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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 distributional 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