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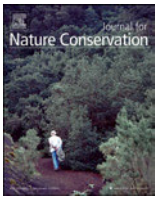

Shifts in fisher (*Pekania pennanti*) diet in response to climate-induced tree mortality in California assessed with DNA metabarcoding

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ABSTRACT

A recent climate-induced tree mortality event in California, USA has led to dramatic landscape-level changes in the southern Sierra Nevada. Wide-spread conifer mortality was documented in habitat occupied by fisher (*Pekania pennanti*), a mature-forest associated species of conservation concern in this region. We analyzed fisher scats collected on the Sierra National Forest from the pre-tree-mortality period (PreTM, 2011 – 2013) and post-tree-mortality period (PostTM, 2017 – 2018). We used DNA metabarcoding to successfully identify taxa and summarized diet composition for 109 PreTM and 102 PostTM fisher scats. We observed 48 different diet items (33 assigned to species and 15 to genus). Mammals, birds, and plants of the *Ribes* genus (gooseberries and currents) comprised the highest proportions of diet items, although scats also contained DNA from reptiles, insects, arachnids, snails, and fungi. The frequency of occurrence of mammalian prey items was lower in PostTM (49.0%) versus PreTM scats (81.7%) with a reduction in the occurrence of two tree squirrels (Douglas squirrel and Humboldt's flying squirrel). A higher proportion of scats collected PostTM (46.1%) contained DNA from *Ribes* spp. versus scats collected PreTM (19.3%). Our data reveal potential cascading effects of climate-induced tree mortality on fisher diet in the southern Sierra Nevada. Flexibility in fisher diet, however, may allow resilience to ecological change though future studies should consider the behavioral, energetic, demographic or fitness consequences from a shift away from medium-sized mammalian prey to plants.

1. Introduction

Climate change can severely impact animals and the habitat upon which species rely on worldwide (Iknayan and Beissinger 2018, Hoffman et al. 2019, Cunningham et al. 2021). Some climate-change-related impacts to ecosystems are direct and relatively obvious, while others are gradual or cascading in nature and thus more challenging to observe (Deschamps et al. 2017, Hoffman et al. 2019). Extreme climate events can contribute to direct loss of habitat and mortality of individual animals (e.g., heat waves), but moderate to mild climatic changes can still have substantial impacts on wildlife populations by degrading habitat leading to increased individual energetic costs and potentially lowering fitness (Birnie-Gauvin et al. 2017, Foden et al. 2019, Mukul et al. 2019, Bourne et al. 2020, McKechnie et al. 2021). One response of individual species to ecological change may be shifts in their diet. For predators, this might be shifts in prey or other food items, or changes in foraging behavior as a response to changes in availability or distribution of food items (Van de Ven et al., 2020a; Cunningham et al. 2021). When such shifts in diet are detected, they can be indicators of ecological stress requiring management intervention and / or enhanced protection of the

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species (Deschamps et al. 2017, Van de Ven et al., 2020b, Bourne et al. 2020).

The southern Sierra Nevada region of the western USA experienced extreme drought conditions starting in late 2012. Between 2015 and 2017, water stressed trees were unable to defend themselves from bark beetles, primarily western pine beetle (*Dendroctonus brevicomis*) leading to extensive outbreaks (AghaKouchak et al. 2014, Young et al. 2017). By 2017, the combination of drought and bark beetle attack led to an estimated 129 million dead trees in California (USDA, 2017). In the southern Sierra Nevada, medium to large diameter pines and firs (particularly ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), and white fir (*Abies concolor*)) had particularly high mortality due in part to vulnerability to specific bark beetles (Fettig et al. 2019, Pile et al. 2019). As forests in this region become more open, drought-tolerant trees (e.g., hardwoods like the California black oak (*Quercus kelloggii*; Knops et al. 1994)) and shrub species that can respond to increased light are becoming more prevalent as live conifer cover is reduced (Fettig et al. 2019, Stephens et al. 2018). These changes to the landscape may have significant impacts on food resources and habitat for wildlife that rely on dense canopy cover, a connected network of mature forest, and conifer-dependent prey species.

The southern Sierra Nevada region where tree mortality has been most pronounced overlaps considerably with the distribution of fisher (*Pekania pennanti*). The isolated population of fishers in the southern Sierra Nevada were recently listed as “Threatened” by the state of California (CDFW 2019), and as “Endangered” by the U.S. Fish and Wildlife Service (USFWS 2020). This population is of focal conservation and management concern as they exist in isolation in the southernmost latitude for fisher, have low population numbers, and have a unique genetic makeup compared to other populations of fishers (Knaus et al. 2011, Tucker et al. 2012, 2014). Fishers are tree-climbing members of the weasel family (Mustelidae) that are associated with features of late successional forests, including dense canopy cover, large-diameter trees, and structures with hollows (Powell et al. 2003, Aubry et al. 2013, Green et al., 2019a). These mesocarnivores are active throughout the year and their long, lean bodies have high metabolic requirements and, in general, limited fat reserves (Powell et al. 2003). Female fishers give birth once a year in spring to a small litter of kits which stay with the mother until the fall (Green et al., 2018). Similar to other mustelids, fishers have small litter size, small body size, and diverse diet (Zielinski et al. 1999, Wisely et al. 2004, Lofroth et al. 2011, Green et al., 2018).

Fishers are omnivores, eating a wide variety of items including vertebrates (e.g., mammals, birds, reptiles), invertebrates, fruit, and fungi (Zielinski et al. 1999, Weir et al. 2005, Golightly et al. 2006, McNeil et al. 2017, Raley and Aubry 2020, Happe et al. 2021). Where data are available, the diet of fishers appears to vary seasonally, likely tied to differences in availability of food items, energetic needs of individuals (e.g., females with young; Raley and Aubry 2020), and individual capacity to catch or acquire certain prey (e.g., males versus females; Powell and Leonard 1983, Weir et al. 2005, Raley and Aubry 2020). In the Sierra Nevada, previous studies indicate that fishers have considerable flexibility in what they can or will eat, but there may be selection in acquiring some food items over others to meet daily energetic requirements (Golightly et al. 2006). Medium to large-bodied mammalian prey items such as tree squirrels appear to provide the best energetic balance (Golightly et al. 2006). A diet study by Zielinski et al. (1999) using scat collection and dissection techniques concluded that fishers had a generalist diet that was dominated by mammals (e.g., squirrels, smaller rodents), but included birds, reptiles, insects, plants, and fungi. A more recent study by Smith et al. (2022) using isotope values from hair samples during a period of drought and tree mortality also found a varied diet, but interestingly documented higher than expected occurrence of fungi in the summer diet as well as differences based on geographic location within the southern Sierra Nevada. Two key prey species of fishers across their historical distributions are the North American porcupine (*Erethizon dorsatum*) and snowshoe hare (*Lepus americanus*; Murray 2003, Powell et al. 2003, Roze and Ilse 2003). Where present, these species appear to influence fisher foraging activity and habitat use – likely because they represent a large source of calories (Powell 1979). However, neither prey species is available at the population level in the southern Sierra Nevada. Porcupines have largely been extirpated presumably due to poisoning in the 1900 s, and the range of snowshoe hares barely extends into the northernmost section of the isolated area presently occupied by fishers in the southern Sierra Nevada (Allen and Casady 2012, Murray 2003).

We expect that recent and dramatic landscape-level changes associated with drought and wide-spread tree mortality in pines and firs in the southern Sierra Nevada may impact fishers due to changes in availability of prey species and other sources of food. We studied fisher dietary responses within the Kings River Study Area on the Sierra National Forest which encompasses an area of approximately 300 km^2 of the southern Sierra Nevada mountains in California. The Kings River Fisher Project (KRFP) was initiated as part of a long-term study of fisher ecology by the Pacific Southwest Research Station (PSW) of the USDA forest Service. In the study area, estimates of the percent of forested areas impacted by tree mortality in areas used by denning females was 12.8 % in 2015, 43.6 % in 2016, and 50.8 % in 2017 (Green et al., 2019b).

Non-invasive scat surveys were conducted annually from 2007 to 2018 for the KRFP with the initial goal to assess fisher use of the landscape relative to management activities. We took advantage of this long-term monitoring effort to evaluate diet items in fisher scats collected in the years before (PreTM) and after (PostTM) established tree mortality of conifers. We used DNA metabarcoding to identify diet items within the scats (de Sousa & Silva 2019; Pompanon et al. 2012). For many species of conservation concern like fishers, information on dietary changes and how that may impact habitat use, behavior, survival, and ultimately fitness can help guide future conservation and forest management and restoration plans (Lofroth et al. 2011, Purcell et al. 2009).

2. Methods

2.1. 2.1 Sample collection and preparation

Trained detection dog teams from Conservation Canines, University of Washington, surveyed an established hexagonal sampling grid (each cell = 14 km^2) within the KRFP study area twice per year from 2007 to 2018 (Fig. 1). Survey methods have been described in detail previously (see Thompson et al. 2012, Zielinski et al. 2013); but in brief, surveys involved an early session (between late May – early July) and a late session (between late September – early November) during which grid cells were visited 3 times (for a total of 6 visits per cell per year). Tracklogs were collected along each survey route and detection teams (1 human handler, 1 trained dog) endeavored to cover different portions of a grid on each route within a sampling session (i.e., limited overlap of area traversed in each season). Scats were located by the dogs, and the handler recorded the coordinates of the site, dried and labeled samples, and then sent scats to the USDA Forest Service’s National Genomics Center for Wildlife and Fish Conservation for genetic species identification.

From 4,979 scats collected during the study from 2009 to 2018, we confirmed 1,880 as being from fisher via *16S* sanger sequencing (see methods in Happe et al., 2020). We used a subset of these fisher scats collected from 10 of the sampled survey grids (Fig. 1) that had sufficient survey effort and enough scats collected from before and after established tree mortality to use for diet analysis. Out of a possible 334 and 458 fisher scats collected from PreTM and PostTM time periods respectively (Table 1), we selected scats that were spatially stratified to minimize resampling of individuals or locations. Scat samples selected for diet analysis were spread equally across two early and two late season sampling periods, when energetic requirements and food availability may differ seasonally.

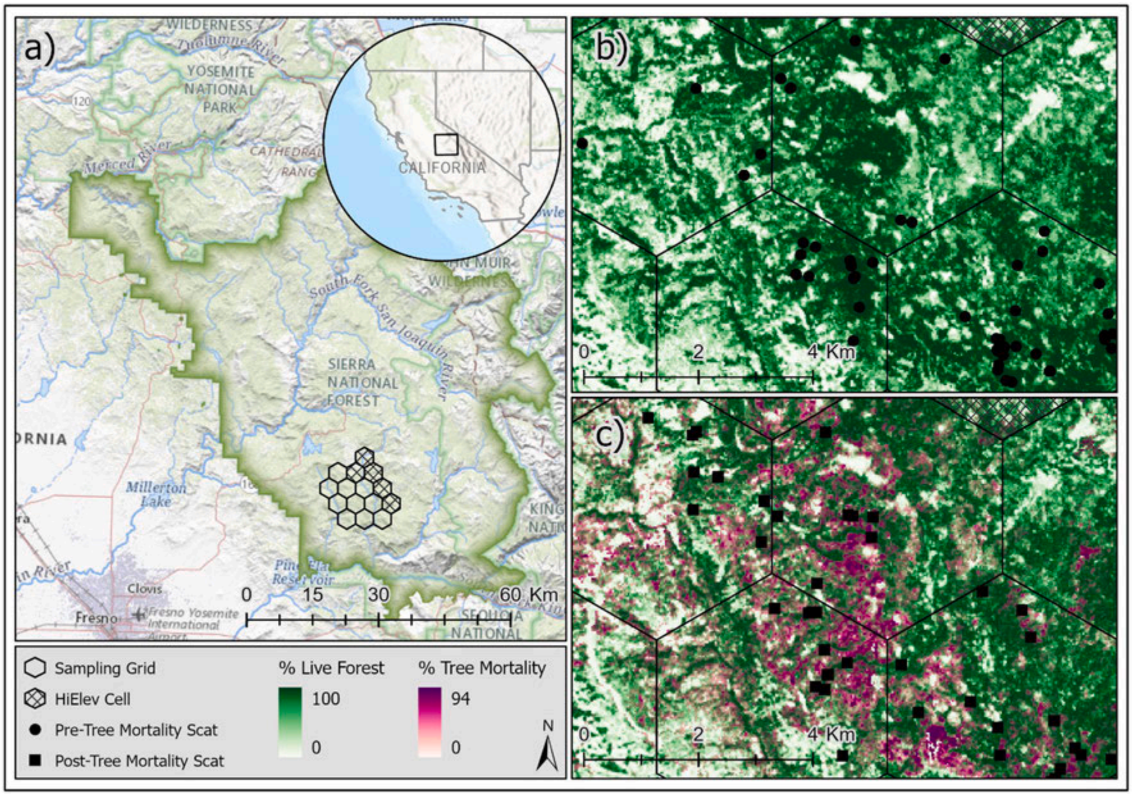

Fig. 1. Location of the Kings River Fisher Project study area in the southern portion of the Sierra National Forest, southeast of Shaver Lake, California, USA. Panel (a) shows the 10 survey cells scats selected for scat diet analysis (open hexagons). Hashed hexagons are 5 cells from slightly higher elevations (see Supplemental results). Panel (b) shows the location of scats relative to live forest within example sampling hexagons during the pre-tree mortality period (PreTM), while panel (c) shows an example of scat locations relative to live and dead forest in the post-tree mortality period (PostTM).

Table 1

Summary of scat samples collected during detection dog surveys as part of the Kings River Fisher Project on the Sierra National Forest, and the subset used for DNA metabarcoding diet analysis. Diet items were recovered from 109 PreTM scats and 104 PostTM scats (two of the PostTM scats contained chicken presumably from baited camera stations). Early season sampling was late May – early July and late session was late September – early November.

Summary of scats collected and refined for use in metabarcoding analysis	Pre-tree mortality samples by season				Post-tree mortality samples by season			
	Late 2011	Early 2012	Late 2012	Early 2013	Early 2017	Late 2017	Early 2018	Late 2018
Total number of scats from surveys	250	242	339	240	352	254	191	142
Scats confirmed as fisher by DNA	68 (27 %)	56 (23 %)	111 (33 %)	99 (41 %)	210 (60 %)	101 (40 %)	110 (58 %)	37 (26 %)
Subset of scats selected for diet analysis	23 (34 %)	24 (43 %)	31 (28 %)	43 (43 %)	38 (18 %)	41 (41 %)	23 (21 %)	19 (51 %)
Scats with diet components	21 (91 %)	19 (79 %)	30 (97 %)	39 (91 %)	31 (82 %)	36 (88 %)	20* (87 %)	17* (89 %)

* One scat contained chicken DNA only.

We analyzed a total of 242 fisher scat samples: 121 PreTM collected from 2011 to 2013 (67 early and 54 late season) and 121 PostTM collected from 2017 to 2018 (61 early and 60 late season; Table 1). Elevation range associated with the sample locations for PreTM was 1,125 – 1,998 m (mean = 1,562 m) and for PostTM was 1,121 – 2,014 m (mean = 1,463 m). DNA from scats were analyzed for diet components using DNA metabarcoding targeting three mitochondrial and one chloroplast genes (Supplemental DNA Methods; Table A1). For the mitochondrial regions, two primer sets targeted vertebrates (12S RNA), one primer set targeted mammals (16S RNA), and one primer set targeted invertebrates (COI).

2.2. 2.2 Data filtering and analysis

To remove low-abundance and potentially erroneous sequences, we required greater than 500 reads to make a taxonomic assignment for potential animal and fungi items and 1,000 reads for plant diet items. We used the higher threshold for plant diet items due the increased risk of exogenous DNA inputs from the environment, but we found that inferences were robust across a wide range of possible read abundance thresholds (Supplemental Fig. A1). We further manually curated the resulting list of potential diet items to remove species which are highly unlikely to represent diet times and instead stem from presence in the environment or secondary consumption (Tercel et al. 2021). First, we removed reads from molds, soil pathogens, and parasitic flatworms which were likely associated with the soil or fecal environment. As fungi can include mold and yeasts, we restricted our assessment of fungi to macro-fungi (those species with a fruiting body aboveground) that would be available to fisher as a diet item. We removed all sequences from human and domesticated dog, both of which were likely introduced as part of the scat detection and collection process. We assumed that detections of fisher DNA in this study were prominently from cells from the digestive tract or hair consumed during grooming and excluded these from the diet summary.

We conducted Permutational Multivariate Analyses of Variance (PERMANOVA) based on species composition to assess whether diet composition differed by season (early and late) and time period (PreTM and PostTM), based on Jaccard index (the intersection divided by the union of species compositions between groups). All analyses were conducted in the R package *vegan* (Oksanen et al. 2022; R Core Development Team 2020) using the function *adonis2* and 1,000 permutations. We report results as frequency of occurrence (percentage of scats containing a particular food item). Using frequency of occurrence of a food item can underestimate the nutritional value of individual items (see Powell 1979). For reference, we also provide mean weight or length metrics of individual diet items (Supplemental Table A2).

3. Results

Twenty-nine scats contained fisher DNA exclusively, leaving 213 with diet items (109 PreTM and 104 PostTM; Table 1). Fisher DNA was identified in all scats, likely from cells in the digestive tract or hair from grooming, although the possibility of occasional intraspecific predation cannot be refuted (Supplemental Fig. A2). The 29 scats without diet items are likely due to DNA degradation of prey items, the small size of scat available that may not have contained cells from diet items, or both.

During manual curation of the taxonomic assignment results, we removed sequences from four taxa which were not likely to represent direct consumption by fishers. Three scats contained DNA from bottle flies (genus *Lucilia*), which are known to be associated with feces. Two scats had DNA from mistletoe (*Phoradendron* spp.); as *Phoradendron* mistletoe berries have coevolved with birds as primary dispersers and have secondary compounds that may deter mammals (Kuijt, 1969; Mathiasen et al. 2008), we suspect these were present in birds that were consumed by fisher. Two fisher scats had DNA from black cottonwood (*Populus trichocarpa*), unlikely to be a diet item for fisher, and we assume to be secondary consumption due to the presence of DNA from downy woodpecker (*Picoides pubescens*) and mountain quail (*Oreortyx pictus*) in these scats. One scat with DNA from western gray squirrel (*Sciurus griseus*) also had DNA reads from a parasitic nematode in the genus *Citellinema* known to infect this squirrel species (Lichtenfels 1971). Finally, we removed from further consideration two scats collected in 2018 which, contained DNA from chicken (*Gallus gallus*). Camera stations baited with chicken were present in the study area in spring 2018 and chicken is otherwise an unlikely food source in this area.

After removing all non-diet items, 211 of the tested scat samples yielded diet items for diet comparison for before and after tree-mortality (87 %), including 109 PreTM and 102 PostTM scats. We identified 48 taxa from these scat samples: 38 vertebrate, 6 insect, and one each from plant, arachnids, mollusks, and fungi (Table 2). We were able to resolve 33 diet items to species and 15 to genus (Table 2). As observed in other studies, fishers consumed a wide variety of diet items in our study area (Table 2). Mammals, birds, and plants were the most frequently observed diet items across all scats, while reptiles, insects, arachnids, mollusks, and fungi were less common diet items (Fig. 2; Supplemental Fig. A3). Scats collected during the PreTM period had nearly equal proportions of scats with 1 or 2 diet items, and occasionally 3 items; in contrast most PostTM scats contained only 1 diet item (Supplemental Fig. A4).

Mammalian diet items included DNA from 13 species and 5 genera (Table 2, Supplemental Fig. A5). In the PreTM scats, 81.7 % had DNA from at least one mammal prey item, compared to only 49.0 % of the PostTM scats (Fig. 2). This reduction was driven by two medium to large-bodied tree squirrels: Douglas squirrel (*Tamiasciurus douglasii*) and Humboldt's flying squirrel (*Glaucomys oregonensis*; Arborgast et al. 2017, Fig. 3, Supplemental Fig. A5). PostTM, the frequency of scats with DNA from the two most common tree squirrels declined significantly; Douglas squirrel detections dropped from 30 to 12 %, and Humboldt's flying squirrel detections went from 20 to 3 % (Fig. 3). However, frequencies of other common mammal species were more constant with gray squirrels remaining at 7 %, chipmunks declining from 9 to 6 %, and mice increasing from 10 to 13 %. Surprisingly, frequency of detection of California ground squirrel (*Otospermophilus beecheyi*), a species typically associated with open areas, declined from 8 to 1 % between PreTM and PostTM scats. Gray fox (*Urocyon cinereoargenteus*) was not documented in PreTM scats but was present in four PostTM scats.

Table 2
Summary of fisher diet items confirmed by DNA metabarcoding from scats collected on the Sierra National Forest (2011–2013 and 2017–2018). Percent of scats with a given diet item are provided from scats collected before established tree mortality (PreTM; n = 109) or after (PostTM; n = 102). Taxa are grouped by class and arranged by relative weight of food items prior to consumption (based on references). Most taxa were identified to species, but some were confirmed only to genus.

Taxon group and common name	Scientific name	PreTM %	PostTM %
Mammals			
Black bear	*Ursus americanus*	0.92	0.00
Botta's pocket gopher	*Thomomys bottae*	1.83	3.92
Broad-footed mole	*Scapanus latimanus*	1.83	2.94
Brush rabbit	*Sylvilagus bachmani*	0.92	2.94
California ground squirrel	*Otospermophilus beecheyi*	8.26	0.98
Chipmunk	*Neotamias* spp.	9.17	5.88
Coyote	*Canis latrans*	0.92	0.00
Douglas squirrel	*Tamiasciurus douglasii*	30.28	11.76
Feral pig	*Sus scrofa*	0.92	0.00
Golden-mantled ground squirrel	*Callospermophilus lateralis*	1.83	0.00
Gray fox	*Urocyon cinereoargenteus*	0.00	3.92
Humboldt's flying squirrel	*Glaucomys oregonensis*	20.18	2.94
Mouse	*Peromyscus* spp.	10.09	12.75
Shrew	*Sorex* spp.	1.83	0
Vole	*Microtus* spp.	0.00	0.98
Western gray squirrel	*Sciurus griseus*	7.34	6.86
Western spotted skunk	*Spilogale gracilis*	0.92	0.00
Woodrat	*Neotoma* spp.	0.92	2.94
Birds			
Band-tailed pigeon	*Patagioenas fasciata*	0.00	0.98
California gull	*Larus californicus*	0.00	0.98
California scrub jay	*Aphelocoma californica*	0.00	0.98
Cooper's Hawk	*Accipiter cooperii*	0.92	0.00
Dark-eyed junco	*Junco hyemalis*	5.50	4.90
Downy woodpecker	*Picoides pubescens*	0.00	0.98
Mountain quail	*Oreortyx pictus*	4.59	5.88
Northern flicker	*Colaptes auratus*	0.92	2.94
Northern goshawk	*Accipiter gentilis*	0.92	0.00
Purple finch	*Haemorhous purpureus*	3.67	4.90
Song sparrow	*Melospiza melodia*	0.92	0.00
Steller's jay	*Cyanocitta stelleri*	3.67	0.98
Townsend's solitaire	*Myadestes townsendi*	0.92	0.00
Varied thrush	*Ixoreus naevius*	1.83	1.96
Western spotted towhee	*Pipilo maculatus*	12.84	3.92
Wren	*Troglodytes* spp.	0.00	0.98
Wrentit	*Chamaea fasciata*	0.00	1.96
Reptiles			
Alligator lizard	*Elgaria* spp.	0.92	1.96
Gilbert's skink	*Eumeces gilberti*	0.00	1.96
Gopher snake	*Pituophis catenifer*	0.00	0.98
Insects			
Ant	*Tapinoma* spp.	1.83	0.00
Bumblebee	*Bombus* spp.	0.92	0.98
Cricket	*Gryllus* spp.	0.92	0.00
Cutworm or dart moth	*Orthosia pulchella*	1.83	0.98
Ground yellow jacket	*Vespula* spp.	6.42	0.00
Ten-lined June beetle	*Polyphylla decemlineata*	1.83	0.00
Arachnids			
Spider	*Sergiolus* spp.	1.83	0.00
Mollusks			
Snail	*Galba* spp.	0.92	1.96
Plants			
Sierra gooseberry or current	*Ribes* spp.	19.27	46.08
Fungi			
Mushroom	*Suillus* spp.	3.67	8.82

Avian diet items consumed by fishers included 16 species and 1

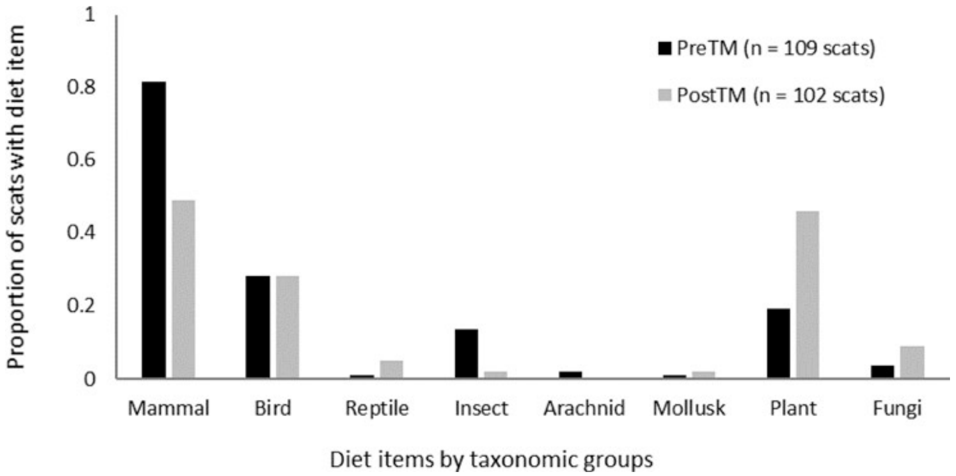

Fig. 2. Proportion (frequency of occurrence) of fisher scats that contained diet items belonging to eight taxonomic groups. Scats were collected during surveys prior to and after a major tree mortality event in the southern Sierra Nevada (PreTM = pre-tree mortality 2011 – 2013; PostTM = post-tree mortality 2017 – 2018).

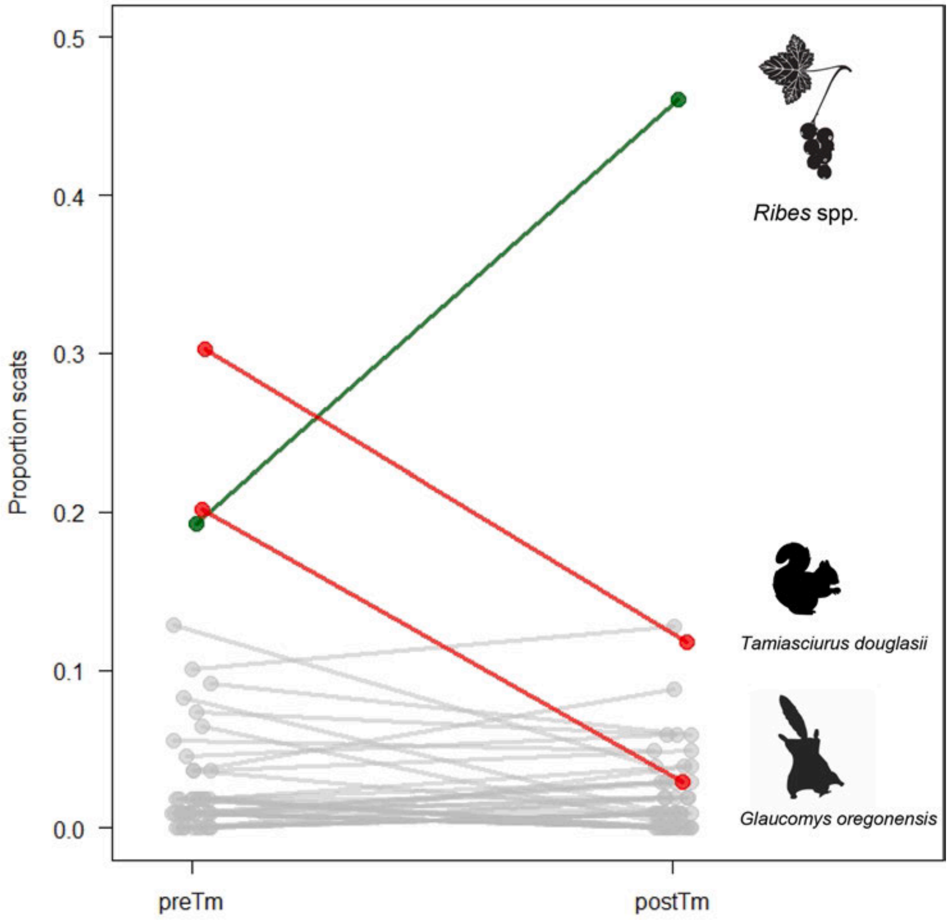

Fig. 3. Proportion (frequency of occurrence) of scats collected prior to tree mortality (PreTM) and after tree mortality (PostTM) containing 48 different diet items. Highlighted are three diet items with the greatest change between the two time periods. *Ribes* spp. (green line) were more frequent while *G. oregonensis* and *T. douglasii* (red lines) were less frequent after established tree mortality.

additional genus (Table 2, Supplemental Fig. A6). The percent of scats with avian DNA was comparable between PreTM and PostTM at 28.4 % and 30.4 % respectively (Fig. 2), although species composition changed (Table 2, Supplemental Fig. A6). The most common bird species detected were western spotted towhee (*Pipilo maculatus*), mountain quail (*Oreortyx pictus*), dark-eyed junco (*Junco hyemalis*) and purple finch (*Haemorhous purpureus*). Spotted towhee was the most frequent bird found in PreTM scats, but this species declined sharply post-tree mortality from 13 to 4 %; in contrast, each of the other three most common species remained relatively stable with frequencies around 4 to 6 % (Supplemental Fig. A6). DNA from two raptors, Cooper's hawk (*Accipiter cooperii*), and northern goshawk (*Accipiter gentilis*) were documented, as

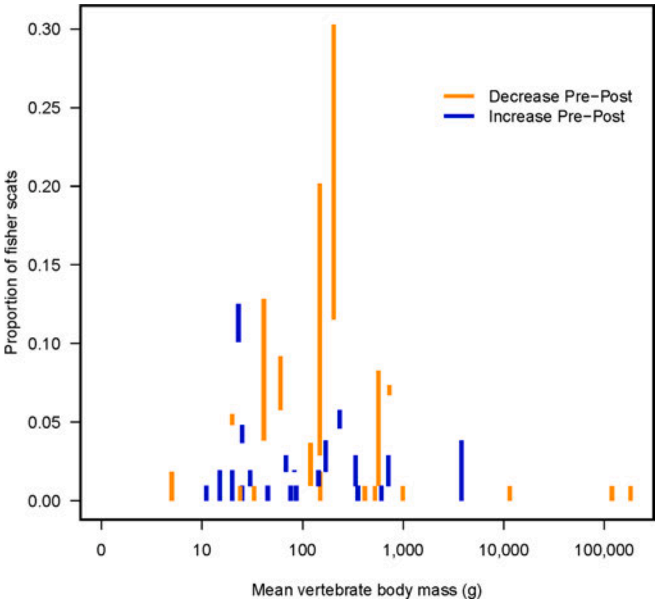

Fig. 4. The proportion (frequency of occurrence) of fisher scats containing each vertebrate diet item (Table 2) item plotted as a function of that species' typical mass (Supplemental Table A3). Proportion of fisher scats pre-tree mortality (PreTM) and post-tree mortality (PostTM) are connected by vertical line segments where blue indicates that the proportion increased PreTM to PostTM and orange that the proportion decreased. The most substantial shifts in diet composition after tree mortality was the loss of mid-sized, mammalian prey.

was that of a large gull (*Larus californicus*), likely scavenged and/or associated with nearby Shaver Lake or Wishon Reservoir.

We identified 13 taxa of non-vertebrate diet items from the fisher scats (Table 2). Plants in the genus *Ribes* increased in frequency from 19 % in PreTM to 46 % PostTM scats, which was the largest change of any diet item (Table 2, Figs. 2, 3). Fungi from the genus *Suillus*, the order commonly known as boletes, increased slightly in frequency from 4 % PreTM to 9 % PostTM (Table 2, Supplemental Fig. A7). Additional identified taxa comprising reptiles (2 lizards, 1 snake), insects (ant, wasp, bee, moth, cricket, and beetle), arachnid (spider), and 1 mollusk (snail) each comprised < 10 % of diet items in the fisher scat (Table 2, Supplemental Fig. A7).

Our PERMANOVA analysis for species composition was based on 48 diet item taxa. We excluded any scats where no diet items or only *Gallus gallus* DNA was detected ($n = 31$). There was no significant difference between early and late season diet compositions for PreTM ($P = 0.134$, $n = 109$) or PostTM ($P = 0.730$, $n = 102$) scats. However, diet composition did differ significantly between PreTM and PostTM periods both when split by season ($P < 0.001$, $n = 108$ and $P = 0.002$, $n = 103$ for early and late, respectively) and when season data were combined ($P < 0.001$, $n = 211$). This shift was largely driven by a decrease in the prevalence of mid-sized mammal prey and an increase in the presence of *Ribes* plant diet items from PreTM to PostTM (Figs. 3 and 4). When we evaluated vertebrate diet items based on size, we found a substantial decrease in medium-sized vertebrates (Fig. 4) present in PostTM scats compared to PreTM scats due primarily to the loss of mid-sized, mammalian prey.

4. Discussion

This is the first study to use scats collected from long-term monitoring efforts to better understand the feeding ecology of fisher in the wake of widespread tree mortality. Our findings from molecular genetic analysis of fisher scats collected in the southern Sierra Nevada indicate a diverse diet comprised largely of mammalian, avian and plant taxa along with insects, fungi, arachnids, and mollusks. The diversity of diet items we observed for fisher in the southern Sierras is consistent with previous studies of fisher diet conducted in California and Oregon (Zielinski et al. 1999, Golightly et al. 2006, Raley and Aubry 2020), though our study identified a higher number of taxa (48) than has been reported previously. We found a notable difference in diet items in scats collected before and after a major tree mortality period, suggesting that fisher diet is strongly influenced by this type of disturbance. Douglas squirrel and Humboldt's flying squirrel were the most common diet items in pre-tree mortality scats, but detections dropped by 18.5 % and 17.3 % respectively post-tree mortality. In contrast, frequency of plants in the *Ribes* genus (presumably eaten as berries from currant and/or gooseberry plants) in scats increased from 19.3 % pre-tree mortality to occurring in nearly half of all scats post-tree mortality.

Our results suggest that fishers in this region have the flexibility to eat a wide variety of foods from mammals of all sizes (some of which may be eaten as carrion), as well as multiple species of birds, reptiles, insects, spiders, plants, and fungi. With respect to mammals, fishers regularly consumed small-bodied prey such as mice and chipmunks before and after tree mortality occurred, and infrequently consumed species such as shrews (*Sorex* spp.) and moles (*Scapanus latimanus*). While none of these small mammals represent a high-calorie meal for a fisher, they may play an important role in supplementing the diet in an area where large prey could be limited in availability. Some species of mice and chipmunks use or explore disturbed areas – so may continue to be a key diet item as the region recovers from extensive tree mortality. In lodgepole pine (*Pinus contorta*) forests in Utah small and medium mammal prey were found to be more abundant following tree mortality (Stone 1995).

Medium-sized mammalian prey such as squirrels have been hypothesized to be an energetically efficient choice for fishers due to the amount of energy provided relative to time invested in capture. Tree squirrels such as Douglas and Humboldt's flying squirrels have the additional benefit of occurring in areas that overlap with other fisher habitat requirements – large trees, decadent forest, and canopy cover. The decline of these two species in the diet is concerning as it likely reflects a decline in local abundance. California ground squirrels – which were consumed more during pre-tree mortality than post-tree mortality often occur in open areas where fishers may be at increased risk of predation. Other medium-sized mammalian prey, such as Botta's pocket gophers (*Thomomys bottae*) and woodrats (*Neotoma* spp.), may be caught opportunistically or where they are locally abundant. The post-tree mortality shift away from medium-sized prey mammalian species that are thought to be the most energetically efficient choice has implications for both conservation and management (Golightly et al. 2006).

Of the remaining large and very large-bodied mammalian prey, the most regularly consumed prey species in our study was the western gray squirrel. While occurring at a frequency of 7.1 % in all scats (Supplemental Fig. A5), western gray squirrels average 731gm and did not decline in the diet post-tree mortality. These squirrels may be less impacted by tree mortality compared with other tree squirrels due to their association with oaks (Carraway and Verts 1994). Oak species in the southern Sierra Nevada are more drought resistant (Knops et al. 1994) than conifer species and are not targeted by bark beetles. Western gray squirrels may be of particular value to female fishers with young due to their size (Raley and Aubry 2020). An observation of a reproductive female fisher in our study area actively hunting a western gray squirrel in summer provides support for this claim (R. Green, pers. obs.).

Brush rabbits are another large-bodied prey species of potential value to fishers in this region, but their local distribution generally only overlaps with that of fishers at the lower elevations limiting general availability of this prey item. Other large mammal species are likely to be consumed as a result of opportunistic encounters or as carrion (e.g., feral pig). Surprisingly, consumption of mule deer (*Odocoileus hemionus*) as carrion was not documented in the scats we collected, although we have seen fishers locally at deer carcasses via remote cameras (R. Green, unpublished data) and this has been confirmed as a source of food for fishers in northern California (Golightly et al. 2006).

We identified several carnivores as prey items in the fisher scat. Two carnivores were likely the result of direct predation. Gray foxes have been shown to be excluded in some areas by fishers (Green et al., 2018, Green et al. 2022), so perhaps consumption in our study area was the result of predation to eliminate competitors or as a food resource. Interestingly, gray fox was not documented in the PreTM fisher diet but was present in four PostTM scats (collected over three seasons) and may reflect an increase in gray fox density in a more open landscape (Green et al 2022). Similarly, fisher have been known to kill and consume Pacific marten (*Martes caurina*) where the species overlap (McCann et al. 2011). We documented fishers consuming other carnivores (e.g., black bears (*Ursus americanus*) and coyotes (*Canis latrans*)) which we assume were scavenged due to their large size.

Fishers consumed a wide variety of birds both pre- and post-tree mortality. Based on the diversity of species, we expect many birds are consumed as the result of opportunistic encounters as opposed to fishers targeting particular species. However, three of the most frequently consumed species spend much of their time on or near the ground: dark-eyed junco, western spotted towhee, and mountain quail. As these species often forage and nest on the ground, they may be more susceptible to predation by fishers. Spotted towhees declined from 12.8 % in pre-tree mortality scats to only 3.9 % of scats post-tree mortality. This decline of spotted towhees in the fisher diet may be less due to tree mortality and more the result of a general decline in this species (Sakai 2016). In contrast, the small-bodied juncos and medium-bodied mountain quail stayed at low but consistent frequencies (5–6 %) in the diet despite tree mortality. As with gray squirrels, mountain quail may continue to be an important diet item in this region as this species is an energetically efficient size for fishers, remained constant in the diet post-disturbance, and may not be as negatively impacted by conifer mortality compared to other birds. We found DNA from two avian predators, the Cooper's hawk, and northern goshawk. Whether this involved consumption of eggs, nestlings or adults is unknown, but these species overlap with fisher in habitat and may represent potential prey.

While mammals and birds comprised the bulk of the animal diet for fishers in this region, fishers also appear to be capitalizing on opportunities to consume lizards, snakes, a variety of insects, as well as the occasional arachnid or snail. Sample sizes are limited for all of these taxa and the presence of DNA does not tell us anything about potential energetic benefits that might be gleaned based on the size of the reptiles involved or the number of insects, arachnids, or snails eaten in a single meal. However, these findings further confirm that fishers can be flexible in their capacity to find, catch, and consume a wide variety of animal prey. We might expect regional reptile species to at least remain constant or even increase in availability as the forests go through successional stages and begin recovery. While young lizards and snakes may be small in size, adult alligator lizards (*Elgaria* spp.), skinks (*Eumeces gilberti*), and gopher snakes (*Pituophis catenifer*) documented here could be an important source of nutrition – especially in summer months when female fishers are either still feeding young or teaching them to hunt. The overall contribution of insects to fisher nutrition is less clear as they do not fall into a size class that is generally energetically efficient for fishers. Yellow jackets (*Vespula* spp.) were the most numerous insect species in scats from our study, and fisher may take advantage of nests dug up by themselves or black bears. Zielinski et al. (1999) found vespid wasps comprised 16.4 % of the total diet of fishers and up to 34.6 % of the autumn fisher diet in the Sierra Nevada. As a group, insects are widely available thus they may help supplement the diet as needed when other prey cannot be found, or as young animals are learning to support themselves.

Plants in the genus *Ribes* were present in the diet at a moderate level pre-tree mortality but increased dramatically in frequency (and thus in apparent value to fishers) post-tree mortality. The *Ribes* genus in the southern Sierra Nevada includes several species of currant and gooseberry. While our DNA methods did not allow identification to species, we suspect it more likely that fishers are eating currants which have berries with smooth exteriors as opposed to gooseberries which are prickly. We do not know if the increase in use of these plants corresponded with an increase in abundance of berries, a decrease in other typical mammalian prey, or perhaps a combination of both. But fishers have been documented eating fruit in other geographic areas. If fishers are shifting to eat more fruit because medium-sized mammalian prey are less available, persistence in the local area may be of concern. First, *Ribes* fruits are not available year-round, so this resource may be limited to mostly summer-fall months. We observed a seasonal difference in the pre-mortality scats, with 6.4 % of the scats collected early season containing *Ribes* compared to 12.8 % collected late season, whereas scats collected post-tree mortality had similar proportions for early and late sampling (21.6 % and 24.5 % respectively). This is consistent with a diet study on Pacific marten that found that most scats collected in the fall and winter contained fruit (Eriksson et al. 2019). Second, the nutritional value to energetics ratio required to obtain berries is likely lower than that ratio for tree squirrels. Third, foraging for berries on the ground for extended periods may put fishers at greater risk of predation compared to foraging for arboreal or semi-arboreal mammals. The fact that fisher can utilize berries may have important management implications. *Ribes* shrubs often grow in small clumps and may be compatible with objectives like tree planting and forest thinning for fuel reduction.

Finally, fungi were present at relatively low frequency (roughly 4 % pre-tree mortality, 9 % post-tree mortality) in scats. This differs from a recent fisher diet study using hair samples and isotopes by Smith et al. (2022) that found fungi to be common in the summer diet of fishers in the southern Sierra Nevada, especially post-tree mortality. The study by Smith et al. (2022) also included samples from across the entire southern Sierra Nevada region, so local conditions may have influenced findings on both studies. DNA references for fungal species in public databases (BOLD and Genbank) are lacking compared to other taxa (Meiklejohn et al. 2019) and it is possible that some of our unassigned DNA reads could be from other macro-fungi. We did not use fungi-specific PCR primers in our metabarcoding work, which may have also limited our recovery of fungi from the scat. Fungi may be a consistent food item (also noted by Zielinski et al. 1999) in this region, although they again represent a largely seasonal food source, and the total nutritional value is unknown without a better estimate of fungi consumed per meal.

Our study design and use of DNA metabarcoding provided direct evidence of diet shifts for fishers; however, there were limitations in our methods. First, we had higher sequencing effort for and potential PCR bias towards vertebrates and thus we likely underreport diet items from invertebrates, fungi, and plants. It should be noted that the presence of a diet item does not indicate proportionality, and similarly the brief time period that a scat sample reflects does not necessarily describe the totality of an individual's consumption patterns. Further, our data represents diet regionally and not the exact locations where prey were consumed. Future studies could have higher ecological precision by evaluating diet by sex and individual as we expect that females may preferentially select smaller prey most of the year but would require the highest energetic advantage during lactation. Pairing diet information with foraging strategies from fine-scale GPS or video monitoring could better reveal patterns not possible from diet analysis of scats alone.

One benefit of using molecular approaches to understanding diet, however, is the superior number of diet items identified relative to other diet studies using different approaches (Monterroso et al. 2018, Thuo et al. 2019). We were able to identify 48 genera, compared to previous methods which identified 14–26 genera (Arthur et al. 1989, Weir et al. 2005, Golightly et al. 2006). Although the difference in number may be due to different study areas, sample sizes, or other study specific reasons, it is consistent with observations that molecular diet analysis can detect cryptic food items in predator diets (Farrell et al. 2000) that may not be detected using other methods.

Overall, we observed different patterns in the DNA metabarcoding results in the periods prior to and after a major climate-induced tree mortality event that indicate a shift from a diet dominated by mammalian prey species to one dominated by plants (presumably in the form of small berries). Such cascading effects of climate change have the potential to impact body condition, reproduction, and survival of fishers. Our findings also suggest opportunities for forest management that may help sustain fishers in a landscape altered by tree mortality, such as promoting habitat that supports tree squirrels (especially Douglas squirrel, Humboldt's flying squirrel, western gray squirrel), a diversity of bird species (especially those that forage and nest on the ground such as mountain quail and spotted towhee), and fruiting shrubs (such as those in the *Ribes* genus).

While a flexible diet may allow fishers in the southern Sierra Nevada to compensate during challenging or changing conditions, it is important to consider that reproductive females in particular need to be able to consistently locate large and nutritious food items during daily foraging trips away from their early season dens, and medium-to-large size food items (e.g., squirrels) that can be carried back to dependent kits during the summer. Future research efforts that combine findings from this and other recent diet studies to identify moderate-to-high quality foraging habitat for fishers in the southern Sierra Nevada could be of great value in supporting this southernmost population's persistence into the future.

CRediT authorship contribution statement

Kristine Pilgrim: Methodology, Validation, Formal analysis, Investigation, Supervision, Writing – original draft, Project administration. **Rebecca Green:** Conceptualization, Methodology, Visualization, Formal analysis, Resources, Supervision, Project administration, Writing – original draft. **Kathryn Purcell:** Conceptualization, Methodology, Resources, Writing – review & editing, Project administration, Funding acquisition. **Taylor Wilcox:** Methodology, Software, Formal analysis, Data curation, Writing – review & editing, Visualization. **Eric McGregor:** Resources, Writing – review & editing, Visualization. **Larissa Gleason:** Resources, Writing – review & editing. **Sam Wasser:** Methodology, Writing – review & editing. **Michael Schwartz:** Resources, Writing – review & editing, Supervision.

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.

Data availability

Our DNA metabarcoding data used is in the supplemental file

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Appendix A. Supplementary material

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