



Niche overlap of competing carnivores across climatic gradients and the conservation implications of climate change at geographic range margins



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ABSTRACT

There is considerable interest in factors controlling “warm-edge” limits – the lower elevation and latitudinal edges of a species' range. Understanding whether conservation measures can mitigate anticipated change in climate requires consideration of future climate as well as species interactions. We explored niche relations of martens and fishers at their southern range margins to understand their spatial and temporal dynamics, and how they may be affected by climate change. We used large-scale non-invasive surveys and home range data from radio-marked individuals to explore the spatial dynamics of each species. Marten and fisher were allopatric in the northern/wetter regions but sympatric at intermediate latitudes with lower precipitation. In the driest/southernmost region only fishers occurred. Martens were not detected when annual precipitation was < 900 mm and rare where minimum temperatures exceeded 4 °C. Fishers were absent where spring snow was > 650 mm. Classification trees, accounting for multivariate interactions, supported these results. Where sympatric, ~70% of a marten's home range overlapped with at least one fisher but martens tended to avoid this area. In sympatry, marten expanded their niche into areas with reduced snowpack, warmer temperatures and uncharacteristic lower elevation habitats. Future climate scenarios predict conditions that favor fishers, but our data suggest martens may be capable of shifting their niche somewhat to warmer and less snowy habitats. The conservation of interacting species at their warm range limits will require land managers be aware of interspecific tolerance, how each may respond uniquely to future climates, and how potential climate refugia can be integrated with existing habitat.

1. Introduction

Understanding the causes of shifts in range limits is a fundamental issue for ecology and conservation (Sexton et al., 2009). Range limits can be a testing ground to understand the environmental conditions to which populations can adapt (Brown et al., 1996; Sexton et al., 2009) and the conditions that we need to preserve and connect as climate changes. “Warm-edge” limits – the margins of a species' range that are closest to the equator or at the species' lower elevational limits – are very likely to be affected by climate change and biotic factors such as competition for resources and predation that accompany these changes (Cahill et al., 2014; Louthan et al., 2015). Consequently, predicting how range limits might respond to climate change requires evaluation of both climatic factors and species interactions.

North American martens (*Martes americana* and *M. caurina*) and the fisher (*Pekania pennanti*) are good subjects for the study of distribu-

tional patterns because important biotic and abiotic effects on their geographic ranges have previously been explored. Additionally, both species are the focus of conservation concerns with the southern Sierra Nevada fisher population under consideration as a threatened species at both the state and federal level, and marten designated a sensitive species by the US Forest Service. Precipitation interacts with competitive advantage and habitat selection to influence marten and fisher distributions. Specifically, deep snow has been proposed to limit the distribution of fishers whereas marten distribution has been shown to be limited by the abundance of the larger-bodied fisher (Raine, 1983; Krohn et al., 1995, 1997, 2004). The geographic distributions of two species are described as either allopatric (non-overlapping), sympatric (overlapping) or parapatric (adjoining), but they are actually a continuum (Bull, 1991). The interactions between fishers and martens lead to the general pattern of parapatric ranges in the western mountainous regions of North America, with martens at higher

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latitudes and elevations than fishers (Hagmeier, 1956; Grinnell et al., 1937; Gibilisco, 1994; Buskirk and Powell, 1994; Kucera et al., 1995; Zielinski et al., 1995, 1997, 2005). Moreover, martens are generally associated with conifer forests and fishers associated with mixed conifer-hardwood forests, habitats that are generally stratified by elevation (Buskirk and Powell, 1994). Whether this is due to differential ability to exploit resources in these forest types, or because these types occur at different elevations with different snow depths is unknown. We do know, however, that marten and fisher distributions have varied with past climate changes (Krohn, 2012) and are expected to change in the future with projected changes in temperature, snowfall, and the severity of wildfire (Lawler et al., 2012; Spencer et al., 2015b).

Until recently, North American martens and fishers were considered congeneric, a relationship that typically implies that competition is, or has been, intense between them. Although recent revisions of their taxonomy have them placed in different genera (Dawson and Cook, 2012; Sato et al., 2012), the similarity of their diets (Martin, 1994; Zielinski and Duncan, 2004), habitat associations (Buskirk and Powell, 1994; Thomasma, 1996) and general environmental factors where they co-occur suggests that competition between them may be acute and affect their distributions (Krohn et al., 1997; Manlick, 2015). Community interactions may be particularly influential in determining marten and fisher distributions, not only because of the interaction between their relative competitive abilities and their mobility in snow but also because of interactions with larger predators. For example, fishers have responded to the absence of larger predators in some parts of their range by increasing their distribution and body size (LaPoint et al., 2015).

Ecological modeling reveals variation in whether the presence of one species can predict the occurrence of the other. Several studies conducted in the snow-free season discovered that model fit was not improved by using one species to predict the other (Gompper et al., 2016; Spencer et al., 2015b). Using surveys in winter, however, Fisher et al. (2013) discovered that the absence of one species significantly explained the occurrence of the other. Surprisingly, Manlick (2015) found that marten occurrence was positively associated with fishers in Wisconsin, yet there were no differences in spatiotemporal segregation, habitat selection or diet. He attributed this “niche collapse” to the homogenization of the forest environment caused by human disturbance. Despite the hypothesis that differences in prey enable the coexistence of martens and fishers (Rosenzweig, 1966), their diets in sympatry are similar (Zielinski and Duncan, 2004; Manlick, 2015).

In western North America, martens and fishers occur in largely peninsular distributions that correspond with the distribution of montane forests in the Rocky Mountains, Cascades, and Sierra Nevada (Gibilisco, 1994; see also <http://maps.iucnredlist.org/map.html?id=41648> and <http://maps.iucnredlist.org/map.html?id=41651>). However, the dynamics of their contemporary distributions have not been explored in detail in any of these bioregions. The climate at the southern end of their distributions – in the southern Sierra and the southern Rockies – is decidedly drier and warmer than farther north and the distribution of habitat for both species becomes reduced from north to south (Gibilisco, 1994; Spencer et al., 2015a). How the warmer and drier environment at the southern margin of their current ranges (the “warm edge”) affects their distributions there may provide insights about how a warmer and drier future climate may affect their distributions and interactions farther north.

Climate change can complicate interspecific interactions at species distributional boundaries. Changes in competitive interactions have been reported at range margins under changing climatic regimes (Letcher et al., 1994; Gaston, 2003). Rubidge et al. (2011), for example, compared historical and modern distributions of three species of montane chipmunks and found evidence of climate change-mediated competitive release at an elevational species boundary. MacArthur (1972) argued that the southern limits of many northern hemisphere species are determined largely by competitive interactions. A recent

review, however, found that warm-edge range limits were more often set by abiotic factors (Cahill et al., 2014).

Here we test competing hypotheses about the drivers of occurrence patterns between two closely related species by examining dynamics at their southern range boundaries (also called the “trailing edges”, see Morelli et al. [2012]). We use spatial data on marten and fisher occurrence in the southern Sierra Nevada to explore the species' niche relations across latitudinal, elevational and climatic gradients. We use data from 2 sources: large-scale and multi-year camera, track-plate, and hair snare surveys from the southern Sierra Nevada carnivore monitoring program (Tucker, 2013; Zielinski et al., 2013), and data on overlap of marten and fisher home ranges from a sample of radio-marked individuals. These sources make it possible to examine the spatial patterns at two resolutions. At the landscape scale, we explore the spatial pattern of how these species distributions change along strong elevational, latitudinal and climatic gradients. Landscapes can also change due to anthropogenic causes, such as timber or vegetation management. However, we focused on climate for 2 reasons: (1) unlike climate, for which there are established models to predict future conditions, there are no reliable models on which to forecast landscape change due to anthropogenic effects. Forest planning typically projects 10 years into the future and what is planned is often not realized due to changing political, social or economic factors, and (2) historically the northern Sierra has been much more affected by landscape change due to the history of clearcut logging in this region, compared to our study area in the southern Sierra where much less disturbing selection logging was the norm (McKelvey and Johnston, 1992).

At the home range scale, we test whether interference competition determines how the species interact spatially and temporally where they occur in sympatry. We predict that approaching the southern margin of their ranges there will be more overlap and more potential for interactions. In effect, we use the current distributions at relatively low latitudes in the mountains of western North America as a surrogate for the environmental conditions expected when a warming climate renders forests at higher latitudes warmer, drier and perhaps with less precipitation in the form of snow. In this way, we foreshadow the changes in interspecific interactions and distributions that may occur with predicted changes in climate in the southern Sierra, and elsewhere in their range where these species co-occur. This perspective will help conservation biologists and land managers understand the characteristics of potential climate refugia for both population persistence and connectivity and whether key interacting species may be able to share such refugia (Morelli et al., 2016).

2. Methods

2.1. Study area

The study area includes the west slope of the Sierra Nevada Mountains south of the Merced River in Yosemite National Park (Fig. 1). This encompasses the great majority of the known current range of native fishers in the Sierra Nevada (Zielinski et al., 1995; Spencer et al., 2015a) but only a portion of the larger marten range, which extends northward through the Sierra Nevada and into the Cascades (Kucera et al., 1995; Zielinski et al., 2005). The study occurred primarily on the Sierra, Sequoia and Inyo National Forests and Yosemite and Sequoia-Kings Canyon National Parks.

The study area has a Mediterranean climate characterized by hot, dry summers and cool winters with most of the precipitation occurring between October and May. Precipitation in the middle to high elevations falls primarily as snow. The Sierra Nevada become higher, steeper, narrower, and drier from north to south and consequently within the study area there are elevational and precipitation gradients with the northern region having a lower mean elevation and higher annual precipitation than in the south. The southern end of the study area is bisected by the Kern River canyon, east of which lies the Kern Plateau

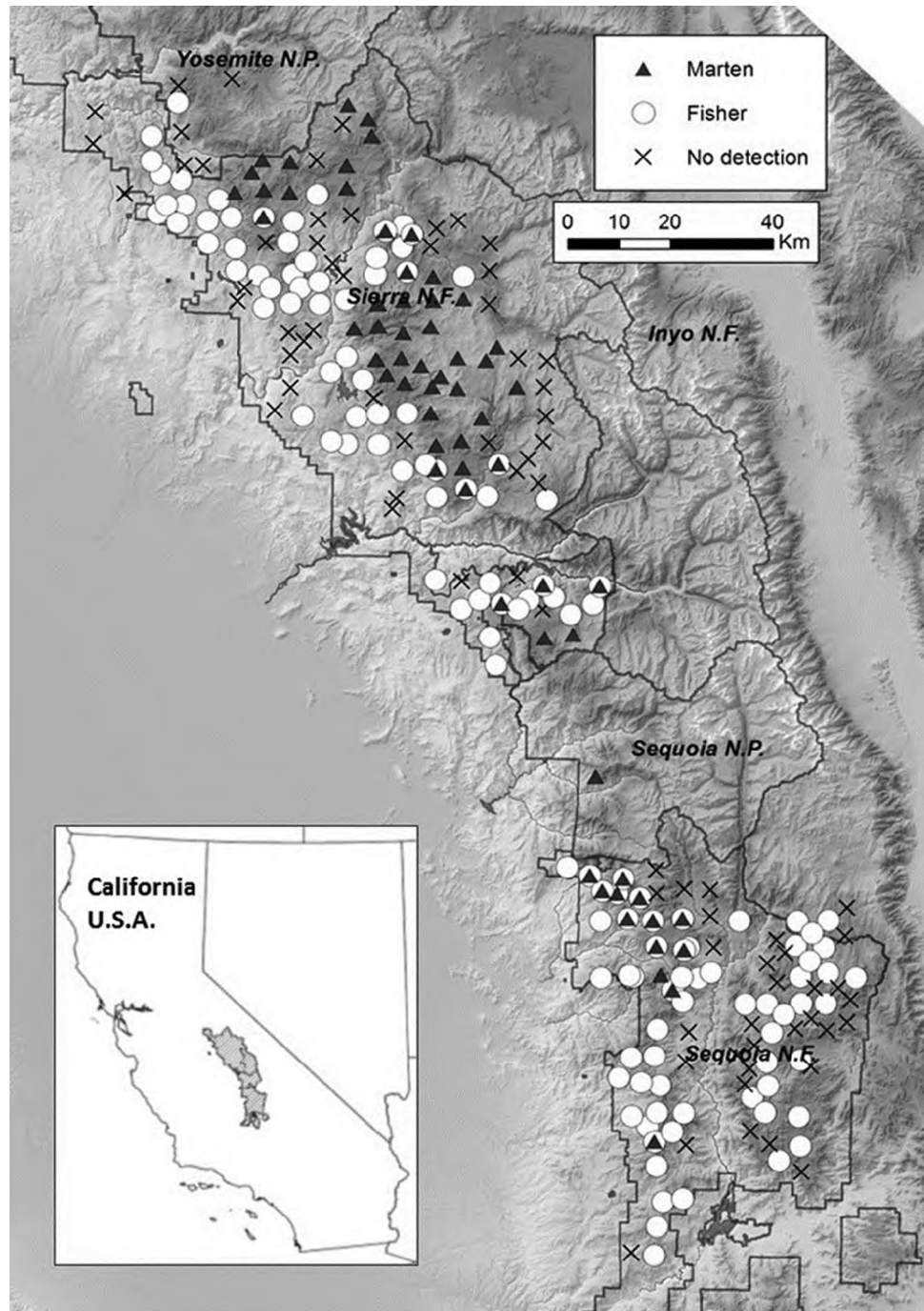


Fig. 1. The locations of 249 sample unit centers and fisher and marten detections in the regional surveys completed through the Sierra Nevada Carnivore Monitoring Program, 2002–2014. Units with marten detections denoted with black triangles, fisher detections with white circles, and units that did not detect either species with an x.

(Fig. 2), a high elevation plateau drier than the rest of the study area and the only portion of the study area on the eastern slope of the Sierra.

2.2. Regional survey data

Marten and fisher data came from two sources. The first was survey results from 12 years of occupancy monitoring by the southern Sierra Nevada carnivore monitoring program (Tucker, 2013; Zielinski et al., 2013; US Forest Service, 2015). This program uses track plates, camera, and non-invasive genetic sampling devices at multi-station sample units that were baited and checked at defined intervals. Sampling principally occurred within the elevational range of 1000 m–3400 m (Fig. 1) from

June–October.

From 2002 to 2009, sample units were comprised of an array of 6 stations encompassing an area of $\sim 0.8\text{km}^2$, checked every 2 days over a 10 day period. At this time, due to the limitations of film cameras, track plates were the primary detection device. Analysis of the first 8 years of data suggested that detection and occupancy estimates would not suffer lower precision with reduced sample effort (Zielinski et al., 2013; J. Baldwin pers. comm). Therefore, to increase efficiency, in 2011 the sampling protocol was revised and the number of stations in a unit was reduced to 3 (a subset of the original 6) checked every 7 days over a 21 day period. To incorporate technological advances in camera technology, each station was revised to be two devices, a camera and

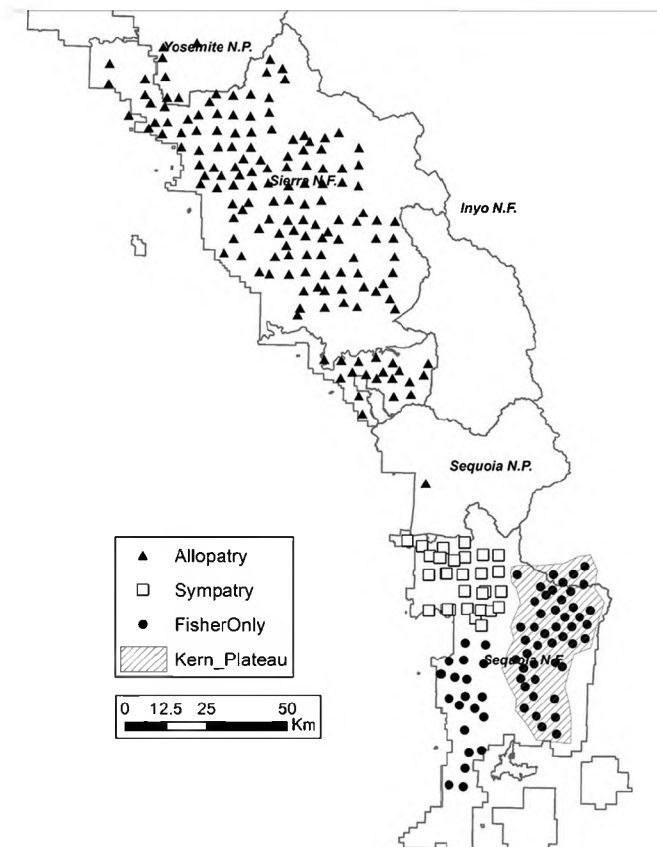


Fig. 2. Regional monitoring sample units by zone designation (allopatric = triangles, sympatric = squares, fisher-only = circles) on a map of national forests and national parks.

track plate enclosure ~100 m apart.

While we did not consider individual stations within a sample unit as spatially independent, they were often at significantly different elevations and vegetation types. Consequently, because we were concerned about the effects of averaging such diverse values across all stations within a unit, we conducted analyses at both the station and unit level. However, we rely primarily on the sample unit results for significance tests because at the station level the results were inflated by the much higher sample size. While the results at the sample unit level may be more robust in that they aggregate the more variable station-level data, the station-level comparisons add resolution to the data.

Data were collected annually from an average of 126 sample units/year over 12 years (2002–2014, no sampling in 2010). Detection was a binomial outcome at each station or unit across all years. Thus, no matter whether a species was detected only once or many times over the 12 years of sampling, the outcome was either “detected” or “not detected”. This is because once a marten or fisher discovers the bait it is likely to return again (Slauson et al., 2012), perhaps over multiple years, and data influenced by this behavior were not useful for our purposes. In this regard we were conservative, and we did not use the number of detections to reflect relative abundance. Probabilities of detection, if present, have been estimated for each species and they are quite high (> 80% for both species; Royle et al., 2008; Zielinski et al., 2015), resulting in little difference between using naïve and adjusted estimates of occupancy.

Preliminary information suggested that overlap in marten and fisher patterns of distribution in the southern Sierra appeared to differ depending on geography (Zielinski et al., 2005; US Forest Service, 2015; J. Tucker pers.obs). North of Sequoia-Kings Canyon National Park the two species were primarily allopatric, whereas they were

primarily sympatric just south of the park (Fig. 1). Although parapatric may be a more appropriate description of some of the distributions in the northern region, for simplicity we refer to this as the allopatric zone. Finally, in the southernmost portion of the study area preliminary information suggested that martens were virtually absent. Thus, to explore how environmental features may explain the patterns of distribution, we divided our analysis into 3 zones: a northern zone where there was little overlap between species (the allopatric zone), a central zone where there was considerable overlap between species (the sympatric zone), and a southern zone (the fisher-only zone) (Fig. 2). We tested the hypothesis that climatic and vegetation characteristics where marten and fisher were detected were different in allopatry versus sympatry. Furthermore, we predicted that in sympatry either 1) landscape heterogeneity was sufficient for each species to occur within the same landscape conditions as is the allopatric zone, or 2) one of the species was associated with atypical landscape characteristics in the sympatric zone. We examined differences in the spatial overlap of marten and fisher detections in relation to vegetation, elevation, precipitation, snowpack, and temperature in the three zones.

We calculated the variable values at stations using a 500 m moving window. This reflected the effective survey area of each station when the distance effects of lure and bait are accounted for and prevented analytical overlap between stations (each station is a minimum of 500 m apart). For the unit level analysis, variables were assessed using a 1 km² moving window around the centroid of all station locations for each unit, which reflects the minimum sampling area encompassed by the perimeter of the stations plus ~150 m buffer for bait and lure distance.

2.3. Climate and other environmental variables

Three climatic variables were chosen to represent the general effects of precipitation and temperature. Total annual precipitation (precipitation) was selected to indicate the overall effects of moisture and the depth of the April 1 snowpack (snowpack) was selected because of the suspected relationship between marten and fisher distributions and snow depth (Krohn et al., 1995, 1997, 2004). Average annual minimum temperature (minimum temperature) was chosen to complement the precipitation variables and as a variable that may highlight differences in the species' relative tolerances to cold. Values for the climate variables were obtained from the 2014 California Basin Characterization Model (BCM) downscaled Climate and Hydrology dataset at a spatial resolution of 270 m using 30-year statistical summaries from 1981 to 2010 (Thorne et al., 2012; Flint et al., 2013, <http://climate.calcommons.org/dataset/2014-CA-BCM>). Vegetation type was represented by the California Wildlife Habitat Relationships (CWHR) system (Mayer and Laudenslayer, 1988). We derived CWHR vegetation types for each station from the USDA Forest Service Existing Vegetation (EVEG) data with source imagery from 2000 to 2008 (www.fs.usda.gov/main/r5/landmanagement/gis). Latitude adjusted elevation was obtained from the USGS 1-Arc Second National Elevation Dataset, 2009, adjusted for latitude by the Conservation Biology Institute (www.databasin.org).

2.4. Effects of future climate

To understand how climate may change in the future in respect to the three climate variables (precipitation, snowpack and minimum temperature), and to understand how future climatic conditions in the study area may affect future distributions of martens and fishers, we obtained the results of climate projection models. We used projections from the same source (2014 California BCM) for 18 climate models using 30 year statistical summaries from 2070 to 2099 that encompassed a range of emissions scenarios and greenhouse gas concentrations (IPCC 4th and 5th Assessment Report, 2007, 2013). We conducted qualitative comparisons of the future direction and magnitude of

changes in the three climatic variables in relationship to the associations with these variables we discovered in the marten and fisher ranges.

2.5. Statistical analyses

Due to non-normality of the environmental data associated with the locations of each species in each zone, we calculated the median and interquartile ranges (IQR). IQRs are unbiased estimators that measure statistical dispersion between the first and third quartile and reflect the asymmetry of skewed distributions. We tested the four continuous variables (elevation, precipitation, snowpack, and minimum temperature) for differences in the overlap of fisher and marten locations using two non-parametric statistical tests. The Kolmogorov-Smirnov (ks) test compared the equality of the cumulative distributions of two samples (e.g., Rangel et al., 2007; Alfaro et al., 2013) and the Mann Whitney *U* (mw) test evaluated differences in the mean ranks of the distributions (e.g., Hasegawa and Maekawa, 2006; Arnan et al., 2012), with significant results ($\alpha < 0.05$) indicating that the two samples come from different distributions. We also created multivariate classification trees (Breiman et al., 1984; De'ath and Fabricius, 2000) to understand how the climatic variables interact to predict the conditions at sample units where each species was detected compared to where it was not. Trees were pruned to the smallest tree with a cross-validation error rate that was within 1 SE of the minimum (Breiman et al., 1984). Classification error rates were estimated using bootstrap aggregation with 1000 replications. Analyses were conducted in R version 3.1.2 using the *stats*, *rpart*, *rpart.plot* and *irp* packages.

2.6. Home range overlap via telemetry

The second source of data came from a sample of radio-marked and concurrently monitored fishers and martens on the Sequoia National Forest (Fig. 3). Animals were trapped at locations that were selected based on field intuition and were distributed relatively evenly across the study area. We were interested in determining the degree of spatial and temporal overlap of home ranges in the central zone, where preliminary data indicated sympatry. Home ranges were represented as 100% minimum convex polygons and included locations derived from – in descending order of frequency – homing to resting sites, ground triangulations, aerial locations, trap sites and carcass recoveries. We used home range estimates to delineate 2-dimensional regions of

spatial overlap (km^2) between each pair of overlapping individuals. Total combined home range percent overlap was calculated for each individual by dividing the total area of overlap by the total home range area and multiplying by 100. Frequency of overlap for an individual was calculated as the total number of individuals overlapping each target individual's home range.

To explore the dynamics of overlap in more detail, we used methods proposed by Minta (1992) to test for attraction to or avoidance of an area of overlap and to determine temporal interactions between pairs of martens and fishers that shared a common area (i.e., home range overlap). We tested the null hypothesis that for each pair sharing an area of overlap, each individual would use the area spatially and temporally independently of the other (i.e., random movement). The spatial overlap and temporal interaction 'effect' was categorized as attraction, avoidance, or random. Additionally, the temporal interaction coefficient 'effects' were evaluated relative to the area of spatial overlap between pairs to determine if the joint use of the overlap area was simultaneous, solitary, or random. Because there is only one way to be simultaneously present and three ways to be solitary (i.e., one or the other or both animals), we used odds ratios (Minta, 1992) as a measure of association to distinguish simultaneous or solitary avoidance or attraction to the overlap area. Observations were considered simultaneous if they were within 48 h of each other because shorter time periods did not result in sufficient data for analysis. Statistical significance of spatial and temporal overlap in overlap areas was determined by comparing observed and expected frequencies of presence and absence using χ^2 tests ($\alpha < 0.05$).

3. Results

3.1. Regional surveys

Over 12 years (2002–2014), we surveyed 1439 stations in 249 sample units for a total of 33,519 station visits. Each unit was surveyed an average of 6.2 years, but because the number of stations in each unit was reduced beginning in 2011 (see Methods), each station was surveyed an average of 4.3 years. This resulted in a total, across all years, of 1515 unit surveys and 7613 station surveys completed, of which 742 station/393 unit surveys detected fisher and 367 station/188 unit surveys detected marten (Table 1). When we combined survey results across years, fishers were detected at 392 stations/130 units and martens at 186 stations/62 units (Table 1). Overall 15 stations and

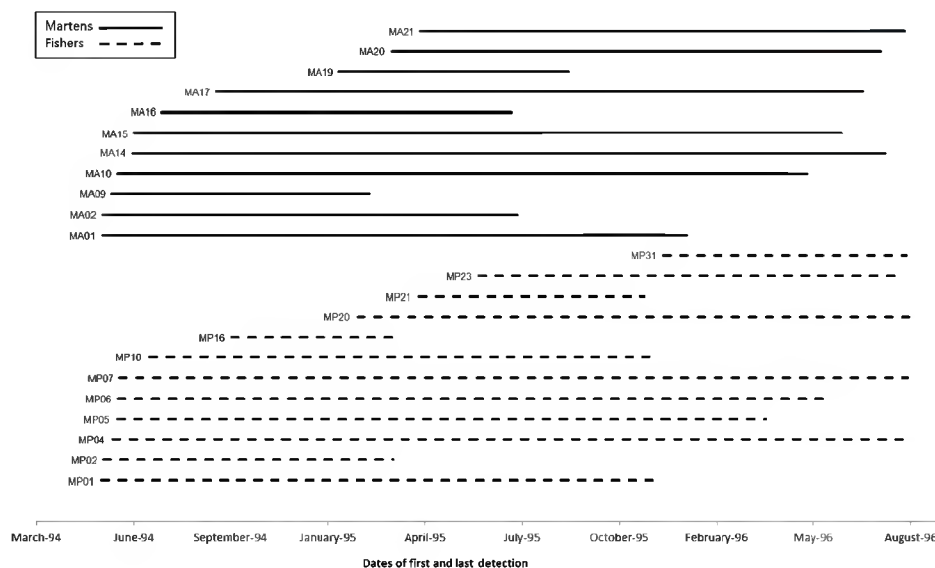


Fig. 3. The dates of first and last detection, and the intervening period, for radio-marked fishers and martens on the Sequoia National Forest (now Sequoia National Monument) demonstrating the concurrence of these data.

Table 1

Number of stations or sample units in each zone (allopatry, sympatry, and fisher-only) and total martens and fishers detections in the southern Sierra Nevada, 2002–2014.

Region	Species	Stations with detection	Total stations (percent)	By year		Years combined	
				Station	Unit	Station	Unit
Allopatry	Marten	144	914 (16)	—	—	—	—
	Fisher	191	914 (21)	—	—	—	—
Sympatry	Marten	42	163 (26)	—	—	—	—
	Fisher	84	163 (52)	—	—	—	—
Fisher only	Fisher	117	356 (33)	—	—	—	—
Total surveys				7613	1515	1439	249
	Marten	186	1433 (13)	367	188	186	62
	Fisher	392	1433 (27)	742	393	392	130

22 units detected both species in the same year (22/1515 units; 1.5%). In the sympatry zone the proportion of units detecting both species in the same year was much higher (18/157 units; 11.5%) and combining detections across years 41% (11/27) of units in the sympatric zone detected both species. In the allopatry zone, fishers were detected at 20% and marten at 16% of the units; in the sympatry zone, fishers were detected at 50% and marten at 23% of the units; in the fisher-only zone fishers were detected at 33% of the units.

Two detection locations were considered outliers and omitted from further analysis. First, we detected a fisher at an unusually high elevation in the allopatric zone that received > 2.5 times the IQR for both precipitation and snowpack for a fisher, a value considered an outlier via the Tukey method (Tukey, 1977). Moreover, this detection was a rarity, occurring at two adjacent stations on a single date out of a possible 216 detection opportunities at that sample unit over 9 years. Secondly, we excluded one sample unit in the fisher-only region that detected marten in 2 out of 10 years surveyed (incidentally the two wettest years during the study). Although the values for all climate variables at this marten detection location fell within the range of what was found at marten detections in the sympatric zone, it was a *spatial* outlier occurring 30 km south of the next nearest marten detection, when the average nearest neighbor distance for all other units was < 5 km (Fig. 1).

3.1.1. Comparisons between species

At the sample unit level, we found the distribution of all four continuous variables elevation, precipitation, snowpack, and minimum temperature to be significantly different between units where fishers and martens were detected in the northern allopatric zone but not significantly different in the central sympatric zone (Tables 2, 3). In the allopatric zone, fishers were detected at significantly lower elevations ($Median_{fisher} = 1923$ m, $Median_{marten} = 2527$ m), lower precipitation ($Median_{fisher} = 1026$ mm, $Median_{marten} = 1157$ mm) and lower snowpack ($Median_{fisher} = 115$ mm, $Median_{marten} = 558$ mm), but higher minimum temperatures ($Median_{fisher} = 4.0$ °C, $Median_{marten} = 0.4$ °C). A similar pattern was found in the sympatric zone but the differences were not statistically significant (Tables 2, 3). There was no overlap in IQR for elevation, snowpack, or minimum temperature in the allopatric

region between fisher and marten, and very small overlap in precipitation. However, in the sympatry zone, the IQR for all variables overlapped. The general distribution patterns and IQR overlap results were consistent between the sample unit and station level analyses; however, at the station level there were statistically significant differences between species for all variables in both the allopatric and sympatric zones.

In the fisher-only zone, fisher detections occurred at significantly higher elevations but lower minimum temperatures and precipitation than where they were detected in either the allopatry or sympatry zones (Fig. 4). The elevation, snowpack and minimum temperature values at fisher detections in the fisher-only zone overlapped the distributions of these variables for both fisher and marten in the other two zones. However, precipitation levels were significantly lower at fisher detection sites in the fisher-only zone (ks test $p < 0.01$, mw test $p < 0.01$), with the entire IQR in this zone below the IQR for both fisher and marten in the other two zones (Fig. 4c, Tables 2, 4).

Each of the three climatic variables appears to have a threshold relationship with the distribution of one or the other species. First, regardless of zone, fishers did not occur where snowpack exceeded 650 mm whereas martens occurred in areas where there was as much as 970 mm snowpack (Fig. 4d). In the fisher-only zone, fishers occurred at elevations that were more characteristic of the elevations where martens occurred in other zones (Fig. 4a). Interestingly, the high elevation areas in the fisher-only zone received much less precipitation than in the zones where martens occurred. Second, martens were never detected at a station with < 911 mm of precipitation per year whereas fishers occurred at stations where precipitation was as low as 400 mm per year (Fig. 4c). Third, martens rarely occurred at locations where the average annual minimum temperature was > 4 °C (this value was exceeded at only 5 of 190 locations with marten detections) but fishers were detected at locations where minimum temperatures as high as 8.8 °C (Fig. 4b).

Classification trees were consistent with these relationships and highlighted the characteristics that separated detection from non-detection locations (Fig. 5). The pruning criteria resulted in a single node tree for fishers, where detections were best predicted by whether snow depth was < 597 mm. The same pruning criteria resulted in a

Table 2

Median and interquartile range (IQR) of environmental variables at regional survey units with fisher or marten detections. Variables include latitude adjusted elevation (m), total annual precipitation (mm), April 1 snowpack (mm) and average annual minimum temperature (°C).

Region		Elevation		Annual precipitation		April 1 snowpack		Min. temp.	
		Fisher	Marten	Fisher	Marten	Fisher	Marten	Fisher	Marten
Allopatry	Median	1923	2527	1026	1157	115	558	4.0	0.4
	IQR	1600–2104	2329–2757	942–1098	1075–1211	25–209	383–735	2.5–5.6	–1–1.7
Sympatry	Median	2073	2207	1030	1074	190	389	2.2	1.5
	IQR	1870–2237	1987–2366	919–1071	1032–1131	58–377	206–481	1.3–4.2	1.2–3.0
Fisher-only	Median	2359	NA	759	NA	278	NA	1.6	NA
	IQR	2037–2608	NA	620–863	NA	153–365	NA	–1.6–3.3	NA

Table 3

Results (p values) of statistical tests (Kolmogorov-Smirnov [ks.test] and Mann Whitney [mw.test]) comparing the distributions of environmental variables at sample units. Significant results ($p < 0.05$, bold text) indicate that the two samples come from different distributions.

Variable	Statistical test	Within species comparisons			Between Species Comparisons	
		Fisher: allopatry/fisher: sympatry	Fisher: sympatry/fisher: fisher-only	Marten: allopatry/marten: sympatry	Fisher: allopatry/marten: allopatry	Fisher: sympatry/marten: sympatry
Elevation	ks.test	0.14	0.02	< 0.01	< 0.01	0.94
	mw.test	0.09	< 0.01	< 0.01	< 0.01	0.33
Annual precipitation	ks.test	0.82	< 0.01	0.04	< 0.01	0.36
	mw.test	0.59	< 0.01	0.02	< 0.01	0.06
April 1 snowpack	ks.test	0.23	0.48	< 0.05	< 0.01	0.56
	mw.test	0.09	0.87	< 0.01	< 0.01	0.15
Minimum temperature	ks.test	< 0.05	0.10	0.02	< 0.01	0.99
	mw.test	0.03	0.06	< 0.01	< 0.01	0.63

slightly more complex tree for the marten where the two criteria of annual precipitation ≥ 1038 and minimum temperature $< 2.9^\circ\text{C}$ classified the vast majority of marten detections. Tree classification error rates were higher for fisher (0.32) than for marten (0.14).

We found a shift in the CWHR types where we detected each species between zones. In the allopatric zone there were greater differences in CWHR types, with fisher being either the only or the more common species at typically low-mid elevation habitats (montane hardwood, montane hardwood conifer, ponderosa pine, Sierra mixed conifer) and marten being the only or the more common species detected at typically high elevation habitats (white fir, red fir, lodgepole pine, subalpine conifer) (Fig. 6). However, in the sympatric zone we found a high degree of overlap between CWHR types used by each species, driven primarily by marten occurrence in the lower elevation vegetation types in fisher-typical habitat (e.g., montane hardwood, ponderosa pine, and Sierra mixed conifer). In the fisher-only zone, the CWHR types typically

Table 4

Frequency of overlap (total number of individuals overlapping each individual's home range) and combined percent overlap (total percent of individual's home range area that overlaps with other individuals) for interspecific comparisons between martens and fishers, where Marten – fisher is from the marten's perspective and Fisher – marten is from the fisher's perspective, on the Sequoia National Forest, Tulare County, California, 1994–1996.

Comparison	Frequency of overlap Mean (SE)	Combined percent overlap Mean (SE)
Marten – fisher	3.18 (0.57)	70.5 (8.21)
Fisher – marten	2.92 (0.50)	15.4 (4.40)

occupied by marten in the other zones (e.g., red fir, subalpine conifer) were used instead by fisher. Moreover, in this zone we found fisher used a broad range of CWHR types including high elevation habitat types

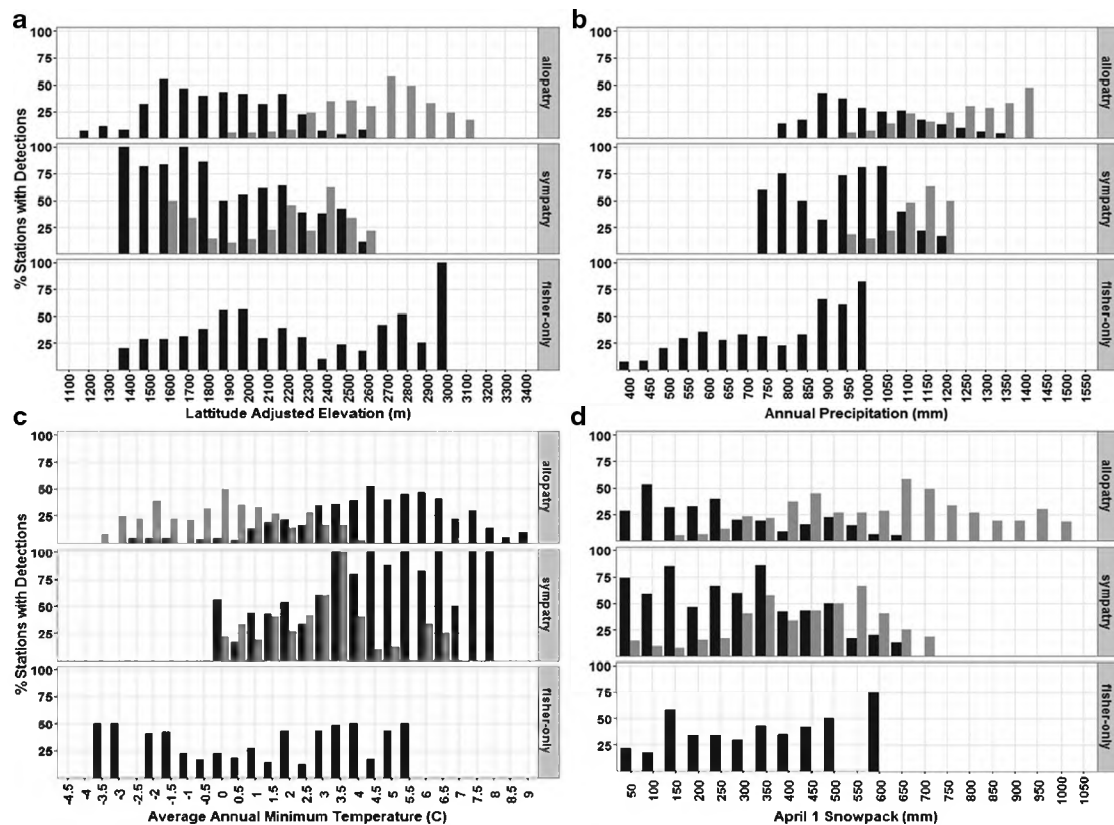


Fig. 4. Distribution of environmental and climatic variables in relation to fisher and marten detections in each zone (allopatry, sympatry and fisher-only) calculated as the percent of stations in which each species was detected (used) divided by the total stations surveyed (available). Fisher detections are black bars and marten detections are gray bars. a) latitude adjusted elevation (m), b) average annual minimum temperature ($^\circ\text{C}$), c) total annual precipitation (mm), d) April 1 snowpack (mm). x-Axis labels reflect the each bin's end point.

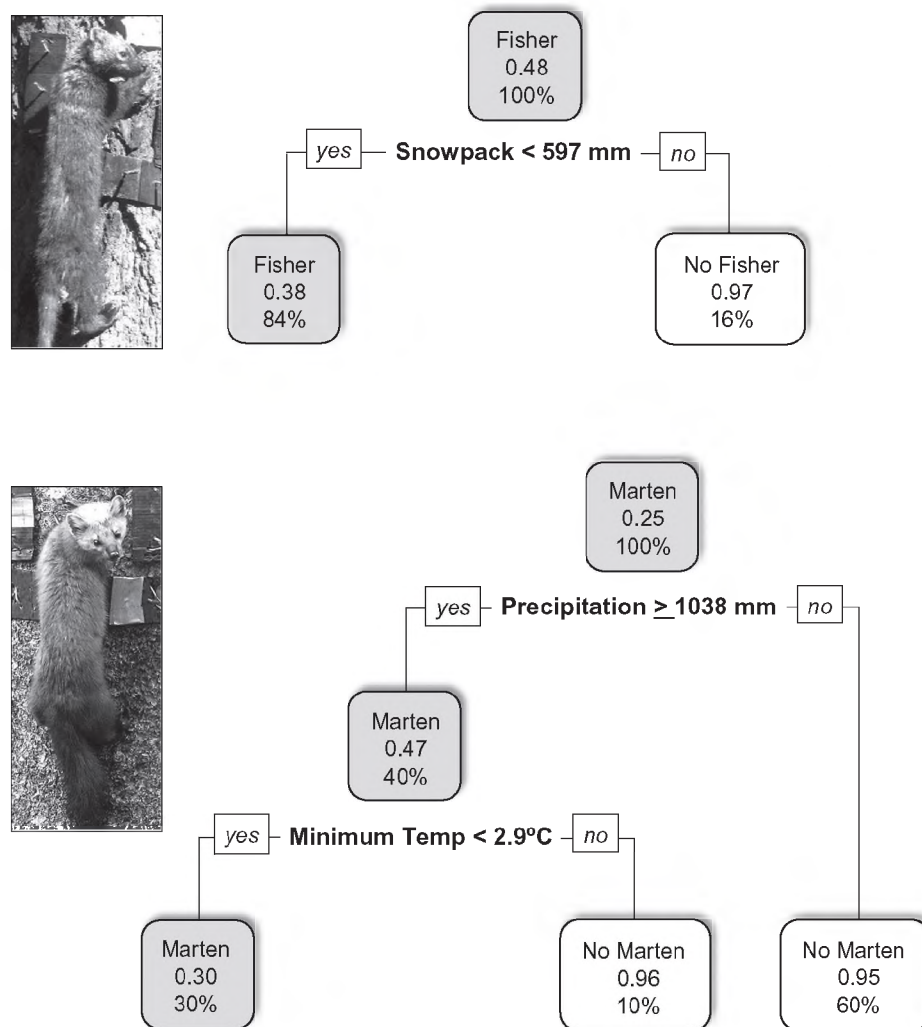


Fig. 5. Classification trees for fisher (top) and marten (bottom) that identify values of one or more climatic variables that best segregate the locations where each species was detected versus where it was not. Trees are based on unit level data from the Sierra Nevada Carnivore Monitoring Program, 2002–2014. Each branch in a tree is labeled with the probability of that class (0–1.0) and the percentage of observations in that node (0–100%).

where fishers had not been detected in other zones (subalpine conifer, pinyon-juniper, and eastside pine) (Fig. 6).

3.1.2. Comparisons within species between zones

3.1.2.1. Fisher: sympatry vs. allopatry. At the unit level, the only significant difference we found was that fishers in the sympatric zone occurred at significantly lower minimum temperatures than in the allopatric zone (Tables 2, 4). However, when the analysis was conducted at the station level, due to greater sample size, fisher detections were also at significantly higher elevation and precipitation in the sympatric zone. In the fisher-only zone at both the unit and station level, elevation was significantly higher and precipitation significantly lower at fisher detection locations than the sympatric zone, whereas minimum temperature was only significantly lower in the station-level analysis.

3.1.2.2. Marten: sympatry vs. allopatry. Distributions of marten detections between zones were significantly different for all variables at both the station and unit level, with marten found at significantly lower elevations, precipitation and snowpack, and higher minimum temperatures in the sympatric compared to the allopatric zone (all $p < 0.02$; Tables 2, 3).

3.2. Home range overlap

We collected data from 11 radio-marked martens (7M:4F) and 12 radio-marked fishers (4M:8F). Individuals were monitored during much of the period from mid-March 1994 through August 1996 (Fig. 3) and the average (SD) number of locations used to estimate a home range was 20.5 (8.0) and 41.0 (18.2) for martens and fishers, respectively. Interspecific home range overlap was common (Fig. 7). All martens overlapped a portion of at least one fisher's home range and 11 of 12 fishers overlapped a portion of at least one marten's home range. Interspecific frequency of overlap averaged 3.18 (range 1–7) for martens (i.e., an average of 3.18 fishers overlapped a marten home range) and 2.92 (range 0–5) for fishers (Table 4). Total combined home range percent overlap averaged 70.5% for martens meaning, on average, more than half of a marten's home range was overlapped by one or more fisher home ranges. However, only 15.4% of a fisher's home range was overlapped by one or more marten ranges.

Of the 35 possible overlapping marten-fisher pairs, 27 (77.1%) had home ranges that overlapped in both time and space (Table 5). From the marten perspective, 13 of the 27 pairs resulted in a significant spatial effect of which 11 exhibited significant spatial avoidance of the overlap area (Table 5). From the fisher perspective, 22 of the 27 pairs resulted in a significant spatial effect, but were split equally between attraction to and avoidance of the overlap area with a marten (Table 5).

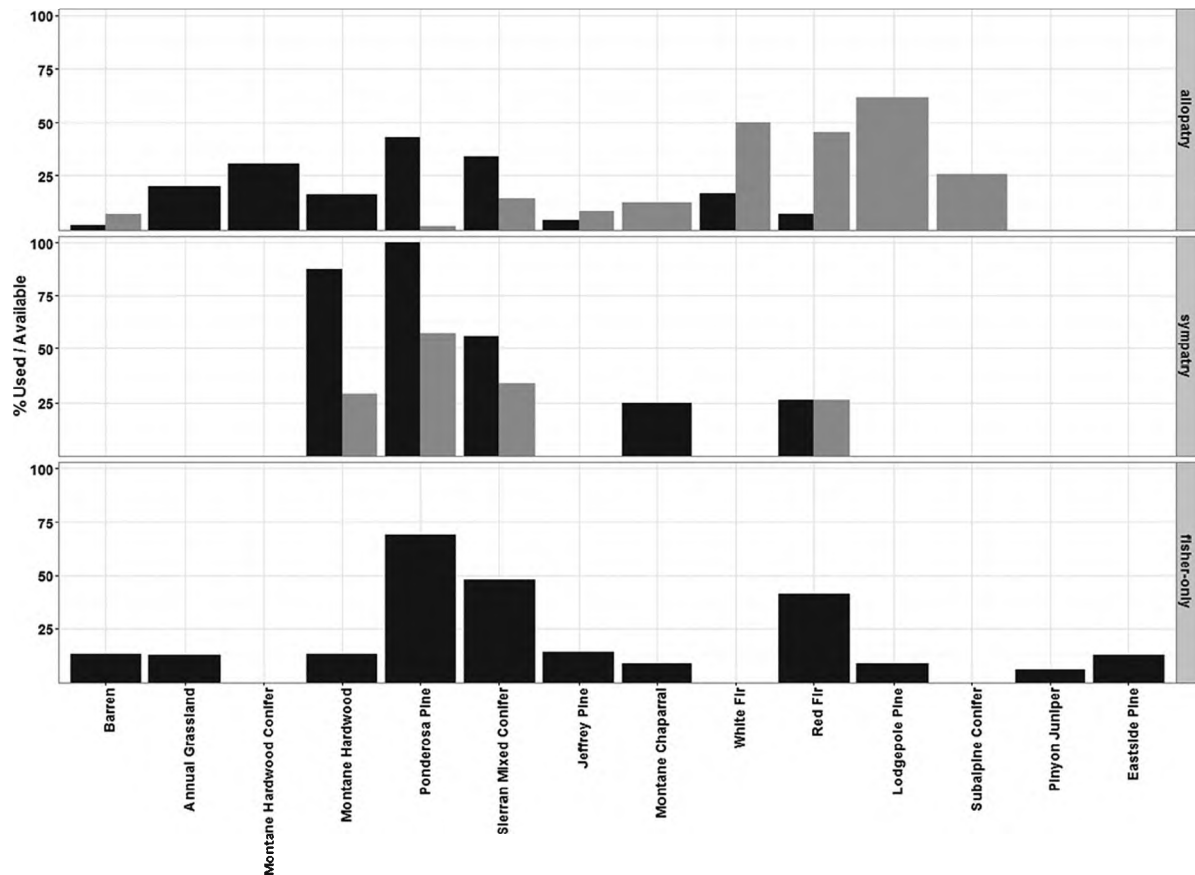


Fig. 6. Distribution of California Wildlife Habitat Relationships system (CWHR) habitat types in relation to fisher and marten detections in each zone calculated as the percentage of stations in which each species was detected (used) divided by the total stations surveyed (available) in that CWHR type. CWHR types are approximately ordered left to right by increasing elevation where the habitat type commonly occurs. Black bars represent fisher and gray bars marten.

Temporal interactions were significant for 74.0% of the interspecific pairs, with the majority (13 pairs) exhibiting simultaneous temporal avoidance of their respective overlap areas (Table 5). In summary, as predicted, marten and fisher home ranges regularly overlapped but martens were more likely than fishers to disproportionately avoid the part of their home range that overlapped with a fisher. However, for cases where there was overlap, both species had a greater likelihood of avoiding the overlap area in the presence of the other in both space and time.

3.3. Climate change projections

The climate change models forecast a variety of outcomes for environmental conditions that may affect marten and fisher distributions in the future. Four models representing the range of variation

found across all 18 models are shown in Fig. 8 (data from all 18 models can be found in the supplementary information: Table S1, Fig. S1). All but one of the 18 climate models projected an increasing mean minimum monthly temperature and decreasing snowpack for the 30 year period 2070–2099. The majority of models predicted an increase in mean minimum temperature of at least 2.5 °C, and a reduction of mean snowpack by > 70%. There was, however, considerable variability in future annual precipitation estimates with half of the models predicting a precipitation increase and half predicting a decrease (predicted mean values ranging from −456 mm to +502 mm).

4. Discussion

We found increasing overlap in the distribution of fisher and marten moving southward across a latitudinal, elevational, and climatic gradient until, in the southernmost and driest zone only fishers were detected. Landscape-level surveys found that the distributions of the species were largely allopatric in the northern and wetter portion of the study area, but extensively overlapped in the central and drier sympatry zone. Because the occurrence of each species is based on an average of 4–6 years of data at each sample unit, the results should reflect established spatial patterns and be insensitive to short-term variations. Telemetry data from the sympatric zone found substantial overlap between species at the home range level. These data clearly demonstrate that the presence of fisher does not preclude the presence of marten. Autecological studies in the early 1990s (Zielinski et al., 2004), together with observations by US Forest Service personnel prior to that time (R. Galloway, pers. comm.), indicate that the area of overlap has persisted for at least 30 years. Previous research has concluded that

Table 5
Spatial and temporal interaction effects within overlap areas for 27 pairs of marten and fisher on the Sequoia National Forest, Tulare County, California, 1994–1996.

	No. of significant pairs (%)	Effect
Spatial overlap - marten	13 (48.1)	Attraction = 2 Avoidance = 11
Spatial overlap - fisher	22 (81.5)	Attraction = 11 Avoidance = 11
Temporal interaction - marten and fisher	20 (74.0)	Simultaneity > solitary = 17 Attraction = 4 Avoidance = 13 Solitary > simultaneity = 3

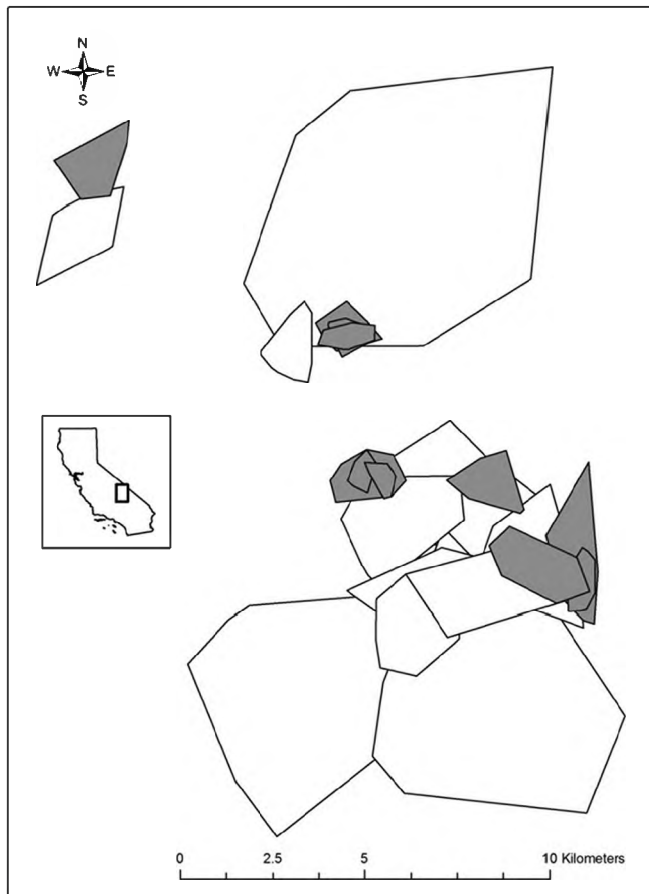


Fig. 7. Spatial distribution of marten (gray) and fisher (white) 100% minimum convex polygon home range estimates, within the sympatry zone on the Sequoia National Forest, from 1994 to 1996.

coexistence of martens and fishers depends on the scale of consideration, in that regions with ample habitat will find them broadly sympatric but within those regions they may not coexist at the same site (Thomasma, 1996). This is not the case in the southern Sierra Nevada where, within a broad zone of sympatry, martens and fishers co-occur at the same sites.

4.1.1. Threshold relationships with abiotic variables

Despite their overlap in the sympatry zone, the occurrences of each species appeared to have a threshold relationship with at least one of the climatic variables. First, there appears to be a snowpack threshold above which fishers do not occur (Fig. 4d). Fishers were not detected at stations with a snowpack depth > 650 mm and, in the classification tree analysis, snowpack was the most influential of the climatic variables with the great majority of fishers occurring where snowpack > 597 mm. Conversely, marten were routinely detected up to 969 mm snowpack, near the maximum snowpack value. This agrees with previous research that fisher distributions are limited by deep snow and that deep snow is an important component of marten habitat (Krohn et al., 1995, 1997, 2004; Manlick, 2015). Second, there appears to be a precipitation threshold below which marten do not occur (Fig. 4c). Marten were never detected below 911 mm precipitation and the classification tree analysis identified precipitation as the most influential variable, with the majority of martens occurring where precipitation ≥ 1038 mm. Fisher, however, were detected across a broad range of precipitation values from a minimum of 400 mm to as high as 1338 mm, which are near the lower and upper limits of

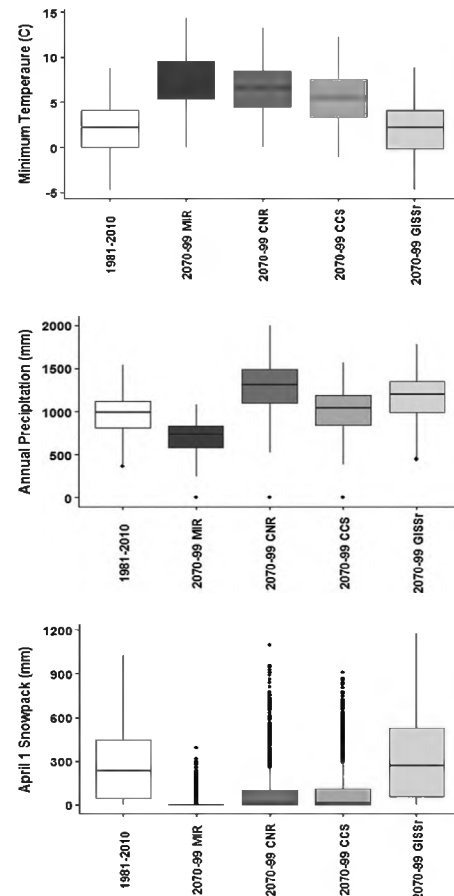


Fig. 8. Boxplots showing changes in climate variables from the current 30 year averages (1981–2010, white) to predictions for 4 future climate change models (2070–99, shades of gray). The central line represents the median value, the lower and upper box ends depict the first and third quartiles defining the interquartile range (IQR), the whiskers show values within $1.5 \times \text{IQR}$, and values $> 1.5 \times \text{IQR}$ plotted as dots.

precipitation in our study area. Finally, there is a less distinct but apparent temperature threshold; martens rarely occurred at locations where the average annual minimum temperature was $> 4^\circ\text{C}$. The classification tree results suggested that, of locations that met the marten's precipitation threshold, those where minimum temperature was $< 2.9^\circ\text{C}$ were the most likely places to detect martens. Fishers, however, were regularly detected at locations exceeding this threshold, and as high as 8.8°C (Fig. 4b). With these limits in mind, how can both species occur together at so many of the sample units in the sympatry zone? The answer is probably related to the variation in topography and elevation in this zone. This heterogeneity means that there are areas where snow is below the fisher's snowpack threshold but also above the marten's precipitation threshold. When these conditions occur at places where minimum temperatures are at intermediate values, conditions for coexistence appear to be met. Theoretical studies suggest a number of other conditions that could facilitate coexistence, in both spatially heterogeneous and spatially homogeneous environments (Amarasekare, 2003).

4.1.2. Dynamics in sympatry

A number of lines of evidence suggest that in sympatry it is martens whose niche expands and that martens, more so than fishers, occupy uncharacteristic habitat in sympatry. First, fishers occur at equivalent latitude-adjusted elevations in both allopatry and sympatry, but martens occur at significantly lower elevations in sympatry than allopatry. This suggests too that, in sympatry, martens should also occupy the vegetation types that typically occur at lower elevations,

which seems to be true. In sympatry there are substantially more marten detections in lower elevation CWHR types – such as ponderosa pine, montane hardwood and mixed hardwood-conifer – than in the allopatry zone. Second, marten detections in sympatry occurred at significantly lower snowpack than in allopatry, including some areas with negligible snowpack, which is uncharacteristic for martens. Third, martens were very rarely detected at units where the minimum temperature was $> 4^{\circ}\text{C}$ (Fig. 4), but all 5 exceptions occurred in the warmer sympatry zone. Conversely, the only difference for fisher was in the distribution of minimum temperatures with fishers occurring at somewhat lower temperatures in sympatry than allopatry. Lastly, fishers and martens were detected at a relatively equivalent proportion of units in allopatry (fisher 20%, marten 16%). However, in sympatry fisher were detected at a much greater proportion of units (50%) than marten (23%), suggesting that in the sympatric zone the conditions may be more favorable for fishers than for martens.

The shift by martens to using lower-elevation habitats when in sympatry with fisher is one of the most intriguing results of this study for two reasons. First, because it would appear to increase risk of predation by fishers. An average of 70.5% of a marten's home range was overlapped by one or more fisher home ranges. The interspecific overlap represents an extraordinary opportunity for interaction between the species. However, the telemetry data suggests that in the majority of the cases where there was a significant *spatial* effect it was the marten that avoided the portion of their home range that overlapped with a fisher. And, of the marten-fisher pairs that demonstrate a significant *temporal* effect, most exhibited simultaneous avoidance of the area of spatial overlap, i.e., both individuals were outside their overlap area, at the same time, more than expected by random movement. Active avoidance may be one reason why we observed no instance of fisher-caused mortality of a marten during the course of the telemetry study. Thus, despite the implication that predation by fishers affects marten distributions (e.g., Krohn et al., 1995; McCann, 2011), this phenomenon does not appear influential in our study area. Second, the occupancy of lower elevation habitats by martens may be one manifestation of adaptive capacity in response to climate change. The degree to which organisms will tolerate new conditions imposed by climate change varies widely but will include phenotypic plasticity via behavioral changes (Staudinger et al., 2013; Beever et al., 2015). Tolerance of lower elevation conditions may indicate phenotypic plasticity in habitat selection behavior by martens.

We also found that in the absence of sufficient precipitation, fishers will expand their niche into areas that are significantly higher and colder and use atypical higher elevation habitats. In the fisher-only zone on the Kern Plateau, fishers were detected in high elevation habitat types more commonly associated with marten (e.g., red fir, lodgepole pine) or types not found elsewhere in the study area (e.g., pinyon-juniper, and eastside pine). The lower minimum temperatures in this zone likely result in a higher percentage of precipitation as snow and comparatively little mid-winter snowmelt resulting in a similar snowpack as in other zones where marten occur. However, we hypothesize that due to significantly lower precipitation, the fisher-only zone does not receive the repeated, deep snow events as the other zones and the lack of periodic deep snow events may enable fisher to expand their niche to occupy higher elevations habitat types that they do not occupy in wetter areas.

4.1.3. Niche partitioning

The evolution of carnivores is hypothesized to be influenced by interspecific competition and, like other species, carnivores should partition niches to minimize these competitive interactions (Dayan and Simberloff, 1996; Johnson et al., 1996; Buskirk et al., 2000; Donadio and Buskirk, 2006). Considering the regional scale across our study area, there appears to be significant niche differentiation between the species. This is supported by our data, as well as some new data on marten and fisher distributions in the allopatry zone (Sweitzer and

Furnas, 2016). Regionally, there are some environmental conditions that, in combination, favor fishers (low snowpack, low precipitation, high minimum temperature, low-elevation forest communities) and these conditions occur in specific locations where fishers primarily occur, e.g., the lower elevation portion of the allopatry zone. Elsewhere there are conditions that, in concert, favor martens (high snowpack, high precipitation, lower minimum temperature, high-elevation forest communities) and these conditions exist where only martens occur, e.g., at higher elevations in the eastern portion of the allopatry zone. We would expect that if competition has been a force in the evolution of martens and fishers that sympatry should not exist or that niche differentiation should be exhibited in the sympatry zone, yet neither appears to be the case. At this scale there is no apparent spatial segregation, habitat segregation, or segregation on the basis of climatic variables in the sympatry zone. Instead our telemetry data suggest that marten may rely on a combination of spatial and temporal avoidance to minimize agonistic interactions. Indeed, active avoidance may be commonly used to reduce risk of encounters among co-occurring carnivores that overlap in habitat (López-Bao et al., 2016).

There are other similarities of the niche of the two species in the sympatry zone. The diets of sympatric fishers and martens in this zone are indistinguishable, exhibiting similar dietary niche breadth and overlap indices (Zielinski and Duncan, 2004). Both species use similar resting locations, which are typically cavities in tree, snags or logs (Lofroth et al., 2010; Spencer, 1987). Thus, in sympatry, marten and fisher niches overlap in respect to the elevations, temperatures and habitats they use, their diets, the snowpack they can tolerate, and amount of precipitation. This pattern of niche similarity was also reported by Manlick (2015) for these species in Wisconsin, but also finds exceptions in the study of guilds of carnivores elsewhere (Dayan and Simberloff, 1996; Meachen and Roberts, 2014).

Niche partitioning depends on the heterogeneity of the landscape, and reduced heterogeneity can alter niche dimensions (Amarasekare, 2003; Harpole and Tilman, 2007; Layman et al., 2007; Manlick, 2015). In our case, there appears to be sufficient *regional* heterogeneity to generate variation in niche overlap from north to south across the study area. However, the relative lack of niche differentiation in the sympatry zone suggests that the landscapes there may be more homogeneous than in allopatry. If so, this would agree with the conclusions reached by Manlick (2015) who found no evidence for spatiotemporal segregation, habitat or dietary differentiation between the species but did observe consistently higher fisher than marten occupancy. He concluded that the homogenous landscape and resulting lack of niche differentiation was limiting the recovery of marten via interspecific competition. Thus, retaining vegetation structural heterogeneity and prioritizing areas with topographic diversity will be important conservation practices, especially for species at their range margins.

4.1.4. Climate change implications

Although the potential changes in precipitation are uncertain, the predicted increases in minimum temperatures and decrease in snowpack by the end of the 21st century appear to favor the environmental conditions associated with fishers and to discriminate against martens. This agrees with the conclusions of others that have modeled future fisher and marten habitat (Lawler et al., 2012; Spencer et al., 2015b) as well as with the conclusion reached by Cahill et al. (2014) that abiotic, more than biotic, factors limit warm-edge range margins. As the southern Sierra Nevada becomes warmer and receives less precipitation as snow, and as these changes also decrease the distribution of sub-alpine conifer forest and increase the mixed hardwood/conifer forest (Rehfeldt et al., 2006; Lenihan et al., 2008), martens will experience more conditions that appear to fall outside their thresholds for occurrence. Our data showing fisher's exclusive presence in the high elevation, but low precipitation conditions on the Kern Plateau indicate that fisher may be able to capitalize on this future potential reduction in snow and expand upslope into higher elevations than where they are

currently found. These changes may produce a larger area of sympatry than currently exists, where – much like it does today – the populations may “spillover” into uncharacteristic habitats, resulting in an increase in fisher-marten interactions. It is possible that the martens that currently occur in the sympatry zone may form the nucleus of a population that is either behaviorally or genetically predisposed to exploit the warmer and drier conditions predicted in the future. However, fishers in the southern Sierra have low genetic diversity (Tucker et al., 2014), which may limit their local adaptation potential to rapidly changing environmental conditions.

We expect the southern margins (i.e., the warm edges) of suitable fisher and marten habitat, and the 3 zones we currently recognize, to migrate north over time. The fisher-only zone may experience the greatest growth if more area falls outside the marten precipitation or temperature thresholds and fishers retain their more flexible habitat associations. Unfortunately, we also expect a new zone to form in this region as climate warms: the exclusion zone. This will occur when abiotic changes produce areas that will be too dry and warm for either species to persist and may require planning for connectivity between this zone and suitable climate farther north or at higher elevations.

Species conservation and habitat management in the face of climate change presents a unique challenge in balancing the need to maintain current habitats as well as anticipate future changes in habitats and species distributions. The conservation of interacting species at the warm edges of their ranges will require land managers be aware of interspecific tolerance, how each species may respond uniquely to future climates and potential changes in habitat and how climate refugia can be conserved and connected to existing habitat (Morelli et al., 2016). Moreover, the few spatial outlying detections of martens in the fisher-only zone may reflect some heretofore unexplained climatic buffering to which individual martens may be responding and that may be worth further examination. Our work also reminds conservationists that managing for habitat conditions associated with vegetation is necessary, but not a sufficient approach. Changes in abiotic conditions that define a species climatic niche, as well as other biotic factors such as species interactions must also be considered when designing adaptive management strategies for species conservation in the era of climate change.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.03.016>.

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