Title: Drought-induced tree mortality affects the space-use and individual plasticity of an endangered forest carnivore

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Abstract

Rapid changes in landscape structure can disrupt the ecology and life history of species of conservation concern. Shifting climate, land-use, and disturbance regimes are generating novel landscape patterns, and it is unclear how these novel conditions may affect imperiled species. In the Sierra Nevada of California, USA, extensive drought-induced tree mortality has rapidly altered forest structure and local microclimates, with potential implications for forest-dependent species. We evaluated the effects of shifting land cover, forest structure, and abiotic conditions on the space-use of federally-endangered fishers (*Pekania pennanti*) in the southern Sierra Nevada during three distinct periods – pre-drought, drought, and post-drought tree mortality. Using 12 years of space-use data from 102 VHF- and GPS-collared fishers, we found that fishers selected for cooler, more forested, and riparian portions of the landscape across time periods. However, during drought and tree mortality, the magnitude of selection shifted strongly, with fishers selecting for remnant live and dead forest, riparian areas, and cooler areas and strongly avoiding open areas. As tree mortality occurred individual variation strongly increased, indicating the potential for adaptive behavior. Our results highlight the importance of individual plasticity and landscape composition in imperiled species persistence and demonstrate the risks of forest loss and change due to shifting climate and disturbance regimes.

1. Introduction

Disturbance regimes influence the temporal and spatial structure of vegetation communities, often with implications for animals occurring within those systems (Betts et al., 2019; McKelvey, 2015). Many species, or species' populations, have evolved to persist in ecosystems typified by intermittent natural disturbances. However, in contemporary systems, climate and land-use change have altered historical disturbance regimes, leading to accelerated landscape change, varied vegetation structure and regeneration, and changes to the composition and configuration of landscape mosaics (Johnstone et al., 2016). Thus, the consequence of altered disturbance regimes is the creation of novel landscape conditions that do not have a historical analog (Seidl et al., 2016b), which may affect the behavior, spatial ecology, and fitness of species occurring within those landscapes. Though responses to changing landscape conditions vary among taxa (Elmqvist et al. 2003), the direction (i.e., positive or negative) and magnitude of species' responses to change likely depend on the status or specialization of the affected species, as well as the landscape conditions that result from change, and the effects of change on resources, predators, and competitors. Understanding how novel disturbance regimes and landscape conditions affect individuals and populations, and the potential adaptive capacity of sensitive species, is of increasing interest and importance (Thurman et al., 2020)

In the western United States, climate and land-use changes have shifted naturally-occurring disturbance regimes. For example, throughout the inter-mountain and western United States (i.e., Sierra Nevada, Cascades, Rocky Mountains), shifting climatic conditions have resulted in increasingly warm, dry conditions, shorter snow-covered seasons, and increased occurrence of drought (Diffenbaugh et al., 2015; Kapnick and Hall, 2010; Mote, 2006). Shifting climate and a century of fire suppression tactics have resulted in increased tree density and mortality (Allen et al., 2010), outbreaks of native and non-native pests (Seidl et al., 2016a), and increasingly frequent and severe wildfire events (Steel et al., 2023). Though high-severity events, such as stand-clearing wildfires, can have deleterious effects on the persistence of forest-dependent species, the effects of nuanced forest disturbances on wildlife vary. For example, a pine beetle (*Dendroctonus* spp.) epidemic in the Rocky Mountains of the United States and Canada resulted in the mortality of millions of hectares of coniferous forest (Kayes and Tinker, 2012). This epidemic altered the structure and composition of forests by reducing canopy cover, altering understory vegetation, and increasing the number of downed logs (Collins et al., 2012; Klutsch et al., 2009; Pec et al., 2015). These rapid changes in forest structure could negatively affect forest-dependent wildlife, but some species persist after tree mortality occurs. For example, elk (*Cervus canadensis*) continued to use areas affected by tree mortality, but shifted their activity patterns to offset the energetic costs of increasing temperature and understory density that resulted from reduced canopy cover (Lamont et al., 2019). Other forest-dependent species, such as Canada lynx (*Lynx canadensis*), continued to use dead forest patches but disproportionately selected for areas with large-diameter, standing dead trees, or complex, remnant live forest (Squires et al., 2020). Though the effects of disturbance on forest-dependent species may vary, changes to forest and landscape structure resulting from novel tree mortality regimes can affect population persistence and induce local extirpations and extinction events.

The fisher (*Pekania pennanti*) is a forest-dependent species of conservation concern that was historically distributed throughout the mixed-conifer and northern hardwood-conifer forests of North America (Raley et al., 2012), but experienced range contractions and local declines due to shifting climate conditions (Tucker et al., 2012) and over-harvest for fur within portions of their range during the 19th and early 20th centuries (Powell and Zielinski, 1994). Though fisher populations in western North America evolved in systems that were historically typified by intermittent disturbances, their distribution continued to contract during the 20th century due to changing forest conditions and shifts in landscape structure, climate, and co-occurring species (Laliberte and Ripple, 2004). In the Sierra Nevada, decreasing snow-pack, rising temperatures, and increasing drought length and frequency have altered tree mortality dynamics (Allen et al. 2010) and fire regimes (Miller et al. 2009), resulting in novel disturbances and landscape structure. For example, a multi-year, climate-induced drought, and subsequent infestation of pine beetles, in the southern Sierra Nevada mountains of California resulted in extensive, heterogeneous, mortality of coniferous trees (Fettig et al., 2019; Young et al., 2017). Here, fishers occur as part of a small and isolated federally-endangered population that has been the focus of recent conservation concern (U. S. Fish and Wildlife Service, 2019). However, little is known about the effects of rapid, widespread tree mortality on fisher ecology, and uncertainties remain about the mechanisms driving patterns of individual- and population-level space-use and population decline. Understanding how individual fishers select or avoid conditions in novel post-disturbance landscapes may offer insights into the capacity of fishers, or other forest-dependent species, to persist in landscapes experiencing changing disturbance regimes (Steel et al., 2023; van Mantgem et al., 2009).

We assessed the effects of tree mortality on an endangered fisher population studied during a 12-year period in the southern Sierra Nevada, California, USA. Given that fishers are forest-adapted carnivores sensitive to forest loss and thermal thresholds (Kuntze et al., 2024), we hypothesized drought and resultant tree mortality would alter fisher resource selection. Based on previous work (Green et al., 2019; Kordosky et al., 2021; Kuntze et al., 2024; Purcell et al., 2009; Sweitzer et al., 2016), we predicted proximity to streams, land cover composition, complex forest structure, surface temperature, and topography would influence resource selection during pre-drought years. During drought and post-drought tree mortality years, we predicted fisher selection for riparian areas, forest cover and complex forest structure, and cooler areas would increase. Finally, we predicted that there would be greater individual variation from population-level patterns in drought and post-drought tree mortality years as forest structure and land cover composition shifted.

2. Methods

2.1 Study area

We collected data from June 2007 through March 2020 within the Sierra National Forest in the southern Sierra Nevada of California, USA (Figure 1). Elevation ranged from 915 to 2,385m and most precipitation occurred as rain in the fall and snow in the winter at elevations ≥ 1,500 m. Precipitation levels were consistent with historical trends during most of the study, but conditions were atypically hot and dry from 2012 to 2014 (Mann and Gleick, 2015), which led to a widespread tree mortality event that occurred from 2015 to 2017 (Young et al., 2017). Consequently, we discretized our study into three distinct temporal periods – "pre-drought" (2007 – 2011) "drought" (2012 – 2014), and "tree mortality" (2015 – 2020). Dominant tree species in the study area included incense cedar (*Calocedrus decurrens*), ponderosa pine (Pinus ponderosa), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), California black oak (*Quercus kelloggii*), and canyon live oak (*Q. chrysolepis*). Patches of deciduous forest, meadows, rock outcrops, and montane chaparral occurred at middle to high elevations within our study area, with mixed chaparral at lower elevations (Fites-Kaufman et al., 2007; Keeley and Davis, 2007).

2.2 Location Data Collection and Home Range Estimation

We trapped fishers primarily during fall and winter months and avoided trapping from March to June to preclude capturing pregnant or lactating females (Green et al., 2017). We captured fishers using live traps (model 108; Tomahawk Live Trap, Hazelhurst, Wisconsin) and sedated fishers with Ketamine (22.5 mg/kg) with Diazepam or Midazolam (0.125 mg/kg) for processing (Green, 2017). From 2007 to 2017, fishers ≥ 1.7 kg were primarily fitted with Holohil radio-collars (model MI-2M, 31 g; Holohil Systems Ltd, Carp, Ontario, Canada), although early in the project some were fit with Advanced Telemetry Systems (ATS) collars (model 1920, 38 g; ATS Inc., Isanti, Minnesota). Beginning in fall of 2017, we began shifting from VHF to GPS collars and attached Lotek GPS collars with RF (LiteTrack 40 (45 g) for females and small males, LiteTrack 60 (63 g) for larger males). Collars were fit with handmade breakaways to minimize injury and fall off over time if fisher was not recaptured. Fishers were classified into 3 age groups – juveniles (< 1 year), sub-adults (≥ 1 and < 2 years), and adults (≥ 2 years; Green et al., 2018). We adhered to protocols approved by California Department of Fish and Wildlife (Permit SC-2730) and the University of California-Davis' Institutional Animal Care and Use Committee (UC-Davis: IACUC #18022) and followed the American Society of Mammalogists' guidelines for the use of mammals in research (Sikes, 2016).

From 2007 to 2020, fishers were relocated via VHF- or GPS-collar tracking. Relocations included ground and aerial triangulation, rest or den sites (i.e., animal residing in single structure), rest areas (i.e., when the animal was tracked to within 50m but could not be located to a single structure), dropped collars, mortality locations, and GPS-collar locations. We excluded VHF-collar locations (e.g., bi-angulations, tri-angulations) with estimated error > 0.1 km^2, 3D GPS-collar locations with horizontal dilution of precision > 10.0, and 2D GPS-collar locations with horizontal dilution of precision > 5.0 (Frair et al., 2010) from subsequent home range estimates. Individual home ranges were estimated for each year, with March 10 to March 9 denoting the beginning and end of the fisher year, respectively. This annual period aligns with average birth dates of fishers within our study area and allowed us to account for fishers transitioning between age classes (e.g., juvenile to sub-adult, sub-adult to adult) (Green et al., 2018). To focus analyses on resident animals, we did not estimate home ranges of juvenile animals and did not estimate home ranges of any individual with fewer than 35 locations collected during the year of interest.

To minimize spatiotemporal autocorrelation of GPS-collar data, we rarified GPS locations to one location per 24 hours. We estimated home ranges using a second-generation kernel density estimator (KDE) with plug-in bandwidth selection (Gitzen et al., 2006). We selected KDE with a plug-in bandwidth selection as it provides more precise home range estimates than similar second-generation home range estimators, and performs similarly to third-generation home range estimators that incorporate time into estimation of utilization distributions (Walter et al., 2015). All data processing and analyses were completed in R v 3.6.2 (R. Core Team, 2021).

2.3 Landscape Covariates

We acquired or created topographic, hydrologic, thermal, and vegetative covariates to test hypotheses about the effects of drought-induced tree mortality and forest and landscape structure on resource selection of fishers. We calculated topographic position index (TPI) – a measure of terrain relief within a given cell compared to surrounding cells – within a 450 m radius (De Reu et al., 2013) from a 30 m resolution elevation raster (U. S. Geological Survey, 2019a) using the ‘‘tpi’’ function in the ‘‘spatialEco’’ package (Evans, 2021). Higher TPI values reflect more prominent (e.g., ridgelines) areas while lower TPI values reflect less prominent (e.g., drainages, valleys) areas. To determine distance to stream, we used the “distance” function in the “terra” package (Hijmans et al., 2021) to create a 30 m resolution raster representing the Euclidean distance from each pixel center to the nearest perennial or intermittent stream (U. S. Geological Survey, 2019b). We captured thermal characteristics of the landscape at a 30 m resolution by calculating summer (21 June – 21 September) mean composites of land surface temperature (LST) in Kelvin units using Landsat satellite data. Landsat data were acquired and processed in Google Earth Engine following Ermida et al. (2020).

We included several vegetation covariates in home range summaries and resource selection models. We created a 30 m resolution annual, fractional land cover dataset using Landsat imagery and random forest regression models for years when drought-induced vegetation change occurred on the landscape – 2014 to 2018. This dataset includes a series of raster layers that provide a continuous measure (i.e., 0 – 100%) of live forest, shrub, open areas (e.g., herbaceous cover, bare ground), or tree mortality (Figure 1). Unlike other regions, pre-drought open areas here generally reflected natural openings include meadows, herbaceous cover, and rocky portions of the landscape. Fractional cover value represents the percentage of the pixel covered by a given land cover type. We used land cover data from 2014 to represent conditions from 2007 – 2014, as land cover during that period was relatively stable with no major disturbances (e.g., wildfire, timber harvesting, tree mortality) within the study area. For 2019 and early-2020, we used 2018 fractional cover data after determining through local observations and visual inspection that land cover remained similar to conditions in 2018. The 2020 Creek Fire, which burned substantial portions of the study area, occurred after data collection for this analysis. Taken together, these land cover covariates capture the restructuring of the landscape as severe tree mortality occurred in the southern Sierra Nevada. Additional details on the creation and accuracy assessment of this dataset are available in McGregor et al. (2021). We also included 30m old growth structural index (OGSI) and basal area of California black oak to represent forest structure and composition characteristics not captured by fractional cover data. (LEMMA Lab, Oregon State University, Corvallis, OR; lemma.-forestry.oregonstate.edu).

2.4 Resource Selection

We evaluated resource selection by fishers during pre-drought, drought, and tree mortality periods by fitting generalized linear mixed-effects models using “glmmTMB” (Magnusson et al., 2017). We generated 10 available locations per used location for each fisher (Northrup et al., 2013) and available locations were assigned weight W = 1000 to facilitate convergence to the inhomogeneous Poisson process likelihood (Muff et al., 2020). For each temporal period, we created a global resource selection model that included: 1) fixed-effects for all landscape covariates to represent population-level selection, 2) random intercepts for individual fishers, 3) random slopes for individual fishers for all covariates to represent individual fisher responses to these covariates. We mean-centered and scaled all covariates and excluded correlated (i.e., Spearman’s correlation coefficient ≥ 0.7) covariates. We identified important predictors at the population-level based on 90% confidence intervals (CIs) of fixed coefficients not overlapping zero and at the individual-level when variance (σ^2) > 1.

3. Results

3.1 Fisher Capture and Tracking, Home Range Estimates, and Composition

From 2007 – 2020, we captured 196 fishers (105 females, 91 males) on 472 occasions and collared 174 fishers. We collected 42,874 VHF (i.e., rest and den sites, rest areas, bi-angulations, tri-angulations, dropped collars, mortality locations), live-capture, and GPS-collar locations. After removing imprecise locations and individuals with fewer than 35 locations from the dataset, we used 20,867 locations to estimate 249 annual home ranges from 102 unique individuals – 65 females and 37 males. Home range sizes were variable between sexes and among individual fishers, but male fishers generally exhibited much larger home ranges than females (Table S1). Regardless of sex or temporal period, fisher home ranges were largely comprised of forest cover – live forest during pre-drought and drought periods, and both live and dead forest during the tree mortality period – with smaller amounts of open areas and shrub cover used (Table S1,

Figure S1). By 2018, approximately 20% of pre-drought live forest experienced tree mortality and open areas increased by approximately 10%. Post tree mortality, open areas were larger in size, and included increased amounts of bare ground due to post-tree mortality management actions.

3.2 Resource Selection

Across temporal periods, fishers consistently selected for forested areas, including live forest and forest affected by tree mortality, and selected against warm areas, areas further from streams, and areas with higher TPI. Though fishers used open areas during the pre-drought and drought periods, these were generally small and proximal to forest patches and fishers were less likely to select for open areas as their availability increased (). There was a strong shift in the direction and magnitude of this relationship after tree mortality occurred with fishers strongly avoiding open areas. Variation in individual-level fisher selection was greatest during the tree mortality period (Table 1, Figure 2, Figure 3).

At the population-level during the pre-drought period, fishers selected (β [90% CIs]) for forested areas (0.43 [0.32 – 0.57]) and open areas (0.14 [0.05 – 0.23]) and selected against warm areas (-0.35 [-0.48 – -0.22]), areas further from streams (-0.21 [-0.28 – -0.14]), and higher TPI (-0.32 [-0.39– -0.25]). There was little effect of basal area of black oaks (0.02 [-0.03 – 0.07]), OGSI (-0.01 [-0.07 – 0.05]), or shrub cover (0.00 [-0.12 – 0.11]) on population-level resource selection. There was strong individual-level variation in fisher selection of shrub cover (σ^2 = 2.4), live forest (σ^2 = 1.9), distance to nearest stream (σ^2 = 1.3), surface temperature (σ^2 = 6.7), and TPI (σ^2 = 1.7) and little variation in fisher selection for open areas (σ^2 = 0.1), basal area of black oaks (σ^2 = 0.6), and OGSI (σ^2 = 0.8).

At the population-level during the drought period, fishers selected for forested areas (0.61 [0.50 – 0.72]), OGSI (0.11 [0.04 – 0.19]), open areas (0.13 [0.03 – 0.24]) and selected against warm areas (-0.25 [-0.38 – -0.11]), areas further from streams (-0.32 [-0.40 – -0.25]), and higher TPI (-0.26 [-0.34 – 0.18]). Fishers weakly selected for basal area of black oaks (0.05 [0.00 – 0.11]) and shrub cover (0.12 [0.00 – 0.23]). There was strong individual-level variation in fisher selection for OGSI (σ^2 = 1.5), shrub cover (σ^2 = 1.3), surface temperature (σ^2 = 5.9), and TPI (σ^2 = 1.5) and little variation in fisher selection for open areas (σ^2 = 0.02), basal area of black oaks (σ^2 = 0.7), live forest (σ^2 <0.01), and distance to nearest stream (σ^2 = 0.9).

At the population-level during the tree mortality period, fishers selected for both live forest (0.22 [0.13 – 0.30]) and forest affected by tree mortality (0.16 [0.11 – 0.22]), as well as basal area of black oaks (0.06 [0.02 – 0.09]). Fishers selected against open areas (-0.24 [-0.31 – -0.18]), warm areas (-0.26 [-0.37 – -0.15]), shrub cover (-0.25 [-0.34 – -0.17]), areas further from streams (-0.20 [-0.26 – -0.14]), and higher TPI (-0.17 [-0.24 – 0.11]) and little effect of OGSI (0.00 [-0.06 – 0.06]). There was strong individual-level variation in fisher selection for open areas (σ^2 = 1.0), OGSI (σ^2 = 2.3), shrub cover (σ^2 = 3.5), distance to nearest stream (σ^2 = 2.9), surface temperature (σ^2 = 10.6), TPI (σ^2 = 2.7), live forest (σ^2 = 2.9), and forest affected by tree mortality (σ^2 = 1.2). There was weak individual-level variation in fisher selection for basal area of black oaks (σ^2 = 0.7) (Figure 2, Figure 3).

Variability in resource selection among fishers and temporal periods can at least partially be explained by differences in individual-level habitat availability. For example, though fishers selected for open areas at the population-level pre-drought, they were less likely to select for open areas as their availability increased (Figure 4). After tree mortality occurred, population- and individual-level selection for open areas switched as all fishers avoided open areas and avoidance increased as availability increased due to tree mortality and post-mortality forest treatments (Figure 4). Conversely, fishers exhibited similar selection strength for live forest regardless of availability or temporal period (Figure 4). Across all temporal periods, fishers selected most strongly against distance to stream when streams and riparian areas were more available and selected most strongly against topographically prominent areas when they were more available (Figure 4). Selection of basal area of black oaks and OGSI exhibited less clear patterns, but pre-drought and post tree mortality fishers with the greatest availability of these features were the most likely to select for them (Figure 4).

4. Discussion

Using more than a decade of space-use data that spanned a drought and consequent tree mortality event in the southern Sierra Nevada, we demonstrated the importance of remnant forest structure and thermal microrefugia to fishers in an increasingly dynamic system. Regardless of temporal period, live forest and standing-dead trees, cool areas and areas closer to streams, and less prominent areas were consistently used by fishers. These features provide important resting and denning locations, cover from predators and competitors, and thermal refugia from hot and dry conditions that can induce physiological stress (e.g., Aubry et al., 2018; McGinn et al., 2023). Interestingly, rapidly shifting forest structure and land cover composition resulted in increased individual plasticity in resource selection, and also increased the strength of fisher avoidance of open areas on the landscape. Increasing heterogeneity in landscape composition and forest structure may induce increased plasticity in space-use of territorial carnivores, but given population-level patterns, this plasticity may also come with unanticipated fitness costs. The southern Sierra Nevada fisher population exists at the southern extent of the species' continental range, with previous work suggesting that the population may have limited capacity to adapt to warming climate (Green et al. 2018). We acknowledge that we were unable to quantify seasonal habitat use, where needs may vary due to shifts in physiological costs (e.g., hot vs. cold), reproductive status, and resource availability (e.g., Creel et al., 2016; Kuntze et al., 2024; Martin et al., 2021), and variation between higher fidelity resting and denning habitat vs. general space-use (e.g., Olson et al., 2024). Nonetheless, our work elucidates important conditions that support fisher space-use in a rapidly changing system, and can inform future restoration and conservation efforts.

Drought conditions had direct and indirect effects on vegetation structure, land cover composition, and fisher space-use. Across temporal periods, fishers selected live forest similarly regardless of availability, but also selected stands affected by tree mortality. Given fishers are territorial, and much of their perception and use of the landscape is likely shaped by previous experiences (e.g., Jakopak et al., 2019; Merkle et al., 2019), standing-dead trees still represent parts of established territories. Alternatively, areas affected by tree mortality were also proximal to remnant live forest (Figure 1; Cheng et al., 2024), and it is likely that stands with standing-dead trees provide connectivity to remnant live forest (Restaino et al., 2019). Importantly, during pre-drought and tree mortality periods, fishers exhibited a functional response to open areas, where they were less likely to select for open areas as their availability increased (Figure 4). The magnitude of this relationship strengthened after tree mortality occurred, when all fishers selected against open areas regardless of availability (Figure 2). Open areas were less common on the landscape pre-drought, and became more common post-drought as tree mortality and management actions to remove dead trees occurred on the landscape. These areas likely present greater risk of predation and competitive interactions due to a lack of cover (Wengert, 2013), may have less prey (e.g., Sollmann et al., 2015), and are likely more thermally stressful (Li et al., 2022). Despite the compromised condition of beetle- and drought-killed trees, they still provide a viable and important, though temporary, alternative to the loss of vegetation in drought-altered landscapes.

Despite observing shifts in the magnitude of selection for land cover and forest structure, we observed consistent selection of fishers for abiotic conditions that may provide thermal refugia in this landscape. Across temporal periods, fishers selected against higher surface temperatures. Surface temperatures can be affected by vegetation structure, with greater vegetation heterogeneity and cover providing more stable temperatures than open or structurally simple areas (Frey et al., 2016; Gilbert et al., 2022). Fisher use of cooler areas may be directly influenced by temperature (e.g., Alston et al., 2020) but could also be indirectly linked to the complex forest structure associated with stable microclimates that provide cover from predators and competitors (e.g., Green et al., 2019; Weir et al., 2005). Across temporal periods, fishers were also more likely to avoid areas further from streams and were more likely to avoid topographically prominent areas. Riparian areas that have perennial and seasonal water exhibit more resilient vegetation, and cooler, wetter microclimates than areas further from streams (Selmants et al., 2023). Similarly, less prominent areas, including drainages and depressions, may be cooler and have greater vegetation cover, complexity, and less exposure than prominent areas such as ridgelines and hilltops (Underwood et al., 2010). The availability of these features to individual fishers influenced the strength of selection and avoidance – fishers with fewer riparian areas were less likely to select against distance to streams and fishers in less topographically complex areas exhibited weaker avoidance of prominent features. Importantly, these findings, as well as aforementioned variability in habitat selection of land cover and vegetation structure, stress the importance of clarifying the context in which individual fishers are responding to their surroundings.

Though our work shows fishers are behaviorally plastic, there are likely fitness effects of tree mortality and shifting climate and land cover composition that were not captured by our analyses. In this area, previous research shows fisher survival decreases as temperatures increase and as forest heterogeneity decreases (Kuntze et al., 2024) and that tree mortality and loss can induce physiological stress (Kordosky et al., 2021). Further, tree mortality has likely altered the availability of energetically important prey, including tree squirrels (e.g., *Sciurus griseus*, *Tamiasciurus douglasii*) that depend on mast no longer provided by dead and dying trees. During the post-drought tree mortality period in the southern Sierra Nevada, two studies found fishers consumed plants and non-mammalian prey more often (Pilgrim et al., 2023) and as a larger proportion of diet (Smith et al., 2024) than pre-tree mortality, which likely incurs energetic costs due to increased handling time, lower digestibility and lower caloric value of these food groups. Increasing temperatures, loss of forest cover, and shifts in prey activity and density can also influence the physiological costs of foraging, with potential negative implications for fitness and population persistence (Briscoe et al., 2022; Scharf et al., 2016). As landscape conditions continue to shift in this dynamic landscape it is possible that fisher fitness will decline without targeted conservation and restoration efforts to support reforestation and key prey populations.

5. Conclusions

Given the increasing prevalence of high-severity wildfire, tree mortality, and shifting climate patterns, implementing practices to recruit and restore resilient vegetation is essential to avoid the acute loss of forested ecosystems (Bernal et al., 2023; Paz-Kagan et al., 2017; Steel et al., 2023). For example, efforts to continue the shift from fire suppression to prescribed fire and selective fuels removal and basal area reduction can reduce the severity of wildfires and likelihood of drought stress and beetle-kill in portions of the Sierra Nevada (Bernal et al., 2023; Hankin et al., 2023; North et al., 2022) and can increase forest resilience. There can be short-term negative effects of fuels reduction on fisher behavior and space-use due to smoke exposure and loss of understory complexity (Sweitzer et al., 2016; Thompson and Purcell, 2016; Truex and Zielinski, 2013). However, given their strong avoidance of open areas in a landscape affected by tree mortality, and other areas affected by high severity fire (Collier, 2024; Green et al., 2022), it is essential to avoid future catastrophic losses. Though nuance and landscape context are important to ensure conservation actions yield benefits (Binley et al., 2025), these practices are important to ensure the retention and recruitment of resilient forest structure and support the persistence of fishers and other forest-dependent species over time (Jones et al., 2022).

Data Accessibility

Code for resource selection and home range analyses is available at https://github.com/mellenmartin/KRFP_RSF. Fisher data to fit resource selection models are provided without geographic coordinates given the sensitive status of fishers in this region.

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Author Contributions

REG, CMT, KLP conceived the study design, collected, collated, and proofed data, and edited the manuscript. **MEM** proofed data, completed space-use and resource selection analyses, and wrote the manuscript. **ELM** completed spatial analyses, proofed the data, and wrote the methods. **SMM** provided assistance with analyses and interpretation of results, and edited the manuscript. All authors approved of the final version of the manuscript.

Declaration of Interest

The authors declare no conflict of interest

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Table 1. Population-level (i.e., “fixed” effects) selection-coefficients (lower – upper 90% CIs) of fishers (*Pekania pennanti*) monitored in our study area in the southern Sierra Nevada, California, USA. We present population-level coefficients for habitat covariates of interest for three temporal periods – “Pre-Drought” (2007 – 2011), “Drought” (2012 – 2014), and “Tree Mortality” (2015 – 2019). Parameters whose 90% confidence intervals did not overlap zero are indicated in bold.

	Period		
Covariate	Pre-Drought	Drought	Tree Mortality
Live forest	**0.44 (0.32 – 0.57)**	**0.61 (0.50 – 0.72)**	**0.22 (0.13 – 0.30)**
Land surface temperature	**-0.35 (-0.48 – -0.22)**	**-0.25 (-0.38 – -0.11)**	**-0.26 (-0.37 – -0.15)**
Basal area of *Quercus kelloggii*	0.02 (-0.03 – 0.07)	0.05 (0.00 – 0.11)	**0.06 (0.02 – 0.09)**
Old growth structural index	-0.01 (-0.07 – 0.05)	**0.11 (0.04 – 0.19)**	0.00 (-0.06 – 0.06)
Open	**0.14 (0.05 – 0.23)**	**0.13 (0.03 – 0.24)**	**-0.24 (-0.31 – -0.18)**
Shrub	0.00 (-0.12 – 0.11)	0.12 (0.00 – 0.23)	**-0.25 (-0.34 – -0.17)**
Distance to nearest stream	**-0.21 (-0.28 – -0.14)**	**-0.32 (-0.40 – -0.25)**	**-0.20 (-0.26 – -0.14)**
Topographic position index	**-0.32 (-0.39 – -0.25)**	**-0.26 (-0.34 – -0.18)**	**-0.17 (-0.24 – -0.11)**
Tree mortality	*NA*	*NA*	**0.16 (0.11 – 0.22)**

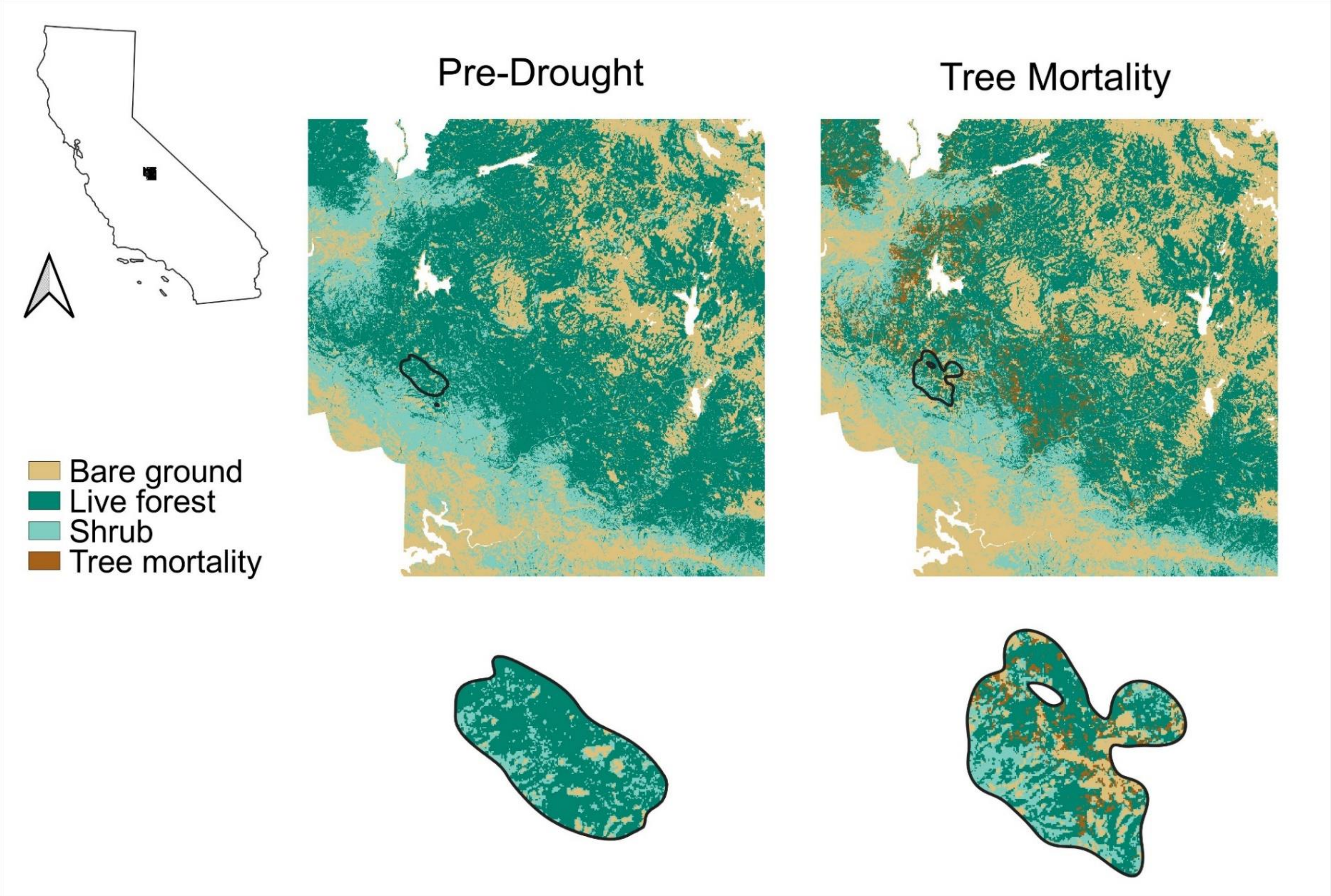
Figure Captions

Figure 1. Our work took place in a portion of the Sierra National Forest in the southern Sierra Nevada, California, USA. We collared and tracked fishers (*Pekania pennanti*) from 2007 – 2020, spanning pre-drought (2007 – 2012), drought (2012 – 2015), and tree mortality (2015 – 2020) periods. Tree mortality due to drought and beetle infestations affected much of the pre-drought live forest, and the amount of the landscape that was characterized as open areas increased substantially as tree mortality and removal occurred post-drought. Female fisher F71's pre-drought (2014: left) and post-drought tree mortality (2017: right) 95% home range contours are depicted to visualize the shift in land cover composition and availability within home ranges.

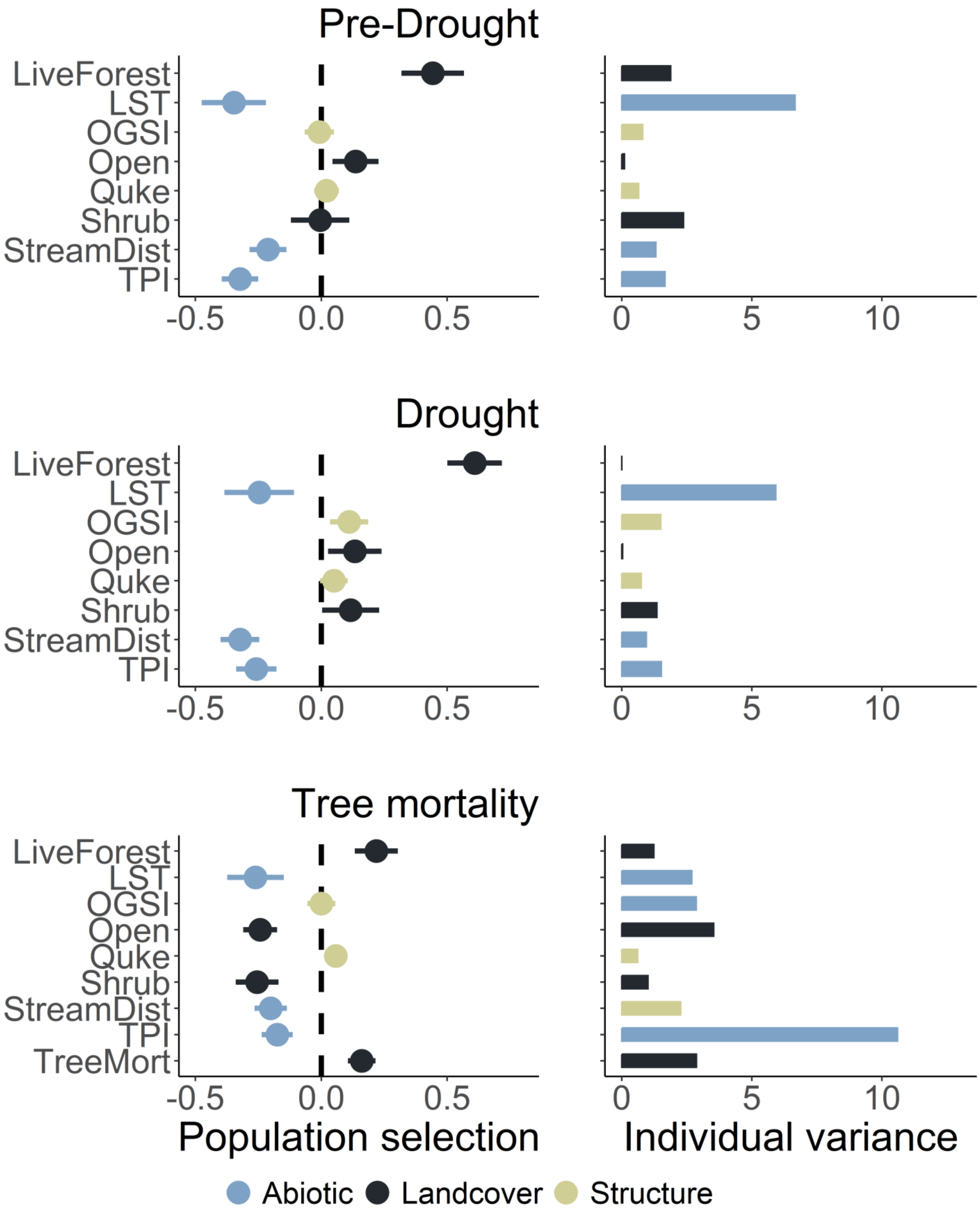
Figure 2. Population-level habitat selection-coefficients (left panels) and individual-level variance (right panels) of fishers (*Pekania pennanti*) in our study area in the southern Sierra Nevada, California, USA from 2007 – 2020. All covariates were centered and scaled prior to inclusion in mixed-effects resource selection models, and the depicted selection coefficients represent the strength of selection for or against the covariate of interest relative to the other covariates. Individual-level variance represents cumulative variance of individual-level selection-coefficients from the population-level selection-coefficient for each covariate. Covariates included open areas (Open), live forest (LiveForest), land surface temperature (LST), old-growth structural index (OGSI), basal area of black oak (*Quercus kelloggii*, Quke), shrub (Shrub), distance to stream (StreamDist), and topographic position index (TPI).

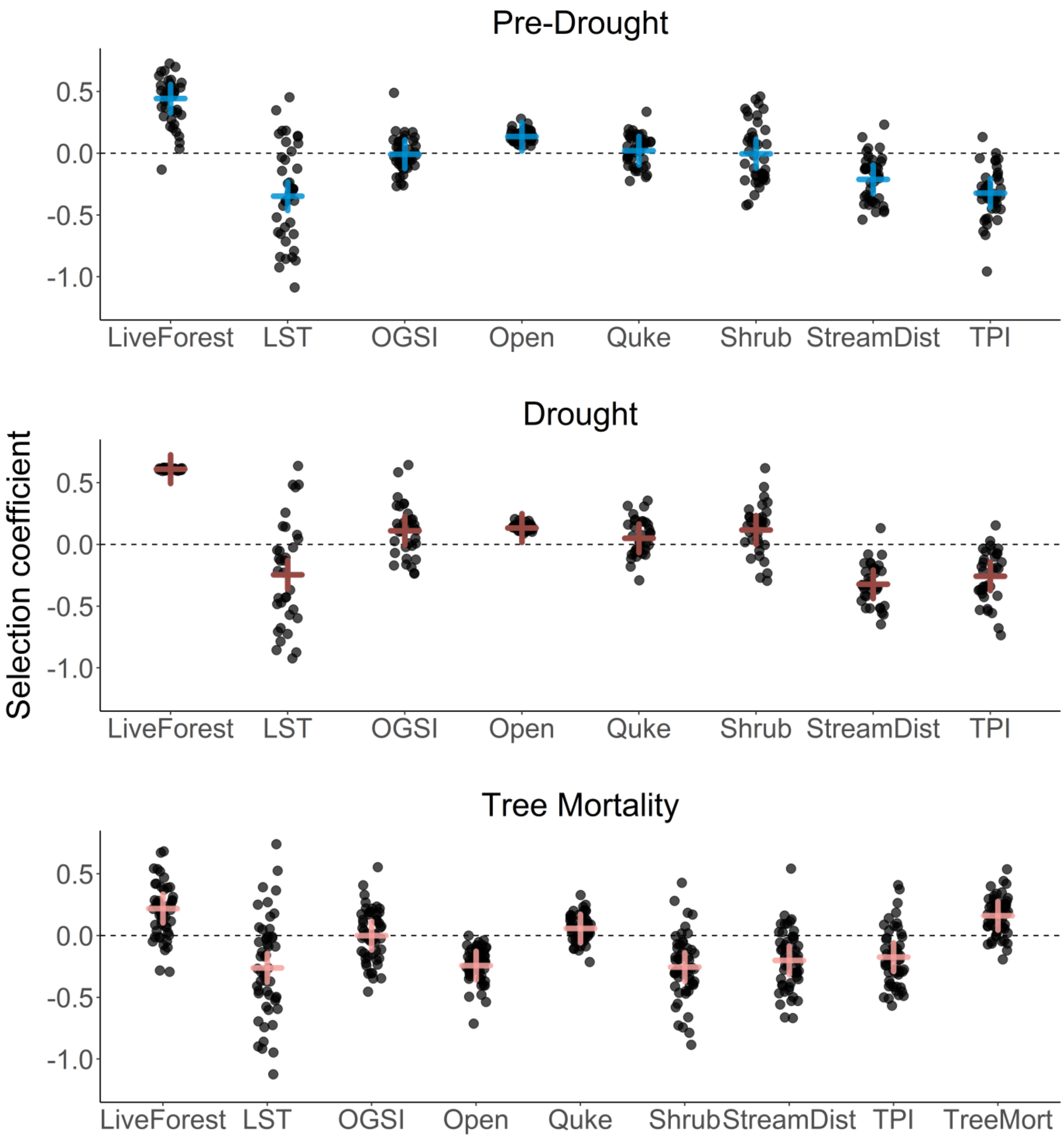
Figure 3. Population-level (colored plus signs) and individual-level (black circles) selection-coefficients of fishers (*Pekania pennanti*) in our study area in the southern Sierra Nevada, California, USA from 2007 – 2020. All covariates were centered and scaled prior to inclusion in mixed-effects resource selection models, and the depicted selection coefficients represent the strength of selection for or against the covariate of interest relative to the other covariates. Covariates included open areas (Open), live forest (LiveForest), land surface temperature (LST), old-growth structural index (OGSI), basal area of black oak (*Quercus kelloggii*, Quke), shrub (Shrub), distance to stream (StreamDist), and topographic position index (TPI).

Figure 4. Functional responses of fishers (*Pekania pennanti*) to habitat covariates of interest in our study area in the southern Sierra Nevada, California, USA from 2007 – 2020. The x-axis of each graph represents the average available covariate value for each fisher, while the y-axis represents individual fishers' selection coefficient for that covariate. Flatter lines indicate fishers consistently selected for a covariate regardless of its availability, while steeper slopes suggest fishers more strongly selected for or against a covariate as its availability increased. Covariates included open areas (Open), live forest (LiveForest), land surface temperature (LST), old-growth structural index (OGSI), basal area of black oak (*Quercus kelloggii*, Quke), shrub (Shrub), distance to stream (StreamDist), and topographic position index (TPI).

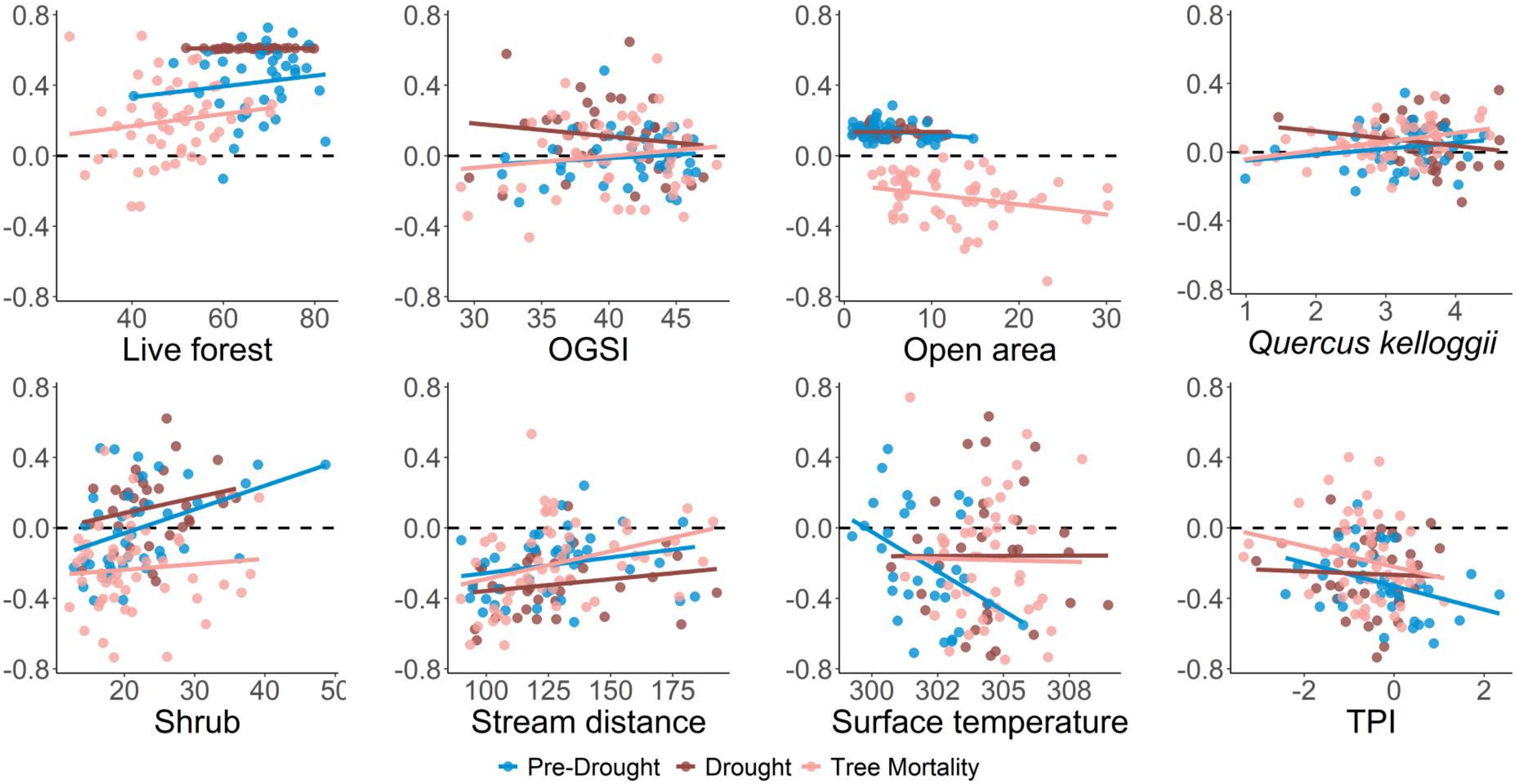

Pre-Drought
Tree Mortality
Bare ground
Live forest
Shrub
Tree mortality

772


Pre-Drought
Drought
Tree mortality
LiveForest
LST
OGSI
Open
Quke
Shrub
StreamDist
TPI
TreeMort
-0.5
0.0
0.5
0
5
10
Population selection
Individual variance
Abiotic
Landcover
Structure


Pre-Drought
Drought
Tree Mortality
Selection coefficient
0.5
0.0
-0.5
-1.0
LiveForest
LST
OGSI
Open
Quke
Shrub
StreamDist
TPI
TreeMort

775



0.8
0.4
0.0
-0.4
-0.8
40
60
80
Live forest
30
35
40
45
OGSI
0
10
20
30
Open area
1
2
3
4
Quercus kelloggii
20
30
40
50
Shrub
100
125
150
175
Stream distance
300
302
305
308
Surface temperature
-2
0
2
TPI
Pre-Drought
Drought
Tree Mortality

Title: Drought-induced tree mortality affects the space-use and individual plasticity of an endangered forest carnivore

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Table S1. Home range sizes and land cover composition within home ranges of fishers (*Pekania pennanti*) monitored in our study area during three temporal periods – "Pre-Drought" (2007 – 2011), "Drought" (2012 – 2014), and "Tree Mortality" (2015 – 2019). Home ranges were estimated from VHF-collar telemetry data (i.e., rest and den sites, rest areas, bi-angulations, and tri-angulations), live-capture locations, and systematically rarified GPS-collar data. For each sex, we report the number of unique fishers, median, minimum, maximum, and standard deviation (SD) of 95% home range contour size estimates in km^2.

	Female			Male		
	n	Median (±SD)	Range (Min. – Max.)	*n*	Median (±SD)	Range (Min. – Max.)
Pre-drought						
Size (km^2)	30	7.15 (5.54)	1.57 – 34.09	10	29.43 (34.66)	7.82 – 127.41
Open	–	2% (2.7)	0 – 13	–	5% (3.2)	2 – 11
Live forest	–	80% (8.6)	50 – 92	–	73% (7.9)	57 – 84
Shrub	–	18% (7.0)	8 – 45	–	19% (6.5)	14 – 36
Drought						
Size (km^2)	22	7.86 (3.51)	3.22 – 15.68	12	24.99 (11.07)	16.83 – 52.19
Open	–	2% (2.4)	0 – 9	–	4% (2.9)	1 – 12
Live forest	–	78% (7.9)	1 – 90	–	75% (6.0)	65 – 88
Shrub	–	20% (6.4)	9 – 32	–	19% (5.2)	11 – 32
Tree Mortality						
Size (km^2)	41	6.74 (4.81)	1.23 – 31.90	27	23.19 (18.09)	6.46 – 89.80
Open	–	5% (6.1)	1 – 29	–	8% (6.5)	2 – 30
Live forest	–	56% (13.4)	38 – 89	–	53% (14.0)	23 – 81

Shrub	–	17% (6.8)	7 – 43	–	17% (9.5)	11 – 53
Tree mortality	–	15% (12.7)	0 – 44	–	19% (9.0)	0 – 29

Supplementary Figure 1. Land cover composition within home range contours of fishers (*Pekania pennanti*) in our study area in the southern Sierra Nevada, California, USA from 2007 – 2019. We present composition for male and female fishers separately during three temporal periods – “Pre-Drought” (2007 – 2011), “Drought” (2012 – 2014), and “Tree Mortality” (2015 – 2020).