of martens to a food shortage in northcentral Ontario. The Journal of Wildlife Management 51, 824–835.

Thompson, I.D., Colgan, P.W., 1990. Prey choice by marten during a decline in prey abundance. Oecologia 83, 443–451.

Thompson, C.M., Gese, E.M., 2007. Food webs and intraguild predation: community interactions of a native mesocarnivore. Ecology 88, 334–346.

Thompson, C.M., Zielinski, W.J., Purcell, K.L., 2011. Evaluating management risks using landscape trajectory analysis: A case study of California fisher. Journal of Wildlife Management 75, 1164–1176.

Tucker, J.M., Allendorf, F.W., Truex, R.L., Schwartz, M.K., 2017. Sex-biased dispersal and spatial heterogeneity affect landscape resistance to gene flow in fisher. Ecosphere 8, e01839.

USFWS, 2020. Endangered and threatened wildlife and plants; endangered species status for southern Sierra Nevada distinct population segment of Fisher. Fed. Regist. 85, 29532–29589.

Watts, K., Whytock, R.C., Park, K.J., Fuentes-Montemayor, E., Macgregor, N.A., Duffield, S., McGowan, P.J.K., 2020. Ecological time lags and the journey towards conservation success. Nature Ecology and Evolution 4, 304–311.

Wengert, G.M., Gabriel, M.W., Matthews, S.M., Higley, J.M., Sweitzer, R.A., Thompson, C.M., Purcell, K.L., Barrett, R.H., Woods, L.W., Green, R.E., Keller, S.M., 2014. Using DNA to describe and quantify interspecific killing of fishers in California. J. Wildl. Manag. 78 (4), 603–611.

Xiao, H.W., Xiao, H.Y., A. min Long, and Y. L. Wang., 2012. Who controls the monthly variations of NH4+ nitrogen isotope composition in precipitation? Atmos. Environ. 54, 201–206.

Zhong, W., Wang, G., Zhou, Q., Ma, L., Wan, X., Liu, W., 2016. Spatial niche partitioning of coexisting small mammals in sand dunes. Italian Journal of Zoology 83, 248–254.

Zielinski, W.J., Duncan, N.P., 2004. Diets of sympatric populations of American martens (Martes americana) and fishers (Martes pennanti) in California. J. Mammal. 85, 470–477.

Zielinski, W.J., Spencer, W.D., Barrett, R.H., 1983. Relationship between food habits and activity patterns of pine martens. J. Mammal. 64, 387–396.

Zielinski, W. J., R. L. Truex, C. V Ogan, and K. et al Busse. 1997. Detection surveys for fishers and American martens in California, 1989-1994: Summary and interpretations. Martes: Taxonomy, Ecology, Techniques, and Management. Provincial Museum of Alberta. Edmonton, Alberta, Canada. (Editors: Proulx, G.; Bryant, H. N.; Woodard, P. M).

Zielinski, W.J., Duncan, N.P., Farmer, E.C., Truex, R.L., Clevenger, A.P., Barrett, R.H., 1999. Diet of fishers (Martes pennanti) at the southernmost extent of their range. J. Mammal. 80, 961–971.

Zielinski, W.J., Truex, R.L., Schmidt, G.A., Schlexer, F.V., Schmidt, K.N., Barrett, R.H., Schmidt, G.A., Schmidt, K.N., Barrett, R.H., 2004. Home range characteristics of fishers in California. J. Mammal. 85, 649–657.

Zielinski, W.J., Truex, R.L., Schlexer, F.V., Campbell, L.A., Carroll, C., 2005. Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. J. Biogeogr. 32, 1385–1407.

Zielinski, W.J., Baldwin, J.A., Truex, R.L., Tucker, J.M., Flebbe, P.A., 2013. Estimating trend in occupancy for the southern sierra Fisher Martes pennanti population. J. Fish Wildl. Manag. 4, 3–19.

Zielinski, W.J., Tucker, J.M., Rennie, K.M., 2017. Niche overlap of competing carnivores across climatic gradients and the conservation implications of climate change at geographic range margins. Biol. Conserv. 209, 533–545.